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# Why are so few island bryophytes endemic?

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## ABSTRACT

Endemism, a hallmark of island biodiversity, reaches its lowest levels among bryophytes compared with other land plants. Whether this pattern reflects low diversification rates, and why, or whether it is a result of loss of endemicity due to extinctions or subsequent continental (back-)colonization, is examined here through a review of available evidence in the Macaronesian flora. Significant genetic differentiation ($G_{ST}$, based on allele frequencies) was consistently found between Macaronesian and continental populations, ruling out the hypothesis that intense migrations necessarily hamper differentiation. A significant phylogeographical signal in the data ($N_{ST} > G_{ST}$; where $N_{ST}$ is a $G_{ST}$ analog incorporating phylogenetic relationships among alleles), involving higher mutation rates than dispersal rates and evidencing incipient speciation, was further found in more than 1/3 of the species investigated. The significantly higher average $N_{ST}$ between extra-European regions and Macaronesia compared to Europe and Macaronesia suggests, however, that incipient speciation is more likely to occur between distant (Macaronesian *versus* extra-European) than closer (Macaronesian *versus* European) populations. In line with this, ancestral area estimations in Macaronesian endemic bryophyte species revealed that at least 50% of them have an extra-European origin, in contrast with the almost exclusively (>90%) European/Mediterranean origin of Macaronesian endemic spermatophytes. Allopatric speciation *via* long-distance dispersal and subsequent divergence of a single endemic species prevails in island bryophytes, wherein sympatric radiations virtually never occur. Such a speciation mode does not trigger high rates of endemism, in contrast to radiations in Macaronesian spermatophytes, which contribute to 56% of the total number of endemics. Several mechanisms may explain the failure of island bryophytes to diversify *in situ*, including the fact that oceanic islands are too small or insufficiently isolated from each other or from continents to promote sympatric speciation, the lack of key innovations, and phylogenetic niche conservatism for stable habitats not prone to trigger radiations. In comparison with spermatophytes, continental (back-)colonization further largely prevails in bryophytes and, unlike in many instances in angiosperms, is not followed by *in situ* speciation on the mainland. The consequent loss of the endemic status of species that did speciate on islands but subsequently enlarged their range further accounts for the low rates of endemism among island bryophyte floras and invalidates the use of endemism rates as a proxy of speciation rates in this group.

*Key words*: speciation, endemism, evolution, island biogeography, island syndromes, hybridization, Macaronesia.

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CONTENTS

## I. INTRODUCTION

Due to geographic isolation that limits interchange with neighbouring mainland, strong environmental gradients, and buffered climatic conditions, islands are among the areas of the world with the highest levels of endemism (Schrader *et al.*, 2024). Thus, 21% of the world vascular plant species are endemic to islands. When standardized by area, endemic richness is 9.5 times higher on islands than in continental regions (Kier *et al.*, 2009). Due to the uniqueness of their biota, islands have been identified as biodiversity hotspots of prime conservation relevance (Whittaker, Fernández-Palacios & Matthews, 2023).

With an estimated 22,000–25,000 species within the three main lineages of the liverworts, mosses and hornworts (Goffinet & Shaw, 2009), bryophytes, the second most diverse group of land plants after spermatophytes, notably deviate from these patterns. In fact, bryophytes exhibit the lowest rates of island endemism across land plants (Fig. 1). In liverworts, species endemism rates are 2% in the Azores, 2% in Madeira, and 0.7% in the Canary Islands. In mosses, these proportions are of 2.0, 2.0 and 1.7%, respectively. These proportions pale by comparison with species endemism rates in spermatophytes, which reach 41% in the Azores, 21% in Madeira, and 47% in the Canary Islands (Mouton *et al.*, 2023). Three main processes, namely a low evolutionary capacity intrinsic to the group, low speciation rates on islands associated with high connectivity between island and mainland populations, and the loss of endemic status due to extinctions and/or subsequent continental (back-) colonization, may account for these patterns.

### (1) The evolutionary capacity of bryophytes

Bryophytes have long been perceived as organisms with low evolutionary capacities. This perception was initially based on the apparent similarity of ancient fossil and extant taxa and the sharing of trans-oceanic distribution ranges assumed to result from vicariance by bryophyte species and spermatophyte genera or families, as if bryophyte species were of equal age to the latter and had remained unchanged for tens of million years [see Vanderpoorten *et al.* (2010a) and references therein]. This hypothesis has progressively been challenged through mounting evidence for a much more recent origin of bryophyte species disjunctions than what a vicariantist hypothesis would suggest, invalidating the notion that bryophyte species remain morphologically consistent for long periods of time (Patiño & Vanderpoorten, 2018). Although overall estimates of net species diversification in bryophytes are approximately 30% of those described for spermatophytes, some recently diverging lineages underwent bursts of diversification comparable to those reported in spermatophytes (Laenen *et al.*, 2014).

The idea that bryophytes have low evolutionary capacities has gained support more recently through two lines of evidence. First, rates of molecular evolution, which, in plants, correlate with species diversity (Barraclough & Savolainen, 2007) and rates of phenotypic evolution (Davies & Savolainen, 2006), were found to be lower in bryophytes than in spermatophytes (Stenøien, 2008). Second, a major effect of the bryophyte life cycle is that genes are directly exposed to selection in the dominant haploid generation. The masking hypothesis predicts that selection is more efficient in haploids than in diploids because deleterious mutations would be more effectively purged in a haploid genome, while beneficial alleles would be rapidly fixed in the population, together resulting in slower evolutionary rates (Immler & Otto, 2018). Genome-wide analyses revealed, however, that the rates of non-synonymous substitutions in nuclear genes are actually substantially higher in mosses than in spermatophytes (Liu *et al.*, 2019). This, together with evidence that selection is not more efficient in bryophytes due to their haploid condition (Szövényi

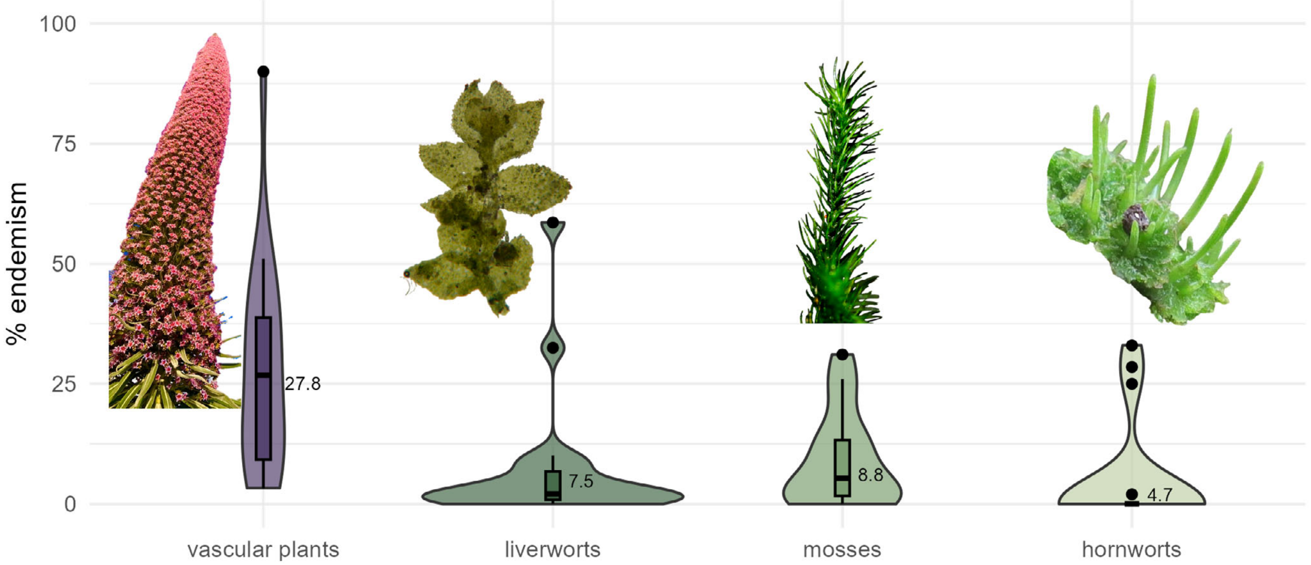

**Fig. 1.** Comparative rates of species endemism in oceanic islands and archipelagos ($N = 19$, Table S1) across vascular plants, liverworts, mosses, and hornworts. The boxplots show the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre line, with the mean value indicated), 1.5× interquartile range (whiskers) and extreme values beyond the whiskers. Images from left to right: *Echium perezii*, an iconic wooody echium endemic to La Palma, Canary Islands (photograph: S. Mirolo); *Cololejeunea schaeferi*, an endemic liverwort species from Madeira and Canary Islands (photograph: R. Gabriel); *Echinodium renauldii*, an endemic moss species from the Azores (photograph: R. Gabriel); *Anthoceros cristatus*, an endemic hornwort species from Ascension island (photograph: Silvia Pressel).

*et al.*, 2013; Linde *et al.*, 2021), calls for alternative explanations for the low levels of endemicity in bryophytes.

### (2) Speciation rates in island bryophytes

Oceanic islands, which originated *de novo* in the sea and never had any physical connection to the mainland, have offered a model of prime importance to analyse the mechanisms of plant speciation (Crawford & Stuessy, 1997; Savolainen *et al.*, 2006; Crawford & Archibald, 2017). Heaney's (2000) conceptual model proposes that when connectivity with continental areas is high, intense gene flow prevents genetic divergence, and hence, speciation. At the other extreme, geographically remote islands experience very rare colonization events, leading to some of the most spectacular island radiations in the absence of competition (Losos & Ricklefs, 2009). Radiations, i.e. increases in the rate of speciation within a clade, can result from selective (adaptive radiations) or neutral (geographic radiations) processes (Simões *et al.*, 2016). While adaptive radiations are primarily driven by 'key innovation' and take place in sympatry under strong divergent natural and sexual selection in different environments, geographic radiations result from allopatric differentiation (Rundell & Price, 2009; Simões *et al.*, 2016).

