

The Macaronesian region

A history of its plant diversity through time

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Summary

The Macaronesian region: a history of its plant diversity through time.

Oceanic islands are important, dynamic ecosystems with high endemism rates, making them natural laboratories for understanding how diversification, dispersal, and disturbance shape biotas. Within this global pattern, the North Atlantic region of Macaronesia, comprised of the archipelagos of the Azores, Madeira, Canary Islands, and Cape Verde, is a perfect model system to investigate how island properties, natural climatic variations, and recent human impacts interact to shape insular floras. Yet, sharp contrasts exist among major land-plant lineages: while Macaronesian spermatophytes exhibit high rates of endemism, bryophytes display the lowest insular endemism rates reported across land plants. This thesis aims at identifying the ecological and evolutionary mechanisms underlying such strikingly different patterns of endemism and to evaluate how climate and humans have influenced the demographic trajectories of endemic insular plants.

Two main questions guide the work: (Q1) which mechanisms explain the contrasted endemism patterns between bryophytes and spermatophytes in Macaronesia, and what do they reveal about islands as refugia or stepping-stones for continental diversity? (Q2) to what extent have human disturbance and natural climatic cycles shaped demographic histories of Macaronesian endemic plant species? These questions are approached through (i) a synthesis and re-analysis of published phylogeographic and biogeographic evidence across land-plant lineages, (ii) targeted phylogeographic analyses of broadly distributed (amphi-Atlantic) bryophytes to evaluate colonization routes and the timing of island-continent exchanges, and (iii) population genomic inferences of demographic change in endemic Canarian and Macaronesian vascular plants from the two historically most disturbed ecosystems, namely the thermo-sclerophyllous woodland and laurel forest.

To address the question of the lower endemism rates of bryophytes as compared to spermatophytes, the thesis evaluates three non-exclusive processes: (1) intrinsically low evolutionary capacity, (2) reduced island speciation due to high connectivity and/or differences in speciation modes, and (3) the loss of endemic status via extinctions and/or subsequent (back-) colonization of mainland areas. The evidence assembled here challenges the simplest “high dispersal prevents speciation” view. Our results show that island and mainland bryophyte populations often retain measurable genetic structure and, in a substantial subset of species, a significant phylogeographic signal consistent with long-term isolation and incipient divergence. Similarly, coalescent-based assessments of migration scenarios do not systematically favor high migration rates, implying that chance long-distance dispersal potential does not necessarily translate into frequent successful migration. In contrast to spermatophytes, where a limited number of iconic radiations generated a large proportion of the island endemic flora, bryophyte insular endemics are found to arise mostly through allopatric speciation, with little evidence for subsequent in situ diversification. This difference suggests that endemism patterns reflect not only dispersal and isolation, but also differences in how often islands generate radiations versus single, geographically structured lineages.

A key outcome of this thesis is that bryophyte endemism rates may substantially underestimate island-driven diversification because bryophyte lineages that originate (or diversify) on islands can more easily expand on other territories. Evidence consistent with Macaronesian origins was found for different bryophyte species distributed across islands and mainland areas, and accounting for such cases would raise Macaronesian bryophyte endemism rate well above the known insular endemism percentage. This supports a dynamic view of islands as contributors to continental biodiversity through back-colonization and *de novo* colonization, potentially facilitated by shifts in wind regimes during glacial periods and by temporary stepping-stones such as seamount chains known as Palaeo-Macaronesia.

Regarding demographic history, population effective sample size reconstructions of endemic plants reveal strong temporal heterogeneity but generally place major expansions or contractions well before the onset of human occupation in the Canary Islands (~2000 years ago), suggesting limited detectability of recent anthropogenic impacts in extant genomic variation. The clearest exception is a localized population decline globally concomitant with the earliest human settlement of people from Berber/Amazigh origin. Across species, signals more often align with pre-human climatic dynamics, including post Last Glacial Maximum changes and mid-Holocene variability (notably the African Humid Period), while differences among taxa are plausibly mediated by life-history traits and dispersal ecology. These results also highlight the hypothesis of a genetic extinction debt, whereby recent habitat disruption does not always translate into an immediate genetic signature, even in insular settings.

Overall, this thesis concludes that Macaronesia is a system shaped by both diversification and migrations. Spermatophyte endemism largely reflects island radiations and the retention of narrow-range lineages, whereas bryophyte endemism is reduced not only by dispersal, but by the combination of limited *in situ* radiations and comparatively frequent post-speciation (back-) colonization of continents. Demographic histories of Macaronesian and Canarian endemic plants largely track Quaternary climate dynamics, while recent anthropic perturbations may have weaker, more localized, or genetically delayed impacts. Together, these findings caution against interpreting island endemism as a universal proxy for speciation and strengthen a dynamic view of islands as both refugia and sources of biodiversity at broader spatial scales.

Resumen

La región macaronésica: una historia de su diversidad vegetal a lo largo del tiempo.

Las islas oceánicas son ecosistemas importantes y dinámicos, con tasas elevadas de endemismo, lo que las convierte en laboratorios naturales para comprender cómo la diversificación, la dispersión y las perturbaciones configuran las biotas. Dentro de este patrón global, la Macaronesia, región del Atlántico Norte formada por los archipiélagos de las Azores, Madeira, las Islas Canarias y Cabo Verde, constituye un sistema modelo ideal para investigar cómo las propiedades insulares, las variaciones climáticas naturales y los impactos humanos recientes interactúan para dar forma a las floras insulares. Sin embargo, existen contrastes importantes entre los principales linajes de plantas terrestres: mientras que las espermatófitas de Macaronesia presentan altas tasas de endemismo, los briófitos muestran las tasas de endemismo insular más bajas registradas entre las plantas terrestres. Esta tesis tiene como objetivo identificar los mecanismos ecológicos y evolutivos que subyacen a estos patrones de endemismo contrastados, y evaluar cómo el clima y los seres humanos han influido en las trayectorias demográficas de las plantas endémicas de esa región.

Dos preguntas principales guían este trabajo: (Q1) ¿qué mecanismos explican los patrones contrastados de endemismo entre briófitos y espermatófitas en Macaronesia, y qué revelan sobre el papel de las islas como refugios o como “stepping-stones” para la diversidad continental? (Q2) ¿hasta qué punto las perturbaciones antrópicas y los ciclos climáticos naturales han configurado la historia demográfica de las especies vegetales endémicas de Macaronesia? Estas preguntas se abordan mediante (i) una síntesis y un reanálisis de la evidencia filogeográfica y biogeográfica publicada en distintos linajes de plantas terrestres, (ii) análisis filogeográficos dirigidos de briófitos de amplia distribución (anfi-Atlántico) para evaluar las rutas de colonización y la cronología de los intercambios isla-continente, y (iii) inferencias de genómica de poblaciones sobre cambios demográficos en plantas vasculares endémicas canarias y macaronésicas procedentes de los dos ecosistemas históricamente más perturbados: el bosque termo-esclerófilo y la laurisilva.

Para abordar la cuestión de las bajas tasas de endemismo de los briófitos en comparación con las espermatófitas, se evalúan tres procesos no excluyentes: (1) una baja capacidad evolutiva intrínseca, (2) una menor especiación insular debido a una alta conectividad y/o a diferencias en los modos de especiación, y (3) la pérdida del estatus de endémico por extinciones y/o por una “retro-colonización” posterior de áreas continentales. La evidencia reunida aquí cuestiona la visión más simple de que “una alta dispersión impide la especiación”. Nuestros resultados muestran que las poblaciones insulares y continentales de briófitos a menudo conservan una estructura genética medible y, en una parte sustancial de las especies, una señal filogeográfica significativa compatible con un aislamiento prolongado y una divergencia incipiente. Del mismo modo, las evaluaciones basadas en coalescencia de escenarios de migración no favorecen de manera sistemática tasas de migración elevadas, lo que implica que el potencial de dispersión a larga distancia no necesariamente se traduce en un gran número de migraciones exitosas. En contraste con las espermatófitas, donde un número limitado de radiaciones emblemáticas

generó una gran proporción de la flora insular endémica, se observa que los endemismos de briófitos insulares surgen mayoritariamente por especiación alopátrica, con escasa evidencia de diversificación in situ posterior. Esta diferencia sugiere que los patrones de endemismo reflejan no solo la dispersión y el aislamiento, sino también diferencias en la frecuencia con la que las islas generan radiaciones frente a linajes únicos estructurados geográficamente.

Un resultado clave de esta tesis es que las tasas de endemismo de los briófitos pueden subestimar de forma sustancial la diversificación impulsada por el contexto insular, porque los linajes de briófitos que se originan (o se diversifican) en las islas pueden expandirse con mayor facilidad a otros territorios. Se encontró evidencia compatible con orígenes macaronésicos en distintas especies de briófitos distribuidas tanto en islas como en áreas continentales; considerar estos casos elevaría la tasa de endemismo de los briófitos de Macaronesia muy por encima del porcentaje de endemismo insular comúnmente reconocido. Esto apoya una visión dinámica de las islas como contribuyentes a la biodiversidad continental mediante la “retro-colonización” y la colonización de novo, potencialmente facilitadas por cambios en los regímenes de viento durante los periodos glaciares y por “stepping-stones” temporales como cadenas de montes submarinos conocidas como Paleo-Macaronesia.

En cuanto a la historia demográfica, las reconstrucciones del tamaño efectivo de las poblaciones de plantas endémicas revelan una fuerte heterogeneidad temporal, pero en general sitúan las expansiones o contracciones principales mucho antes del inicio de la ocupación humana de las Islas Canarias hace cerca de 2000 años, lo que sugiere una detectabilidad limitada de los impactos antropogénicos recientes en la variación genómica actual. La excepción más clara es un declive poblacional localizado, globalmente concomitante con los primeros asentamientos humanos de origen bereber/amazigh. Entre especies, las señales se alinean con mayor frecuencia con dinámicas climáticas previas a la ocupación humana, incluidos los cambios posteriores al Último Máximo Glacial y la variabilidad del Holoceno medio (en particular, el Periodo Húmedo Africano), mientras que las diferencias entre taxones probablemente están mediadas por rasgos de historia de vida y por las capacidades de dispersión variables. Estos resultados también ponen de relieve la hipótesis de una deuda de extinción genética, según la cual una perturbación reciente del hábitat no siempre se traduce en una firma genética inmediata, incluso en contextos insulares.

En conjunto, esta tesis concluye que Macaronesia es un sistema moldeado tanto por la diversificación como por las migraciones. El endemismo de las espermatófitas refleja en gran medida las radiaciones insulares y la retención de linajes de distribución restringida, mientras que el endemismo de los briófitos se ve reducido no solo por la dispersión, sino por la combinación de radiaciones in situ limitadas y una “retro-colonización” de los continentes relativamente frecuente tras la especiación. Las historias demográficas de las plantas endémicas macaronésicas y canarias siguen en gran medida la dinámica climática del Cuaternario, mientras que las perturbaciones antrópicas recientes pueden tener impactos más débiles, localizados o retardados genéticamente. En conjunto, estos resultados aconsejan prudencia al interpretar el endemismo insular como un proxy universal de la especiación y refuerzan una visión dinámica de las islas como refugios y como fuentes de biodiversidad a escalas espaciales más amplias.

Résumé

La région macaronésienne : une histoire de sa diversité végétale au cours du temps.

Les îles océaniques sont des écosystèmes importants et dynamiques, présentant des taux élevés d'endémisme, ce qui en fait des laboratoires naturels pour comprendre comment la diversification, la dispersion et les perturbations façonnent les communautés biologiques. Plus particulièrement, la Macaronésie, région du Nord de l'océan Atlantique composée des archipels des Açores, de Madère, des îles Canaries et du Cap-Vert, constitue un système modèle idéal pour étudier comment les propriétés insulaires, les variations climatiques naturelles et les impacts humains historiques interagissent pour structurer les flores insulaires. Les grandes lignées de plantes terrestres y ont des diversités fortement contrastées : alors que les spermatophytes macaronésiens présentent des taux d'endémisme élevés, les bryophytes possèdent les taux d'endémisme insulaire les plus faibles rapportés parmi les plantes terrestres. Cette thèse vise à identifier les mécanismes écologiques et évolutifs à l'origine de ces patterns d'endémisme fort contrastés, et à évaluer comment le climat et les activités humaines ont influencé les histoires démographiques des plantes endémiques de cette région.

Ce travail est guidé par deux questions: (Q1) quels mécanismes expliquent les différences de patterns d'endémisme entre bryophytes et spermatophytes en Macaronésie, et que révèlent-ils quant au rôle des îles en tant que refuges ou « stepping-stones » pour la diversité continentale ? (Q2) dans quelle mesure les perturbations anthropiques et les variations climatiques naturelles ont-elles façonné l'histoire démographique des espèces végétales endémiques de Macaronésie ? Ces questions sont abordées au moyen (i) d'une synthèse et d'une réanalyse des données phylogéographiques et biogéographiques publiées sur différentes lignées de plantes terrestres, (ii) d'analyses phylogéographiques ciblées de bryophytes à large aire de distribution (amphi-Atlantique) afin d'évaluer les voies de colonisation et la chronologie des échanges îles-continents, et (iii) d'inférences de génomique des populations sur les changements démographiques d'angiospermes endémiques des Canaries et de Macaronésie, issues des deux écosystèmes les plus durement perturbés : la forêt thermo-sclérophylle et la forêt de lauriers.

Pour traiter la question des faibles taux d'endémisme des bryophytes par rapport aux spermatophytes, trois processus non exclusifs sont évalués : (1) une faible capacité évolutive intrinsèque, (2) une spéciation insulaire réduite en raison d'une forte connectivité et/ou de différences dans les modes de spéciation, et (3) une perte du statut d'endémique via des extinctions et/ou une « rétro-colonisation » ultérieure des régions continentales. Les éléments rassemblés ici remettent en cause la vision simpliste selon laquelle de grandes capacités de dispersion empêcheraient la spéciation. Nos résultats montrent que les populations insulaires et continentales de bryophytes conservent une structuration génétique significative et, pour une part importante des espèces, un signal phylogéographique significatif, compatible avec un isolement de longue durée et les prémisses d'une divergence. De même, l'évaluation des scénarios de migrations fondée sur des approches de coalescence ne favorisent pas systématiquement des taux de migration élevés, ce qui implique que le potentiel de dispersion à longue distance ne se traduit pas nécessairement par un grand nombre d'événements de

migration réussis. Contrairement aux spermatophytes, chez lesquels un nombre limité de radiations emblématiques a généré une grande part de la flore insulaire endémique, les bryophytes insulaires endémiques sont majoritairement issues de spéciations allopatriques, avec peu de preuves de diversification ultérieure in situ. Cette différence suggère que les patterns d'endémisme reflètent non seulement la dispersion et l'isolement, mais aussi des différences quant à la fréquence à laquelle les îles génèrent des radiations, par opposition à des lignées uniques structurées géographiquement.

Un résultat majeur de cette thèse est que les taux d'endémisme des bryophytes ne reflètent pas nécessairement leurs taux de spéciation car les lignées de bryophytes qui apparaissent (ou se diversifient) sur les îles peuvent rapidement étendre leur aire de distribution à d'autres territoires, perdant ainsi leur endémicité. La prise en compte de tels cas augmenterait le taux d'endémisme des bryophytes de Macaronésie bien au-delà du pourcentage d'endémisme insulaire généralement rapporté. Ces résultats soutiennent une vision dynamique des îles comme participant à la biodiversité continentale via « rétro-colonisation » et colonisation de novo, possiblement facilitée par des changements dans les régimes de vent durant les périodes glaciaires et par des « stepping-stones » temporaires tels que des chaînes de monts sous-marins, connues sous le nom de Paléo-Macaronésie.

Concernant l'histoire démographique, les reconstructions de taille efficace des populations de plantes endémiques révèlent une forte hétérogénéité temporelle mais situent généralement les expansions ou contractions majeures bien avant le début de l'occupation humaine des îles Canaries il y a environ 2000 ans, témoignant d'une empreinte limitée des impacts anthropiques récents dans la diversité génétique actuelle. L'exception la plus claire est un déclin localisé de population, globalement concomitant aux premiers peuplements humains d'origine berbère/amazighe. Pour la plupart des espèces, les signaux concordent plus souvent avec des dynamiques climatiques antérieures à l'occupation humaine, notamment les changements postérieurs au Dernier Maximum Glaciaire et les variabilités de l'Holocène moyen (en particulier la Période Humide Africaine), tandis que les différences entre taxons sont vraisemblablement médiées par des traits d'histoire de vie et des capacités de dispersion variables. Ces résultats mettent également en évidence l'hypothèse d'une dette d'extinction génétique, selon laquelle une perturbation récente des habitats ne se traduit pas toujours par une signature génétique immédiate, même en contexte insulaire.

Dans l'ensemble, cette thèse conclut que la Macaronésie est un système façonné à la fois par la diversification et les migrations. L'endémisme des spermatophytes reflète largement les radiations insulaires et la persistance de lignées à aire de distribution réduite, tandis que l'endémisme des bryophytes est réduit non seulement par la dispersion, mais aussi par un nombre limité de radiations in situ et l'importance de la « rétro-colonisation » des continents après spéciation. Les histoires démographiques des plantes endémiques macaronésiennes et canariennes suivent en grande partie la dynamique climatique quaternaire, tandis que les perturbations anthropiques récentes peuvent avoir des impacts plus faibles, localisés ou retardés génétiquement. Enfin, ces résultats incitent à la prudence quant à l'interprétation de l'endémisme insulaire comme proxy universel de la spéciation et renforcent une vision dynamique des îles à la fois comme refuges et comme sources de biodiversité à des échelles spatiales plus larges.

List of contributions

Papers / Manuscripts

- I. **Miroló, S.**, Ledent, A., González-Mancebo, J. M., Gabriel, R., Sim-Sim, M., Collart, F., Patiño, J.*, & Vanderpoorten, A.* (2026). Why are so few island bryophytes endemic? *Biological Reviews*, brv.70127. <https://doi.org/10.1002/brv.70127>
- II. **Miroló, S.***, Ledent, A.*, Patiño, J., Collart, F., & Vanderpoorten, A. (2026). Unveiling historical connections between island and continental floras: phylogeographic evidence from Macaronesian bryophytes. (Submission to *Plant Biology*)
- III. **Miroló, S.**, Jay-García, L. S., Mouton, L., Reyes-Betancort, A., Naranjo Cigala, A., Morente-López, J., Arjona, Y., Menezes de Sequeira, M., González Montelongo, C., García, A., Acevedo, A., Patiño, J.*, & Vanderpoorten, A.* Molecular echoes of Guanche legacies: unraveling human impact on the flora of the Canary Islands through comprehensive genomic exploration. *Manuscript*.

Ongoing study

- IV. Petrosino, C.*, **Miroló, S.***, Fichant, T.*, Fraïsse, C., Patiño, J., & Vanderpoorten, A. Genetic diversity and historical connections in the Canary Islands endemic flora: implications for conservation management.

Paper in Appendix S1

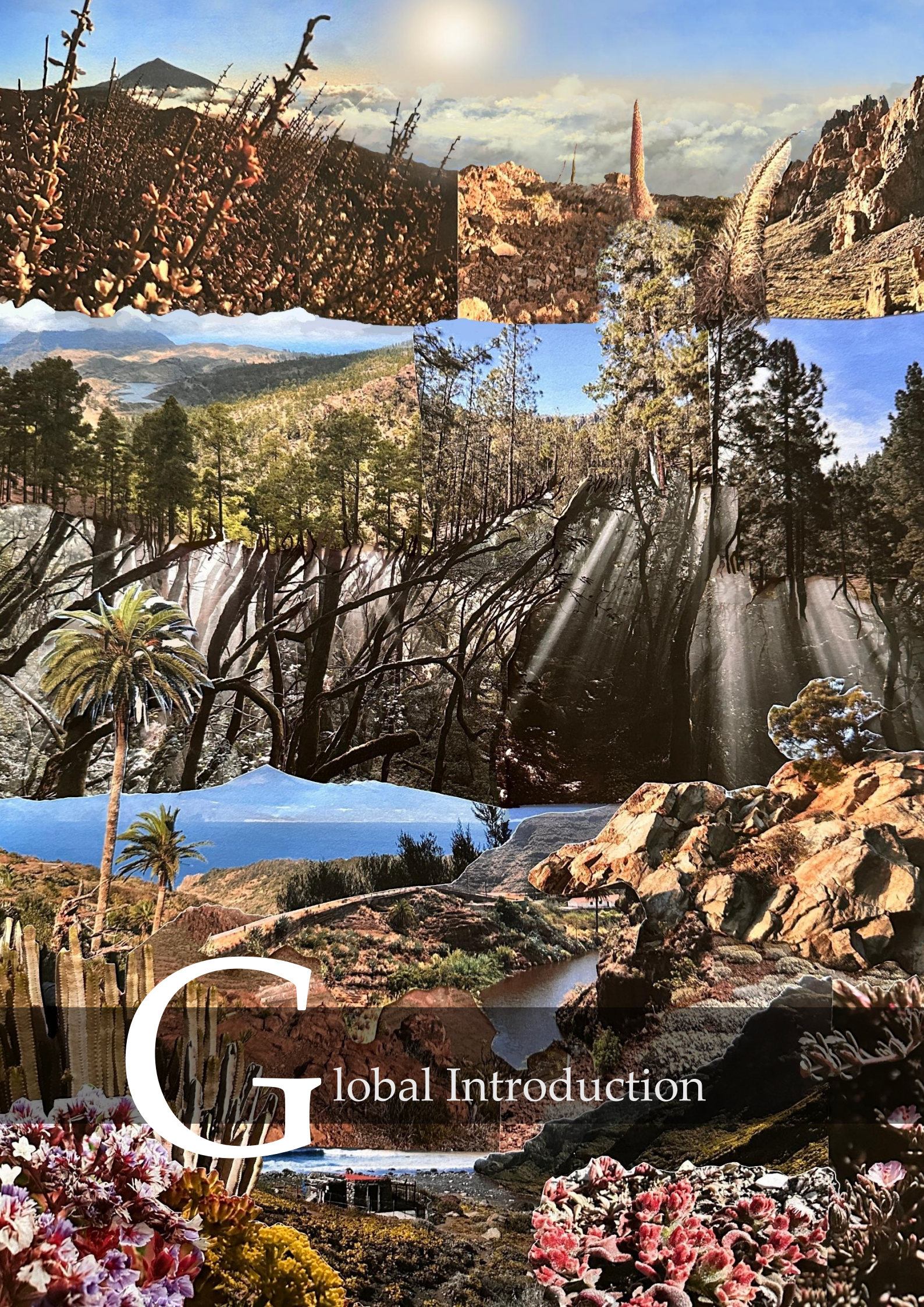
- V. Patiño, J.*, Collart, F.*, Vanderpoorten, A., Martin-Esquível, J. L., Naranjo-Cigala, A., **Miroló, S.**, & Karger, D. N. (2023). Spatial resolution impacts projected plant responses to climate change on topographically complex islands. *Diversity and Distributions*, 29(10), 1245–1262. <https://doi.org/10.1111/ddi.13757>

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G lobal Introduction

Islands, and oceanic islands in particular, are peculiar environments, as they account for only 5% of global emerged land but are home to 21% of the world vascular plant species (Schrader et al., 2024). Their ecosystems are very different from those on continents, with for example a tree line limit up to 2000m lower on oceanic islands than on mainland (Karger et al., 2019). The endemic richness is 9.5 times higher on islands than in continental regions, once standardized by area (Kier et al., 2009). This huge difference can be attributed to the combination of geographic isolation and strong environmental gradients, from sea level to alpine summits, that typically characterize oceanic islands and promote speciation (Schrader et al., 2024). During glacial cycles, and particularly the Last Glacial Period (LGP) and Last Glacial Maximum (LGM), islands further experienced a substantial increase in size, and hence, of their carrying capacity, owing to lower sea levels under climatically buffered conditions, thereby increasing speciation rates and decreasing extinction rates (Fernández-Palacios et al., 2016). Additionally to their high biodiversity, islands also include the most fragile ecosystems in the world. Approximately 50% of all threatened species are endemic to islands, and around 75% of all known extinctions concern insular species (Fernández-Palacios et al., 2021), even without taking into account ‘dark extinctions’ (see Orihuela-Rivero et al., 2025). Current major threats to insular ecosystems include the introduction of invasive species (Haines et al., 2024), changes in land cover and habitat loss and fragmentation (Otto et al., 2017), climate change and the associated rise of sea level (Veron et al., 2019), which are altogether well-established responsible causes for the ongoing biodiversity crisis and disruption of ecosystem services (Moustakas et al., 2025; Zittis et al., 2025; Fernández-Palacios et al., 2021; Russell & Kueffer, 2019).

As they were the last places on earth being colonized by humans, islands are good model systems to study anthropic environmental disturbances (Nogué et al., 2021; Whittaker et al., 2017; Vitousek, 2002). It was shown that all colonized islands suffered major biodiversity losses, with high vegetation turnover corresponding to the period of human settlement (Nogué et al., 2025, 2021). Anthropic modifications in insular environments have had much more dramatic impacts than in mainland environments on native ecosystems. Indeed, island species evolved in almost complete isolation, which promoted the evolution of a series of traits, collectively referred to as the island syndromes, such as the loss of defensive and competitive traits and dispersal capacities (Barton & Fortunel, 2023). We can therefore say that current insular ecosystems were shaped through various key events, both climatic and anthropic.

To study these processes, the Macaronesian region is an ideal model as it is, along with Hawaii and the Galápagos, one of the best studied insular systems in the world (Cerca et al., 2023; Florencio et al., 2021). Macaronesia is considered a hotspot of biodiversity (Hoffman et al., 2016).

Endemic species represent almost half of the native plant species and 35% of the global biota, with a total of around 7000 endemic species (Fernández-Palacios et al., 2025; Mouton et al., 2023). It is home to some of the most impressive oceanic island radiative evolutions, as best exemplified by the genera *Echium*, *Argyranthemum* or *Aeonium* in plants, and the lizard genus *Gallotia* or the chaffinches *Fringilla* in animals.