Between these two extremes, at intermediate migration levels, radiations are expected to be hampered by recurrent colonization events, preventing species from diversifying due to competition with already established species sharing the same niche [the niche pre-emption hypothesis (Silvertown, 2004; Silvertown, Francisco-Ortega & Carine, 2005)]. Allopatric speciation, wherein each speciation event is tied to an immigration event and subsequent divergent evolution, so that each endemic taxon has its sister taxon on the mainland, is expected to prevail (Rosindell & Phillimore, 2011).

Heaney's conceptual model provides an ideal framework to interpret the strikingly low levels of island endemism and the almost complete prevalence of allopatric speciation in bryophytes (Patiño *et al.*, 2014a). We hypothesize that at close to moderate distance from a source, intense gene flow would prevent speciation. Bryophyte endemics are hence thought to originate primarily from geographically remote sources through chance long-distance dispersal and allopatric speciation (Vanderpoorten *et al.*, 2011).

The underlying idea that the high dispersal capacities of bryophytes, as well as other efficient dispersers such as fungi (Stallman, Robinson & Knope, 2023), erode genetic divergence on geographically close islands and prevent sympatric speciation on remote islands, is supported by two lines of evidence. First, the shallower slope of the species–area relationship in bryophytes compared to spermatophytes reflects the larger range size and lower compositional turnover of the former due to their higher dispersal capacities, leading to the higher homogenization of bryophyte floras as compared to spermatophyte floras (Patiño *et al.*, 2014b; Yu *et al.*, 2020). Second, species richness on oceanic islands typically varies as a function of island age, which reflects both dispersal limitations and opportunities for speciation as islands reach their highest elevation (Borregaard *et al.*, 2017; Whittaker, Triantis & Ladle, 2008). In bryophytes, time *per se* has little independent role in explaining bryophyte species richness and principally features as a variable accounting for the changing area and topographic complexity during the life cycle of oceanic islands (Aranda *et al.*, 2014a; Patiño *et al.*, 2013b; Pócs, 2006; Sundberg, Hansson & Rydin, 2006; Tiselius *et al.*, 2019; Torre *et al.*, 2019; Yu *et al.*, 2019a,b). As a result, species richness standardized by area is not, in contrast with the predictions of the MacArthur & Wilson (1967) island biogeography model, necessarily lower in bryophytes on oceanic islands than on continents (Patiño *et al.*, 2015b).

Bryophytes primarily disperse by means of spores. In the life cycle of land plants, bryophyte spores are homologous to the pollen grains of spermatophytes. The cell wall of both spores and pollen is impregnated by sporopollenin, a highly resistant biopolymer against physical abrasion, desiccation, decay and ultraviolet (UV) radiation that confer on them the ability to remain viable under the harsh conditions of air currents. While the role of zoochory in the dispersal of bryophyte [Chmielewsky & Eppley (2019) and references therein] and fern (Brock, 2025) spores has been increasingly acknowledged, spores are, in fact, primarily dispersed by wind, as suggested by two pieces of evidence. First, wind connectivity contributes substantially more to the similarity of bryophyte and fern floras among islands than geographic distance (Muñoz *et al.*, 2004; but see Brock, 2025). Second, species range size and viability of spores under the conditions of desiccation and frost that prevail in high-altitude air currents are strikingly correlated (van Zanten, 1978). Globally, spores exhibit similar features to pollen grains in terms of dispersal traits and capacity (Table 1). While pollen grains contribute to gene flow, dispersal in spermatophytes occurs *via* seeds. Seed dispersal capacities substantially differ depending on their dispersal syndromes (Arjona *et al.*, 2018; but see Heleno & Vargas, 2015; Green, Baltzinger & Lovas-Kiss, 2022). Orthodox seeds, i.e. seeds capable of being dried to internal moisture of <12% water, share with spores the ability to tolerate desiccation due to similar physiological mechanisms involving late embryogenesis abundant proteins (Alpert & Oliver, 2002), but dispersal traits and kernels point to much higher dispersal capacities of spores compared to seeds. In particular, spores are substantially smaller, have slower settling velocities, and much fatter-tail dispersal kernels than anemochorous seeds (Table 1).

With concentrations reaching up to 100 spores per m$^3$ 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). Spore-trapping experiments revealed that while spore density is highest within the nearest vicinity of the source, the majority of spores are dispersed across distances in excess of hundreds of metres from the source, at densities that become decoupled from any distance-dependent effect (Lönnell *et al.*, 2012; Lönnell, Jonsson & Hylander, 2014; Sundberg, 2005). Similarly, the composition of propagule rain communities shows little similarity with that of ground communities and is unrelated to distance from potential propagule sources (Barbé, Fenton & Bergeron, 2016). Finally, a decay of the isolation-by-distance signal beyond 100 m from the source was revealed in a meta-analysis of spatial genetic structures in bryophytes (Vanderpoorten *et al.*, 2019). Altogether, these observations point to an inverse isolation effect (Szövényi, Sundberg & Shaw, 2012), counteracting genetic differentiation, and hence, potentially, hampering speciation (Barbé *et al.*, 2016; Sundberg, 2005), and resulting in a higher genetic diversity of colonizing propagules with increasing isolation. Therefore, and in contrast to the common assumption that island populations are genetically depauperate due to founder effects (Barrett, 1996; Frankham, 1996, 1997, but see Caujapé-Castells *et al.*, 2017; Fernández-Mazuecos & Vargas, 2011; García-Verdugo *et al.*, 2015), island bryophyte communities would be expected to exhibit comparable or even higher genetic diversity than continental populations due to the accumulation of lineages from numerous sources.

If an inverse isolation effect applies in bryophytes, the probability of finding spores from different sources is expected to increase with distance from the latter, providing the ideal setting for the establishment of secondary contacts and subsequent gene flow in insular habitats among genotypes previously isolated in the mainland (or in other insular

Table 1. Comparison of dispersal traits and kernels in fern and bryophyte spores and anemochorous seeds. Dispersal distance: distance (in m) at which a certain percentile of diaspores disperse.

| | Bryophyte spores | Fern spores | Anemochorous seeds |
|---|---|---|---|
| Size (mm) | 0.01–0.03 (–0.3[*]) (Boros *et al.*, 1993) | 0.02–0.1 (Gómez-Noguez *et al.*, 2017) | 0.05–>100 (Arditti & Ghani, 2000) |
| Settling velocity (m/s) | 0.005–0.085 (Zanatta *et al.*, 2016) | 0.01–0.11 (Gómez-Noguez *et al.*, 2017) | 0.02–9.02 (Casseau *et al.*, 2015; Liu *et al.*, 2021; Pietsch & Chapman, 2023; Song *et al.*, 2020) |
| Dispersal distance | 25–50th percentile: 1 m (*Sphagnum*; Sundberg, 2005)<br>40–60th percentile: >100 m (*Discelium*) (Lönnell *et al.*, 2015) | 95th percentile: *ca.* 1 m[†] (Rose & Dassler, 2017) | 50th percentile: 0.2–0.9 m<br>95th percentile: 2.9–17.9 m (Bullock *et al.*, 2017) |

[*] Record size in the genus *Archidium*.
[†] Estimated based on the ratio of the number of spores deposited at 0.1 m *versus* 1 m from the source.

regions). Mounting evidence suggests that the resulting high levels of genetic variation are critical to the emergence of adaptations or key innovations promoting radiations, as proposed by the surfing syngameon hypothesis (Caujapé-Castells, 2011). Central to this hypothesis, originally formulated for spermatophytes (Caujapé-Castells *et al.*, 2017) and tested here for bryophytes, is the idea that islands serve as contact zones for distinct, divergent lineages.

Bryophytes exhibit, however, significantly higher proportions of bisexual species and of species producing specialized asexual diaspores in islands than on the mainland (Patiño *et al.*, 2013a). In bryophytes, bisexual species are characterized by high selfing rates, resulting in completely homozygous sporophytes producing spores that are genetically identical to their single haploid parent (Haig, 2016). Whether these patterns reflect actual shifts in mating systems or simply are a reflection of the fact that bisexual species produce more sporophytes than unisexual ones (Longton & Schuster, 1983), and are hence more likely to reach islands, remains to be determined. Nevertheless, high rates of selfing and clonal reproduction may, potentially, compromise introgression among distinct lineages underlying the application of the surfing syngameon hypothesis.

### (3) Loss of endemic status: extinctions and dispersal from islands to mainland

The low rates of island endemism in bryophytes may alternatively result from the loss of their endemic status through extinctions or dispersal. The hypothesis that species that originated on islands lose their endemic status is at odds with the Oceanic Island Theory, according to which 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.*' (Wilson, 1961, p. 185). Underlying this assumption is the perception of Darwin (1859), supported by subsequent biogeographers (e.g. Carlquist, 1966, 1974), of island species as poor dispersers (Burns, 2019). In bryophytes, significant shifts in life-history traits towards increased production of specialized asexual diaspores and decreased sporophyte production on oceanic islands might indeed point to a global loss of long-distance dispersal ability (Patiño *et al.*, 2013a). While spores are highly resistant to harsh environmental conditions thanks to their sporopollenin-impregnated walls, this is not the case for specialized asexual diaspores. The latter are, hence, less well equipped for long-distance dispersal by wind and are thought to contribute primarily to colony growth and short-distance dispersal [Laenen *et al.* (2016b) and references therein]. The idea that island species inevitably lose dispersal capacity has, however, been increasingly challenged. Recent evidence in spermatophytes even suggests that dispersal ability may actually be favoured on islands because traits enhancing wind dispersal would be positively selected when habitat availability is high (García-Verdugo *et al.*, 2017). Changes in the applicability of the loss of dispersal syndromes have led to a paradigm shift, wherein islands are no longer considered as the end of the colonization road (Bellemain & Ricklefs, 2008). This perception of islands as dynamic systems, from which continents can be (back-)colonized, is fully compatible with the application of MacArthur & Wilson's (1967) island biogeography model in a glacial/interglacial context (Fernández-Palacios *et al.*, 2016), wherein islands exhibited a higher carrying capacity and were more connected to mainland during glacial periods. In fact, islands experienced buffered climates and were larger, higher, and less isolated from continental landmasses during glacial periods, so that extinction rates were lower, migration rates higher, and thus, species richness and speciation rates higher than during interglacial periods (Weigelt *et al.*, 2016). Such characteristics could account for the crucial role of islands as climatic refugia, acting as reservoirs or sources of novel biodiversity for subsequent (back-)colonization of continents (Caujapé-Castells, 2011; Condamine, Leslie & Antonelli, 2017; Yamada *et al.*, 2021).

Here, we address the question of the strikingly low rates of endemism among island bryophytes through a review and analysis of available evidence. We organize our review in the following hypothetical framework: (*i*) intense migrations between islands and nearest mainland areas erode founder effects and prevent genetic divergence, thereby hindering speciation (H1). Endemic speciation can therefore only take place following chance long-distance dispersal from remote continents (H2). (*ii*) Frequent migrations between island and mainland areas result in comparable genetic diversity levels on islands as compared to mainland (H3), generating a suitable context for the application of the surfing syngameon hypothesis. However, high levels of genetic diversity on islands do not drive diversification, as elevated rates of selfing and/or clonality prevent admixture (H4). (*iii*) Low endemism levels are not a result of limited speciation opportunities but rather of extinctions or the redistribution of endemic species into continental areas (H5).

## II. MATERIALS AND METHODS

### (1) Study area

The above hypotheses were tested using the bryophyte flora of Macaronesia, a biogeographic region that has been central to furthering our understanding of the particularities of macroecological patterns and interaction networks on islands, as a model. The Macaronesian archipelagos appear as some of the best-known oceanic archipelagos of the world in terms of the characterization of their flora and available genetic data (Florencio *et al.*, 2021), thus providing an ideal setting to document patterns and infer processes regarding endemic speciation (Caujapé-Castells *et al.*, 2017).

Whether or not Macaronesia should be recognized as a distinct biogeographic region, and its geographic circumscription, has long been debated. Initially defined as a biogeographic region comprised of the Azores, Madeira, and

Canary Islands (Engler, 1879), Macaronesia was subsequently broadened to include the Cape Verde islands as well as continental enclave areas in North Africa and Iberia (Sunding, 1979). Based on the sharing of three distinct floristic elements, namely the Palaeotropical-Tethyan flora, considered as the relict of a flora spanning across Europe and North Africa in the Tertiary (but see Kondraskov *et al.*, 2015), the African Rand flora, currently disjunct with the coastal margins of Africa and Arabia, and the neoendemic flora, Fernández-Palacios *et al.* (2024) recognized Macaronesia as a biogeographic region including the Azores, Madeira, the Canary Islands and the Cape Verde islands. Such a circumscription, however, does not fit with bryophytes (Vanderpoorten, Rumsey & Carine, 2007). In fact, the Cape Verde islands include very few shared endemics with the other Macaronesian archipelagos (none in liverworts and two in mosses) and exhibit strong affinities with the bryophyte flora of sub-Saharan Africa (Table 2, see online Supporting Information Figs S1, S2 and Table S1). By contrast, the floras of the Canary Islands, Madeira, and the Azores include a much higher proportion of Macaronesian endemics shared between two or more archipelagos and are largely dominated by a European-Mediterranean element (Tables 2, S1, Figs S1 and S2). This led us to focus here on the Azores, Canary Islands, and Madeira (Fig. 2).

### (2) Population genetic structure and diversity of non-endemic species

Our literature search yielded 25 species out of a total of 805 species present in Macaronesia, for which patterns of genetic structure and diversity were documented (Aranda *et al.*, 2014b; Carter, 2012; Cezón *et al.*, 2010; Désamoré *et al.*, 2016; Devos *et al.*, 2011; Feldberg *et al.*, 2016; Freitas & Brehm, 2001; Fuselier *et al.*, 2009; Hedenäs, 2010; Hutsemékers *et al.*, 2012; Laenen *et al.*, 2011; Ledent *et al.*, 2019; Patiño *et al.*, 2015a, 2016, 2017; Pisa *et al.*, 2015; Shaw *et al.*, 2015; Stenøien *et al.*, 2014; Vanderpoorten *et al.*, 2005, 2008; Vilnet *et al.*, 2012; Table S2). To standardize the population genetic statistics considered and allow comparisons within the same analytical framework, the following statistics were recomputed.

Genetic divergence between island and mainland populations was assessed through $G_{ST}$ and, for DNA sequence data, $N_{ST}$ to test the hypothesis that frequent migrations between islands and nearest mainland areas eroded founder effects and prevented genetic divergence, and hence, speciation (H1). $G_{ST}$ is a measure of genetic divergence among populations in terms of allele frequencies, regardless of the molecular divergence among alleles. $N_{ST}$ is a measure of genetic differentiation among populations analogous to $G_{ST}$ but considering the phylogenetic relationships between alleles (Pons & Petit, 1996). $N_{ST}$ values were computed from a Tamura & Nei's distance matrix (Tamura & Nei, 1993) as implemented in Arlequin 3.5.2.2 (Excoffier & Lischer, 2010). A key property is that $N_{ST} > G_{ST}$ when alleles within populations are more closely related than alleles between populations. This generates a phylogeographic signal in the data, indicating a higher diversification rate than dispersal rate and pointing to incipient speciation (Pons & Petit, 1996). The hypothesis that $G_{ST}$ and $N_{ST} > 0$ was tested through 1000 permutations of specimens across regions. The hypothesis that $N_{ST} > G_{ST}$ was tested through 1000 permutations of rows and columns of the distance matrix among alleles. A paired *t*-test was then conducted to test the hypothesis that $G_{ST}$ ($N_{ST}$) was, on average, significantly higher between Macaronesia and the extra-European region than between Macaronesia and Europe across species.

Table 2. Patterns of endemism and floristic similarities of the moss and liverwort+hornwort floras of the Azores, Madeira, Canary Islands and Cape Verde islands. Endemism is considered at the level of single archipelagos and is split into single (SIE) and multiple (MIE) island endemics as well as at the level of one or more archipelagos (multiple archipelago endemics) and quantified as the percentage of endemic species as compared to the entire flora. Floristic similarities are quantified as the percentage of the bryophyte flora of each archipelago that is shared with other regions of the world. See figshare online repositories for species distributions (liverworts and hornworts at https://doi.org/10.6084/m9.figshare.29881025.v1, and mosses at https://doi.org/10.6084/m9.figshare.29881028.v1).

| Archipelago (number of species) | Europe + Mediterranean | North America | South America | Sub-Saharan Africa | Archipelago endemics (SIEs–MIEs) | Multiple archipelago endemics |
|---|---|---|---|---|---|---|
| **Liverworts and hornworts** | | | | | | |
| Azores (156) | 86 | 54 | 38 | 36 | 0.0–1.9 | 4.5 |
| Madeira (182) | 86 | 54 | 33 | 34 | 1.1–1.1 | 6.0 |
| Canary Islands (148) | 87 | 49 | 32 | 38 | 0.0–0.0 | 6.1 |
| Cape Verde (49) | 67 | 49 | 45 | 84 | 0.0–0.0 | 0.0 |
| **Mosses** | | | | | | |
| Azores (294) | 88 | 53 | 30 | 46 | 1.0–1.4 | 2.7 |
| Madeira (361) | 88 | 56 | 29 | 46 | 1.9–0.3 | 4.4 |
| Canary Islands (359) | 91 | 59 | 26 | 46 | 0.5–1.0 | 3.6 |
| Cape Verde (133) | 65 | 48 | 42 | 78 | 0.7–5.2 | 1.5 |

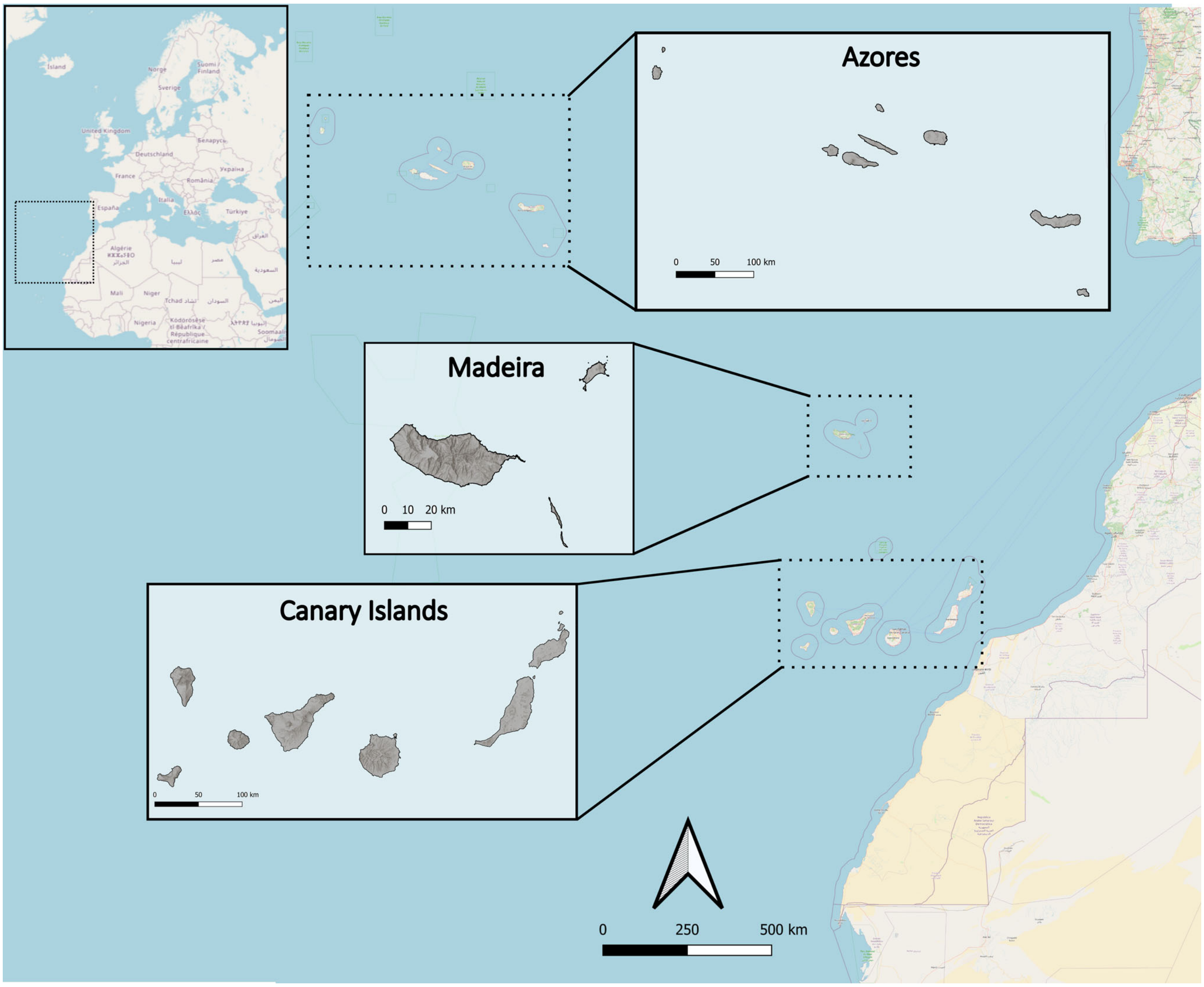

**Fig. 2.** Map of the study area, including the archipelagos of the Azores, Madeira, and Canary Islands. Background maps from OpenStreetMap.