Macaronesia was first circumscribed in the 19th century as a biogeographic region comprised of three oceanic islands archipelagos of the North Atlantic ocean, namely the Azores, Madeira, and Canary Islands (Engler, 1879). The circumscription of the region was subsequently broadened to include the Cape Verde islands, but also continental enclaves in North Africa and Iberia due to their floristic similarities (Sunding, 1979). Based on the same floristic criteria and excluding the small Selvagens islands, Macaronesia was recently recognized as the biogeographic region comprised of the Azores, Madeira, Canary Islands, and Cape Verde islands (Fernández-Palacios et al., 2024) (Figure 1). From these four archipelagos, only Cape Verde is an independent country, while the Azores and Madeira are two autonomous regions of Portugal, and Canary Islands are an autonomous region of Spain (see Table 1 for some key features of each archipelago).

Table 1 – Macaronesian archipelagos: geographical and demographical parameters. From Fernández-Palacios et al. (2025).

Parameter	Azores	Madeira	Selvagens	Canary Islands	Cape Verde	Macaronesia
<i>#islands >1km²</i>	9	5	1	11	14	40
<i>Area (km²)</i>	2764	815	3	7447	4033	15062
<i>Elevation (m)</i>	2351	1862	154	3718	2835	3718
<i>Distance to continent (km)</i>	1369	630	375	96	571	96
<i>Oldest emerged island age (My)</i>	6	14	27	23	16	27
<i>Human colonization</i>	1432	1420	/	~2000BP	1462	~2000BP
<i>Population density (inhabitants/km²)</i>	91	430	/	295	124	212

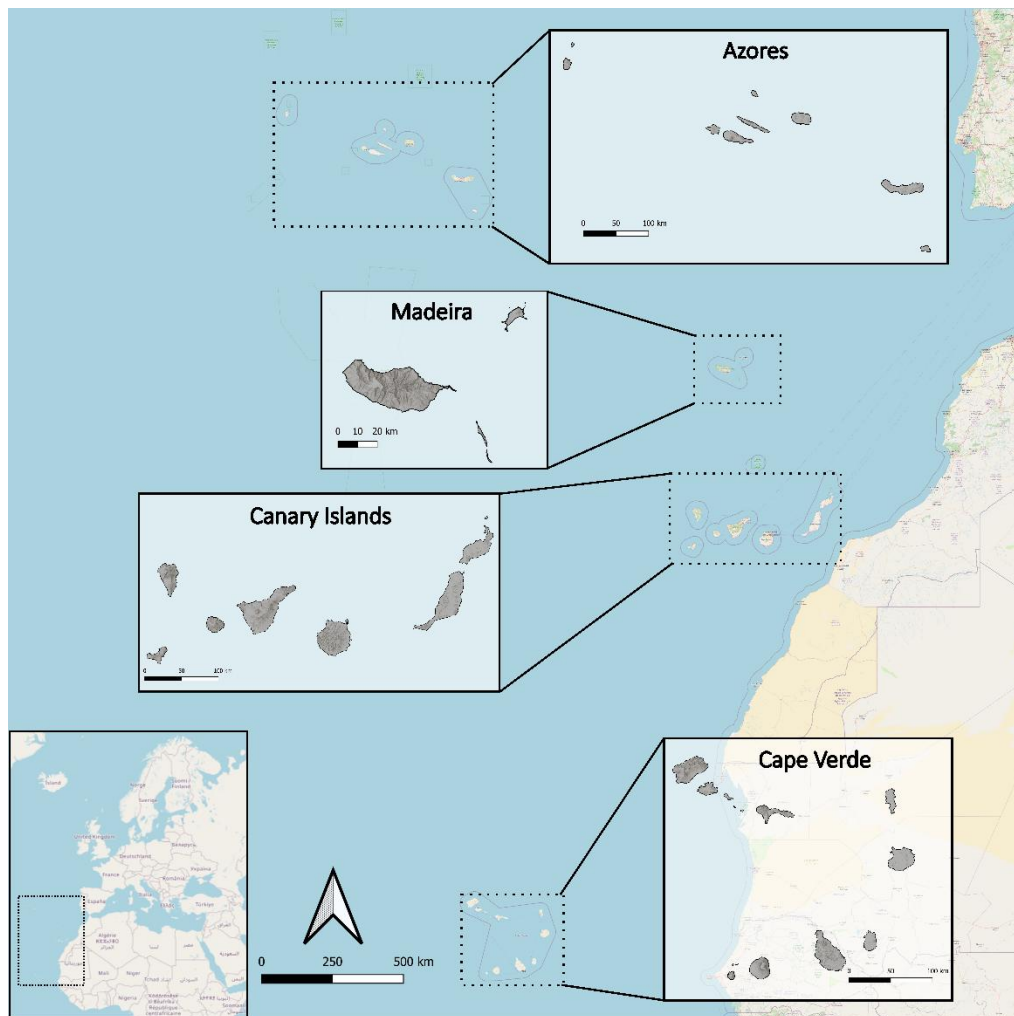


Figure 1 – Map of the Macaronesian region with its 4 archipelagos highlighted. From top to bottom: the Azores, Madeira, the Canary Islands, Cape Verde. Map created by F. Collart, background maps from OpenStreetMap.

This region is characterized by three different floristic components (Figure 2) (Fernández-Palacios et al., 2024):

- The Palaeotropical-Tethyan flora, including laurel forest taxa, is shared by the three northern archipelagos of the Azores (A), Madeira (M) and Canary Islands (C). It includes most canopy tree species of the laurel forest ecosystem, some species only shared between Madeira and the Canary Islands, like *Apollonias barbujana* or *Persea indica*, but also *Morella faya* that is common across the three archipelagos where it covers large areas. We can also cite examples from the genera *Ilex* (A: *perado* ssp. *azorica*, M: *perado* ssp. *perado*, C: *perado* ssp. *platyphylla* and ssp. *lopezlilloi*), *Laurus* (A: *azorica*, M-C: *novocanariensis*), or *Picconia* (A: *azorica*, M-C: *excelsa*).
- The African Rand flora is shared by the three southern archipelagos of Madeira (M), Canary Islands (C) and Cape Verde (V). This flora is disjunct between Macaronesia and the coastal margins of Arabia and North Africa. It includes species from the thermo-sclerophyllous woodland and succulent scrub ecosystems, and was probably widely distributed across Africa during more humid periods, now persisting only in small fragmented areas after extinction events, leading to speciation. Famous examples are the species of *Dracaena* (M-C: *draco*, C: *tamaranae*, V: *caboverdeana*) and *Sideroxylon* (M: *mirmulans*, C: *canariense*, V: *marginatum*).
- The neoendemic flora constitutes the third characteristic floristic element of Macaronesia present on the four archipelagos, and includes famous examples of insular secondary woodiness. Many species in this flora are believed to have a Mediterranean origin, with numerous cases of subsequent radiative evolution events (e.g., the *Aeonium* alliance (62 species), *Echium* (22 species), and *Argyranthemum* (24 species)) leading to a highly diversified floristic element (Carine et al., 2010; Price et al., 2018).



Figure 2 – Examples of species from the three floristic elements characteristic of the Macaronesian region. Palaeotropical-Tethyan flora (left) = *Apollonias barbujana*; African Rand flora (center) = *Dracaena draco*; Neoendemic flora (right) = *Echium perezii*. All pictures taken by Sébastien Mirolo.

Major historical climatic events had huge consequences on the biodiversity of Macaronesian islands. A recent palynological record on the island of Gran Canaria attests of the important changes that occurred during the transition from the LGP, through the LGM, into the Holocene, with the laurel forest replaced by a pine forest during the LGM before making way to a thermo-sclerophyllous woodland (Martin-Ramos et al., 2025). Another notably important climatic period that impacted Macaronesian ecosystems was the African Humid Period (AHP), as evidenced by palynological records (Castilla-Baltrán et al., 2021; Nogué et al., 2013). A vegetation turnover was recovered at the end of the AHP around 5500BP, when hygrophilous taxa were replaced by less water-demanding species. This more humid period was linked to a higher latitude limit of the West African monsoon, probably reaching the Canary Islands (Pausata et al., 2016), but there is still no clear consensus on the matter (but see Martin-Ramos et al., 2025). Other punctual natural events are also responsible for the current distribution and state of the ecosystems in Macaronesia, like volcanic eruptions or hurricanes. Studies on the ecosystem recovery following the latest volcanic eruption in the Canary Islands, Tajogaite volcano (also known as Cumbre Vieja) on the island of La Palma in December 2021, demonstrated the adaptation and resistance of the pine forest ecosystem to this kind of disruption (Guerrero-Campos et al., 2025). Hurricanes were also documented as temporarily increasing trees growth rate, with very local effects detected (Rozas et al., 2023).

More recently, Macaronesian ecosystems have been impacted by human disturbance. High rates of deforestation since the European colonization of the archipelagos during the 15th century led to very low surface of native vegetation cover (Norder et al., 2020). In the Canary Islands, the picture is more complicated since this archipelago was colonized twice: first by people of Berber/Amazigh origin around 2000 BP (Santana et al., 2024), and second by Europeans during the 15th century. The former introduced species like goats and sheep, while the latter arrived with rat infested vessels. Both extensively deforested for agriculture and logging purposes, leaving around a quarter of the native ecosystems potential natural area. This proportion is probably much higher than it would have been before the 1940s, when rural lands were abandoned after the second world war, and until the 1970s with the beginning of a tourism-based economy and rural exodus (Rozas et al., 2023; del Arco Aguilar et al., 2010). Anthropogenic impacts in the Canary Islands are extensively discussed in Box 1.

In the Canary Islands, only 26.7% of the land is currently covered by natural vegetation, meaning that almost three quarters of the islands surface is degraded (data from 2010, see Table 2 and Figure 3). Among the six vegetation belts composing the majority of the altitudinal gradient, the most impacted one is the thermo-sclerophyllous woodland, with only 8.4% of its former potential

surface area remaining. The historical over-exploitation of this ecosystem for agriculture and pastoralism led to an advanced state of degradation, which is currently worsening with the extension of human development from the coast to higher altitude (del Arco et al., 2010). The evergreen laurel forest ecosystem was also strongly affected by humans, leaving for example only 1% of its former natural distribution on the island of Gran Canaria, and with a missing potential of 88.2% of its former natural distribution globally (Table 2).

Table 2 – Actual and potential area covered by vegetation across the 6 vegetation belts present in the Canary Islands (data from del Arco Aguilar et al., 2010).

Ecosystem	Actual area [ha]	Potential area [ha]	Canary total potential surface	% Missing potential (area [ha])
Coastal halophilous belt	2124	2609	0.35%	18.6 (485)
<i>Euphorbia</i> scrubs	49046	355227	47.77%	86.2 (306181)
Thermo-sclerophyllous woodland	6432	76980	10.35%	91.6 (70548)
Evergreen laurel forest	10181	86624	11.65%	88.2 (76443)
Canary pine woodland	60678	112697	15.16%	46.2 (52019)
Meso-oromediterranean summit broom scrub	15247	16341	2.20%	6.7 (1094)

BOX 1 – The Canary Islands: historical account of human impact on their biodiversity

Pre-Colonization Period

The Canary Islands are a peculiar archipelago within the North Atlantic ocean, as it is the only one that was colonized twice: once by North African Amazigh people starting during the 1st century CE (Santana et al., 2024), and the second time in the 14th century CE by Europeans. Beside the timing of colonization, here defined following Pozo (2024) as the permanent settlement of people, these islands were already known by other civilizations as corroborated by Pliny the Elder (23-79 CE) who irrevocably mentioned them in his *Natural History* (book VI, chapter 37). The Roman Tyrian purple dye factory, found on Lobos and dated to the 1st century BCE, offers direct evidence of Antiquity civilizations' knowledge of the existence of this archipelago (Mitchell, 2024). Other Antiquity authors might have written about the Canary Islands, such as the Carthaginian's *Periplus* of Hanno the Navigator (5th century BCE), but these sources are impossible to verify except for the technological navigation capacity of such a journey (Mauny, 1955). Other types of data also point to ancient human presence, such as palynological records dating the arrival of men around 2300 years ago, with an increase in frequency of wildfires (de Nascimento et al., 2016).

The pre-colonization period led to limited attested human impact on biodiversity, as only Eastern islands show traces of resources exploited by Romans. Aside from settlements focusing on the harvesting of *Stramonita haemastoma*, a sea snail, from which the highly prized Tyrian purple dye was extracted, there were probably also a few settlement areas in the South of Lanzarote for seasonal high sea fishermen (Mitchell 2024; del Arco Aguilar et al., 2016). More recently, genetic evidence suggests that goats were maybe brought and then left at this period to these islands, where they became feral. Another explanation hypothesizes the overlapping presence of Romans and Amazigh people, where the former would have taken goats from the latter (Díaz-Pérez et al., 2025).

The Amazigh Period

Amazigh people, also known as Berbers, probably colonized all Canarian islands between the 1st and 5th centuries CE, likely within about 200 years (Santana et al., 2024). The rapid colonization helps to explain similitudes between the different cultures of each island in the first centuries. The currently accepted story gives a westward direction to the colonization. It would have started from Lanzarote and Fuerteventura, and expanded subsequently to Gran Canaria, Tenerife, La Gomera, and finally La Palma and El Hierro. Each island's culture then evolved independently in isolation, but from the same shared background (Mitchell, 2024; Santana et al., 2024 but see Pozo, 2024 for discussions about who were the first Canarians and when they arrived).

A range of evidence from Gran Canaria suggests that, around the 11th century CE, a new colonization event from North Africa took place in the Canaries, leading to co-existing cultural traditions such as funerary practices (Alberto-Barroso et al., 2022), dietary habits (Lécuyer et al., 2021), a rediscovery of the marine environment (Delgado-Darias et al., 2023), and a global technological innovations era (Velasco-Vázquez et al., 2021). However, this second colonization wave is contested (Santana et al., 2025). Ancient DNA genetic data, however, point to a more complex history than the unique Amazigh colonization, with some clear differences between people from the Eastern and Western islands such as different genome ancestral components, but also no direct evidence of a second colonization as hypothesized from Gran Canaria data alone (Serrano et al., 2023; Fregel et al., 2019). The only observed consensus between all studies and all types of data is the complete isolation of people from different islands at the time of European colonization, probably for centuries, suggesting an absence of communication, trade, and exchanges of any kind (Hagenblad et al., 2025, 2017; Morales et al., 2023, 2009; Fregel et al., 2019 but see Pozo, 2024 for discussion on the matter).

Major environmental changes are linked to the colonization, and then exploitation, of the Canary Islands by Amazigh people. They introduced the so-called “Mediterranean farming package” at its Westernmost expansion, which consisted here in 5 domestic animals, some of them becoming problematic invasive species like goats (*Capra hircus*), sheep (*Ovis aries*) and cats (*Felis catus*) (Biota, 2025), and various crops like wheat (*Triticum durum*), barley (*Hordeum vulgare*), lentil (*Lens culinaris*), bean (*Vicia faba*), pea (*Pisum sativum*) and figs (*Ficus carica*) (Morales et al., 2023, 2009). Forests clearcutting and burning took place to cultivate those species (de Nascimento et al., 2020), leading to soil erosion and degradation (Morales et al., 2009), and landscape modifications (Castilla-Beltrán et al., 2021) with for instance the complete extinction of indigenous forests on Fuerteventura (Machado Yanes, 2007). Many animal species also went extinct due to hunting pressure, habitat modification and the introduction of predators, for example Canarian giant lizards (*Gallotia* spp.), birds (e.g., *Puffinus holeae*, *Coturnix gomerae*, *Emberiza alcoveri*) or rodents (*Canariomys* spp., *Malpaisomys insularis*) (Fernández-Palacios et al., 2025). Native plant species were impacted as well but it is difficult to determine to what extent due to the lack of fossil evidence. The only known examples are two extinct tree species based on evidence from pollen grains found in sediments (de Nascimento et al., 2009) and the extinct *Ruta museocanariensis* found in mummy shrouds (Marrero-Rodríguez et al., 2023). We can, however, expect that two millennia of grazing by introduced ovicaprids induced some extinctions as well (see Orihuela-Rivero et al., 2025 on the “dark extinction” phenomenon).

The European Period

The Canary Islands were colonized by European people during the 15th century, but the archipelago was first rediscovered, mapped, and then widely visited in the 14th century CE. The Castilian conquest started with the invasion of Lanzarote in 1402 by Norman nobles and ended with the fall of Tenerife in 1496 in the hands of the Castilian crown. Thousands of aboriginal people were killed and sold as slaves across Europe and other archipelagos such as Madeira, but also within the Canary Islands themselves, a genocide that eradicated their whole culture (Adhikari, 2017). Subsequently, the islands became an important slave-based agricultural center and an inevitable hub for transatlantic trade (Crosby, 1972). Agriculture was the basis of the economy in the archipelago until the second half of the 20th century, when it turned itself toward a tourism-based development model (García-Rodríguez et al., 2018).

The European colonization accelerated the degradation of the environment through deforestation for intensified agriculture and introduction of invasive species, which led to many documented extinctions (Orihuela-Rivero et al., 2025; Castilla-Beltrán et al., 2021; Parsons, 1981). Some ecosystems were actively restored during the 20th century, like pine forests (Parsons, 1981), and the abandonment of agricultural practices led to natural regeneration of laurel forests since the 1940-1980 period (Rozas et al., 2023; Fernández-Palacios et al., 2017), even if only 11.8% of its natural distribution remains (del Arco Aguilar et al., 2010). By contrast, the condition of thermo-sclerophyllous woodlands remains poor, making it the most threatened ecosystem in Canary Islands with only 8% of its natural distribution remaining (del Arco Aguilar et al., 2010; Fernández-Palacios et al., 2008), and coastal *Euphorbia* scrubs are decreasing due to urbanism and tourist development (del Arco Aguilar et al., 2010). Despite more than 40% of its surface being protected (Gobierno de Canarias, 2024), only one quarter of the archipelago is covered in natural vegetation (del Arco Aguilar et al., 2010).

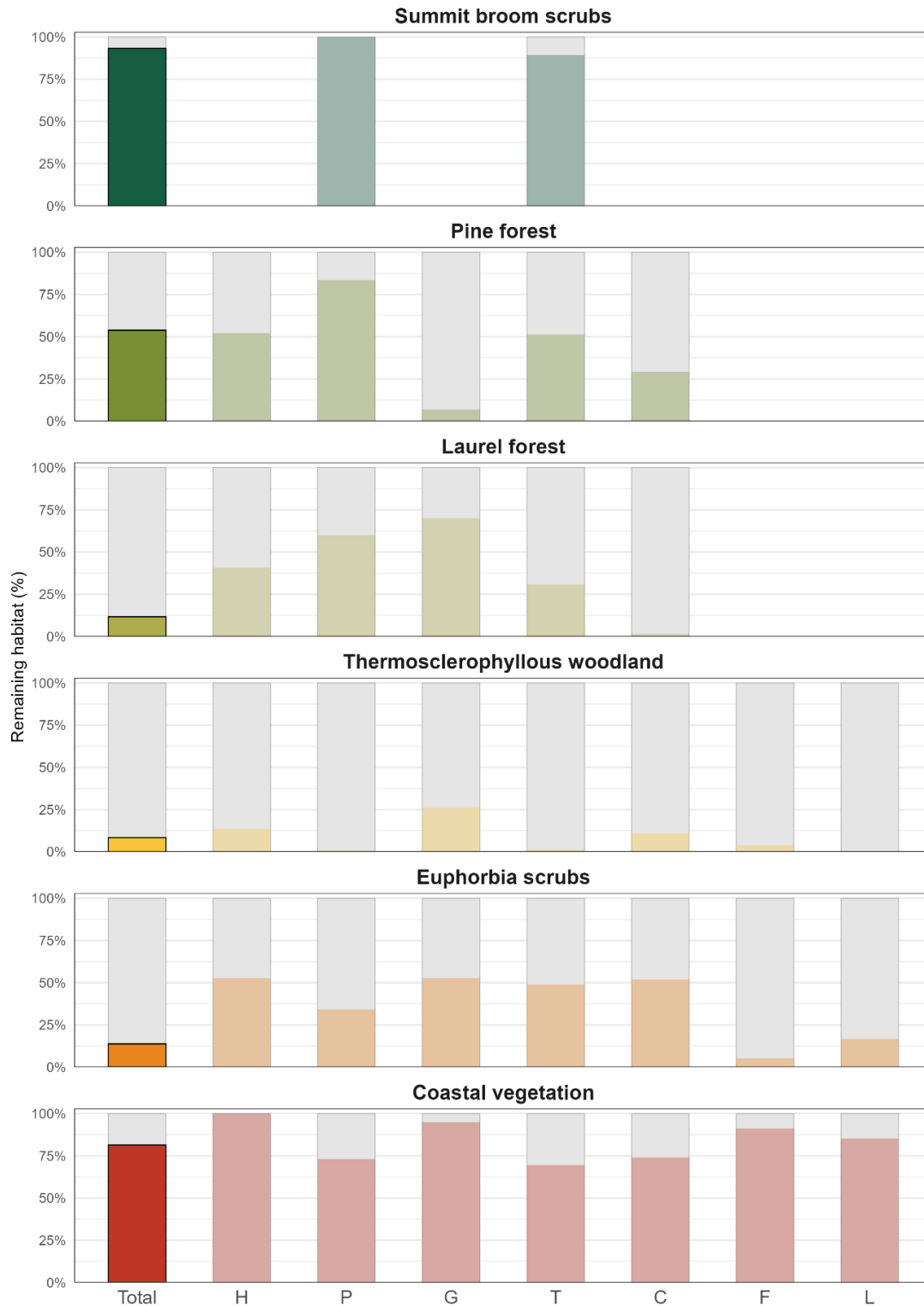


Figure 3 – Proportion of remaining habitats across the 6 vegetation belts present on the Canary Islands. The filled colored portion of the bars represents the preserved fraction of a given vegetation type on a given island (or Total across all islands). The absence of bar means represents the absence of this vegetation type on this particular island. H = El Hierro, P = La Palma, G = La Gomera, T = Tenerife, C = Gran Canaria, F = Fuerteventura, L = Lanzarote. Data from del Arco Aguilar et al. (2010).

The concept of Macaronesia by Engler (1879) and subsequent biogeographers (Sunding, 1979; Bramwell, 1976, 1972; Takhtajan, 1969; Dansereau, 1961) placed particular emphasis on the endemic element of the vascular flora. Engler (1879) was the first to interpret the origin of this substantial endemic element in terms of the relict from a formerly widespread subtropical flora that covered southern Europe and North Africa during the Tertiary, complemented by *in situ* speciation of ancient Mediterranean clades. Palaeogeographical and paleontological data do not, however, provide irrefutable evidence for Engler's refugium model. The latter has been supported (e.g. Santos et al., 2026) and challenged based on molecular phylogenetic evidence, which suggests that the patterns of relationship and evolution of the Macaronesian endemic vascular flora are much more complex than what Engler's refugium model would predict (Kondrakov et al., 2015; Carine, 2005; Carine et al., 2004). The debate concerning the concept of Macaronesia has, to date, largely focused on the spermatophyte flora (Fernández-Palacios et al., 2024). The cryptogamic, and in particular, the bryophyte floras, have received much less attention.

Bryophytes are the second most diverse land plant group after spermatophytes, with an estimated 22,000-25,000 species (Goffinet & Shaw, 2009). They primarily disperse by tiny spores of about 10-20 µm that can travel considerable distances. Bryophytes therefore tend to exhibit large, trans-oceanic distribution ranges (Patiño & Vanderpoorten, 2018) and in fact, 9% of the mosses and 14.4% of the liverwort species occurring in Macaronesia are absent from the close Palearctic region and disjunct in more remote areas, in particular, the Neotropics (Mirolo et al., 2026). Consequently, it has been hypothesized that the extremely low rates of endemism in the Macaronesian flora result from the high long-distance dispersal capacities of bryophytes, counter-acting genetic drift and thereby, limiting speciation opportunities (Patiño et al., 2014; Vanderpoorten et al., 2011).

Despite this, the origin of the Macaronesian bryophyte flora has traditionally been interpreted in the context of Engler's relictual model (see Vanderpoorten et al., 2007 for review). This perception was in part supported by fossil evidence. The moss genus *Echinodium*, for instance, is currently known only from Macaronesia and Australasia, but Baltic and Saxon amber fossils attest to a formerly much wider range (Frahm, 2004). Such an interpretation has, however, been challenged by phylogenetic evidence of the polyphyly of the genus (Stech et al., 2008), questioning the relationship between fossil and extant species. As with spermatophytes, or perhaps even more, the application of Engler's refugium model has been increasingly challenged. In particular, recent phylogeographic evidence suggests that the Macaronesian bryophyte flora would have either served as a refugium for continental biodiversity during the glacial period (Hutsemékers et al.,

2011; Laenen et al., 2011) or even a source of novel biodiversity that would have subsequently colonized the western fringe of Europe (Patiño et al., 2015), offering strong support to mounting evidence for a substantial role of islands as reservoirs for continental biodiversity, in sharp contrast to Engler's refugium model (see Box 2 for a historical overview of the back-colonization concept).

1.1 Objectives of the thesis

The present thesis focuses on the biogeographic history of the Macaronesian flora. Based on a phylogeographic approach, it addresses two main questions: what have been the mechanisms through which the evolution of bryophytes and spermatophytes led to so contrasting patterns of endemism? To what extent have human disturbance and natural climatic cycles impacted species demographic history? To address these broad questions, the thesis was divided into two main sections.

Patterns of endemism in bryophytes and spermatophytes

The first section is divided in two chapters addressing different but complementary aspects of the mechanisms that led to strikingly opposed endemism patterns between bryophytes and spermatophytes.

The first chapter aims at disentangling the mechanisms responsible for the lower endemism rate in bryophytes compared to spermatophytes through a review of available evidence and re-analyses of published data. More specifically, three main hypotheses will be tested: (i) high migration rates prevent genetic divergence, and hence, speciation from geographically close continents, so that endemic speciation only happens after long-distance dispersal from remote continents; (ii) high rates of clonality and selfing prevent admixture, hampering chances for recombination and hybrid speciation; (iii) insular endemic species rapidly back-colonize continental regions, thereby losing their endemic status.