Genetic diversity per region (Macaronesia, Europe and the Mediterranean, extra-European, i.e. sub-Saharan Africa, North America, South America, and others) was described for each species to test the hypothesis that frequent migrations between island and mainland areas result in comparable genetic diversity levels on islands compared to mainland (H3). Genetic diversity was characterized by expected heterozygosity (He) and nucleotidic diversity ($\pi$, the average of the genetic distance between alleles weighted by allele frequency, with the genetic distance computed using Tamura & Nei's distance). Linkage disequilibrium within island and mainland populations was computed for each pair of loci (chloroplast DNA being considered as one locus) using Arlequin 3.5.2.2 to test the hypothesis that, on islands, high rates of selfing and/or clonality prevent admixture among populations (H4). A paired *t*-test was subsequently used to determine whether, on average, the proportion of loci with significant linkage disequilibrium was higher in island than mainland populations.

### (3) Phylogeographic origin of Macaronesian endemic species

Evidence on the biogeographic origin of Macaronesian endemic bryophyte species was reviewed to test the hypothesis that endemic speciation can only occur following chance long-distance dispersal from remote continental sources (H2). The list of Macaronesian endemic bryophyte species and the sources of their phylogenetic trees and data is presented in Table S3. Species were included in ancestral range estimation analyses when (*i*) DNA sequence data were available for the target endemic species as well as for >50% of the species included in the genus and/or clade including the Macaronesian endemic species taxon; and (*ii*) the target endemic species is (are) included in a genus and/or clade of >5 species. We focused on clades sampled at >50% because ancestral area estimations, like all methods of ancestral state reconstructions, infer ancestral states from information collected on extant taxa, making them highly sensitive to taxon sampling. Therefore, the accuracy of ancestor reconstructions depends strongly on the density of species sampling [Ponti, Arcones & Vieites (2020) and references therein]. Paleoendemic taxa, for which the actual area of origin cannot be inferred from ancestral area estimations, were excluded. A paleoendemic origin was inferred from two pieces of evidence: (*i*) a stem age that is much older than any of the extant Macaronesian islands, a condition that is, however, weakened by the potential errors in molecular dating and the existence of paleo-islands, some of which may have emerged 60 million years ago (Ma) (Fernández-Palacios *et al.*, 2011) and (*ii*) their position on long, basal branches in the phylogeny. Three taxa met these conditions: *Andoa berthelotiana*, *Hedenasiastrum percurrens* and *Alophosia azorica*. Polyphyletic species, or endemic species included in a taxonomically challenging group of polyphyletic species, were also excluded because monophyletic species are the sampling unit in ancestral range estimations. This was the case for the genera *Isothecium* (Draper & Hedenäs, 2024; Draper, Hedenäs & Grimm, 2007) and *Pelekium* (Norhazrina *et al.*, 2016), for which molecular phylogenies resolve currently recognized species as polyphyletic.

Based on these criteria, 10 of the 21 and 7 of the 36 Macaronesian endemic liverwort and moss species, respectively, were included in formal ancestral range estimation analyses, as detailed in Appendix S1. For comparison with vascular plants, we reviewed existing literature from *Scopus* to find phylogenies of genera including Macaronesian endemic species with the following key words: Macaronesia, Canary Islands, Madeira, Azores, endemic*, phylogen*. The resulting papers and their bibliography were also searched for additional relevant publications.

## III. THE GENE FLOW HYPOTHESIS: POPULATION GENETIC STRUCTURE BETWEEN ISLANDS AND MAINLAND

Although relatively low, significant differences in allele frequencies ($G_{ST}$) between Macaronesian and mainland populations were found across most species (Fig. 3, Table S2), indicating that migration does not completely erode genetic

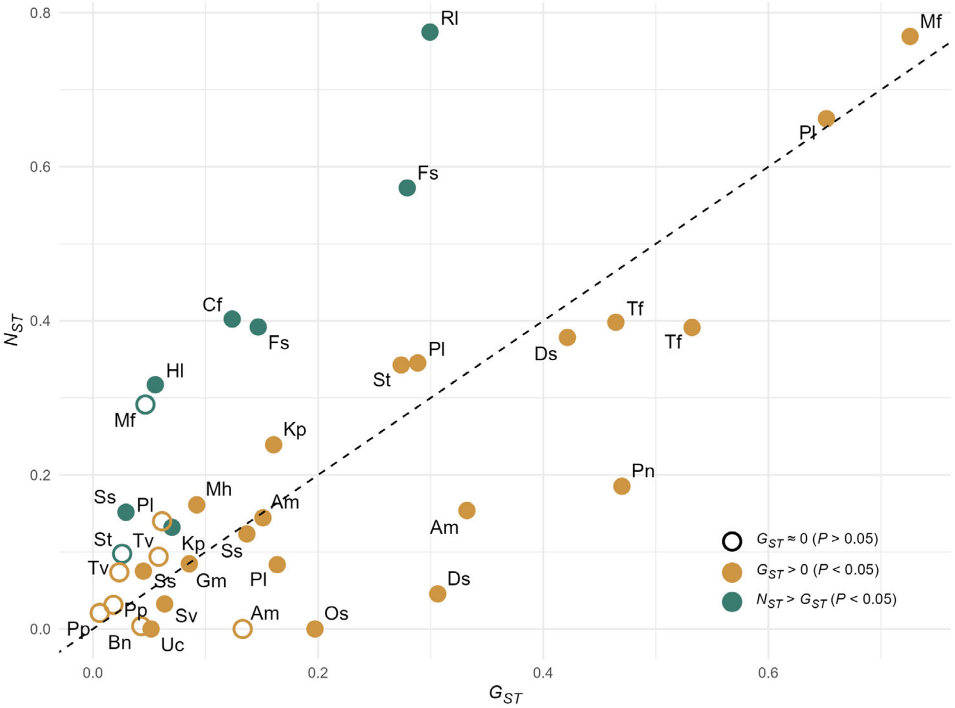

**Fig. 3.** Unilocus genetic structure of non-endemic Macaronesian bryophyte species for which suitable sequence data were available (see Table S2), as expressed by pairwise $G_{ST}$ (genetic differentiation based on allele frequencies) and $N_{ST}$ ($G_{ST}$ analogue incorporating phylogenetic relationships among alleles) between Macaronesia, Europe (including the Mediterranean) and other regions (see Table S2 for raw data). Open dots: $G_{ST}$ not significantly different from 0 ($P > 0.05$); filled orange dots: $G_{ST}$ significantly different from 0 ($P < 0.05$); filled green dots: $N_{ST}$ significantly higher than $G_{ST}$ ($P < 0.05$). The dashed line represents $G_{ST} = N_{ST}$. Am = *Amphidium mougeotii*; Bn = *Bryoxiphium norvegicum*; Cf = *Calypogeia fissa*; Ds = *Dicranum scottianum*; Fs = *Fissidens serrulatus*; Gm = *Grimmia montana*; Hl = *Homalia lusitanica*; Kp = *Kindbergia praelonga*; Mf = *Metzgeria furcata*; Mh = *Myurium hochstetteri*; Os = *Odontoschisma sphagni*; Pl = *Pulvigera lyellii*; Pn = *Ptychomitrium nigrescens*; Pp = *P. polyphyllum*; Rl = *Radula lindenbergiana*; Ss = *Sematophyllum substrumulosum*; St = *Scleropodium touretii*; Sv = *Saccogyna viticulosa*; Tf = *Tetrastichium fontanum*; Tv = *T. virens*; Uc = *Ulota calvescens*.

differentiation by drift (H1). Limited gene flow was further evidenced by the presence of a significant phylogeographic signal ($N_{ST} > G_{ST}$) in 6 of the 21 species for which DNA sequence data were available (Fig. 3). A significant phylogeographic signal in the data involves a higher mutation than dispersal rate, providing evidence that island populations have evolved in isolation for sufficient time to generate related endemic genotypes (Demenou *et al*., 2020; Heuertz *et al*., 2014; Ley *et al*., 2014). Thus, a significant phylogeographic signal is indicative of incipient speciation (Dauby *et al*., 2010). In Macaronesian spermatophytes, a similar signal was found among taxa included within *Erica scoparia s.l.* (Désamoré *et al*., 2012), but not among conspecific spatially disjunct populations (e.g. between Madeiran and Canarian *Olea* (Garcia-Verdugo *et al*., 2010)) or between Macaronesian and mainland *Erica arborea* (Désamoré *et al*., 2011), *E. scoparia s.str.* (Désamoré *et al*., 2012), and *Dracaena draco* (Durán *et al*., 2020).