The second chapter aims at better understanding the biogeographic history of more widely distributed bryophyte species, and at testing the role of islands as stepping-stones at continental scale. Here, we use amphi-Atlantic species distributed in Macaronesia and both sides of the North Atlantic to address two main questions: what have been the historical relationships between island and mainland populations? Is the timing of Macaronesian archipelagos colonization and any subsequent back-colonization of mainland regions compatible with the hypothesis that islands were biodiversity refugia during glacial periods as they had higher carrying capacity and lower geographic isolation, making them more available for migrants of

allochthonous origin at the same time as many species went extinct on mainland areas due to the advance of the ice sheet?

Human impact on endemic plant species

The second section comprises the third chapter in which we aim at determining to what extent human actions and climatic events shaped current demographic history of Macaronesian plant species. By taking Canarian and Macaronesian endemic plant species from the two historically most disturbed ecosystems, namely the thermo-sclerophyllous woodland and laurel forest, we seek for signatures of human disturbance, disentangling the impact of the first settlement and of the European colonization, and compare this impact with that of major climatic events.

BOX 2 – Historical overview of the back-colonization concept

The study of island biogeography was formalized by MacArthur and Wilson in the 1960s with their funding concept of the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1967). At the same period, the plate tectonics theory led to a paradigm shift, along with new cladistic approaches, markedly influencing biogeographers, and dividing them into teams of supporters for vicariance vs dispersal mechanisms (e.g., Nelson & Platnick, 1981; Rosen, 1978). Vicariance explains species distributions through the fragmentation of an ancestral continuous range by geological or environmental events, which isolated populations that diverged and evolved independently. In contrast, dispersal explains distributions through the active or passive movement of organisms across geographic, ecological, or other barriers, founding new populations that subsequently evolve on their own. Dispersal theories, such as the ETIB, were still explaining most of the observed diversity patterns found on oceanic islands, but vicariance theory gained more and more support. Species were grouped by phenotypic similitudes through cladistic analyses, and geographically coherent groups were explained by tectonic plates movements. For island clades, transitory landbridges were hypothesized to explain their presence but also their differences through long-term isolation (Queiroz, 2005). The development of molecular techniques, in particular genetic sequencing, uncovered more detailed interpretations of island biodiversity, and conclusions were often at odds with vicariance theory, favoring dispersal mechanisms, but also frequently opposed to both (Heaney, 2007; Queiroz, 2005).

In a traditional island biogeography framework, islands represent evolutionary dead-ends that can be colonized from mainland, but island species cannot disperse towards continents. This view is exemplified by Wilson's (1961) statement that "[a taxon] *can shift its headquarters from a large land mass to a smaller one but not in the opposite direction*" (Wilson, 1961). Yet, the premises of a paradigm shift were already apparent in the early biogeographic literature. Ball (1878) and Hooker (1878), in particular, both had already hypothesized a Macaronesian origin for endemic plant species growing on the Moroccan coast (Fernández-Palacios & Whittaker, 2020). This pattern of continental species embedded in insular groups was frequently recognized, although several decades of skepticism were necessary before acknowledging continent colonization by island taxa as a credible concept (Park et al., 2001; Seidel, 1988). Various names were given, such as 'reverse colonization', 'retro-colonization', 'boomerang event', or 'back-colonization' (Figure A) (Fernández-Palacios & Whittaker, 2020; Caujapé-Castells, 2004).

To our current knowledge, the first case of a modern back-colonization hypothesis was formulated in 1959 by Hillenius, stating that the Chamaeleon clade was of Malagasy origin (Hillenius, 1959). Even if it was finally refuted (Tolley et al., 2013), this hypothesis has been followed by various researchers for decades (Raxworthy et al., 2002). Herpetologists hypothesized that multiple clades were of insular origin during the 1980s and 1990s. Some of these hypotheses were refuted, like a Caribbean origin of North American *Trachemys* ssp. (proposed by Seidel, 1988; refuted by Stephens & Wiens, 2003) or a Malagasy origin of some East African Gekkonidae species (proposed by Kluge & Nussbaum, 1995; refuted by Austin et al., 2004), others proved to be accurate (e.g., a Caribbean origin of American *Anolis* Norops species first proposed by Jackman et al., 1997). The back-colonization hypothesis was also suggested in other animal clades, such as a Cuban origin of continental frogs *Eleutherodactylus* spp. (proposed by Hedges, 1989; demonstrated by Crawford & Smith, 2005), a Malagasy origin of East African Nesomyines rodents (proposed by Jansa et al., 1999; refuted by Poux et al., 2005), a Pacific islands origin of multiple clades of Australian monarchs bird species (proposed and

demonstrated by Filardi & Moya, 2005), or a Hawaiian origin of some continental flies *Scaptomyza* spp. (proposed by O'Grady & DeSalle, 2008; debated for the whole genus).

In plants, the back-colonization concept arose in the Macaronesian region, where many examples have been documented. The first case supported by molecular data, in 1996, revealed that East African *Aeonium* species come from a Canarian ancestor (Mes et al., 1996; Mes & Hart, 1996), therefore showing the first back-colonization example resulting from long-distance dispersal (Machado et al., 1998). We can also cite the Macaronesian origin of Portuguese *Convolvulus* species among the first cases (proposed by Pinto da Silva & Teles, 1981; demonstrated by Carine et al., 2004). Other archipelagos were also shown as sources of diversity for continental flora (e.g., Price & Wagner, 2018 for a review of Hawaiian cases).

The paradigm shift regarding the back-colonization concept was made possible thanks to molecular phylogenies and genetic sequencing technologies (reviewed in Bellemain & Ricklefs, 2008). New insular biogeography theories arose to cope with this new and more dynamic view of islands diversity, like the General Dynamic Model of oceanic island biogeography (Whittaker et al., 2008), or the more recent glacial-sensitive model of island biogeography (Fernández-Palacios et al., 2016). These models build on the ETIB, accounting for island ontogeny in the former case and the dynamics of glacial cycles in the latter case, adding the notion of windows of opportunities (Carine, 2005) for long distance dispersal during glacial periods, when islands reached their largest size and elevation. The buffered climatic conditions and larger surfaces during glacial periods thus made islands perfect glacial refugia for continental species, and thus reservoir of biodiversity for back-colonization.

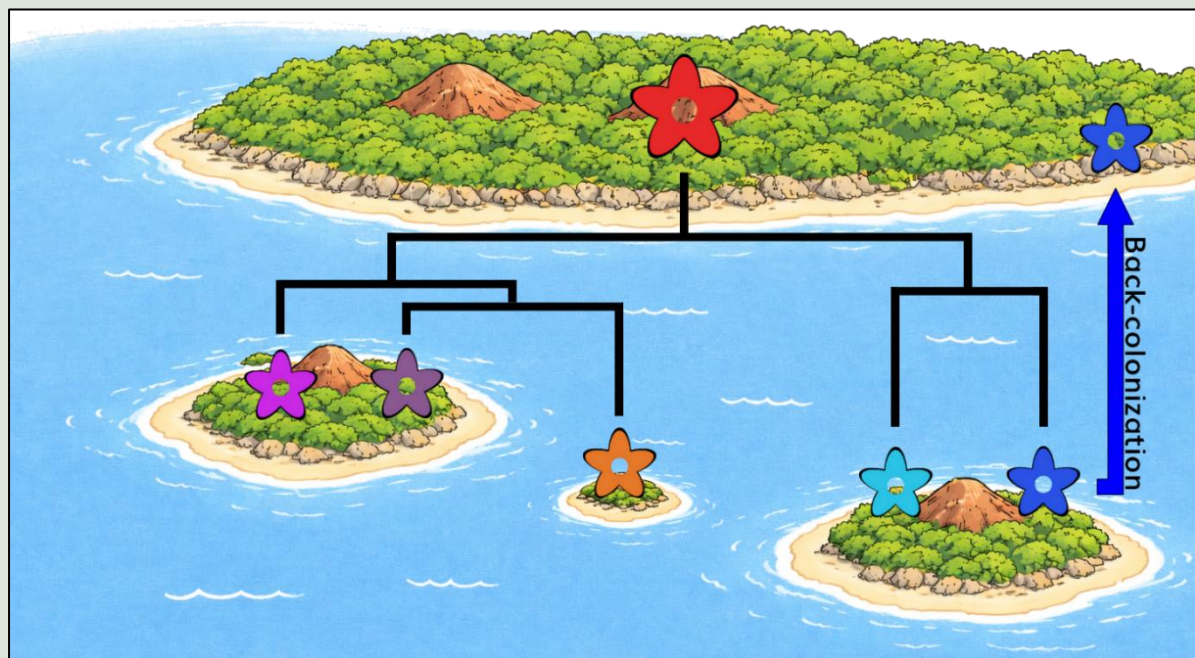


Figure A – Schematic representation of a back-colonization event. A continental ancestor (red flower) colonizes the islands, where it radiates in five new endemic species (pink, purple, orange, turquoise, and blue flowers). The blue flower colonizes back the continent from which its ancestor originated (blue arrow). Figure made by J. Mirolo.



Chapter 1

Why are so few island bryophytes endemic?

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 endemism 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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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

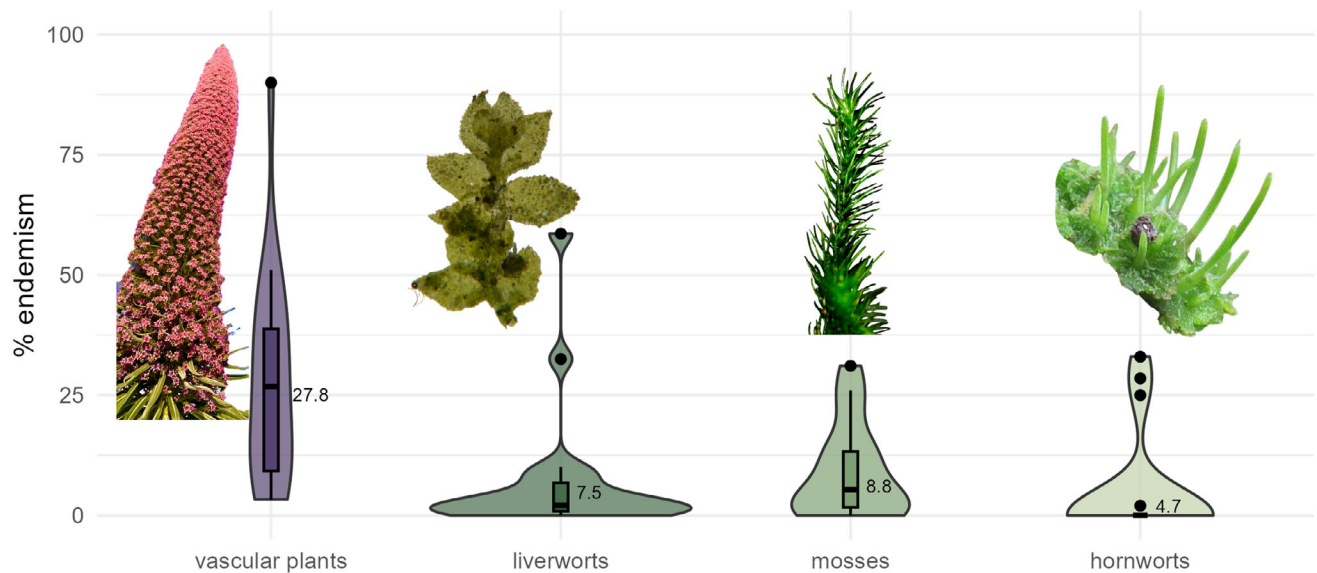


Fig. 1. Comparative rates of species endemism in oceanic islands and archipelagos ($N = 19$, Table S1) across vascular plants, liverworts, mosses, and hornworts. The boxplots show the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre line, with the mean value indicated), 1.5 $\times$ interquartile range (whiskers) and extreme values beyond the whiskers. Images from left to right: *Echium perezii*, an iconic woody 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 endemism 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 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). 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 <i>et al.</i> , 1993)	0.02–0.1 (Gómez-Nogues <i>et al.</i> , 2017)	0.05–>100 (Arditti & Ghani, 2000)
Settling velocity (m/s)	0.005–0.085 (Zanatta <i>et al.</i> , 2016)	0.01–0.11 (Gómez-Nogues <i>et al.</i> , 2017)	0.02–9.02 (Casseau <i>et al.</i> , 2015; Liu <i>et al.</i> , 2021; Pietsch & Chapman, 2023; Song <i>et al.</i> , 2020)
Dispersal distance	25–50th percentile: 1 m (<i>Sphagnum</i> ; Sundberg, 2005) 40–60th percentile: >100 m (<i>Discolium</i>) (Lönnell <i>et al.</i> , 2015)	95th percentile: ca. 1 m [†] (Rose & Dassler, 2017)	50th percentile: 0.2–0.9 m 95th percentile: 2.9–17.9 m (Bullock <i>et al.</i> , 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 Kondrakov *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

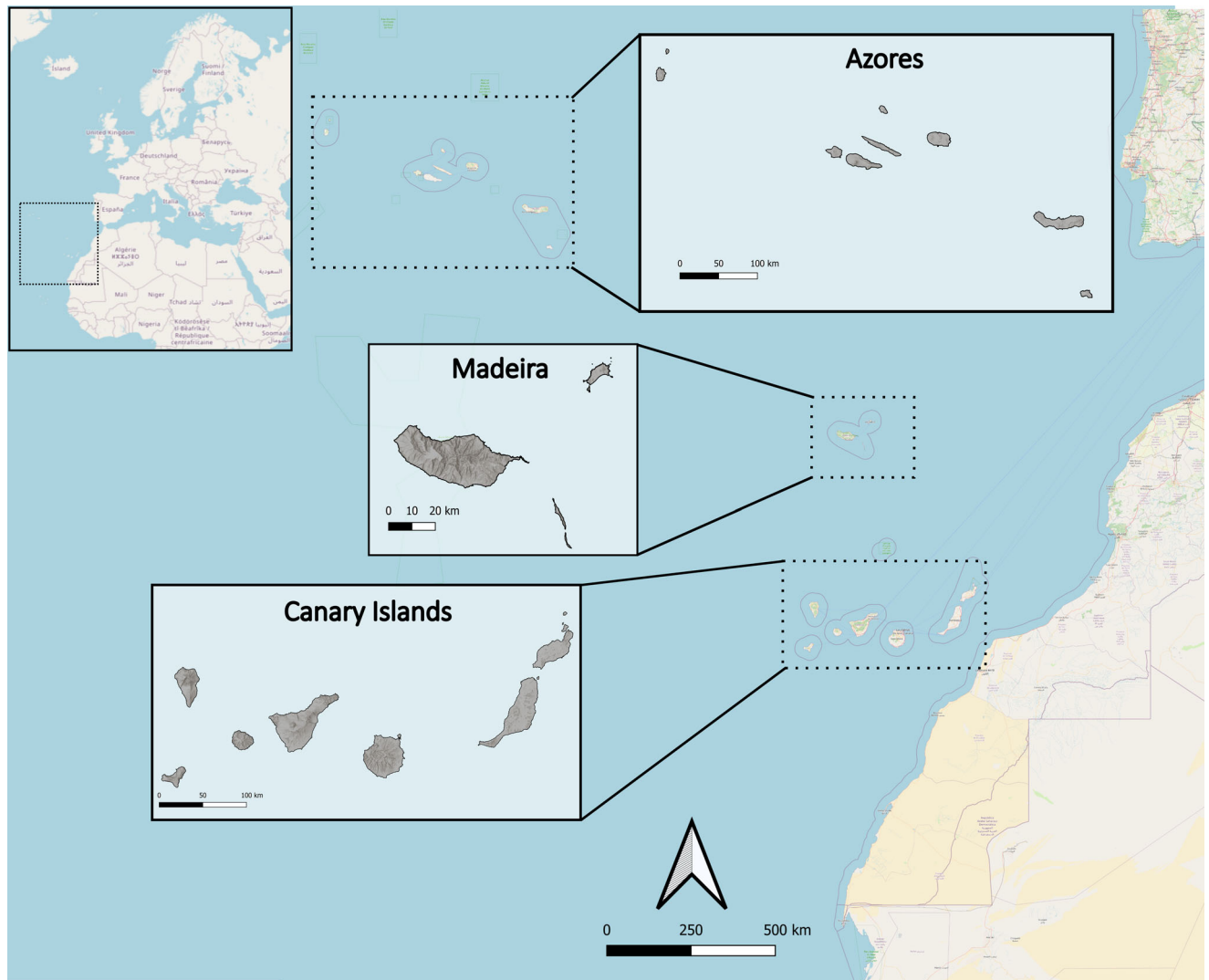


Fig. 2. Map of the study area, including the archipelagos of the Azores, Madeira, and Canary Islands. Background maps from OpenStreetMap.

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 (H_e) and nucleotide diversity (π , 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*, *Hedenasiastrium 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 *Isoethecium* (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

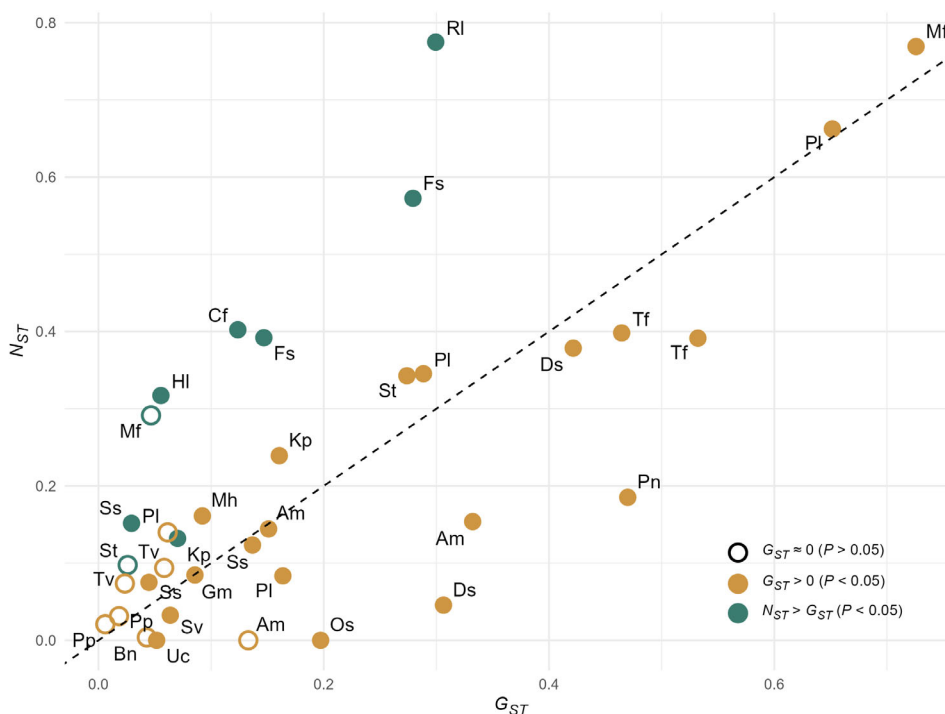


Fig. 3. Unilocus genetic structure of non-endemic Macaronesian bryophyte species for which suitable sequence data were available (see Table S2), as expressed by pairwise G_{ST} (genetic differentiation based on allele frequencies) and N_{ST} (G_{ST} analogue incorporating phylogenetic relationships among 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*; Pt = *Pulvigeria lyellii*; Pn = *Pycomitrium nigrescens*; Pp = *P. polyphyllum*; Rl = *Radula lindenbergiana*; Ss = *Sematophyllum substrumulosum*; St = *Scleropodium touretii*; Sv = *Saccogyna viticulosa*; Tf = *Tetrastichium fontanum*; Tv = *T. virens*; Uc = *Ulota calvoscens*.

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* (García-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*, *Plagioclila* 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*, *Pelekiium*, *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

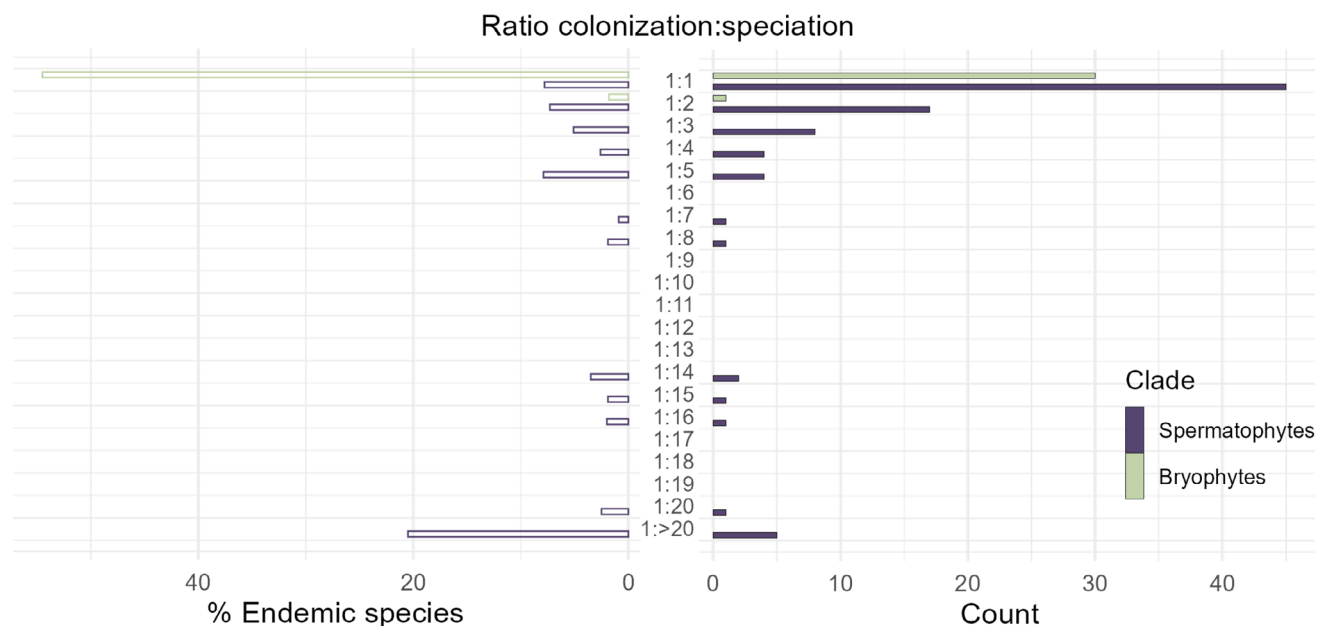


Fig. 4. Comparative patterns of *in-situ* diversification in Macaronesian spermatophytes (purple) and bryophytes (green). Right panel shows ratio between the number of speciation events (endemic species) and the number of colonization events per clade. Left panel shows contribution (%) of clades to the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

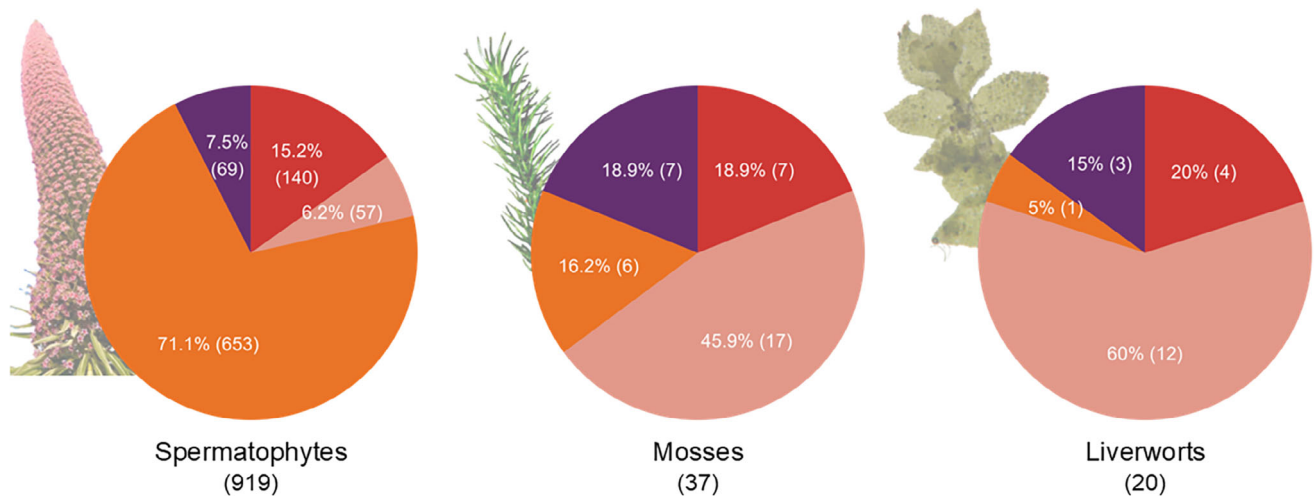


Fig. 5. Proportions of single and multiple archipelago endemic species in spermatophytes, mosses and liverworts (no Macaronesian hornworts are endemic). Numbers and percentage of endemic species are shown in each slice of the pie diagram, with the total number of endemic species in each group indicated 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 *Isoetecium*, 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

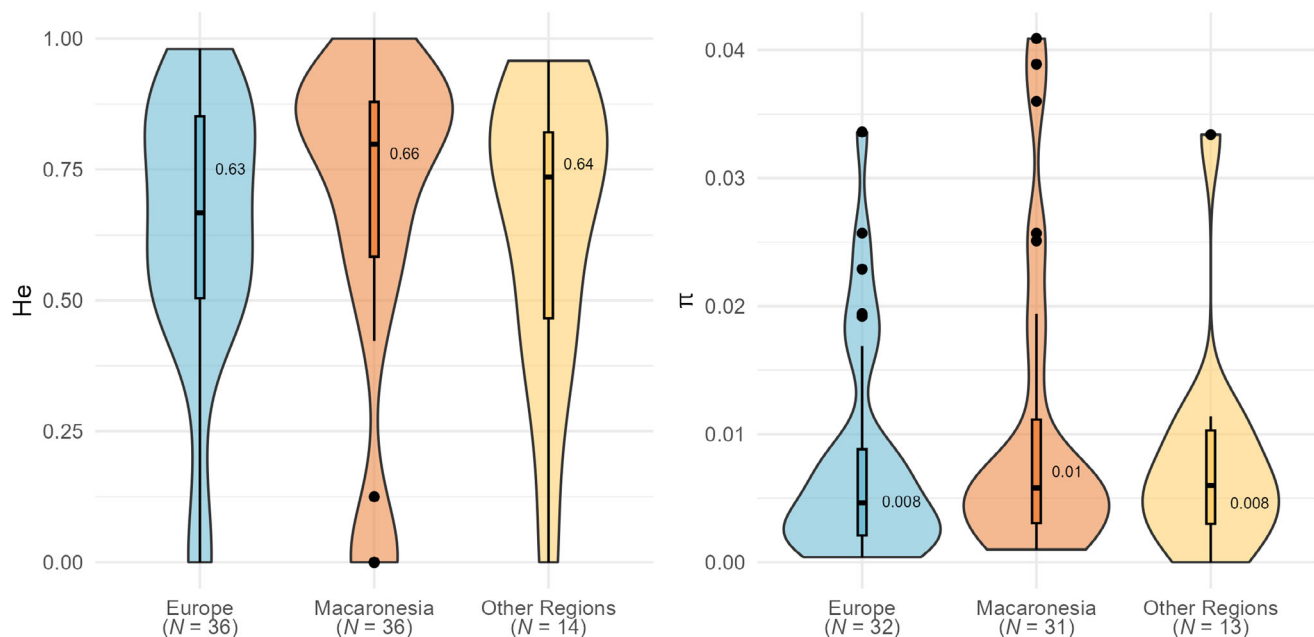


Fig. 6. Unilocus genetic diversity of non-endemic Macaronesian bryophyte species, as expressed by expected heterozygosity (H_e ; left) and weighted mean genetic distance between alleles (π ; right). The box-plots show the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre line, with mean value indicated), 1.5 $\times$ 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 endemism 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			
<i>Dicranum scottianum</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Epipterygium atlanticum</i>	Single European accession nested within a Macaronesian clade (Hanusch <i>et al.</i> , 2020)	None	0
<i>Fissidens serrulatus</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Frullania calcarifera</i>	Ancestral range estimations (Fig. S5)	None	0
<i>Frullania teneriffae</i>	Ancestral range estimations (Fig. S5)	None	0
<i>Homalia lusitanica</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Lejeunea lamacerina</i>	European accessions nested within a Macaronesian clade (Heinrichs <i>et al.</i> , 2013)	None	0
<i>Myurium hochstetteri</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Ptychomitrium nigrescens</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Ptychomitrium polyphyllum</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Radula lindenbergiana</i>	Ancestral range estimations (Laenen <i>et al.</i> , 2011)	None	0
<i>Sematophyllum substrumosum</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Saccogyna viticulosa</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Tetrastichium fontanum</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Tetrastichium virens</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
<i>Thamnobryum maderense</i>	Nested within a clade of Macaronesian endemics (Olsson <i>et al.</i> , 2011)	None	0
<i>Ulotia calvescens</i> *	Coalescence simulations (Patiño <i>et al.</i> , 2015a)	None	0
Spermatophytes			
<i>Aeonium alliance</i> *	Continental species nested within a Macaronesian clade (Mort <i>et al.</i> , 2002)	<i>Aeonium leucoblepharum</i> , <i>A. arboretum</i> subsp. <i>korneliuslemsii</i> , <i>A. stuessyi</i>	1:3
<i>Convolvulus</i> *	Continental species nested within a Macaronesian clade (Carine <i>et al.</i> , 2004)	<i>Convolvulus femandesii</i>	1:1
<i>Dracaena draco</i> *	Ancestral range estimations (Durán <i>et al.</i> , 2020)	None	0
<i>Euphorbia</i> *	Continental populations nested within a Macaronesian clade (Barres <i>et al.</i> , 2011, 2017; Martín-Hernanz <i>et al.</i> , 2023; Rincón-Barrado <i>et al.</i> , 2024)	<i>E. pedroi</i> , but none in the case of <i>E. balsamifera</i> and <i>E. regis-jubae</i>	1:1
<i>Limonium</i> *	Ancestral range estimations (Koutroumpa <i>et al.</i> , 2021; Lledó <i>et al.</i> , 2005, 2011)	<i>L. fallax</i> , <i>L. mucronatum</i>	1:2
<i>Lotus</i> *	Ancestral range estimations (Jaén-Molina <i>et al.</i> , 2021)	<i>L. assakensis</i> , <i>L. pseudocreticus</i> , <i>L. criticus</i>	1:3
<i>Matthiola</i> *	Continental populations nested within a Macaronesian clade (Jaén-Molina <i>et al.</i> , 2009)	<i>M. sinuata</i> , but none in the case of <i>M. bolleana</i>	1:1
<i>Sonchus pinnatifidus</i> *	Continental populations nested within a Macaronesian clade (Cho <i>et al.</i> , 2019; Lee <i>et al.</i> , 2005)	None	0
<i>Tolpis</i> *	Ancestral range estimations (Gruenstaedtl <i>et al.</i> , 2017)	<i>T. virgata</i> , but none in the case of <i>T. barbata</i>	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 endemism 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 endemism 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 hot-spots, 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>.

X. REFERENCES

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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 (H_e), and mean genetic distance between alleles weighted by allele frequency (π).

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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ILES CANARIES

Chapter 2

Unveiling historical connections between island and continental floras: phylogeographic evidence from Macaronesian bryophytes.

Unveiling historical connections between island and continental floras: phylogeographic evidence from Macaronesian bryophytes

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Running title: Phylogeography of Macaronesian bryophytes

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. This suggests that, in groups with high long-distance dispersal capacities like bryophytes, floristic similarity is 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.

Key words: bryophytes, oceanic islands, island biogeography, Approximate Bayesian Computation, coalescence, endemism, Macaronesia

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 center of distribution on the oceanic archipelagos of the Azores, Canary Islands, Madeira, and Cape Verde, collectively forming the Macaronesian biogeographic region (Fernández-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 (Tolley *et al.* 2013; Fritz *et al.* 2024; Austin *et al.* 2004; Poux *et al.* 2005) or supporting (Nicholson 2002; Nicholson *et al.* 2005; Crawford & Smith 2005; Filardi & Moyle 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 (Heaney 2007; de Queiroz 2005; 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 McArthur & Wilson's equilibrium theory of island biogeography (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, McArthur & 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 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 transoceanic 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 and with the hypothesis of severe extinctions in mainland areas, making the latter largely available for migrants of allochthonous origin?

MATERIAL & 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 total number of accessions ranging between 21 and 179 and 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.

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 (Fernández-Palacios *et al.* 2016), mainland populations experienced a bottleneck at LGM followed by an expansion during inter-glacial 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 yrs BP and 15,000 yrs BP; the Last Glacial Maximum (LGM), between 19,000 and 26,000 yrs BP; the pre-LGM period, between 29,000 and 250,000 yrs 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 yrs 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

$$N_e = \theta / \mu \text{ (eq.1),}$$

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 centered 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 equaled 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 5km^2 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 over-specific 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 $Ne_0 \in [2; 100]$. Subsequent population expansion was modelled using a growth rate r defined as:

$$Ne_t = Ne_0 e^{rt} \text{ (eq.2),}$$

where t is the time interval between the founder event and the end of the considered period, and Ne_t the effective population size of the population of interest at the considered period, as estimated using eq.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 splitted 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 laid between $1e-10$ to $1e-6$, and a second set, wherein the sampled rates laid between $1e-5$ to $1e-1$. 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 analyzed 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 1). 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*.

Coalescence simulations generated data that were compatible with the observed summary statistics of genetic structure and diversity (Figs. S1 to S9). The procedure of model selection was characterized by low rates of false positives ranging between 3 and 14% (Table S4). 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 species and a continental origin of Macaronesian populations, including two from Europe, two from extra-European origins, and one 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 (5 species) or during the current interglacial period (2 species), than before the LGM (2 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).

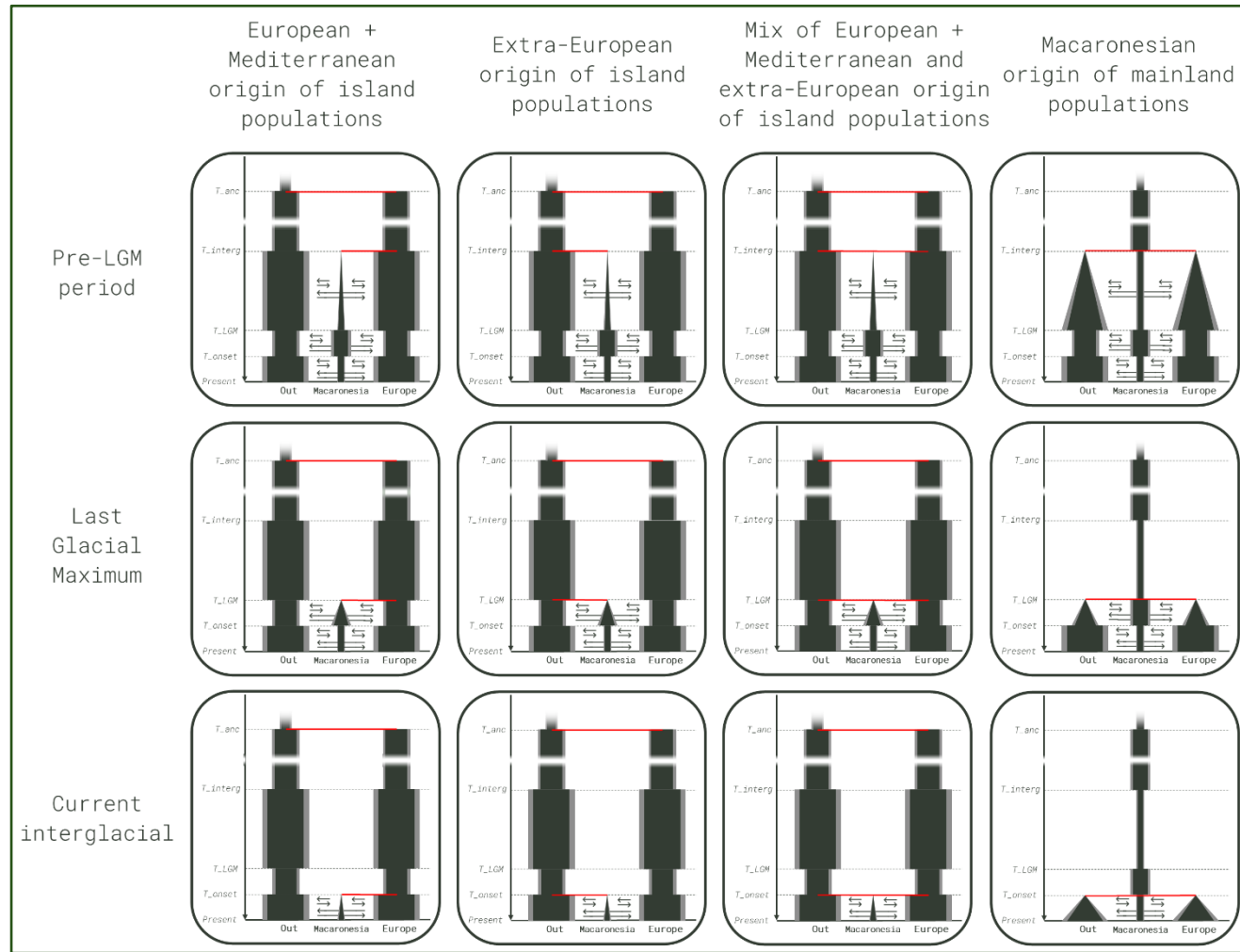


Figure 1 – Hypothetical phylogeographic scenarios for the relationships between populations from Macaronesia, Europe and the Mediterranean basin (Europe), and other regions (Out) since the last interglacial period. A combination of four scenarios of geographic origin (columns) and timing of colonization (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.

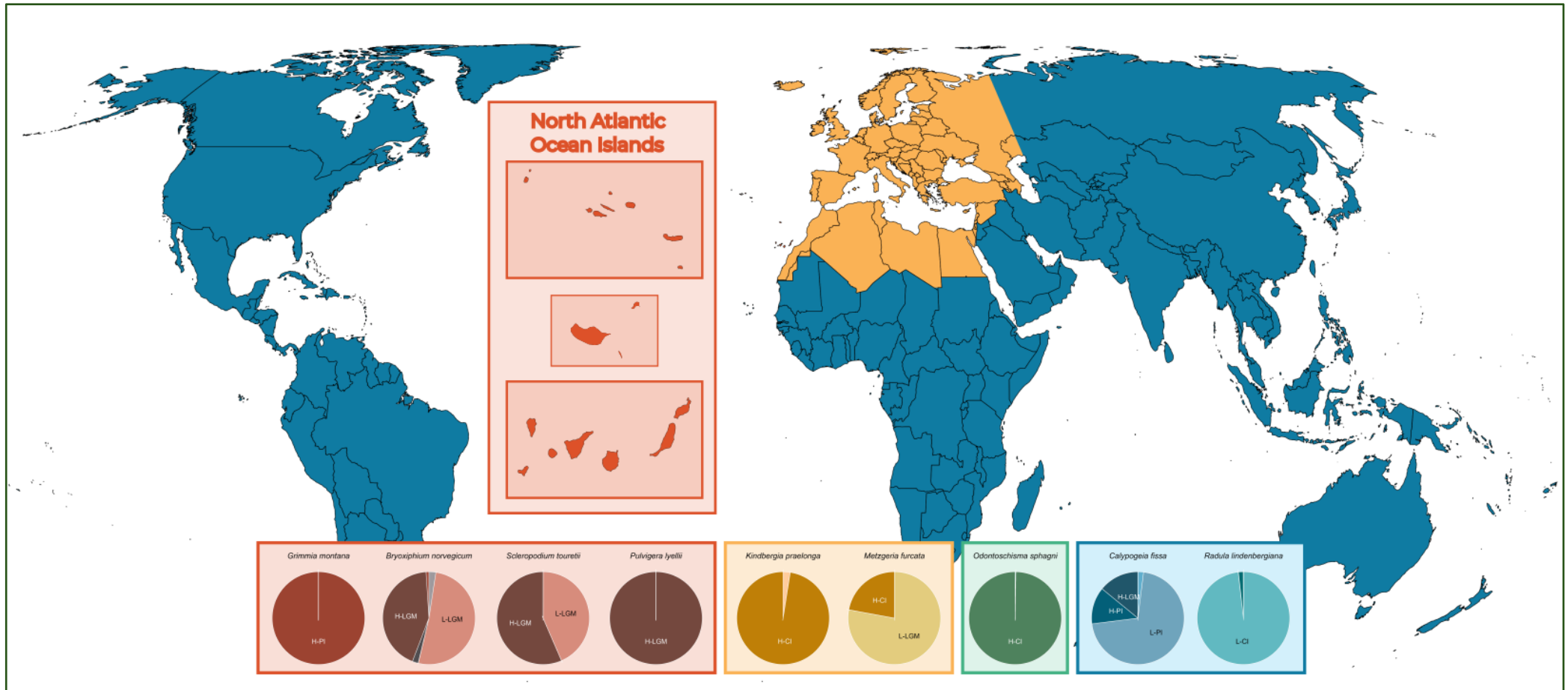


Figure 2 – Phylogeographic history of selected amphi-Atlantic bryophyte species inferred from coalescence analyses. Pie diagrams indicate the posterior probability of competing scenarios, involving (i) an origin of island populations from Europe and the Mediterranean (in yellowish tones), from extra-European origin (in blueish 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 & 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 emphasised 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. 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). 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 (Lönnell *et al.* 2012, 2014; Sundberg 2005), accounting for the decay of the isolation-by-distance signal beyond 100m 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 2009 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, i.e., the systematic over- or under-representation 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 simple 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 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 transoceanic 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 Mediterraneo-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 *Pulviger a 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, trans-continental 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 shortcomings with the coalescence simulations. Indeed, the time unit in the latter is a generation, which needs to be translated into years through the generation time. While the estimation of the latter is straightforward in annual species, it is more complicated in perennial species. It is generally defined as the age at which an individual reproduces, but its actual estimation is challenging and can lead to substantial differences (Jonasson *et al.* 2022). Here, following Patiño *et al.* (2015) and Ledent *et al.* (2019), we fixed the generation time at 5 years. This generation time is consistent with estimates in other perennial

mosses, such as *Polytrichum*, wherein Pressel *et al.* (2025) 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 *et al.* 2017, 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 relatively 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 holds great promises 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.

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SUPPLEMENTARY DATA

Article title: Unveiling historical connections between island and continental floras: phylogeographic evidence from Macaronesian bryophytes

Authors: Sébastien Mirolo, Alice Ledent, Jairo Patiño, Flavien Collart, Alain Vanderpoorten

The following supplementary data are available for this article:

Table S1	Amphi-Atlantic bryophyte species included in a meta-analysis on the relationships between Macaronesian and continental populations.
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Table S2	Numbers of climatically pixels of 5km ² 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.
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Table S3	Genetic structure and diversity of amphi-Atlantic bryophyte species across their Macaronesian, European and Mediterranean, and extra-European range.
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Table S4	ABC-GLM model validation.
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Figures S1:S9	PCA analysis on the simulated and observed genetic summary statistics for each of the nine species investigated in the present study.
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Table S1 – Amphi-Atlantic (i.e., species distributed across Europe and the Mediterranean basin, North/SouthAmerica, 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 of 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.

Species	#genes	Gene partition	Europe	Macaronesia	Extra-European	Data sources
<i>Bryoxiphium norvegicum</i>	1	rpoC1-rps4-trnG-trnLF (c)	5	3	27	Patiño et al., 2016
<i>Calypogeia fissa</i>	1	atpIH-psbD-trnL (c)	33	27	12	Ledent et al., 2019
<i>Grimmia montana</i>	1	psbA1-psbT-trnLF (c)	25	8	19	Vanderpoorten et al., 2008
<i>Kindbergia praelonga</i>	2	ITS (n)	45	17	24	Hedenäs 2010
		trnG (c)	46	16	22	
<i>Metzgeria furcata</i>	2	ITS2 (n)	48	5	2	Ledent et al., 2019 + Fuselier et al., 2009
		trnG (c)	161	11	7	
<i>Pulviger a lyellii</i>	4	AW108 (n)	104	14	33	Ledent et al., 2019
		AW317 (n)	117	16	56	
		AW454 (n)	111	12	41	
		trnG (c)	115	13	53	
<i>Odontoschisma sphagni</i>	1	trnLF (c)	7	6	8	Aranda et al., 2014 + Vilnet et al., 2012 + Shaw et al., 2015 + Feldberg et al., 2016
<i>Radula lindenber giana</i>	1	aspB-rps4-trnG-trnL (c)	35	39	4	Laenen et al., 2011 + Patiño et al., 2017 + Devos et al., 2011
<i>Scleropodium touretii</i>	2	ITS (n)	14	8	21	Carter 2012 + Vanderpoorten et al., 2005 + Cezón et al., 2010
		psbA2-rps4-trnG (c)	14	13	22	

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Table S2 – Numbers of climatically pixels of 5km² 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.

Species	Present			LGM			Bottleneck		Expansion
	Europe	Extra-European	Macaronesia	Europe	Extra-European	Macaronesia	Europe	Extra-European	Macaronesia
<i>Amphidium mougeotii</i>	5600904	10716290	9081	4620577	8031956	16562	0.82	0.75	1.82
<i>Pulviger a lyellii</i>	3866988	4094126	17880	2362794	6281526	28908	0.61	1.53	1.61
<i>Calypogeia fissa</i>	1911427	2188530	19598	1555536	1872982	29483	0.81	0.85	1.50
<i>Metzgeria furcata</i>	3690913	1738304	16229	2190364	1632695	29083	0.59	0.94	1.79
<i>Diplophyllum albicans</i>	3651395	6479002	19009	3621444	3279615	29483	0.99	0.50	1.55
<i>Homalothecium sericeum</i>	3101434	3506129	18917	3446306	4992677	29427	1.11	1.42	1.55
<i>Metzgeria conjugata</i>	2938867	3091006	17761	1187987	2171825	29482	0.40	0.70	1.66
<i>Lewinskya affine</i>	1632291	1399826	5272	2251808	1457573	18141	1.38	1.04	3.44
<i>Plagiothecium denticulatum</i>	3631259	4114643	7042	2560838	3478729	23186	0.70	0.84	3.29
<i>Plagiomnium undulatum</i>	3111173	3776529	17117	1049196	1828414	29064	0.34	0.48	1.69
<i>Plagiothecium undulatum</i>	2119284	2721412	6938	1612026	1420863	15935	0.76	0.52	2.296
<i>Scorpiurium circinatum</i>	793017	4445319	19686	837134	4085604	29445	1.05	0.92	1.49

0.34	0.48	1.49
1.38	1.53	3.44

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.

SPECIES	Locus	Gst_mac_out	Gst_mac_eur	Gst_eur_out	Nst_mac_out	Nst_mac_eur	Nst_eur_out	He_out	He_mac	He_eur	p_out	p_mac	p_eur
<i>Bryoxiphium norvegicum</i>	rpoC1-rps4-trnG-trnLF (c)	0.02	0.05	0.057	0	0	0.11	0.96	1	0.9	0.006	0.006	0.005
<i>Calypogeia fissa</i>	atpIH-psbD-trnL (c)	0.17***	0.06**	0.14***	0.54***	0.05*	0.43***	0.82	0.85	0.89	0.011	0.007	0.01
<i>Grimmia montana</i>	psbA1-psbT-trnLF (c)	0.07*	0.08*	0.11***	0.1	0.04	0.1***	0.89	0.86	0.88	0.006	0.005	0.004
<i>Kindbergia praelonga</i>	ITS (n)	0.05	0	0.15***	0.12**	0.01	0.16***	0.82	0.65	0.46	0.011	0.002	0.002
	trnG (c)	0.23**	0.2*	0.084*	0.24**	0.2*	0.24***	0.68	0.12	0.46	0.01	0.002	0.002
	multilocus	0.12**	0.08*	0.12***	0.18**	0.08*	0.2***	0.75	0.39	0.46	0.011	0.002	0.002
<i>Metzgeria furcata</i>	ITS2 (n)	1	0.59**	0.3	1	0.66**	0.31	0	0	0.58	NA	NA	0.017
	trnG (c)	0.07	0.03	0.04	0.34**	0.29**	0.24*	0.9	0.82	0.7	0.033	0.006	0.009

<i>Odontoschisma sphagni</i>	trnLF (c)	0.01	0.34*	0.2*	0	0.04*	0	0.79	0.73	0.52	0.006	0.025	0.007
<i>Pulviger a lyellii</i>	AW108 (n)	NA	0.06	NA	NA	0.14*	NA	NA	0.6	0.68	NA	0.009	0.023
	AW317 (n)	NA	0.16*	NA	NA	0.08	NA	NA	0.76	0.53	NA	0.039	0.026
	AW454 (n)	NA	0.65***	NA	NA	0.66***	NA	NA	0	0.56	NA	NA	0.019
	trnG (c)	NA	0.29**	NA	NA	0.35***	NA	NA	0.6	0.5	NA	0.005	0.002
	multilocus	NA	0.3***	NA	NA	0.28***	NA	NA	0.49	0.57	NA	NA	0.017
<i>Radula lindenbergiana</i>	aspB-rps4-trnG-trnL (c)	0.3**	0.17***	0.42***	0.84***	0.42***	0.81***	0.5	0.89	0.67	0.003	0.001	0.002
<i>Scleropodium touretii</i>	ITS (n)	0.34***	0.12**	0.36***	0.34***	0.17*	0.81***	0.43	0.89	0.86	0.003	0.003	0.002
	psbA2-rps4-trnG (c)	0.06	0	0.034	0.14*	0	0.13*	0.74	0.42	0.51	0.001	0.001	0.001
	multilocus	0.23***	0.08*	0.23***	0.3***	0.14*	0.43***	0.58	0.66	0.68	0.002	0.002	0.002

Table S4 – ABC-GLM model validation. False positives (validation of model choice) rates refer to the proportion (%) of false positive, i.e., simulations generated under all the demographic scenarios but the best-fit one and erroneously assigned to the latter. 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).

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>Pulviger a 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

Figure 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 & Methods for details regarding phylogeographic scenarios and summary statistics).

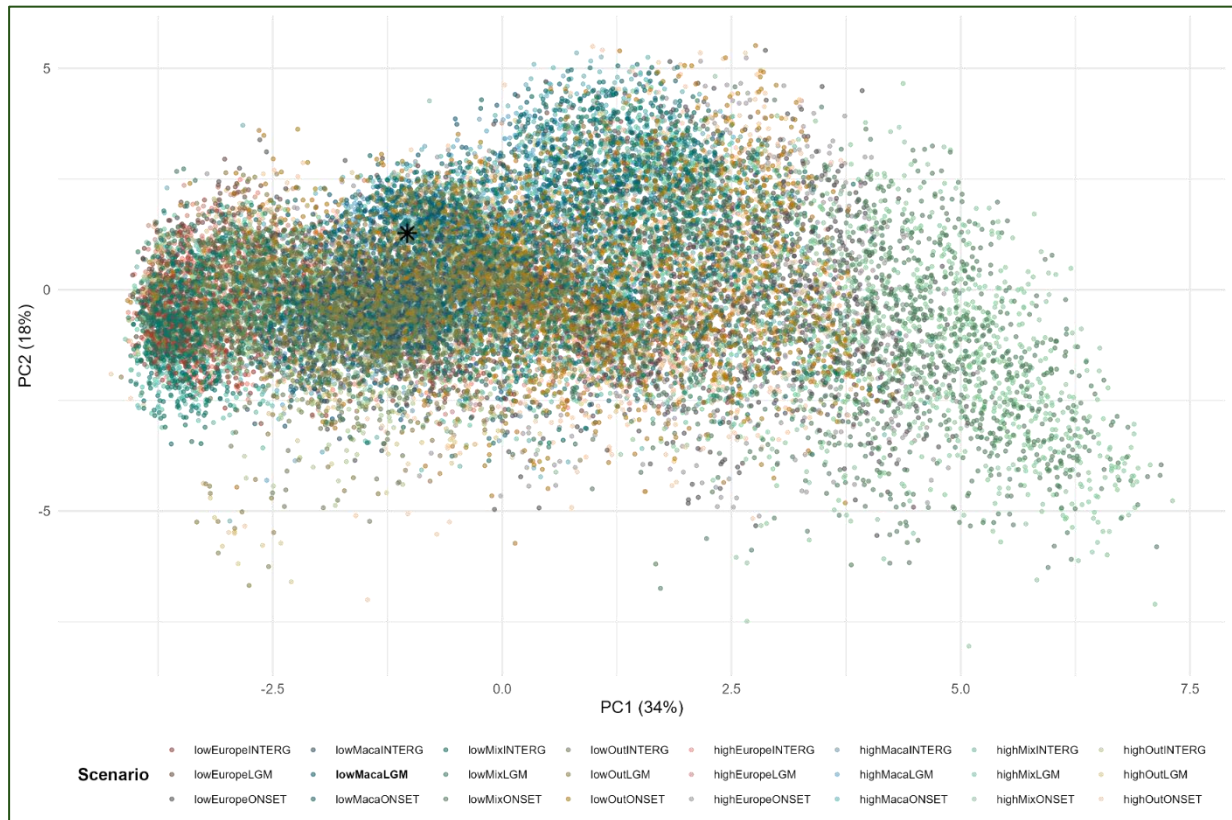


Figure S2 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Calypogeia fissa* in the first plane of a Principal Component Analysis of selected summary statistics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



Figure 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 & Methods for details regarding phylogeographic scenarios and summary statistics).