Thus, the unexpectedly high proportion of bryophyte species with a significant island/mainland phylogeographic signal points to an active diversification process. Whether such differentiation requires taxonomic recognition has been debated in the context of the Linnean shortfall (Brown & Lomolino, 1998), which refers to the gap between formally described species and the number of species that actually exist. For example, the phylogeographic signal found here in *Fissidens serrulatus* corresponds to divergence between a Macaronesian and a mainland clade, which were previously recognized, respectively, as *F. luisieri* and *F. serrulatus s.str.*, until they were combined as synonymous due to their close morphological similarity (Werner *et al*., 2009). Regardless of taxonomic recognition, a significant phylogeographic signal suggests the presence of evolutionarily significant units relevant for conservation (Van Rossum *et al*., 2018). This underscores the need to consider genetic differentiation in conservation programmes (Hedenäs, 2016; Hedenäs *et al*., 2022), even for apparently highly dispersive organisms like bryophytes.

Overall, the idea that frequent migrations in island bryophytes necessarily prevent genetic divergence and, hence, incipient speciation (H1), can be ruled out. Nevertheless, the significantly higher average $N_{ST}$ between extra-European regions and Macaronesia ($N_{ST} = 0.35 \pm 0.30$) compared to Europe and Macaronesia ($N_{ST} = 0.24 \pm 0.25$, $P = 0.04$) suggests that a phylogeographic signal is more likely to occur between distant (Macaronesian *versus* extra-European populations) than between closer (Macaronesian *versus* European) populations. A meta-analysis of spatial genetic structures in bryophytes revealed that, beyond the limits of short-distance dispersal (<100 m from the source), a decay of the isolation-by-distance signal occurs, consistent with the inverse isolation hypothesis (Vanderpoorten *et al*., 2019). This decay, observed at distances of several hundreds to a few thousands of kilometres, i.e. the distance separating Macaronesia from mainland Europe, reflects efficient long-distance dispersal. Above such distances, i.e. at distances between Macaronesia and extra-European mainland, increased genetic divergence among populations occurs, marking the limits of regional dispersal, beyond which an increasingly smaller proportion of spores travel. Altogether, these observations suggest that speciation is more likely to take place in island bryophytes at sufficient distances from the mainland for genetic divergence to take place. As a result, a geographically remote origin of endemic Macaronesian bryophytes is expected (H2).

## IV. BIOGEOGRAPHIC ORIGIN OF MACARONESIAN ENDEMISM

Ancestral range estimations for selected Macaronesian endemic bryophyte species yielded high levels of uncertainty (Figs S3–S12; Table S4). In nine species (*Cololejeunea madeirensis*, *Frullania polysticta*, *F. sergiae*, *Homalothecium mandonii*, *Lewinskya scissa*, *Rhynchostegiella azorica*, *R. bourgeana*, *R. pseudolitorea*, *R. trichophylla*), the reconstructions suggested the fragmentation of a large, trans-oceanic range. This makes it impossible to assign the actual area of origin(s) of Macaronesian populations, suggesting, in line with previous analyses aiming at reconstructing ancestral distribution ranges in bryophytes (Laenen *et al*., 2018), that recurrent long-distance dispersal events have largely eroded the geographical structure of bryophyte phylogenies. An extra-European origin was recovered for *Acrobolbus azoricus* and *A. madeirensis*, *Amphidium curvipes*, *Leptoscyphus azoricus*, *Plagiochila* spp., and *Porella inaequalis*. Although incomplete taxon sampling or species polyphyly in other genera including Macaronesian endemics prevented a formal analysis of their origins, several other species are nested within genera that do not occur in Europe, also pointing to an extra-European origin. This is the case for *Orthotrichum handiense*, nested within a North American clade (Draper *et al*., 2021), *Pelekium atlanticum*, nested within a paleo-tropical clade (Norhazrina *et al*., 2016), and *Cheilolejeunea cedercreutzii* and *Heteroscyphus denticulatus*, which belong to tropical genera. A European origin was only inferred in the case of *Cololejeunea schaeferi*. We also consider *Exsertotheca intermedia*, a Macaronesian endemic species nested within a species-poor genus endemic to Europe (Draper *et al*., 2011), to be of European origin.

The substantial contribution of extra-European areas to the origins of Macaronesian endemic bryophyte species contrasts sharply with the origin of Macaronesian endemic spermatophytes. Our review of the literature for 515 species builds on previous evidence (see Table S5 and references therein) to show that 91% of Macaronesian endemic spermatophyte species originate from the Mediterranean. The striking difference in the rate and area of origin of endemism between Macaronesian bryophytes and spermatophytes is consistent with our second hypothesis that endemic speciation from European colonizers is unlikely in bryophytes and that endemic speciation occurs following chance long-distance dispersal events from geographically remote areas (H2). This explains the discrepancy between the higher floristic similarity of the bryophyte flora with Europe and the

Mediterranean than with any other region of the world (Table 2), whereas the endemic element has a primarily extra-European origin.

Species-level phylogenies on the origin of Macaronesian endemic species further reveal a major difference between bryophytes and spermatophytes: in bryophytes, virtually all island endemic speciation events occur through allopatric speciation with no subsequent *in situ* island diversification (Fig. 4, right panel). In spermatophytes by contrast, although the bulk of island speciation events also originate from allopatric speciation, a number of striking cases of *in situ* island diversification contributed to the majority of Macaronesian endemic species. In fact, the colonization:speciation ratio was 1 for all but one of the 31 genera (out of 39) including Macaronesian endemic bryophytes in Table S4 and Fig. 4, with the only *in situ* diversification events involving two species in the genus *Acrobolbus* (*A. azoricus* and *A. madeirensis*) (Table S4). In spermatophytes, a colonization:speciation ratio of 1 was reported for 44 out of a total of 90 genera analysed, but the almost equal number of radiations (46 genera) contributes disproportionately to 88% of the endemic species reviewed (56% of the total number of endemic Macaronesian species). The most spectacular radiations occurred in *Lotus*, the woody *Sonchus* alliance and the *Aeonium* alliance, which currently include, respectively, 28, 34 and 62 endemic Macaronesian species (Fig. 4, left panel, Table S5).

Several mechanisms may account for the failure of island bryophytes to radiate. First, speciation has a spatial scale that depends on levels of gene flow. Kisel & Barraclough (2010) reported a significant relationship between the minimum island size for speciation to occur and species dispersal capacities, as reflected by the spatial genetic structure ($G_{ST}$), among a large range of organisms. While mounting evidence points to the role of intra-island micro-allopatry in some of the most spectacular radiations of Macaronesian spermatophytes, such as *Argyranthemum* (White *et al.*, 2020) and *Pericallis* (Jones *et al.*, 2014), oceanic islands might be too small or insufficiently isolated from each other or from continents to promote sympatric speciation in bryophytes. Testing this hypothesis is, however, challenging because, in contrast to spermatophytes, for which single-island endemics prevail (Carine & Schaefer, 2010), the vast majority of Macaronesian endemic bryophytes are multiple-island and multiple-archipelago endemics (Fig. 5), making it difficult to determine the area wherein speciation took place.

Second, the niche pre-emption hypothesis posits that congeneric early colonizers, sharing similar ecological requirements due to niche conservatism, rapidly occupy all available niches, limiting opportunities for subsequent radiation. This hypothesis offers an appealing framework to explain the significant relationship between the likelihood of radiation and the number of island colonization events in Macaronesian spermatophytes (Silvertown, 2004). In bryophytes, *Acrobolbus*, the only genus that diversified *in situ*, includes only a single non-endemic species. In four instances (*Heteroscyphus*, *Breutelia*, *Pelekium*, *Trematodon*), endemic species, excluding paleo-endemics, are the only members of their genus in Macaronesia, and yet, failed to diversify further (Table S3), challenging the application of the niche pre-emption hypothesis to bryophytes. This hypothesis is further weakened for bryophytes as its main driver, competition, plays only a marginal role in bryophyte communities

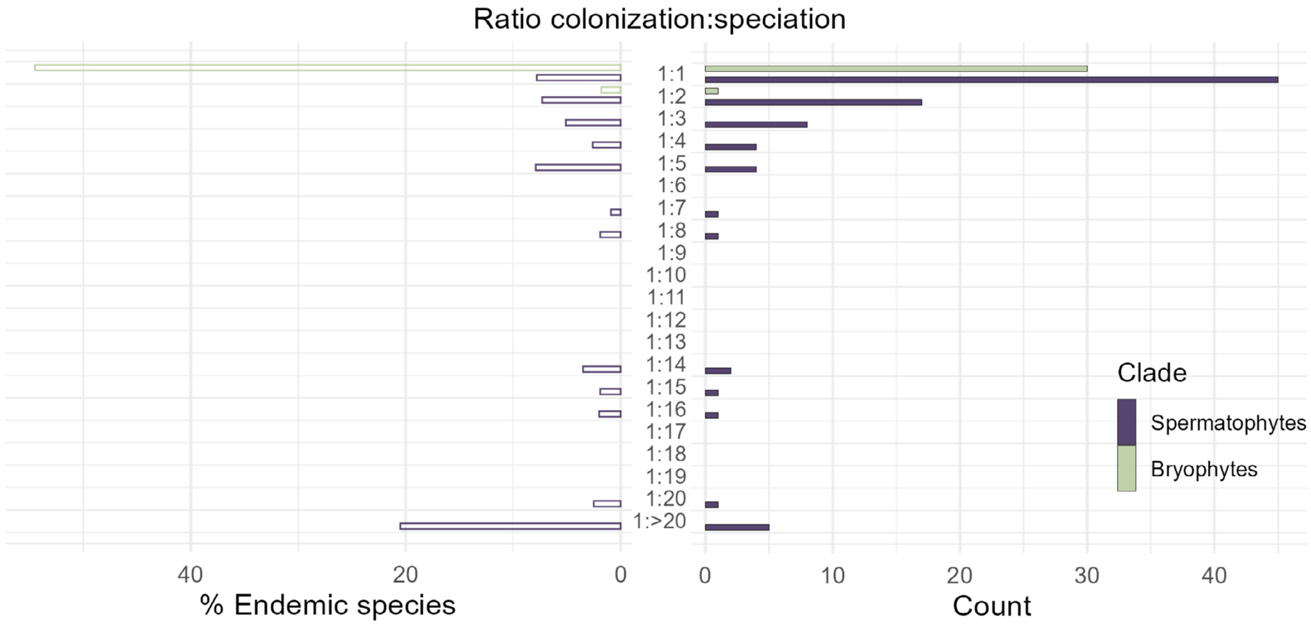

**Fig. 4.** Comparative patterns of *in-situ* diversification in Macaronesian spermatophytes (purple) and bryophytes (green). Right panel shows ratio between the number of speciation events (endemic species) and the number of colonization events per clade. Left panel shows contribution (%) of clades to the total number of Macaronesian endemic species, grouped according to their colonization:speciation ratio (see Tables S4 and S5 for raw data).

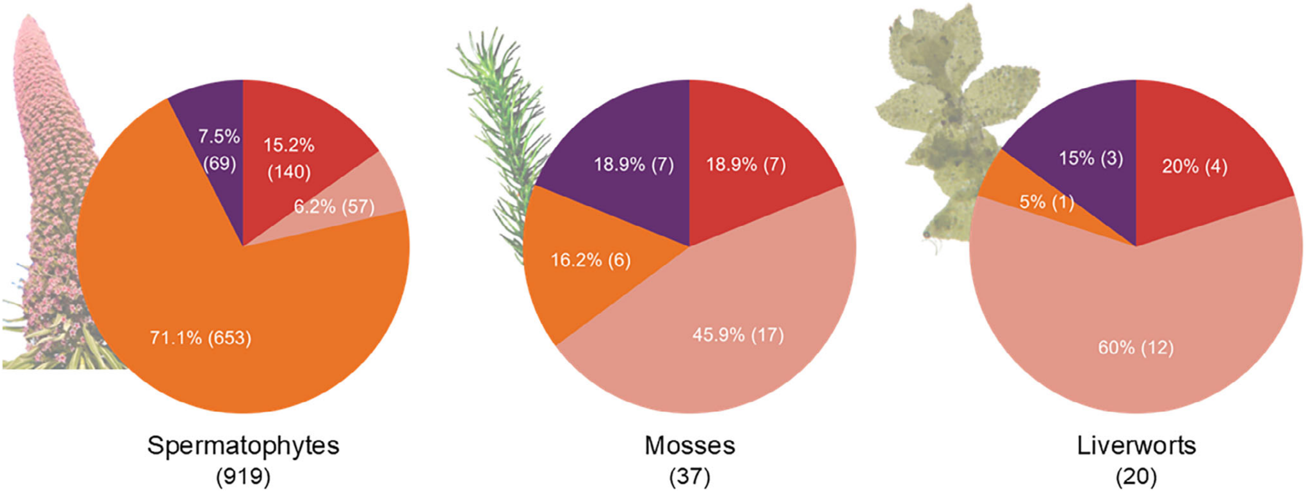

**Fig. 5.** Proportions of single and multiple archipelago endemic species in spermatophytes, mosses and liverworts (no Macaronesian hornworts are endemic). Numbers and percentage of endemic species are shown in each slice of the pie diagram, with the total number of endemic species in each group indicated below the charts. Orange = Canary Islands; purple = Azores; red = Madeira; pink = multiple archipelagos.

[Ma *et al.* (2024) and references therein]. In particular, none of the Macaronesian endemic bryophyte species is an annual, a strategy that would be expected if competition was a limiting factor for *in situ* speciation.

Third, certain traits, termed 'key innovations', have been argued to lead to adaptive radiations by permitting shifts into previously inaccessible ecological niches (Miller, Stroud & Losos, 2023). In island plants, one of the most striking innovations is the evolution of woodiness (Nürk, Atchison & Hughes, 2019). In bryophytes, a shift towards pleurocarpy is assumed to have triggered the radiation of Hypnales (Shaw *et al.*, 2003), while shifts towards bisexuality in liverworts are significantly correlated with increased diversification rates (Laenen *et al.*, 2016a). While a bias towards increased bisexuality was found in island bryophytes as compared to mainland ones, this bias most likely results from the higher production of sporophytes in bisexual species, their higher long-distance colonization capacities, and hence, over-representation on islands, rather than *in-situ* shifts towards bisexuality (Patiño *et al.*, 2013a). Thus, there is to date no evidence for the evolution of key innovations in island bryophytes that would have triggered diversification. Adaptive radiations are, furthermore, intimately associated with strong divergent selection in different environments (Rundell & Price, 2009). Previous experimental work suggested that, in contrast with the vast majority of spermatophytes, physiological and morphological plasticity prevail over ecotypic differentiation in bryophytes (reviewed by Patiño & Vanderpoorten, 2018), thereby offering an explanation for their failure to radiate adaptively. Mounting evidence for local adaptation from genome-wide analyses [see Xing *et al.* (2024) and Wu *et al.* (2025) and references therein], however, increasingly challenges such an interpretation.

In this context, Macaronesian bryophytes may have failed to radiate not because of their inability to adapt locally and diversify, but because of their preference for habitats that are not prone to triggering radiations. In particular, Patiño *et al.* (2014a) attributed the lack of radiation in Macaronesian bryophytes to their strong association with laurel forest, which harbours 16 out of 20 endemic liverworts and 22 out of 36 endemic mosses. The composition of laurel forest might have undergone more rapid composition shifts than previously suggested (Kondraskov *et al.*, 2015) and its extent varied through time due to climate change and human disturbance, which started in the Canary Islands about 2000 years BP (de Nascimento *et al.*, 2020; Castilla-Beltrán *et al.*, 2021; Santana *et al.*, 2025). As an evergreen forest habitat, laurel forest has been characterized by buffered microclimatic conditions throughout its palaeoclimatic history (Fernández-Palacios *et al.*, 2017). Unlike rapidly shifting environments that promote diversification (Pennington *et al.*, 2010), laurel forests may not have the environmentally dynamic conditions necessary for evolutionary radiations (Patiño *et al.*, 2014a). In fact, none of the major radiations of Macaronesian spermatophytes have been inferred to occur within, or to originate from, this habitat (e.g. White *et al.*, 2020). The largely tropical origin of Macaronesian endemic bryophytes from species clades largely restricted to rainforests offers an explanation for the strong preference of Macaronesian endemic species for evergreen forests, a habitat preference that would be fixed across entire species clades due to phylogenetic niche conservatism (Collart *et al.*, 2021).

## V. APPLICABILITY OF THE SURFING SYNGAMEON HYPOTHESIS TO ISLAND BRYOPHYTES

The surfing syngameon hypothesis (Caujapé-Castells, 2011) proposes that high migration rates to suitable areas in the

Canary Islands facilitated secondary contact among lineages previously isolated on the mainland, promoting hybridization and resulting in high genetic diversity that favoured lineage diversification. In line with this hypothesis (H3), genetic diversity was similar in island and mainland populations (Fig. 6). In contrast to spermatophytes (Caujapé-Castells *et al.*, 2017; Curto *et al.*, 2017; Rincón-Barrado *et al.*, 2024), however, high levels of genetic diversity in Macaronesian bryophytes did not trigger diversification (H4), with a colonization:speciation ratio essentially equal to 1 in bryophytes (Table S4).

A key feature of the surfing syngameon hypothesis is the crucial role played by introgression. In bryophytes, allopolyploidization has been reported repeatedly (e.g. Barbulescu *et al.*, 2017; Karlin & Smouse, 2017; Nieto-Lugilde *et al.*, 2018), but the role of homoploid hybridization has long been questioned (Natcheva & Cronberg, 2004; Sawangproh & Cronberg, 2021). In the Macaronesian endemic bryophyte flora, evidence for hybridization is limited to a putative allopolyploid origin of the moss *Grimmia curviseta* (Rodríguez-Romero *et al.*, 2017), while the complete polyphyly of morphospecies within *Isothecium*, including the endemics *I. montanum* and *I. prolixum*, was tentatively interpreted in terms of reticulation (Draper *et al.*, 2007; Draper & Hedenäs, 2024).

Several features of bryophyte reproductive biology, and in particular, strong constraints on sexual reproduction, do not, at first sight, promote hybridization. In particular, in the about two-third of unisexual bryophyte species (Laenen *et al.*, 2016a), sexual reproduction is limited as the sexes need to be in close sympatry as the sperm cells can only travel very short distances to reach the archegonia (typically much less than 1 m but up to 20 m in some species with extremely high sperm cell production, such as *Marchantia polymorpha*; Pressel & Duckett, 2019). Although a fraction of sperm cells is tolerant to desiccation for extended periods (Shortlidge, Rosenstiel & Eppley, 2012), and although sperm release into the air was reported in the liverwort genus *Conocephalum* (Shimamura, Yamaguchi & Deguchi, 2008), sperm dispersal most commonly takes place through a continuous film of water, and thus depends strongly on environmental conditions (Hedenäs & Bisang, 2019; Sundberg, 2002).

Populations of unisexual bryophytes are further characterized by large numbers of individuals that do not have sexual organs and by strongly biased sex ratios with female dominance (reviewed by Bisang *et al.*, 2025). It has therefore long been assumed that bryophytes compensate for limited opportunities for sexual reproduction by higher rates of clonality (During, 2007; Longton & Schuster, 1983; but see Crawford, Jesson & Garnock-Jones, 2009). In bisexual species, intragametophytic selfing largely prevails (Eppley, Taylor & Jesson, 2007). Intragametophytic selfing results in completely homozygous sporophytes, meaning that species reproduce primarily in what is, in effect, a clonal fashion, *via* the union of genetically identical gametes (Haig, 2016; Klips, 2015).