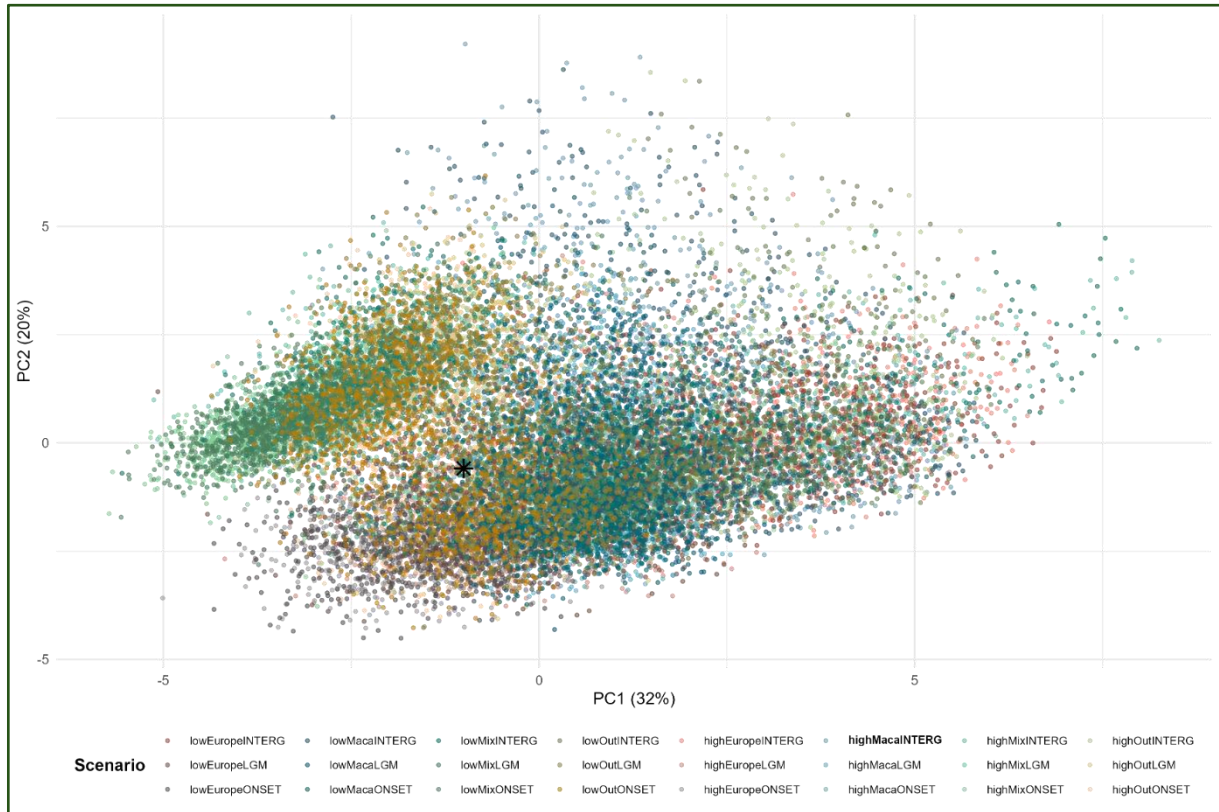


Figure S4 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Kindbergia praelonga* in the first plane of a Principal Component Analysis of selected summary statistics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

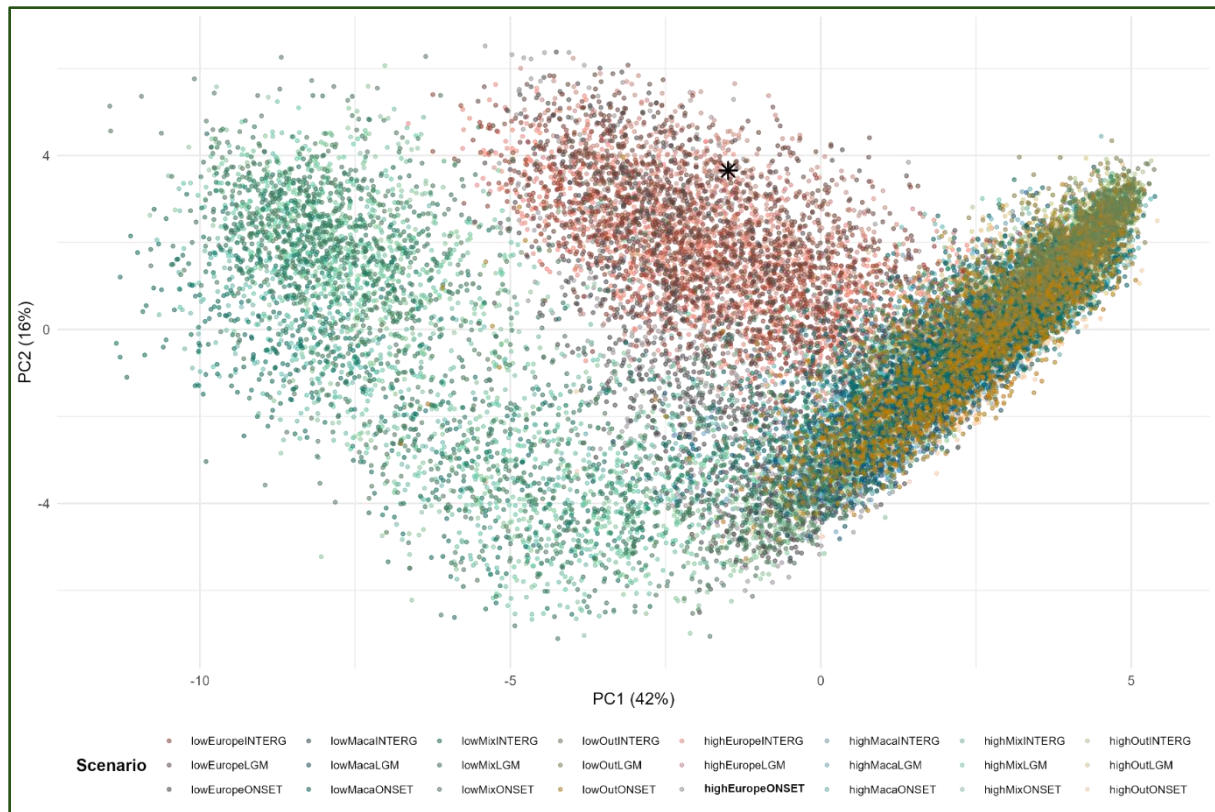


Figure S5 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Metzgeria furcata* in the first plane of a Principal Component Analysis of selected summary statistics of genetic structure and diversity (See Material & Methods for details regarding phylogeographic scenarios and summary statistics).

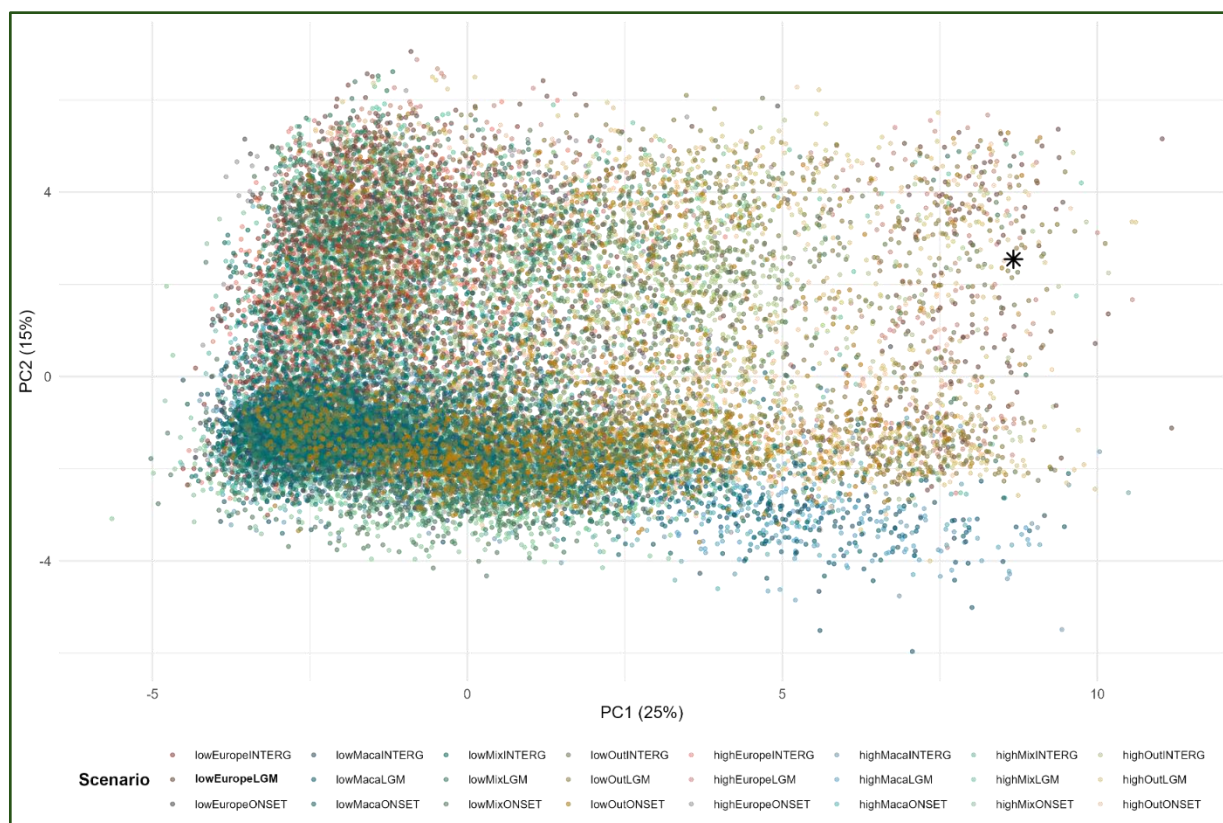


Figure S6 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Pulviger a lyellii* in the first plane of a Principal Component Analysis of selected summary statistics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

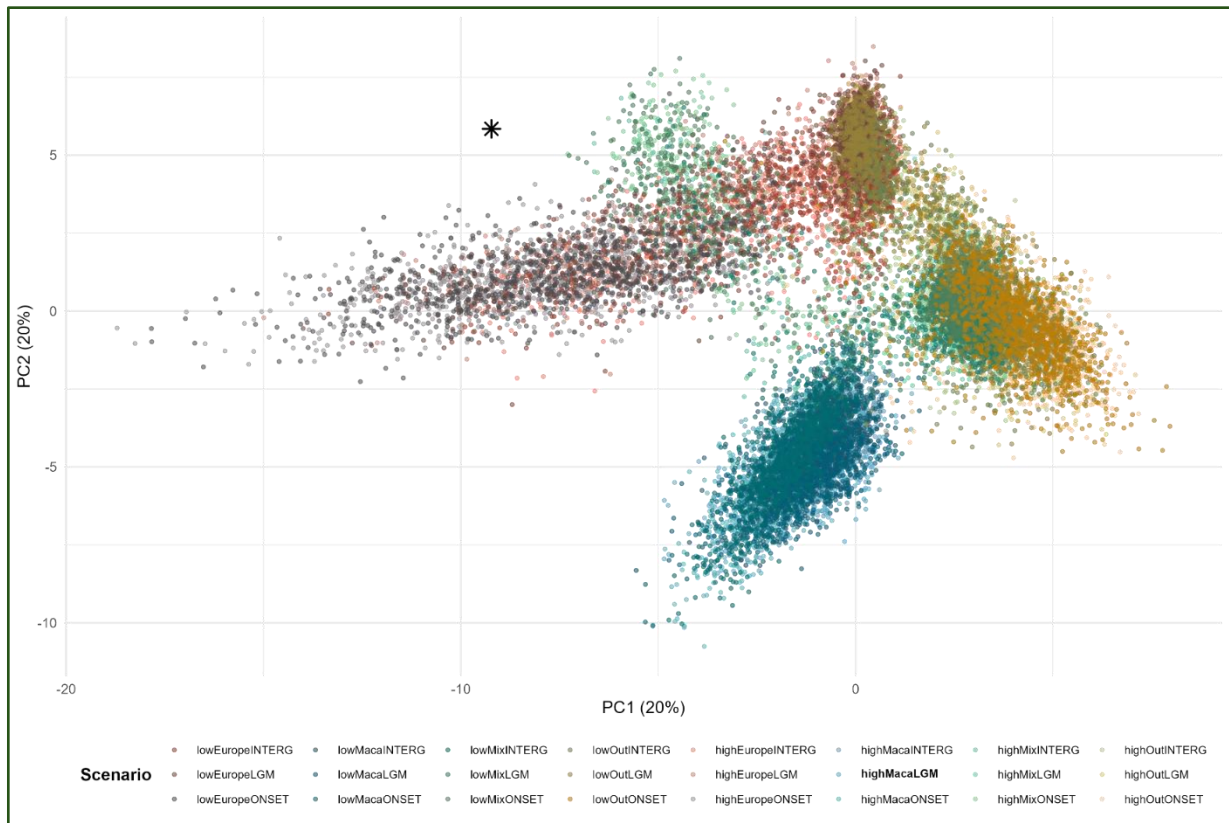


Figure S7 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Odontoschisma sphagni* in the first plane of a Principal Component Analysis of selected summary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

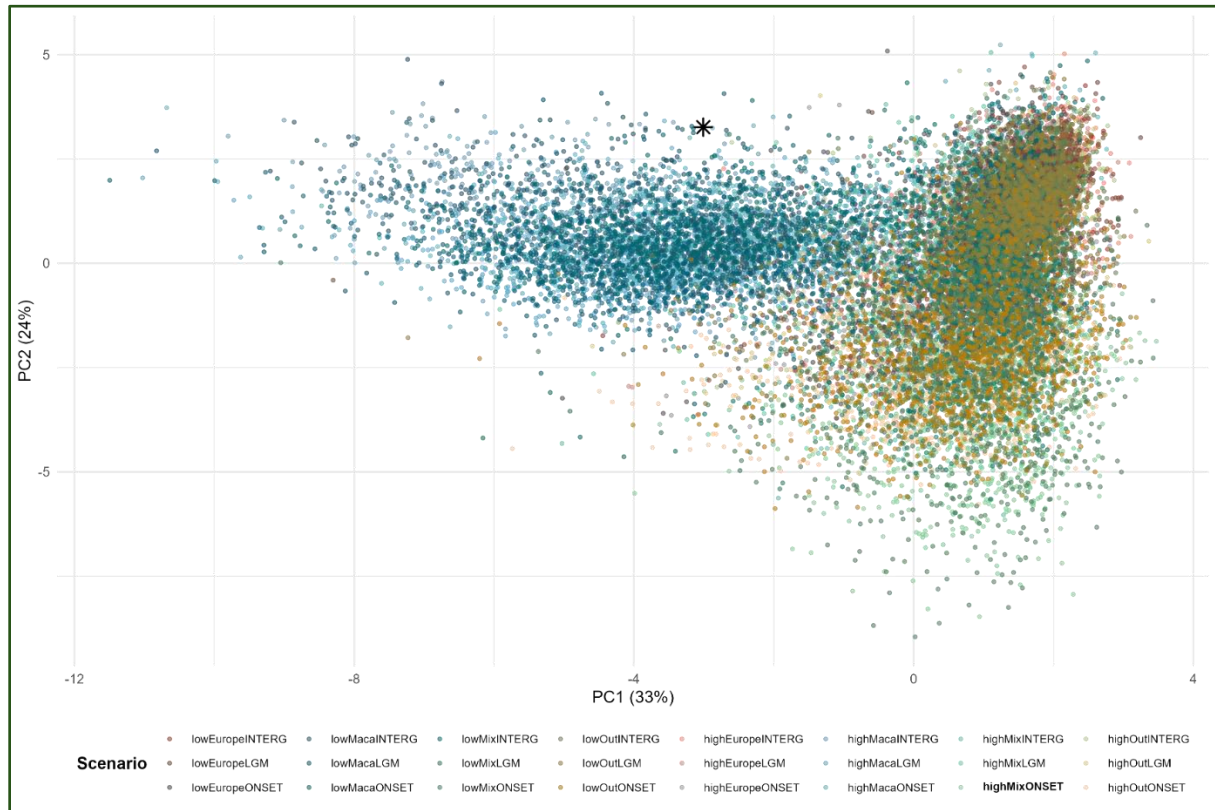


Figure S8 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the liverwort *Radula lindenbergiana* in the first plane of a Principal Component Analysis of selected summary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

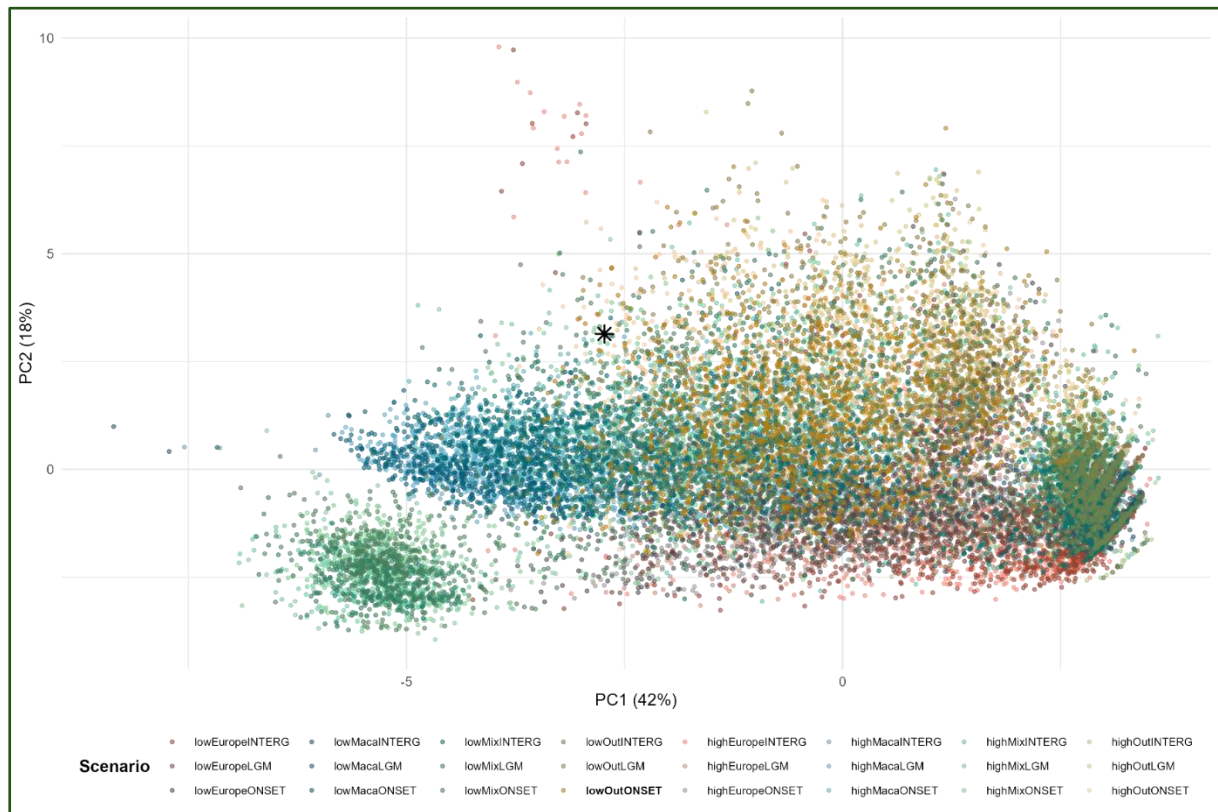
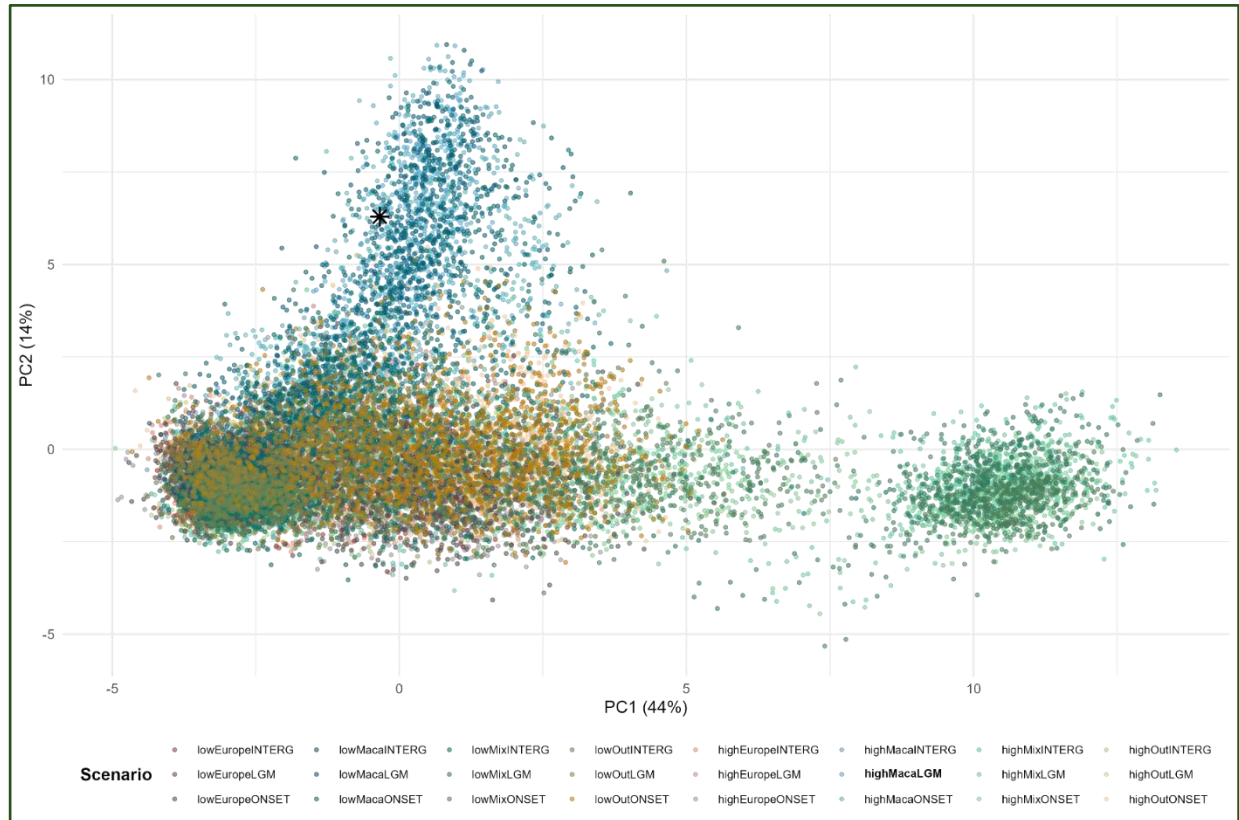
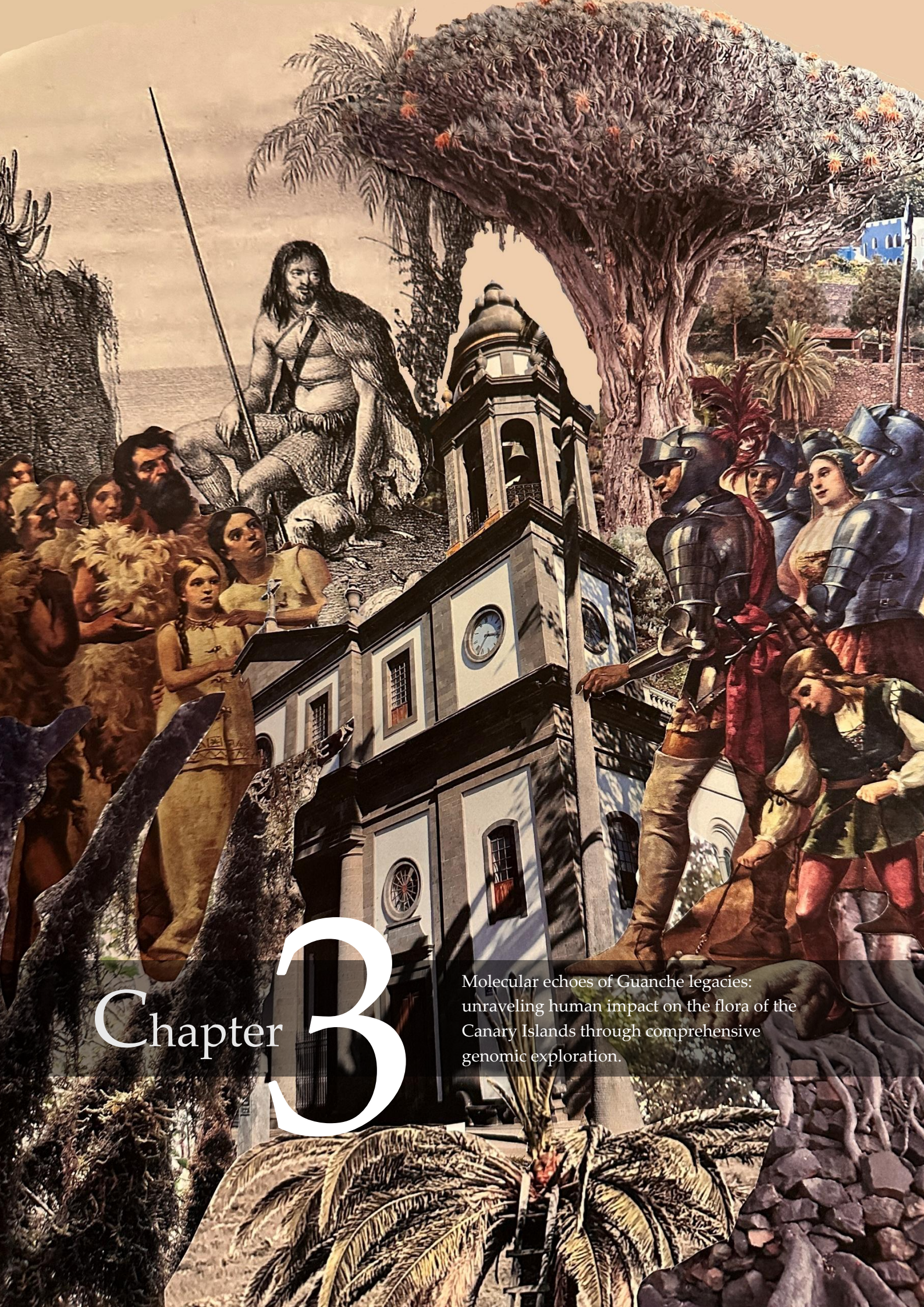


Figure S9 – Representation of the observed (black star) and simulated data under different phylogeographic scenarios (coloured dots) of the origin and timing of colonization of Macaronesia in the moss *Scleropodium touretii*. in the first plane of a Principal Component Analysis of selected summary statistics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





Chapter 3

Molecular echoes of Guanche legacies:
unraveling human impact on the flora of the
Canary Islands through comprehensive
genomic exploration.