Limited opportunities for sexual reproduction and recombination are, at first sight, further compromised on islands, wherein a significantly higher proportion of bisexual species and species producing specialized asexual diaspores was reported (Patiño *et al.*, 2013a). Out of 10 bryophyte species for which suitable data were available, seven exhibited significant linkage disequilibrium among loci (Table S6). In

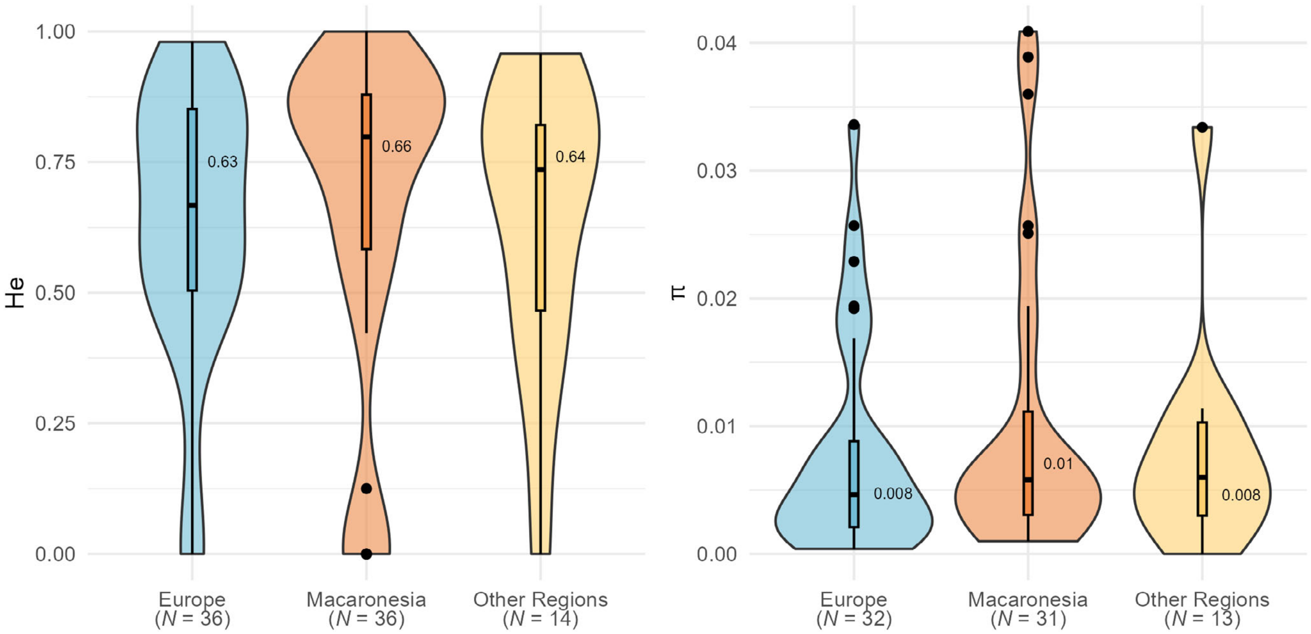

**Fig. 6.** Unilocus genetic diversity of non-endemic Macaronesian bryophyte species, as expressed by expected heterozygosity (He; left) and weighted mean genetic distance between alleles (π; right). The box-plots show the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre line, with mean value indicated), 1.5× interquartile range (whiskers) and extreme values beyond the whiskers.

contrast to our hypothesis H4, which posits that higher rates of selfing in island populations and/or clonality prevent admixture, however, significant linkage disequilibrium was 3.5 times as frequent in continental populations compared to island ones. Previous studies reported ambiguous results. A significant linkage disequilibrium was found in island populations of *Rhynchostegium riparioides* (Hutsemékers *et al.*, 2011), but not in *Porella canariensis* (Freitas & Brehm, 2001). In *Sphagnum palustre*, island and mainland populations exhibited a similar proportion of loci in linkage disequilibrium (Stenøien *et al.*, 2014). There is, hence, no genetic evidence for increased selfing and/or clonality rates on islands that would act as prezygotic barriers to hybridization in island bryophytes. The currently very limited evidence for hybridization in the Macaronesian bryophyte flora may therefore mask an actually much more important phenomenon.

It has been suggested that the role of homoploid hybridization in bryophytes has been greatly underestimated (Natcheva & Cronberg, 2004; Sawangproh & Cronberg, 2021). In fact, the dominance of the haploid gametophytic phase in bryophytes complicates the identification of hybrid specimens based on morphology, since intermediate morphotypes, corresponding to F1 hybrids in spermatophytes, can be observed only in the diploid sporophytes (Longton & Schuster, 1983). Although gene tree incongruence, recurrently reported in bryophyte phylogenies and interpreted in terms of hybridization may, at least in part, result from other processes such as incomplete lineage sorting (Meleshko *et al.*, 2021), genome-wide molecular screening techniques now provide suitable tools to seek molecular signatures of hybridization and indeed have increasingly revealed evidence for interspecific recombination in the nuclear genome [Klink *et al.*, 2024; Sawangproh & Cronberg (2021) and references therein]. Thus, there is no reason to expect that the surfing syngameon hypothesis would not apply to island bryophytes (H3), calling for further research on the role played by hybridization in bryophytes.

## VI. EXTINCTIONS AND (BACK-) COLONIZATIONS

Vegetation on many islands has been characterized by rapid rates of turnover since humans arrived (Nogué *et al.*, 2021), which may have triggered high extinction rates and could potentially account for the observed low rates of endemism in island bryophytes. The history of Macaronesia has been shaped by extensive deforestation, which began in the Canary Islands about 2000 years BP with colonization by aboriginal settlers and peaked across all Macaronesian archipelagos from the 16th century upon Castilian arrival (Castilla-Beltrán *et al.*, 2021; Elias *et al.*, 2022). In the Canary Islands, well-preserved laurel forests cover about 12% of their potential distribution range (Betzin, Thiv & Koch, 2016), but with large variations among islands. In the island of Gran Canaria for instance, less than 1% of the pre-human distribution remains (del Arco Aguilar *et al.*, 2010). Madeira was almost completely deforested during the 17th century with the development of agriculture, and in particular, sugar cane production (Moore, 2010). In the Azores, the original forest was successively replaced by *Erica azorica/Myrsine africana* shrublands and grassy meadows, and from the 19th century, exotic woody species were introduced at a massive scale (Rull *et al.*, 2017). Although laurel forests are the primary habitat for 79% of Macaronesian endemic bryophyte species (Sim-Sim *et al.*, 2014), only two cases of extinctions have been documented (*Nobregaea latinervis* and *Fissidens microstictus*) (Sim-Sim *et al.*, 2014). For Macaronesian spermatophytes, by contrast, 13 cases of extinctions have been reported (Fernández-Palacios *et al.*, 2025; Orihuela-Rivero *et al.*, 2025). Although extinction rates may actually exceed reported cases ('dark extinctions'; Orihuela-Rivero *et al.*, 2025), such bias would need to be extreme in bryophytes compared to spermatophytes to account for the substantial variations in rates of endemism between these two groups. Furthermore, although exotic trees were introduced in Macaronesia from the late 18th century, thus post-dating the large-scale destruction of laurel forest that took place following European colonization in the 15th century, many bryophyte species, including endemic ones, have the ability to colonize substitution habitats. In particular, a rich epiphytic bryophyte flora was documented on introduced *Pittosporum* and *Cryptomeria* in the Azores (Gabriel & Bates, 2005). As a result, degradation of the laurel forest may not necessarily translate into extinctions.

Alternatively, endemic Macaronesian species may have lost their endemicity due to subsequent emigration. Evidence for a Macaronesian origin was found for 18 bryophyte species (about 2% of Macaronesian bryoflora) distributed across Macaronesian and mainland areas (Table 3). This result underscores the crucial role that islands can play in shaping a relevant portion of continental biodiversity, not only as refugia during glacial periods, but also as important centres of speciation. From these insular hotspots, species may have expanded subsequently to continental regions through two distinct processes: back-colonization, where lineages originally from the mainland re-establish themselves there after evolving on islands; and *de novo* colonization, where newly evolved island lineages colonize mainland for the first time (Patiño *et al.*, 2015a). In agreement with our hypothesis H5, the low rates of island endemics in bryophytes thus at least partly reflect loss of their endemic status due to subsequent back- or *de novo* colonization of continental areas. In fact, adding those 18 bryophyte species that speciated in Macaronesia and subsequently colonized mainland areas, would result in a rate of endemism in Macaronesian bryophytes of 10%, corresponding to that reported for pteridophytes (Vanderpoorten *et al.*, 2011).

Continental (back-)colonization may have been facilitated by two processes. First, wind connectivity is currently greater from southwestern Europe and western North Africa towards the archipelagos than the reverse (Hutsemékers *et al.*, 2011), but was inverted during the last glaciations,

Table 3. Evidence for continental (back-)colonization from Macaronesian ancestors. * indicates species for which *in-situ* speciation with subsequent dispersal into mainland areas has been suggested.

| Species | Evidence | Speciation following back-colonization | Ratio colonization: speciation |
|---|---|---|---|
| **Bryophytes** | | | |
| *Dicranum scottianum** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Epipterygium atlanticum* | Single European accession nested within a Macaronesian clade (Hanusch *et al.*, 2020) | None | 0 |
| *Fissidens serrulatus** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Frullania calcarifera* | Ancestral range estimations (Fig. S5) | None | 0 |
| *Frullania teneriffae* | Ancestral range estimations (Fig. S5) | None | 0 |
| *Homalia lusitanica** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Lejeunea lamacerina* | European accessions nested within a Macaronesian clade (Heinrichs *et al.*, 2013) | None | 0 |
| *Myurium hochstetteri** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Ptychomitrium nigrescens** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Ptychomitrium polyphyllum** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Radula lindenbergiana* | Ancestral range estimations (Laenen *et al.*, 2011) | None | 0 |
| *Sematophyllum substrumulosum** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Saccogyna viticulosa** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Tetrastichium fontanum** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Tetrastichium virens** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| *Thamnobryum maderense* | Nested within a clade of Macaronesian endemics (Olsson *et al.*, 2011) | None | 0 |
| *Ulota calvescens** | Coalescence simulations (Patiño *et al.*, 2015a) | None | 0 |
| **Spermatophytes** | | | |
| *Aeonium* alliance* | Continental species nested within a Macaronesian clade (Mort *et al.*, 2002) | *Aeonium leucoblepharum*, *A. arboretum* subsp. *korneliuslemsii*, *A. stuessyi* | 1:3 |
| *Convolvulus** | Continental species nested within a Macaronesian clade (Carine *et al.*, 2004) | *Convolvulus fernandesii* | 1:1 |
| *Dracaena draco** | Ancestral range estimations (Durán *et al.*, 2020) | None | 0 |
| *Euphorbia** | Continental populations nested within a Macaronesian clade (Barres *et al.*, 2011, 2017; Martín-Hernanz *et al.*, 2023; Rincón-Barrado *et al.*, 2024) | *E. pedroi*, but none in the case of *E. balsamifera* and *E. regis-jubae* | 1:1 |
| *Limonium** | Ancestral range estimations (Koutroumpa *et al.*, 2021; Lledó *et al.*, 2005, 2011) | *L. fallax*, *L. mucronatum* | 1: 2 |
| *Lotus** | Ancestral range estimations (Jaén-Molina *et al.*, 2021) | *L. assakensis*, *L. pseudocreticus*, *L. criticus* | 1:3 |
| *Matthiola** | Continental populations nested within a Macaronesian clade (Jaén-Molina *et al.*, 2009) | *M. sinuata*, but none in the case of *M. bolleana* | 1:1 |
| *Sonchus pinnatifidus** | Continental populations nested within a Macaronesian clade (Cho *et al.*, 2019; Lee *et al.*, 2005) | None | 0 |
| *Tolpis** | Ancestral range estimations (Gruenstaeudl *et al.*, 2017) | *T. virgata*, but none in the case of *T. barbata* | 1:1 |

The table excludes sister relationships between a Macaronesian and a mainland lineage that do not involve a source–sink relationship (e.g. the Macaronesian *Ilex perado* and the Asian *I. leucoclada*, *I. latifolia* and *I. rugosa*; Manen *et al.*, 2002) as well as poorly resolved or weakly supported relationships [e.g. *Andryala* (Fehrer *et al.*, 2007; Ferreira *et al.*, 2015), *Helichrysum* (Galbany-Casals *et al.*, 2009)].

during which the westerlies wind regime prevailed (Wang, Jiang & Liang, 2018). Second, a series of seamounts, known as Palaeo-Macaronesia, emerged during glacial periods and may have served as stepping stones (Fernández-Palacios *et al.*, 2011). Despite the high long-distance dispersal capacities of bryophytes, stepping-stones may play a role in their distribution patterns. Although bryophyte spores are efficiently dispersed by air, genetic structure increases with geographic distance beyond the regional dispersal range (Vanderpoorten *et al.*, 2019). In this context, disjunct distribution patterns between the Neotropics, Macaronesia and western Europe in an array of species such as *Leptoscyphus cuneifolius*, *Plagiochila exigua* and *P. bifaria* have been interpreted in terms of a role for Macaronesia as a stepping-stone for the dispersal of trans-oceanic migrants on their 'colonization road' to a new continental environment (Patiño *et al.*, 2015a). Stepping-stones may play a particularly important role in species that fail to reproduce sexually, for which a stepping-stone colonization process among forest patches has been reported (Percel *et al.*, 2024).

(Back-)colonization from Macaronesia to the continent has also been reported repeatedly in spermatophytes (Table 3), raising the question of whether the prevalence of this pattern in bryophytes could offer an explanation for the striking differences in Macaronesian endemism rates between bryophytes and spermatophytes. Despite the substantially larger number of phylogeographic studies in Macaronesian spermatophytes than bryophytes (Tables S5 and S4, respectively), evidence of actual (back-)colonization in spermatophytes has been reported for only nine genera (about 0.7% of the Macaronesian spermatophyte flora) (Table 3). The faster emigration rates of endemic bryophytes as compared to spermatophytes is best illustrated by the proportions of single-island endemics and multiple-archipelago endemics among lineages. Thus, the proportion of single-island endemics in the liverwort and moss flora (Fig. 5, Table 2) differs dramatically from the spermatophyte flora (Mouton *et al.*, 2023), being, for liverworts, mosses and spermatophytes respectively, 0, 1 and 5% in the Azores, 1.1, 1.9 and 14% in Madeira, and 0, 0.5 and 30% in the Canary Islands. Conversely, the proportion of multiple-archipelago endemics is substantially higher in Macaronesian endemic mosses (46%) and liverworts (60%) than in Macaronesian endemic spermatophytes (6%) (Fig. 5).

In spermatophytes, speciation of migrants of Macaronesian origin took place in seven out of the nine genera included in Table 3, for which continental back-colonization was reported, conferring an endemic status to the ancestral insular lineage. In bryophytes conversely, speciation of migrants of insular origin on continents was reported only for the genus *Rhynchostegiella* (Patiño & Vanderpoorten, 2015). Altogether, the higher proportion of species that originated on islands and subsequently emigrated in bryophytes than in spermatophytes, coupled with the fact that, in the latter, Macaronesian endemics conserved their endemicity because of the divergence and speciation of the derived continental lineage, further explains the low levels of endemism in island bryophytes. The low levels of endemicity in island bryophytes therefore does not accurately reflect their actual speciation rate. While, in spermatophytes, island endemism rates provide an easy way to assess one of the most fundamental parameters in evolutionary biology – speciation rates (Emerson & Kolm, 2005; Weigelt *et al.*, 2016) – this is not the case in bryophytes.

## VII. CONCLUSIONS

(1) Incipient speciation occurs in island bryophytes, but is more likely when source populations are geographically remote. Consequently, at least 50% of Macaronesian endemic bryophytes have an extra-European origin. There is a sharp contrast between the strong similarities of the bryophyte floras of Macaronesia with those of the European and Mediterranean region compared with other regions of the world and the widely predominant Mediterranean origin of Macaronesian endemic spermatophytes.

(2) Virtually all island endemic speciation events in bryophytes occur through allopatric speciation with no subsequent *in situ* island diversification. Several mechanisms may explain the failure of island bryophytes to diversify *in situ*, including the fact that oceanic islands are too small or insufficiently isolated from each other or from continents to promote sympatric speciation, the lack of key innovations, and phylogenetic niche conservatism for stable habitats not prone to trigger radiations.

(3) Comparable or even higher levels of genetic diversity were found in island *versus* mainland populations. This could provide a suitable framework for the application of the 'surfing syngameon hypothesis' proposing that high migration rates to islands facilitate secondary contact among lineages previously isolated in the mainland, fostering hybridization that favours lineage diversification. Despite the lack of evidence for higher rates of selfing or clonality on islands, only one endemic Macaronesian bryophyte species is putatively of hybrid origin, highlighting the need for further research on the role played by hybridization in the evolution of island bryophytes.

(4) Islands played a crucial role as refugia or speciation hotspots, from which mainland areas have been (back-)colonized. The substantially higher proportion of continental (back-)colonization events in bryophytes than in spermatophytes, coupled with the fact that, in the latter, the continental lineage often speciated, conferring endemic status to the ancestral insular lineage, further explains the low rates of endemism in island bryophytes. Consequently, rates of endemism substantially under-estimate speciation rates in island bryophytes.

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## IX. DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.29881025.v1 and https://doi.org/10.6084/m9.figshare.29881028.v1.

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## XI. SUPPORTING INFORMATION

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

**Fig. S1.** Number of bryophyte species shared between each of the four Macaronesian archipelagos (Azores, Madeira, Canary Islands and Cape Verde) and four biogeographic regions (Nearctic, Palearctic, Neotropical, Sub-Saharan Africa).

**Fig. S2.** Venn diagram of species distribution overlaps between archipelagos for the Macaronesian bryoflora (left = mosses; right = liverworts).

**Fig. S3.** Ancestral range estimation of the genus *Amphidium* using the BioGeoBEARS R package.

**Fig. S4.** Ancestral range estimation of the genus *Cololejeunea* using the BioGeoBEARS R package.

**Fig. S5.** Ancestral range estimation of the genus *Frullania* using the BioGeoBEARS R package.

**Fig. S6.** Ancestral range estimation of the genus *Homalothecium* using the BioGeoBEARS R package.

**Fig. S7.** Ancestral range estimation of the genus *Leptoscyphus* using the BioGeoBEARS R package.

**Fig. S8.** Ancestral range estimation of the genus *Lewinskya* using the BioGeoBEARS R package.

**Fig. S9.** Ancestral range estimation of the genus *Plagiochila* sect. *rutilantes* using the BioGeoBEARS R package.

**Fig. S10.** Ancestral range estimation of the genus *Porella* using the BioGeoBEARS R package.

**Fig. S11.** Ancestral range estimation of the genus *Rhynchostegiella* using the BioGeoBEARS R package.

**Fig. S12.** Ancestral range estimation of the genus *Acrobolbus* using the BioGeoBEARS R package.

**Table S1.** Percentage of endemic species within native vascular plants, liverworts, mosses and hornworts floras of different oceanic islands and archipelagos.

**Table S2.** Genetic structure and diversity of non-endemic Macaronesian species investigated in this study, as expressed by pairwise $G_{ST}$ (and $N_{ST}$ in the case of DNA sequence data) between Macaronesia (mac), Europe (including the Mediterranean) (eur), and other regions (out), expected heterozygosity (He), and mean genetic distance between alleles weighted by allele frequency ($\pi$).

**Table S3.** Macaronesian endemic moss and liverwort species (after Mouton *et al.*, 2023), excluding *Riccia boumanii* since its discovery in Asia (Xiang *et al.*, 2022), with information on the availability of relevant phylogenetic data for ancestral range estimations and inclusion/exclusion in the present analysis.

**Table S4.** Biogeographic origin of Macaronesian endemic bryophyte species, as inferred from ancestral area estimations (Figs S3–S12) and speciation patterns.

**Table S5.** Summary of studies reporting the biogeographic origins of Macaronesian endemic vascular plants and speciation patterns.

**Table S6.** Linkage disequilibrium in island (Macaronesia) and mainland [Europe and other mainland regions (Out)] Macaronesian bryophyte populations.

**Table S7.** Ancestral range estimations selection procedure for six model combinations.

**Table S8.** Phylogenies clock model and tree prior selection procedure for six model combinations.

**Appendix S1.** Methodology followed for the ancestral range estimation analyses.

**Table S9.** Bryophyte genera selected for ancestral area estimations, with information on the number of loci (n = nucleus, ch = chloroplast) and secondary calibration of the dating analysis based on the genus crown age (in million years ago, Ma) (Laenen *et al.*, 2014).

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