Molecular Echoes of Guanche Legacies: Unraveling Human Impact on the Flora of the Canary Islands through Comprehensive Genomic Exploration

GUACAMOL

GUAnches and aboriginal people from the **CA**nary islands **MO**lecular impact on biodiversity

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INTRODUCTION

Even if the concept of an Anthropocene Epoch is still a subject of debate (McCarthy et al., 2025), it nonetheless can be characterized as an ongoing geological event that marks the deep environmental impact of human activities (IUGS & ICS, 2024). If the actual definition of the Anthropocene still remains controversial, the idea of the recognition of a new geological period characterized by a boom of human activities and its environmental consequences has been around for a long time (Crutzen & Steffen, 2003) and is widely used today (Zalasiewicz et al., 2021). The pressing need to evaluate the extent and dimensions of human impacts and the desire to restore “wild” systems have sparked controversy concerning the value of establishing prehuman baselines.

Some evidence already points toward great ancient human-mediated changes. Rates in ecological change increased drastically in the last millennia across the world, up to unprecedented values compared to their levels in the last 18 thousand years (Mottl et al., 2021). This recent increase is due to human influence, as even major climatic events like the deglaciation period had smaller effects than Late Holocene anthropic turnover (Wood et al., 2017). This is especially true for oceanic island systems, whose biota have experienced unparalleled extinction rates during the past centuries (Wood et al., 2017). The same pattern was clearly shown on island systems with an increase of ecological change rates, i.e., turnover in the vegetation community composition, by a factor of 11, with a global acceleration in the last 5000 years, specifically after human settlement (Nogué et al., 2021).

Humans impacted island ecosystems in many ways, leading to major biodiversity loss (Russell & Kueffer, 2019). This fact has been acknowledged for a long time, and not only for recent European colonizations but for all human settlements (Kirch, 1997), and on virtually all colonized oceanic islands (Nogué et al., 2021). However, these impacts change in magnitude regarding the period of the island colonization: the oldest colonization events resulted in slower vegetal community composition turnover rates than the events that happened 500 Common Era (CE) and onwards (Nogué et al., 2021). This can be interpreted from a technological and knowledge point of view, with older civilizations being less advanced, but also from the ecosystem resilience perspective itself regarding the coexistence with humans for longer periods (Nogué et al., 2025).

The Canary Islands are a perfect model archipelago to look at successive human impacts and their magnitude, as they are the only North Atlantic archipelago colonized twice by humans. Palynological records tend to date the arrival of man around 300 Before CE (BCE), with an increased number of wildfires (de Nascimento et al., 2016). Archeological evidence for that period

is, however, missing. The islands were already exploited by the Romans around the 1st century BCE, as attested by some remains discovered on the islands of Lobos and Lanzarote (Mitchell 2024; del Arco Aguilar et al., 2016), but the first real settlement probably took place at the beginning of the common era, around the 1st and 2nd centuries CE by Berber/Amazigh people (Santana et al., 2024). Europeans colonized a second time the archipelago during the Age of Discovery, which led to the full colonization of the Canary Islands during the 15th century.

Mounting evidence, including extinctions among bird, micro-mammal, and plant species, soil erosion and degradation, vegetation community changes through clear-cutting and burning for agricultural and settlement purposes, introduction of invasive detrimental species (Fernández-Palacios et al., 2025; de Nascimento et al., 2020; Morales et al., 2009), points toward a biodiversity loss in the Canary Islands starting from the Amazigh colonization. The Amazigh were the last to introduce the so-called ‘Mediterranean farming package’, consisting of various animal and vegetal species (Morales et al., 2023). Overgrazing by goats and sheep, and direct predation by both humans and introduced animals, led to significant modifications of the environment, for example by irreversibly destroying the remnants of laurel forest vegetation on Fuerteventura and deeply degrading thermo-sclerophyllous woodlands on all islands (Castilla-Beltrán et al., 2021; Morales et al., 2009; Machado Yanes, 2007). Large herbivores such as pigs, sheep and goats probably further disrupted the ecosystems, leading to chemical, physical and structural modifications (Bescond-Michel et al., 2025).

Europeans have undoubtedly had an impact on the Canary Islands environment, as they have had on other Macaronesian archipelagos since the colonization period. The current distribution of native ecosystems is dramatically smaller than their potential natural area, with about a quarter (26.7%) persisting, and the remaining area divided between substitution vegetation (52.9%) and human infrastructures (20.4%) (del Arco Aguilar et al., 2010). Thermo-sclerophyllous woodlands and laurel forests are the two forest ecosystems with the most drastic reduction in surface area, with respectively 8 and 11.8% of their natural distribution remaining (del Arco Aguilar et al., 2010), and climate change is exacerbating this trend (García-Alvarado et al., 2024). As a comparison, 17% of native vegetation remains in the Azores, 21% on Madeira, and 28.4% in the Cape Verde islands (Norder et al., 2020). The similarity of the proportions of remaining vegetation in the Canary Islands with those reported in other archipelagos that experienced a single, European colonization, tends to suggest that the latter has been the main driver of habitat degradation across Macaronesia. The extent to which vegetation degradation was entirely due to the European colonization, or was initiated during the Amazigh period, is, however, poorly studied. The limited information available through palynological records points toward a clear acceleration in the

ecological turnover at European colonization time, but with an onset at the aboriginal people arrival period (Castilla-Beltrán et al., 2021), suggesting two distinct magnitudes of environmental impact at both periods.

There are two different approaches to study past events. One is based on ‘fossil’ data contemporaneous with studied past events, for example the pollen record (Nogué et al., 2021) or ancient DNA (Ávila-Arcos et al., 2023). The other one is based on ‘present’ data to infer past events. Drastic transformations of the environment, and thus of species demography, profoundly affected island biodiversity and marked native species population structure and diversity. These events can be reconstituted using genomic data through various methods (Marchi et al., 2021), including coalescent-based analyses, which became essential to reconstruct species demographic history.

Taking Canarian and Macaronesian endemic plant species as a model, this study aims at determining the extent to which anthropic disturbance has left a signature in current patterns of genetic structure and diversity, and how this signature compares with that caused by major climatic events.

MATERIAL & METHODS

General framework

We used an integrative approach combining reconstructions of species demographic history from analyses of population genetics and projections of species climatic niches onto present and Last Glacial Maximum (LGM) periods of time to determine whether bottlenecks inferred from genetic analyses match in timing and intensity differences in spatial extent of climatically suitable areas, pointing to a purely climatic interpretation of shifts in population size through time. To do so, we reconstructed, after having identified population genetic structure, the demographic history of each population, identified major shifts in population size, and determined the corresponding population size ratio before and after the shift. To derive an estimate of the shifts in the extent of climatically suitable area between two time periods, we calibrated Species Distribution Models (SDM) from occurrence data under present climatic conditions and projected them onto historical climatic layers. Finally, we determined whether the shifts in population size took place during specific periods of time corresponding to the European period, the Amazigh (Guanche) period, or pre-human major climatic events, and whether bottlenecks inferred genetically are of the same order of magnitude as climate-induced shifts in the extent of climatically suitable areas.

Sampling and molecular protocols

Eleven Canarian or Macaronesian endemic spermatophyte species characteristic of the thermo-sclerophyllous woodland or the laurel forest, the two most widely impacted forest ecosystems found in the Canary Islands (del Arco Aguilar et al., 2010), were selected (Table 1).

Samples were collected during various field campaigns in 2022 and 2023, and dried in silica gel. The samples included specimens from the whole distribution area of the species except for some species not found on El Hierro or relictual populations growing on the cliffs of the natural park of Jandía, Fuerteventura, that was not prospected. The five Canarian islands where laurel forest naturally occurs were visited (Gran Canaria, Tenerife, La Gomera, La Palma, El Hierro) and samples from Madeira were gathered by collaborators (*Persea indica*, *Morella faya*, *Apollonias barbuja*). A total of 1065 samples were collected (see Figure 1 and figshare online Supplementary data for sampling locations; <https://doi.org/10.6084/m9.figshare.31315144>).

DNA extractions were performed following an optimized CTAB protocol (Schenk et al., 2023; Doyle & Doyle, 1987) for all the species. DNA was then purified using AMPure XP beads (Agencourt, Beckman Coulter, Brea, USA) following the manufacturer's protocol. Quality checks were performed using a BioSpec-nano spectrophotometer (Shimadzu, Kyoto, Japan) for DNA detection, and electrophoresis on agarose 1.5% for integrity. Quantification was conducted using Qubit 4 Fluorometer (Invitrogen, Thermo Fisher Scientific, Waltham, USA) and Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Thermo Fisher Scientific, Waltham, USA) following manufacturer's protocols. Following quality check results, 475 samples were selected to maximize DNA concentrations and geographical origin diversity for all species (between 12 and 95 per species). RADseq libraries were prepared by Floragenex (<http://www.floragenex.com>) with the restriction enzyme SbfI, generating fragments with a length varying from 300 to 600bp. Sequencing of the libraries was conducted on an Illumina sequencing platform (Paired-End reads).

Table 1 – Species used in the framework of this study. Ecosystems from del Arco Aguilar et Rodríguez Delgado (2018). Trees ecological and reproductive strategies from Ganivet et al. (2019) (FST = ‘Facultative’ Shade-Tolerant; IST = ‘Itinerant’ Shade-Tolerant; LLP = Long-Lived Pioneer). Harvested = parts or totality of the plant harvested for food, dying property, medicinal use. **Morella faya* is here considered as introduced in Portugal following Gandoger (1920)²⁰.

Species	Ecosystem	Growth form	Ecological strategy	Reproductive strategy	Reproductive morphology	Dispersal mode	Historical use	Endemicity
<i>Apollonias barbujana</i>	Dry laurel forest	Tree	FST	Seedlings + Suckers	Hermaph.	Endozoochory ¹	Firewood ^{5,22} + Carpentry ⁵	Macaronesia
<i>Adenocarpus foliolosus</i>	Substitution vegetation in laurel and pine forests areas	Shrub	Pioneer + Pyrophyte	Seedlings	Hermaph.	Ballochory ⁷	Firewood ^{8,22} + Harvested ^{8,22}	Canary
<i>Brachypodium arbuscula</i>	Thermo-sclerophyllous woodland	Herb	Rhizomatous ³	Geophyte	Hermaph.	Autochory ^{6,10} + Myrmecochory ³	None	Canary
<i>Canarina canariensis</i>	Humid laurel forest	Herb	Tuberous ²	Geophyte	Hermaph.	Endozoochory ⁹	Harvested ^{4,5,18}	Canary
<i>Dracunculus canariensis</i>	Humid laurel forest + Ruderal nitrophilous scrub ¹³	Herb	Rhizomatous ¹²	Geophyte	Hermaph.	Endozoochory ¹⁹	Harvested ¹⁸	Canary
<i>Luzula canariensis</i>	Humid laurel forest	Herb	Rhizomatous ¹⁴	Geophyte	Hermaph.	Autochory ⁶ + Myrmecochory ^{6,15}	None	Canary
<i>Heberdenia excelsa</i>	Laurel forests + Thermo-sclerophyllous woodland	Tree	IST	Seedlings	Hermaph.	Endozoochory ^{1,9}	Firewood ^{5,22} + Harvested ^{5,18} + Carpentry ⁵	Macaronesia

<i>Morella faya</i>	Laurel forests + Substitution vegetation in laurel forest areas	Tree	LLP	Seedlings + Suckers	Dioicous	Endozoochory ¹	Firewood ^{5,22} + Harvested ^{4,5,18} + Carpentry ⁵	Macaronesia*
<i>Persea indica</i>	Humid laurel forest	Tree	FST	Seedlings + Suckers	Hermaph.	Endozoochory ¹	Firewood ^{5,22} + Harvested ¹⁸ + Carpentry ^{5,18}	Macaronesia
<i>Retama rhodorhizoides</i>	Thermo- sclerophyllous woodland	Shrub	Pioneer ¹⁶	Seedlings	Hermaph.	Autochory ⁶ + Endozoochory ¹⁷	Harvested ^{8,22}	Canary
<i>Spartocytisus filipes</i>	Thermo- sclerophyllous woodland	Shrub	Pioneer ²¹	Seedlings	Hermaph.	Ballochory ⁷ + Myrmecochory ^{6,11}	Harvested ²²	Canary

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Data processing

The phred score of the raw sequences, obtained using the software *FastQC* v0.12.1 (Andrews, 2010), was over 30 for all bases. We further processed the raw data using *iPyrad* v0.9.85 (Eaton & Overcast, 2020) to separate reads according to their barcodes and assembled them into loci to generate the Variant Calling Format (VCF) files. The pipeline works in 7 steps to filter reads, sequences and loci, based on various quality parameters and to identify orthologous sequences between individuals of the same species. As the selected species are all non-model species lacking reference genomes, the default parameters for diploid species with *de novo* genome assembly were used except for the *mindepth_majrule* (set to 3 to increase the amount of information in the dataset) and the two parameters *clust_threshold* and *min_samples_locus*. To identify the best combination of values for these parameters and the percentage missing data allowed, we empirically processed in two steps to maximize the number of polymorphic loci and minimize missing data following a similar approach as in García-Olivares et al. (2019).

During the first step, we tested three values (85, 90 and 95%) of the *clust_threshold* parameter that controls for the minimum level of similarity for two sequences from different individuals to be assigned to the same locus and four values (40, 50, 60 and 70% of individuals) of the *min_samples_locus* parameter, which controls for the minimum number of individuals that must share a locus to keep it. This led to 12 combinations, and hence, 12 datasets per species. To choose between these 12 parameter combinations, we ran different analyses of population genetic structure to evaluate the congruence of the signal among datasets. Congruence was assessed based on a set of three analyses: a Principal Component Analysis (PCA) to describe groups of individuals in a visual assessment, a Neighbour-Joining tree to group individuals into clusters based on the Euclidian distance criterion, and a sparse Non-negative Matrix Factorization analysis (sNMF) to quantify the number of ancestral populations and look at admixture patterns. If the results indicated the same groups in the PCA and the NJ tree, and the same number of ancestral populations and admixture patterns in the sNMF, the datasets were considered as congruent. For all species but *Morella faya* and *Luzula canariensis*, congruent results were obtained across the 12 datasets (Table 2), and the dataset yielding the highest number of loci was selected for subsequent analyses. Further filtering removed 9 individuals due to their high number of missing data, leaving a total of 449 samples distributed across the 11 species.

The data were handled using the packages *dartRverse* (Mijangos et al., 2022; Gruber et al., 2018), *vcfR* (Knaus & Grünwald, 2017), *LEA* (Frichot & François, 2015) and *tidyverse* (Wickham et al., 2019). The PCA was performed with the *adeigenet* package (Jombart & Ahmed, 2011; Jombart,

2008), the NJ tree was produced with the *ape* package (Paradis & Schliep, 2019), and the sNMF with the *LEA* package.

In the second step, a single SNP per locus was selected to avoid non-independence in the data. For each locus, SNP selection was performed to minimize the proportion of missing data. All loci with more than 50% of missing data were removed. Different missing data thresholds were used for each species to optimize the number of individuals per island and reduce biased results due to missing data. The thresholds were empirically determined by running multiple times PCA and sNMF analyses with values between 25 and 50% NA, and by comparing the results for outliers. The distribution of missing data through filtering steps and species-specific thresholds can be found in Figures S1 to S11.

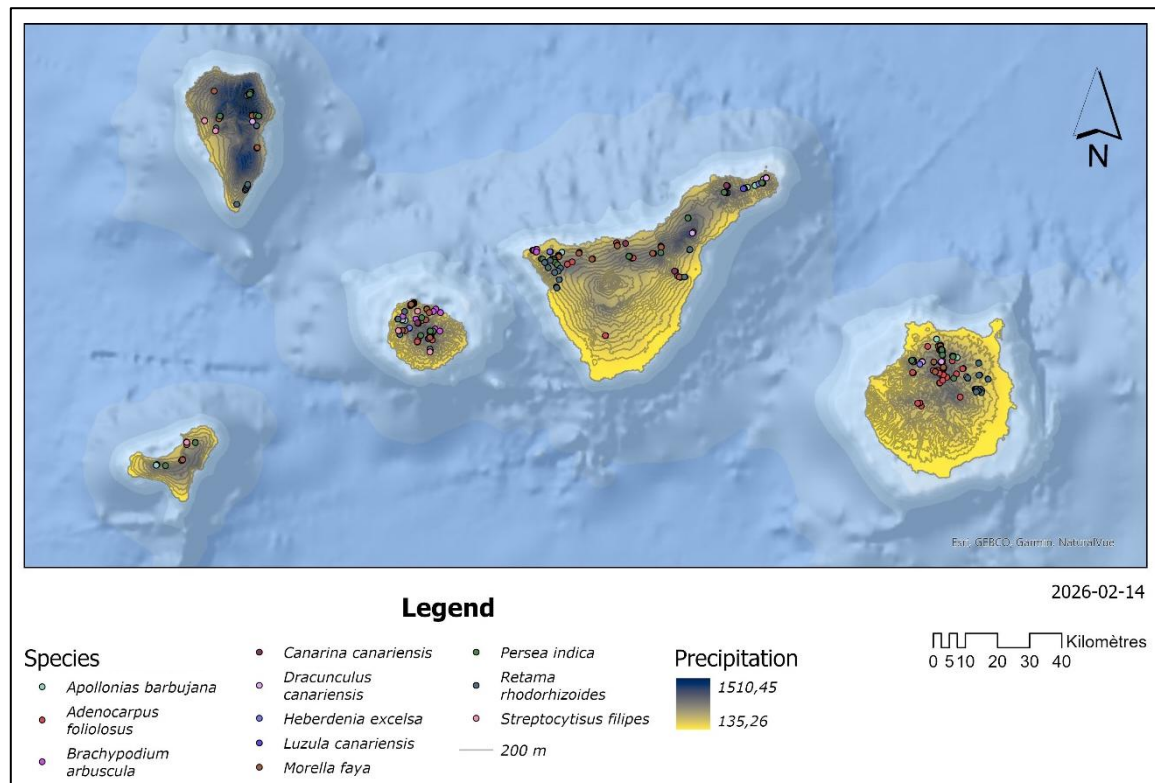


Figure 1 – Collected samples localizations of 11 species of Macaronesian and Canarian endemic plant species across their Canarian distribution area. Background topographic map from Copernicus project. Map created by G. Wislet.

Table 2 – Summary statistics of the selected ipyrad parameter combination complete datasets for each species. sp = species code, param = chosen ipyrad parameter combination, CLU = clust_threshold parameter that controls for the minimum level of similarity for two sequences from different individuals to be assigned to the same locus (three values: 85, 90, 95%), MIN = min_samples_locus parameter that controls for the minimum number of individuals that must share a locus to keep it (four values: 40, 50, 60, 70% of individuals), raw reads = total number of raw reads, filtered reads = total number of raw reads after ipyrad filtering, loci = total number of loci kept, SNPs = total number of SNPs within the dataset, depth = median reading depth across sites and individuals, NA% = proportion of missing data in the SNPs matrix, best K = optimal value of K from the sNMF analysis, pop code = sNMF determined population code names (see Figure 2 for codes geographic signification). *Apollonias barbujana* (AB), *Adenocarpus foliolosus* (AF), *Brachypodium arbuscula* (BA), *Canarina canariensis* (CanC), *Dracunculus canariensis* (DC), *Heberdenia excelsa* (HE), *Luzula canariensis* (LC), *Morella faya* (MF), *Persea indica* (PI), *Retama rhodorhizoides* (RR), *Streptocytisus filipes* (SS).

Sp	Param	#Ind	Raw reads	Filtered reads	Loci	SNPs	Depth	NA%	Best K	Pop code
AB	CLU95-MIN40	46	19402075	19394372	4628	21513	34	20.4	2	East + West
AF	CLU95-MIN40	95	108843872	108670309	2120	18208	56	15.5	3	LG + GC-Anaga + TF-LP
BA	CLU90-MIN40	39	66541510	66504873	7546	41424	107	16.3	2	LG + TF
CanC	CLU95-MIN40	53	7234715	7206176	2727	13049	10	20.1	4	LP + LG + Teno + GC-Anaga
DC	CLU90-MIN40	62	44831826	44719061	5105	15551	12	15.1	2	West + GC
HE	CLU95-MIN40	27	3998906	3995607	1754	7429	19	21.3	3	MAD + Lau + The
LC	CLU85-MIN60	19	2193099	2191207	162	335	34	15.3	2	LG + TF
MF	CLU85-MIN50	17	49852461	49817258	1101	3134	163	23.4	2	MAD + CAN
PI	CLU95-MIN40	27	25651181	25634671	3051	15804	48	25.2	2	MAD + CAN
RR	CLU95-MIN40	61	22814943	22775475	3132	19044	40	14.8	4	LG + Teno + Guimar + LP-GC
SS	CLU95-MIN40	12	2175818	2173555	3027	10126	26	18.2	1	All

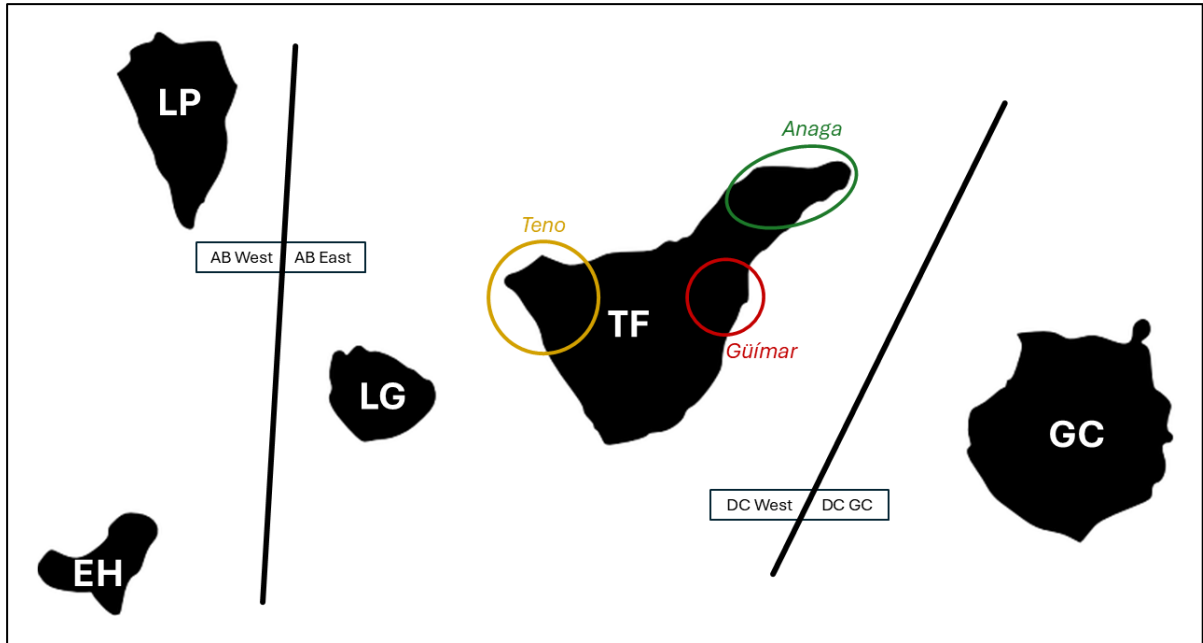


Figure 2 – Codes of the Canarian population inferred in the genetic clustering analyses. Madeira not represented but coded as MAD, and Canary Islands as CAN.

Population genetics

Each species and genetic cluster was characterized by its diversity through a series of statistics computed in R v4.4.1 (R Core Team, 2024) with the packages *popgenstuff* (Bradburd, 2025; <https://github.com/gbradburd/popgenstuff>), *hierfstat* and *adegenet* (Goudet & Jombart, 2022; Jombart, 2008; Jombart & Ahmed, 2011). These analyses included observed and expected heterozygosity (H_o , H_s ; *hierfstat* and *adegenet*), inbreeding coefficients (F_{IS} , F_{IT} ; *hierfstat* and *adegenet*), allelic richness (A_r), proportion of polymorphic loci, nucleotide diversity (π ; *popgenstuff*), Watterson's theta (θ_W ; *popgenstuff*), and effective population sizes (N_e) following the formula $\theta = 4N_e\mu$. Population genetic structure was characterized by global and pairwise Weir & Cockerham F_{ST} (*hierfstat* and *adegenet*), as well as pairwise Nei's genetic distance ($N_ei D$; *hierfstat* and *adegenet*), which measures the amount of allele-frequency divergence accumulated between populations. All graphics, maps and figures were produced with the packages *ggplot2* (Wickham, 2016), *ggrepel* (Slowikowski, 2024), *ggtree* (Xu et al., 2022), *terra* (Hijmans, 2024), *sf* (Pebesma & Bivand, 2023; Pebesma, 2018) and *MetBrewer* (Mills, 2022).

Population demographic history

To infer past species demographic history, we used the software *STAIRWAYPLOT2* (Liu & Fu, 2020), which estimates changes over time in the effective population size (N_e) of each genetic cluster

(as defined by the sNMF analysis) separately to avoid biasing the N_e estimation with structured data. Among the available software reconstructing demographic history, *STAIRWAYPLOT2* is able to detect recent past events. It was tested on real data that retrieved a population growth less than 100 generations ago (Liu & Fu, 2020), which should be enough generations to find recent signal from the Canary Islands anthropic period, at least with our short generation time species. The folded SFS for each genetic cluster was computed using *easySFS* (<https://github.com/isaacovercast/easySFS>). According to the previous results, PCA outliers and individuals with more than 20% admixture were excluded to avoid biases in the coalescent-based demographic inference. Some populations included a low number of individuals, like *Canarina canariensis* from La Palma with only 4 individuals, Madeiran *Persea indica* with only 2 individuals or Madeiran *Heberdenia excelsa* from the laurel forest clade with 3 individuals, and were discarded. We selected an angiosperm mutation rate of $7E-9$ per site per generation for autosomal markers (from Krasovec et al., 2018; following Gibert et al., 2024). The total number of sequenced sites (parameter L) was computed following Kastally et al. (2025) by multiplying the total number of sites retained in the whole dataset (including both variable and invariable positions) by the ratio between the number of SNPs retained by *easySFS* and the total number of loci. The generation time for each species was determined from a literature search based on the age at which individuals first reproduce. To take the uncertainty of this parameter into account (Jonasson et al., 2022), we defined a range based on the different literature reports (Table S1). We followed the defaults parameters implemented by *STAIRWAYPLOT2* for other parameters.

To facilitate the interpretation of the shape of the stairway plots and identify periods characterized by shifts in population size, we implemented a segmentation analysis. We divided the X-axis (log-transformed time) into 10 equally-spaced periods. Within each period, we fitted a LOESS smoother to the log N_e curve (span = 0.01) and used the R package *inflection* (Christopoulos, 2025) to identify maximum curvature points. To reduce dependency on an arbitrary partitioning of the time axis, we repeated the same procedure, taking as period boundaries the middle of the initial 10 time-periods.

Species distribution models

Species and environmental data

Occurrence data at 500m resolution were collected from three different sources : Biodiversity database of Canary Islands (Biota - Banco de Datos de Biodiversidad de Canarias), the Global Biodiversity Information Facility (www.GBIF.org consulted on 12 August 2025; <https://doi.org/10.15468/dl.5kk83j>), and personal observations (see figshare online

Supplementary data; <https://doi.org/10.6084/m9.figshare.31315144>). GBIF data were filtered using the default parameters of the *clean_coordinates* function from the R package *CoordinateCleaner* (Zizka et al., 2019). We further filtered-out data recorded before 1979 and with a resolution coarser than 500m to match with the climatic data temporality and Biota resolution. Finally, only occurrence data located within the distribution range, as defined by Biota (category “Seguro nivel 1 y 2”) to remove potential misidentifications. Occurrence data were finally filtered to keep a single occurrence per pixel via the *dismo* package (Hijmans et al., 2024). The number of occurrence points ranged between 87 and 829 (detail in Table S4), except in *Luzula canariensis*, a narrow endemic species restricted to La Gomera and Tenerife, where it is distributed in few scattered localities, resulting in a number of occurrence points of 39 that did not warrant further analysis (note that the species is also present on the island of La Palma, but only represented by two occurrences on Biota). A set of 10,000 background points were randomly sampled all across the Canary Islands and used for all species. 19 bioclimatic variables were extracted from CanaryClim (Patiño et al., 2023) at 100m resolution and aggregated at 500m resolution by computing the mean across 100m pixels for the present time (1979-2013) and during the LGM period (Patiño et al., in prep.).

Model fitting and evaluation

We applied the first step of the variable selection protocol of Adde et al. (2023), to select the most informative predictors for each species. We first computed univariate binomial distribution Generalized Linear Models (GLM), with a fixed prevalence of 0.5 for every predictor and allowing quadratic terms, and ranked models based upon their p-values. We kept only the predictor with the lowest p-value and, following Dormann et al. (2013), removed all associated predictors with a Pearson’s correlation >0.7 to avoid multicollinearity. This selection protocol was applied until no significant predictor remained.

For each species, Species Distribution Models were generated with 3 different modelling techniques: GLM (McCullagh & Nelder, 1989), Maxnet (Phillips, 2021) and a down-sampled Random Forest (Valavi et al., 2021). For GLM, we performed a step AIC allowing linear and quadratic terms under the binomial family error. For Maxnet, default parameters from *MAXNET* package were applied. For Random Forest, we used 1000 trees, randomly sampling with replacement at each tree a number of background points equal to the number of occurrences, leaving all the other default parameters from the *RandomForest* package. The models were evaluated with 100 cross-validations, using 70% of the data to calibrate the models and the remaining 30% to evaluate them with three metrics: AUC, MaxTSS and the Boyce Index. To take

model uncertainty into account (Araújo & New, 2007), we generated an ensemble model by applying a weighted mean across the 3 techniques, weighting them by their MaxTSS values.

Model projections

Models were projected at present time (Patiño et al., 2023) and during the LGM period (Patiño et al., in prep.). These continuous maps were afterward binarized in order to identify climatically suitable and unsuitable pixels, using a threshold that maximizes the sum of specificity and sensitivity (as recommended by Liu et al., 2013). We computed the total number of suitable pixels for each species at each period to derive the ratio of the extent of suitable areas at both periods.

RESULTS

RAD sequencing

We directly removed 17 samples due to low number of reads (<100 recovered loci after filtering), and proceeded with the demultiplexing of the other 458 individuals. For all 11 species, we obtained a total of 353,540,406 raw reads and removed 457,842 reads through ipyrad filtering. The total per species varied between 2,173,555 (*Streptocytisus filipes*) and 108,670,309 (*Adenocarpus foliolosus*), with a median value of 22,775,475 filtered raw reads. The proportion of missing data varied between 14.8% (*Retama rhodorhizoides*) and 25.2% (*Persea indica*), with a mean value of 18.7% across species, and the median reading depth varied from 10 (*Canarina canariensis*) to 163 (*Morella faya*). A total of 165,617 SNPs were retrieved from all the species ([335; 41,424]) across 34,353 polymorphic loci ([162; 7,546]). Characteristics of the total datasets can be found in Table 2.

The amount of loci recovered varied largely among species, along with the missing data proportion. Most species yielded >2000 polymorphic loci after the various filtering steps, two gave between 1000 and 2000 loci (*Heberdenia excelsa*, *Morella faya*), and only one species had <1000 loci (*Luzula canariensis*, 162 loci). The proportion of missing data varied less between species in this second dataset, with values around 10% ([6.9; 12.4]), but with high heterogeneity between populations from the same species, such as in *Apollonias barbujana* with 33.6% on Gran Canaria specimens, but only 3.8% on El Hierro. Individual repartition and missing data per population can be found in Table 3.

Genetic diversity analyses

Genetic structure

sNMF analyses showed a recurrent pattern of division between the Canary Islands and Madeira (*Heberdenia excelsa*, *Morella faya*, *Persea indica*) except for *Apollonias barbujana* whose Madeiran individuals grouped with those from Gran Canaria for all K values investigated. Most species were divided into island clusters, where individuals from the same island grouped together or in geographically coherent clusters (e.g., La Palma and El Hierro together in a single group). A clear longitudinal gradient was observed in all species, except *Persea indica* and *Morella faya* that did not show any clear pattern beside the two archipelago clusters. For some species, Tenerife was divided into two genetically distinct clusters, with specimens from Teno on the West and from Anaga on the East being separated with different limits (*Canarina canariensis*, *Dracunculus canariensis*, *Heberdenia excelsa*, *Retama rhodorhizoides*), sometimes with

specimens from Anaga showing a mixed genome between clusters from Teno and Gran Canaria (*Adenocarpus foliolosus*). El Hierro individuals, when present, tend to group with La Palma specimens (*Apollonias barbujana*, *Dracunculus canariensis*, *Streptocytisus filipes*), but the groups of specimens from La Palma exhibited different affinities. La Palma specimens were included in their own genetic cluster (*Canarina canariensis*) or grouped with those of El Hierro (*Apollonias barbujana*, *Streptocytisus filipes*), with those of La Gomera (*Heberdenia excelsa*), of Teno or Tenerife in general (*Adenocarpus foliolosus*), or also with those of Gran Canaria (*Retama rhodorhizoides*). The cross-entropy criterion selection gave between 1 and 4 optimal genetic clusters depending on the species (see Table 2 and Figures S12 to S22 for details).

A peculiar case that is worth discussing a little bit more is the one of *Dracunculus canariensis*, whose cross-entropy results were highly uncertain. Indeed, the lowest cross-entropy value was associated with K=6, followed by K=8 and K=2, but all values were similar between 2 and 9 populations. When looking at the admixture pattern while incrementing K from 2 to 9, we see that the populations tend to split according to their longitudinal gradient, with four genetic clusters per island on Gran Canaria and Tenerife when K=9. Specimens from Teno, La Gomera and La Palma progressively form island-specific clusters with increasing K values, and eventually, within-island clusters in the case of La Palma for K=9.

Genetic diversity metrics

Across all populations from the 11 species analyzed in this study, summary statistics revealed a wide range in genetic diversity, inbreeding coefficients and population differentiation metrics values (Figure 3 and Table S2). Patterns were globally similar between the genetic and geographic clusters among species, independently of admixed individuals presence. Observed and expected heterozygosity (H_o and H_s) varied a lot among species, with several taxa exhibiting H_o values below 0.05 (*Adenocarpus foliolosus*, *Canarina canariensis*, *Dracunculus canariensis*, *Luzula canariensis*, *Persea indica*), whereas others have H_o values higher than 0.1 (*Morella faya*, *Streptocytisus filipes*). Expected heterozygosity (H_s) followed the same trends. Nucleotide diversity (π) and Watterson's theta (θ_W) followed these same species specific trends observed for heterozygosity, with the highest values recorded for *Morella faya*, *Streptocytisus filipes* and *Brachypodium arbuscula*, and the lowest values in *Dracunculus canariensis* and *Adenocarpus foliolosus*.

Across species, H_o and H_s were lower within clusters than global estimates among clusters. For species occurring across multiple islands, population-level measures frequently differed in magnitude. For instance, in *Apollonias barbujana*, H_e ranged from low values in El Hierro to

substantially higher levels in Tenerife and La Gomera. Similar patterns among islands were found in *Heberdenia excelsa*, *Retama rhodorhizoides* and *Persea indica*, where some islands consistently harbored the most genetically variable populations. Across species and populations, FIS values varied from 0.02 to 0.4, with several populations showing high levels of heterozygote deficiency. Global FIT values exceeded FIS in all species, reflecting the combined effects of within-population and among-population structure. Global FST values indicated large differences among species in overall population structuring. Species such as *Adenocarpus foliolosus*, *Retama rhodorhizoides*, *Brachypodium arbuscula* and *Morella faya* exhibited FST values around 0.1-0.3, whereas highly structured species, including *Canarina canariensis*, *Dracunculus canariensis*, *Luzula canariensis* and *Persea indica*, reached substantially higher levels of differentiation. Genetic clusters and geographic populations generally displayed similar heterozygosity and allelic richness values, showing no real impact of the filtering-out of admixed individuals in the genetic grouping. Higher FIS values and, in some species, higher FIT were observed when specimens were grouped per island vs genetic clusters due to the inclusion of admixed individuals and the presence of a within-island structure in the case of geographic populations.

Pairwise FST and Nei's D comparisons (Figure 4 and Table S3) revealed strong differences within and among species. In some species, differentiation among population pairs was moderate, with FST values around 0.1-0.3 (*Adenocarpus foliolosus*, *Brachypodium arbuscula*, *Morella faya*), while others had FST values above 0.5 between islands or regions within islands (*Canarina canariensis*, *Dracunculus canariensis*, *Luzula canariensis*, *Persea indica*). In several species, the most differentiated pairs corresponded to distant islands such as El Hierro and Gran Canaria or comparisons involving Madeira, while closer islands showed lower levels of differentiation. Nei's genetic distance followed the same pattern. Pairwise differentiation patterns were broadly comparable when considering genetic clusters or island populations, although geographic populations often yielded wider ranges of FST values. The inclusion of admixed individuals increased the differentiation pattern, and the separation of large genetic clusters comprised of individuals from different islands led to small FST values among islands.

		Ho	Hs	FIS	FIT	Ar	π	θW
BA_TF	Gen	0.080	0.106	0.175	0.363	1.104	0.097	0.119
BA_TF	Geo	0.080	0.106	0.175	0.363	1.104	0.097	0.119
BA_LG	Gen	0.074	0.098	0.163	0.353	1.097	0.092	0.146
BA_LG	Geo	0.074	0.098	0.163	0.353	1.097	0.092	0.146
CanC_LP	Gen	0.052	0.078	0.219	0.648	1.072	0.063	0.078
CanC_LP	Geo	0.050	0.082	0.269	0.564	1.076	0.055	0.079
CanC_LG	Gen	0.049	0.085	0.303	0.685	1.081	0.066	0.087
CanC_LG	Geo	0.047	0.086	0.323	0.597	1.082	0.055	0.082
CanC_Teno	Gen	0.045	0.087	0.345	0.704	1.081	0.061	0.092
CanC_TF	Geo	0.042	0.110	0.400	0.643	1.108	0.066	0.133
CanC_GC	Gen	0.041	0.059	0.184	0.514	1.058	0.050	0.070
CanC_GC-Anaga	Gen	0.041	0.066	0.240	0.657	1.065	0.056	0.099
DC_LP	Geo	0.021	0.025	0.084	0.550	1.024	0.017	0.035
DC_GC	Gen	0.019	0.041	0.218	0.653	1.041	0.035	0.098
DC_GC	Geo	0.019	0.041	0.221	0.617	1.041	0.034	0.099
DC_EH	Geo	0.018	0.019	0.031	0.524	1.019	0.017	0.031
DC_West	Gen	0.016	0.032	0.145	0.620	1.032	0.027	0.120
DC_TF	Geo	0.016	0.034	0.202	0.608	1.033	0.028	0.076
DC_LG	Geo	0.014	0.016	0.050	0.533	1.016	0.013	0.028
LC_LG	Gen	0.048	0.089	0.277	0.759	1.086	0.070	0.102
LC_LG	Geo	0.048	0.089	0.277	0.759	1.086	0.070	0.102
LC_TF	Gen	0.044	0.131	0.388	0.796	1.126	0.109	0.162
LC_TF	Geo	0.044	0.131	0.388	0.796	1.126	0.109	0.162
AF_GC-Anaga	Gen	0.042	0.056	0.149	0.258	1.055	0.050	0.134
AF_GC	Geo	0.040	0.055	0.173	0.256	1.055	0.041	0.128
AF_LG	Gen	0.039	0.049	0.135	0.246	1.049	0.046	0.069
AF_LG	Geo	0.039	0.050	0.153	0.238	1.050	0.040	0.065
AF_LP	Geo	0.038	0.051	0.160	0.244	1.049	0.038	0.055
AF_TF	Geo	0.037	0.054	0.204	0.284	1.054	0.041	0.102
AF_TF-LP	Gen	0.036	0.050	0.166	0.272	1.049	0.045	0.079
SS_LG	Geo	0.148	0.186	0.116	0.287	1.180	0.165	0.208
SS_EH	Geo	0.135	0.171	0.107	0.279	1.161	0.146	0.164
SS_All	Gen	0.131	0.205	0.226		1.757	0.151	0.280
SS_LP	Geo	0.098	0.153	0.229	0.378	1.138	0.086	0.138
MF_Mad	Gen	0.191	0.232	0.094	0.408	1.222	0.198	0.214
MF_Mad	Geo	0.191	0.232	0.094	0.351	1.222	0.198	0.214
MF_LG	Geo	0.139				1.139		0.139
MF_TF	Geo	0.124	0.156	0.136	0.380	1.153	0.129	0.174
MF_Can	Gen	0.121	0.164	0.185	0.467	1.161	0.130	0.196
MF_GC	Geo	0.106	0.132	0.089	0.347	1.123	0.098	0.124
RR_LG	Gen	0.068	0.087	0.140	0.388	1.085	0.073	0.106
RR_LG	Geo	0.068	0.087	0.140	0.331	1.085	0.072	0.105
RR_Teno	Gen	0.064	0.081	0.134	0.384	1.080	0.070	0.114
RR_TF	Geo	0.057	0.085	0.195	0.374	1.085	0.071	0.132
RR_LP-GC	Gen	0.053	0.062	0.101	0.360	1.061	0.058	0.069
RR_LP	Geo	0.052	0.065	0.125	0.319	1.064	0.059	0.068
RR_GC	Geo	0.051	0.059	0.096	0.297	1.059	0.055	0.060
RR_Guimar	Gen	0.049	0.062	0.127	0.378	1.060	0.054	0.064
HE_GC	Geo	0.098	0.115	0.022	0.277	1.107	0.097	0.118
HE_The	Gen	0.090	0.121	0.154	0.596	1.117	0.103	0.149
HE_LauM	Gen	0.071	0.104	0.142	0.590	1.089	0.092	0.097
HE_Mad	Geo	0.063	0.105	0.266	0.457	1.091	0.067	0.097
HE_TF	Geo	0.061	0.130	0.325	0.501	1.127	0.124	0.151
HE_LP	Geo	0.048	0.064	0.125	0.353	1.059	0.038	0.065
HE_LauC	Gen	0.043	0.068	0.220	0.628	1.067	0.062	0.101
HE_LG	Geo	0.040	0.060	0.224	0.427	1.057	0.030	0.066
PI_Mad	Gen	0.054	0.065	0.060	0.726	1.062	0.072	0.076
PI_Mad	Geo	0.054	0.065	0.060	0.410	1.062	0.072	0.076
PI_LG	Geo	0.036	0.050	0.152	0.468	1.048	0.045	0.076
PI_TF	Geo	0.029	0.044	0.163	0.475	1.043	0.043	0.087
PI_Can	Gen	0.028	0.044	0.144	0.751	1.044	0.044	0.137
PI_LP	Geo	0.027	0.042	0.221	0.511	1.039	0.045	0.053
PI_GC	Geo	0.020	0.031	0.256	0.533	1.028	0.034	0.034
PI_EH	Geo	0.016	0.015	-0.025	0.357	1.016	0.015	0.021
AB_LG	Geo	0.086	0.106	0.125	0.297	1.105	0.097	0.120
AB_East	Gen	0.077	0.122	0.243	0.380	1.121	0.088	0.186
AB_TF	Geo	0.077	0.113	0.224	0.376	1.111	0.056	0.138
AB_GC	Geo	0.063	0.114	0.326	0.458	1.103	0.049	0.105
AB_LP	Geo	0.056	0.071	0.137	0.306	1.069	0.064	0.079
AB_West	Gen	0.056	0.070	0.135	0.292	1.070	0.066	0.091
AB_EH	Geo	0.056	0.063	0.066	0.249	1.062	0.058	0.065
AB_Mad	Geo	0.043	0.070	0.249	0.396	1.054	0.035	0.053

Figure 3 – Genetic diversity for all species studied at the population level. Genetic populations (Gen, written in blue) correspond to sNMF results excluding admixed individuals (>20%). Geographic populations (Geo, written in red) correspond to individuals found on a single island. Populations are grouped per species by descending order of observed heterozygosity values, from the lower generation time species to the higher. Species and populations codes can be found in Table 2. Ho = observed heterozygosity, Hs = expected heterozygosity, FIS = within population inbreeding, FIT = total inbreeding, Ar = allelic richness, π = nucleotide diversity, θW = Watterson's theta. All metrics results can be found in Table S2.

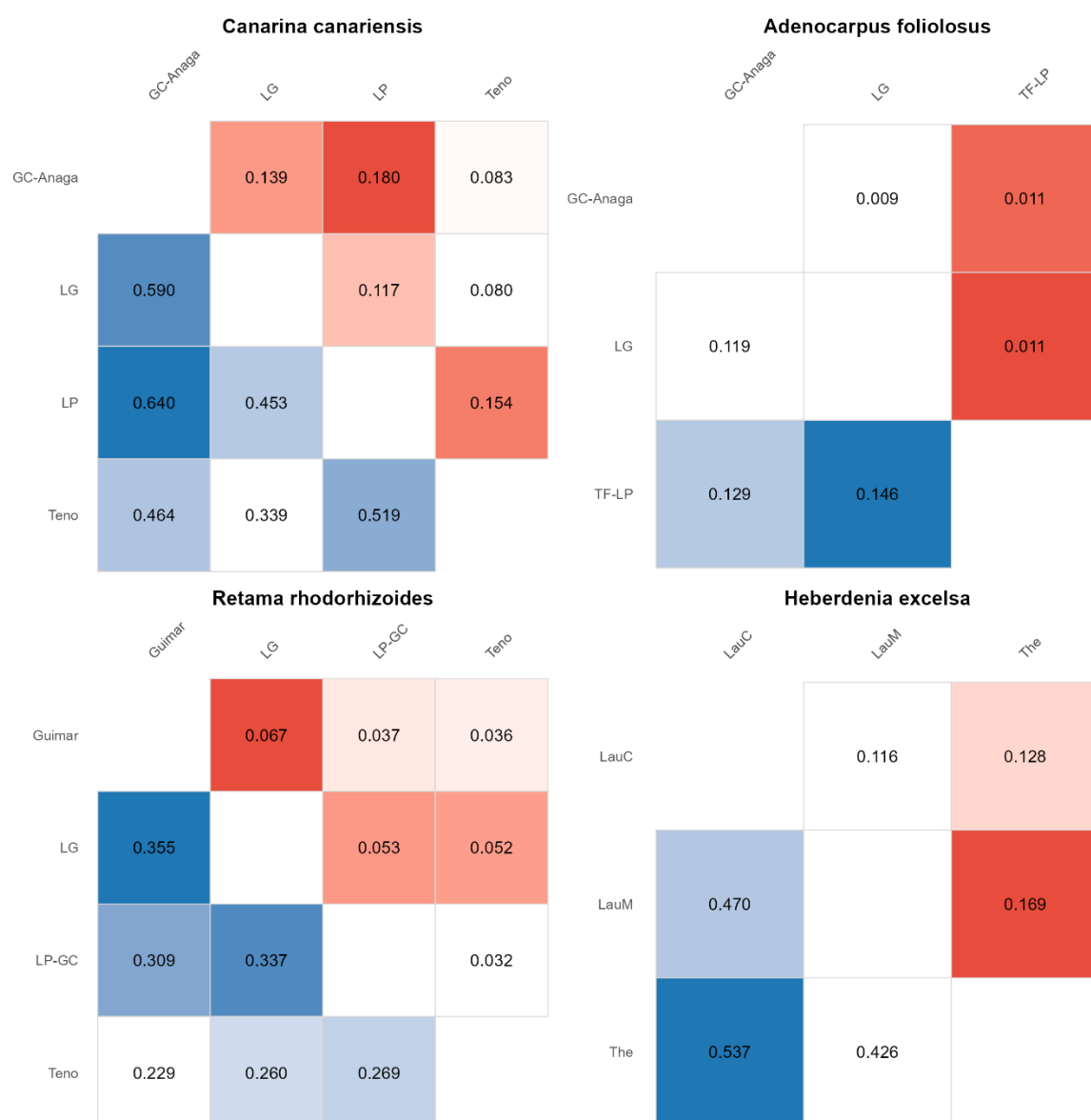


Figure 4 – Overview of the genetic structure among populations, expressed as pairwise F_{st} (below the diagonal, in blue) and Nei's distance (above the diagonal, in red) between genetic clusters. Populations codes can be found in Table 2. All species metrics results can be found in Table S3.

Stairway plots

Among the datasets analyzed in this study, only the *Adenocarpus foliolosus* population from La Gomera showed a potentially human induced genetic bottleneck, with a reduction of almost four times its effective population size (N_e) between the Amazigh colonization period (2000 Before Present, BP) and present time, divided between the Amazigh-only (~3 times) and European periods (~1.3 times). In comparison, the climatic period between the Last Glacial Maximum (LGM, 21000BP) and Amazigh colonization led to a bottleneck of around 1.5 times its N_e values. Other species showed small N_e reductions during the human-presence period, like *Canarina canariensis* from La Gomera and *Streptocytisus filipes*, with both ~1.2 times N_e decrease. Surprisingly, a small genetic expansion was found in *Heberdenia excelsa* laurel forest clade during the human-presence period with a ratio of ~0.9. See Table 3 for all ratios results.

Various species experienced genetic expansions during the climatic period, with the most extreme examples being *Dracunculus canariensis* two populations with ratios of 0.012 and 0.004, i.e., a N_e increase of 83 and 250 times in 19000 years (~1.3 times per century). *Canarina canariensis* Gran Canaria + Anaga population also had a demographic expansion during the climatic period (~0.2 ratio), along with *Luzula canariensis* two populations (0.24 and ~0.5 ratios) and *Retama rhodorhizoides* La Palma + Gran Canarie population (~0.4 ratio). Other species had demographic bottlenecks of moderate intensity, with N_e reductions of around 1.5 times in *Canarina canariensis* La Gomera population, and of ~1.3 times in *Streptocytisus filipes* and *Brachypodium arbuscula* Tenerife population.

Apart from those results, most datasets analyzed showed the same expected pattern of a sharp N_e increase at the beginning of the reconstructions, but at different time periods (see Figure 5 for a summary, and Figures S23 to S33 for the plots themselves by species divided by populations). Some occurred right before the onset of the penultimate glacial period (PGP) 194.000 years ago (ya), like *Streptocytisus filipes* (from 16000 to more than 190000) and *Apollonias barbujana* eastern population (from 24000 to 100000), and some occurred during the PGP, like Canarian *Morella faya* (from around 30000 to 75000) or the *Retama rhodorhizoides* from La Gomera (from 12500 to over 50000) and the *Heberdenia excelsa* thermo-sclerophyllous woodland clade (from 27000 to over 70000). Most of the species and populations had large increases in size during the Last Glacial Period (LGP) that began 115.000ya and ended only recently around 15.000ya. During this period, other populations of *R. rhodorhizoides* (same range as La Gomera population), *Persea indica* (from 6500 to over 500000), western population of *A. barbujana* (from less than 17000 to 60000), *Adenocarpus foliolosus* (from less than 10000 for all three populations to more than

50000 for all except La Gomera population) and the Canarian *Heberdenia excelsa* laurel forest clade (from 15000 to over 150000) started their increase at the beginning of the LGP while *Brachypodium arbuscula* (from 20000 to over 60000 for La Gomera population) and *Luzula canariensis* (from less than 16000 to over 80000) started later during the middle and late LGP. More recent increases are described above.

Another interesting pattern observed across different datasets is the suggested large decrease right before the sharp increase described here above, where most species experienced a rapid population growth in the past at the beginning of their demographic reconstruction. For *Persea indica*, it is even apparent that around the last Interglacial Period (115ka-130ka) N_e dropped dramatically from 6500 to less than 1500 before recovering during the LGP to impressive values over 500000. This suggested pattern is visible through the confidence interval for both *H. excelsa* clades, the eastern population of *A. barbujana*, and also, but more recently, for both *Dracunculus canariensis* populations, the Gran Canaria + Anaga *Canarina canariensis* population and the La Gomera *Brachypodium arbuscula*.

Table 3 – Shifts in effective population size (N_e) across selected Canarian and Macaronesian endemic species at different periods. Ratio represents demographic trends at present time vs European colonization time (Europe), at European colonization time vs Amazigh colonization time (Amazigh), at present time vs Amazigh colonization time (Human), and at Amazigh colonization time vs Last Glacial Maximum (Climate), computed from demographic history reconstructions (see Material and Methods for details). See Figure 2 for genetic clusters codes geographic signification.

Species	Genetic cluster	Ne Present	Ne Europe	Ne Amazigh	Ne LGM	Ratio Europe	Ratio Amazigh	Ratio Human	Ratio Climate
<i>Apollonias barbujana</i>	East	86406	86268	88888	101195	0.998	1.030	1.029	1.138
	West	63401	63087	63931	59120	0.995	1.013	1.008	0.925
<i>Adenocarpus foliolosus</i>	GC-Anaga	83052	83531	83532	80426	1.006	1.000	1.006	0.963
	LG	6017	7944	23218	33626	1.320	2.923	3.859	1.448
	TF-LP	55705	55632	56126	50222	0.999	1.009	1.008	0.895
<i>Brachypodium arbuscula</i>	LG	55680	57632	59058	57574	1.035	1.025	1.061	0.975
	TF	25084	25600	26513	34256	1.021	1.036	1.057	1.292
<i>Canarina canariensis</i>	GC-Anaga	97379	97391	96793	18768	1.000	0.994	0.994	0.194
	LG	13651	14802	15890	23267	1.084	1.073	1.164	1.464
	Teno	23578	23578	23578	23189	1.000	1.000	1.000	0.983
<i>Dracunculus canariensis</i>	GC	541168	539808	542933	6260	0.997	1.006	1.003	0.012
	West	898287	898287	898287	3819	1.000	1.000	1.000	0.004
<i>Heberdenia excelsa</i>	Lau	150728	127876	136630	144282	0.848	1.068	0.906	1.056
	Ther	72033	69541	70364	73050	0.965	1.012	0.977	1.038
<i>Luzula canariensis</i>	LG	86151	86151	86151	20676	1.000	1.000	1.000	0.240
	TF	226364	226364	226364	102894	1.000	1.000	1.000	0.455
<i>Morella faya</i>	Can	77638	76934	78474	79526	0.991	1.020	1.011	1.013
<i>Persea indica</i>	Can	572190	572190	572190	571982	1.000	1.000	1.000	1.000
<i>Retama rhodorhizoides</i>	Guimar	19226	19225	19310	19520	1.000	1.004	1.004	1.011
	LG	55526	52755	56345	56499	0.950	1.068	1.015	1.003
	LP-GC	32570	32615	33614	12765	1.001	1.031	1.032	0.380
	Teno	52897	52870	53156	53593	0.999	1.005	1.005	1.008
<i>Spartocytisus filipes</i>	all	96228	96209	111442	148154	1.000	1.158	1.158	1.329

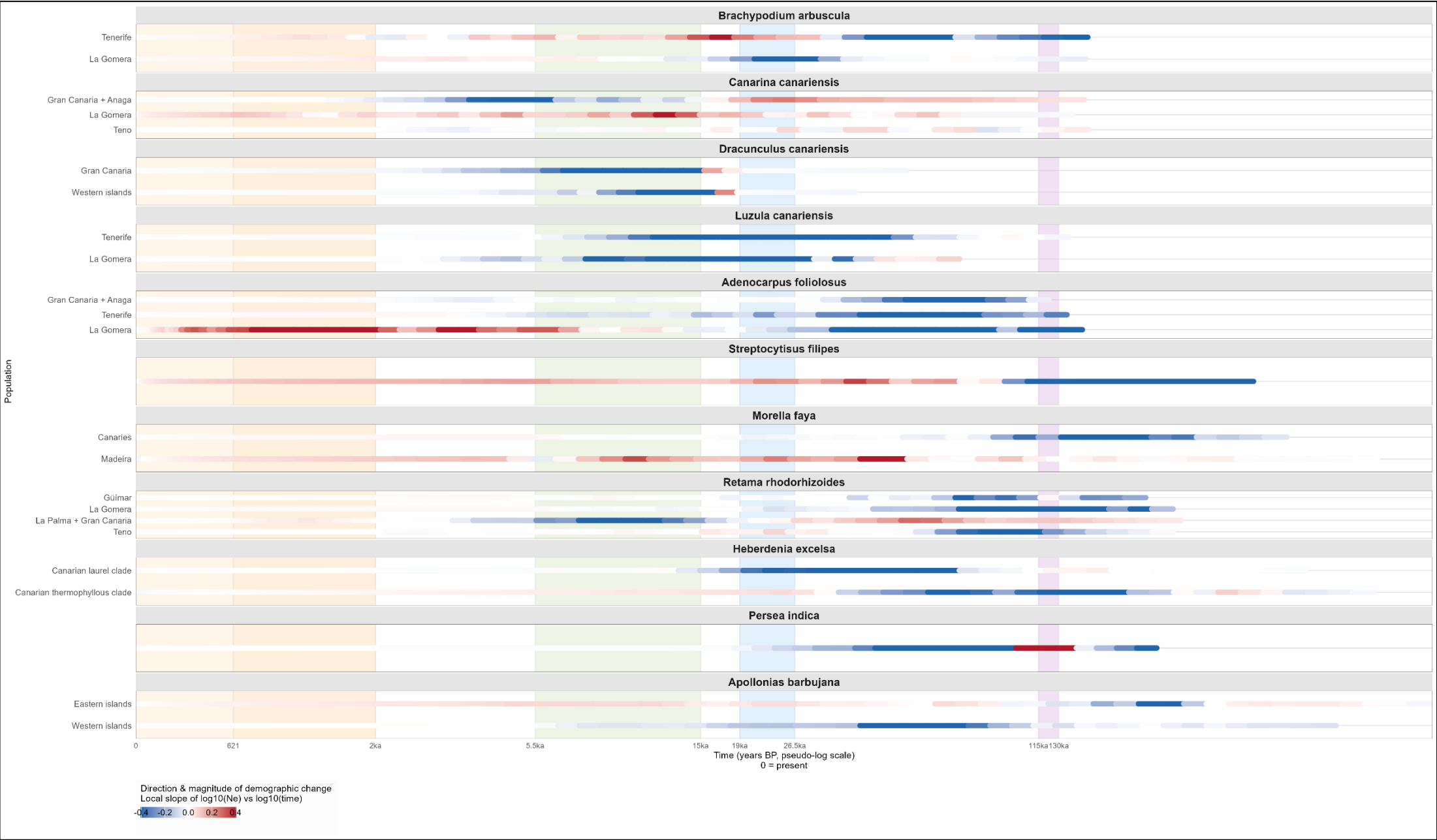


Figure 5 – Summary of the demographic history for all species and populations. The graph shows the variation of the slope of the relationship between N_e and time, inferred from *STAIRWAYPLOT2* analyses, at regular time intervals, with values in blue corresponding to a negative slope, i.e., to an increase of N_e values between two adjacent periods (going forward in time, i.e., from the past to the present), and values in red corresponding to a positive slope, i.e., a decrease of N_e values between two adjacent periods. Important periods are highlighted in the background in different colors (yellow = European period, orange = Guanche period, green = African Humid Period, blue = Last Glacial Maximum, purple = Last Interglacial (Eemian)).

Species Distribution Models

The Species Distribution Models exhibited high levels of accuracy on average (see Table S4 for each model performance including the ensemble model, for every species). The Ensemble models gave a mean AUC value of 0.926 ± 0.015 across all species, a Boyce Index of 0.987 ± 0.013 , and a max TSS of 0.753 ± 0.029 . The results were similar for all individual species. The habitat suitability at present time and during the LGM (21kya) for each species can be found in Figure S34, and pixel ratios, i.e., changes in climatic suitable area between the LGM and present, in Table 4.

Table 4 – Shifts in climatic suitability across selected Canarian and Macaronesian endemic species between the Last Glacial Maximum (LGM) and the present. Ratio represents the ratio of climatically suitable pixels at LGM vs at present time, computed from the projection of species distribution models onto LGM and present climatic layers (see Material and Methods for details).

Species	#Pixel present	#Pixel LGM	Ratio
<i>Apollonias barbujana</i>	4450	2465	0.554
<i>Adenocarpus foliolosus</i>	5326	10878	2.042
<i>Brachypodium arbuscula</i>	4479	6532	1.458
<i>Canarina canariensis</i>	3893	1903	0.489
<i>Dracunculus canariensis</i>	6170	5958	0.966
<i>Heberdenia excelsa</i>	3464	2565	0.740
<i>Morella faya</i>	5746	7936	1.381
<i>Persea indica</i>	4049	5117	1.264
<i>Retama rhodorhizoides</i>	5069	7162	1.413
<i>Spartocytisus filipes</i>	6233	8739	1.402

Substantial variation of climatic suitability, with either evidence for expansion or reduction of the extent of climatically suitable areas between the LGM and present time, was found among species (Table 4). The extent of climatically suitable areas increased from the LGM to the present in *Apollonias barbujana*, *Canarina canariensis*, and *Heberdenia excelsa*. In *Dracunculus canariensis*, no sharp variation of the extent of climatically suitable areas was observed. In all other species, the extent of climatically suitable areas decreased from the LGM to the present. The species predicted to have had the largest decline in climatic suitability was *Adenocarpus foliolosus*, with a reduction of suitable areas corresponding to half its former distribution range during the LGM (ratio = 2.04).

DISCUSSION

Do reconstructions of the demographic history of Canarian endemic forest species allow the identification of signatures of post-human colonization?

The present analyses evidenced substantial variations of effective population size (N_e), but the timing of the major shifts in population size occurred well-before the human colonization of the Canarian archipelago, ruling-out the hypothesis that human disturbance over the past 2000 years left a clear signature in extant patterns of genetic diversity. The only exception was a reduction of the population of *Adenocarpus foliolosus* from La Gomera ~2000BP, concomitant with the colonization of the island by human populations of Amazigh origin (Santana et al., 2024) and the increase of the fire regime (Castilla-Beltrán et al., 2021; Nogué et al., 2013). An anthropogenic interpretation of this pattern is, however, at odds with the fact that, although La Gomera has the best-preserved laurel forest ecosystem across the archipelago, with ~70% of its potential natural area remaining (del Arco Aguilar et al., 2010). Although it does not necessarily mean that the forest remained intact during 2000 years, no recent bottleneck was evidenced in the populations of other islands, where the extent of laurel forest is much more reduced and the conservation status of this ecosystem much more degraded.

Other species and populations showed demographic expansion or reduction concomitant to older climatic perturbation events, spanning various timescales. Some species like *Canarina canariensis* or *Dracunculus canariensis* showed population expansions posterior to the Last Glacial Maximum (LGM), while other species underwent even older expansions, the oldest one dating back up to 200-250 thousand years ago in *Streptocytisus filipes*.

The lack of imprints of recent human disturbance on patterns of genetic structure and diversity was unexpected because mounting evidence points to a global loss of genetic diversity due to human activity, both by direct actions like changes in land use or habitat fragmentation, or by indirect consequences from species introductions, pollution, or climate change, sometimes linked to population extinctions (Shaw et al., 2025; Exposito-Alonso et al., 2022; Almeida-Rocha et al., 2020; Leroy et al., 2018). The impact of ancient civilizations on current patterns of genetic diversity and structure has also been previously reported (Goudie, 2018; Hofman et al., 2015). On islands, the link between genetic loss and human perturbation is even more visible as they are seen as model systems (Whittaker et al., 2017), where colonization happened quite recently and has been shown to have impacted plant communities (Nogué et al., 2021) and their genetic diversity (e.g., Seersholm et al., 2018 in New Zealand; Bourgeois et al., 2024 in La Réunion). In some extreme cases, severe reductions in population size, species introduction, or local

extinctions even led to the entire replacement of ecosystems (Bush et al., 2022), leading to cascading effects (Almeida-Rocha et al., 2020). In the Canary Islands, the extinction of mammal, reptile and bird species has substantial impact on ecosystems (Fernández-Palacios et al., 2025; Pérez-Méndez et al., 2018; Illera et al., 2016). It has, for example, been hypothesized that the summit broom scrubs ecosystem was once a *Juniperus cedrus* woodland, which dispersal network was disturbed (Nogales et al., 2014), leading to extensive community turnover (see discussions from Heinen & Borregaard, 2024; Albert et al., 2020; and Pérez-Méndez et al., 2018).

There might be several explanations for the lack of a signature of human disturbance in extant patterns of genetic diversity. Although it would be interesting to perform Whole Genome Sequencing to obtain more informative loci, and then conduct a Genome-Wide Association Study, a limitation due to the number of markers available is unlikely. In many instances indeed, genetic analyses based on similar genomic data (e.g., Xie et al., 2026; Vintsek et al., 2022), and even datasets yielding lower numbers of markers such as microsatellites (Gonzalez et al., 2014), revealed genetic signatures of recent demographic events (e.g., Bourgeois et al., 2024; Qin et al., 2024; Wang et al., 2023; Liu et al., 2020). With SNP matrices from RAD sequencing comparable in size to the ones generated here, *STAIRWAYPLOT2* analyses proved very efficient in recovering recent demographic events in non-model species (e.g., Wang et al., 2023; Liu et al., 2020).

One interpretation of the lack of any signature of recent anthropic disturbance in the present data is that genetic responses are delayed or result from a genetic extinction debt, a parallel concept to the classic extinction debt that represents the delayed loss of species following habitat deterioration (Tilman et al., 1994; Essl et al., 2015), which has already been found in the Canary Islands, including for vascular plants (Otto et al., 2017). In fact, a genetic extinction debt, i.e., the time lag between disturbing events and genetic responses at the population scale, is an increasingly recognized pattern. Habitat disturbance affects species fitness and survival, and results in genetic drift through the loss or change in frequency of genetic variants. This genetic signature of habitat perturbations can be detected only after a number of generations, as moderately high levels of genetic diversity are preserved through persisting individuals that hold genetic legacies of their ancestors (see Gargiulo et al., 2025, and references therein). In species with short generation times, such as *Canarina canariensis* (estimated at between 2 and 5 years, see Table S1), we would have expected a recent anthropic period signal from 2000BP onward (~400 generations). The failure of our analyses to retrieve the signal of demographic events dating back to 2000ya may reflect the low impact of people from Amazigh origin on the demography of this species, while the European settlement, dating back to only ~100 generations, may have been too recent to leave a detectable imprint in the genome.

The prevalence of ancient vs recent demographic events reported in the present analyses is in line with the results obtained in Afrotropical species on the continent. Little to no demographic signal was found in phylogeographic analyses across various plant species of the African tropical forest. The absence of any recent demographic signal, despite substantial fragmentation during the last glacial/interglacial cycles, was interpreted by Hardy et al. (2021) and Ernst et al. (2025) in the context of Maley's refuge hypothesis (Maley, 1996). This hypothesis posits that repeated Quaternary cold and dry periods contracted and fragmented Afrotropical forests into isolated refugium patches, before expansion phases and populations secondary contacts took place during wet periods. Genetic evidence, however, points toward a more nuanced and species-specific response, wherein species distribution ranges were fragmented, according to a pattern that varied depending on differences in life-history traits and ecological preferences (see reviews by Hardy et al., 2021 and Ernst et al., 2025), in a much similar way as the patterns reported here in species with short (*Canarina canariensis*, *Dracunculus canariensis*) or long (*Apollonias barbujana*, *Persea indica*) generation times. In Afrotropical ecosystems, contrasted demographic histories were recovered for long-lived, shade-tolerant species and pioneer, sun-loving species with different dispersal capacities. In long-lived, shade-tolerant species with limited dispersal capacities, i.e., species with non-assisted seed dispersal, deep signals of demographic shifts dated back to Pleistocene events. In pioneer, sun-loving species with high long-distance dispersal capacities, i.e., with wind dispersed seeds, more recent signals of demographic shifts dating to the LGM and post-LGM period were identified (Piñeiro et al., 2021). Indeed, high dispersal capacities allow for a better genetic mixing, "overwriting" the signature of old demographic variations by more recent events in the genome, whereas low dispersal capacities prevent homogenization of allele frequencies, contributing to maintain genetic structures for longer periods. This same pattern was also visible in meta-analyses, showing that habitat fragmentation and degradation have lower or delayed effects on the genetic diversity of long-lived species, proportionally to the number of generations since the disturbance event (González et al., 2020; Vranckx et al., 2012; Aguilar et al., 2008).

In line with those results, species with short generation times growing in humid conditions like *Canarina canariensis*, *Dracunculus canariensis* or *Luzula canariensis* showed important increases in population size after the LGM and during the African Humid Period (AHP) (see Figure 5 for a summary of demographic events across all species, or supplementary Figure S23 to S33 for detailed results by species). In contrast, species with short generation time, but growing in more arid conditions, like the grass species *Brachypodium arbuscula* or the bush species *Retama rhodorhizoides*, showed different signals. A slow, steady N_e decrease was found for *B. arbuscula*

(Tenerife population) since the LGM period, and 95% IC tends to suggest the La Gomera population also underwent a genetic bottleneck during the AHP (see Figure S25). In *R. rhodorhizoides* (La Palma + Gran Canaria cluster) conversely, a sharp increase in effective population size was identified during the AHP. These patterns can be linked to a West African Monsoon northward limit reaching the Canarian latitude at peak of humid periods during the AHP (Pausata et al., 2016; von Suchodoletz et al., 2010), but also to intrinsic dispersal capacities as *B. arbuscula* has short-distance dispersal capacities, whereas the seeds of *R. rhodorhizoides* are dispersed through endozoochory (Table 1), i.e., long-distance dispersal capacities. A vegetation turnover identified in the pollen record (Nogué et al., 2013; Castillan-Beltrán et al., 2021) further emphasized the importance of the AHP for shaping the Canarian ecosystems, with a rapid decrease in abundance of hygrophilous taxa like *Salix canariensis* or *Phoenix canariensis* around 6000-5500BP in La Gomera, concomitant with an increase in common laurel forest taxa. This palynological pattern was also recorded in continental Africa sediments (Lézine et al., 2025, 2019, 2005), showing important modifications of species distribution during the AHP along strong decreases in freshwater discharges between 7100 and 5500BP (Lézine et al., 2025).

More ancient demographic shifts were inferred for species with longer generation time, which aligns with findings in Afrotropical continental species according to which the inherent inertia associated with long generation time species prevents to detect demographic signatures of relatively recent events such as the LGM in the genome (see reviews by Hardy et al., 2021 and Ernst et al., 2025 on Afrotropical species, and Gargiulo et al., 2025 on genetic response delay). Furthermore, old strong genetic structuring signals were shown to persist even after major population disruptions like habitat reduction and fragmentation, making it possible to date the habitat disruption through this strong signal decline (Sgarlata et al., 2025). Our results show a strong signal of N_e increase during the Last Glacial Period or sometimes even before the last interglacial period (Eemian). This period corresponds to a climatic shift from tropical to Mediterranean like, thus promoting species exchanges between islands and mainland (Caujapé-Castells et al., 2022; García-Verdugo et al., 2019; Fernández-Palacios et al., 2011). This old signal could also represent a complete isolation of the species after the extinction of the taxon on mainland, as has been hypothesized as the “late Pleistocene endemism increase hypothesis” (Caujapé-Castells et al., 2022).

In fact, the signal for ancient demographic events reported here could also reflect departures of our data from the assumptions of the *STAIRWAYPLOT2* analyses. Stairway plots results are recovered from coalescent estimates and according to all hypotheses going along this theory, e.g., a unique panmictic isolated unstructured population (Liu & Fu, 2020). Different recent

theories (Rodríguez et al., 2018; Mazet et al., 2016) show that very similar effective population size demographic histories (or curve trajectories) can arise from various processes like connectivity between populations, population and subpopulation sizes and number, different sampling strategies, etc. (Fedorca et al., 2024; Mazet & Noûs, 2023; Boitard et al., 2022; Chikhi et al., 2018). In an archipelago context, an expansion signal can represent a real population size increase through range expansion, but also an increase in the connectivity between islands during the last glacial period and associated lower sea level (Fernández-Palacios et al., 2016), or a founder event and associated genetic drift.

It is particularly important to be cautious in the interpretation of our results as island endemics often have small distribution ranges and strong genetic structures. In most of the species investigated here, genetic clusters are typically island-specific or shared between two islands. By analyzing each population independently, we attempted at reducing the bias introduced by the genetic structure, but ancient genetic connections among populations may have taken place. Moreover, the results are conditional to the value of the mutation rate and to the definition of the generation time implemented. To take the uncertainty of the latter into account, we ran the analysis using different generation time values to interpret time intervals rather than fixed periods, focusing on comparisons among populations and species and on broadly defined climatic events.

CONCLUSION & PERSPECTIVES

The present study contributes to fill a gap in the quantitative assessment of human impact on genetic diversity in insular systems (Nogué et al., 2025). Focusing on forest plant species from the two most degraded ecosystems, i.e., the thermo-sclerophyllous woodland and laurel forest in the Canary Islands, we found demographic shifts concomitant with major climate change events, but virtually no trace of anthropic perturbations. Different options exist to further investigate the anthropic impact on the current genetic diversity of Canarian endemic species.

First of all, it would be interesting to complement our results with further analyses on the species colonization history across the archipelago to better understand the source-sink dynamic between islands. In particular, explicit hypotheses regarding expected demographic shifts could be tested within a coalescence context (see e.g. Rincón-Barrado et al., 2024a,b). Dated phylogeographies would also be useful to model historical island connections, for example using a multi-species coalescent model approach (e.g., StarBeast3 (Douglas et al., 2022)) or an admixture based approach (e.g., DILS (Fraïsse et al., 2021), dadi-moments (Gutenkunst et al., 2009; Jouganous et al., 2017)). We could also investigate how present genetic diversity will evolve in the current ecosystems regeneration dynamic through a future scenarios modelization approach (e.g., SLiM (Haller et al., 2026)), to determine how it will affect the fitness of the species and the ecosystems.

As an extinction debt was found in the Canary Islands diversity, including vascular plant biodiversity (Otto et al., 2017), we could test for a delayed genetic response regarding recent human perturbations. To do so, land-use history archives would be necessary to compare forest patches between one another and see for example if some particularly impacted forests show unexpected high genetic diversity (e.g., Plue et al., 2026), but to my knowledge, there are no such archives. A proxy could be historical socioeconomic developments like was done in Norder et al. (2020). Another possibility would be to compare genetic diversity between different age classes of the same long-lived species. By comparing young and old individuals, we could detect an anthropic impact or reduction in diversity in the younger population as has been shown in other studies (e.g., Ruiz-Chután et al., 2024). Many species could be good candidates to test this hypothesis: laurel trees like *Persea indica*, *Apollonias barbujana* or *Ocotea foetens*, but also *Juniperus turbinata* or *Juniperus cedrus*.

A more straightforward way to look for anthropic perturbations in the genetic diversity of native species would be to compare past diversity with currently observed results. In the Canary Islands, ancient DNA (aDNA) analyses were conducted on cultivated plant species of cultural importance

to modern and ancient inhabitants (Hagenblad et al., 2025, 2024, 2017; Hagenblad & Morales, 2020; Oliveira et al., 2012). To my knowledge, no study focused yet on native vegetation and compared ancient to current genetic patterns. Promising DNA recovery results obtained in tropical and subtropical ecosystems (Ekram et al., 2025; Dommain et al., 2020), but also on island settings (Pillay et al., 2026), wherein DNA is typically poorly preserved (Kistler et al., 2017), open the door to aDNA and sedaDNA studies in an island context.

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SUPPLEMENTARY DATA

Table S1 – *STAIRWAYPLOT2* metadata. Tot ind. = total number of individuals, population = code of the population estimated from sNMF analysis (see main text Material & Methods for details), #individuals = number of individuals within this population after removing admixed individuals (>20%), generation time = species specific generation time displayed in the results and distribution values used to take uncertainty into account, #SNP retained = number of SNP projected in the SFS, L= estimation of the total number of sites sequenced.

Species	Tot ind.	Population	#individuals	Generation time	#SNP retained	L	Comments and sources for generation time
<i>Apollonias barbujana</i>	38	East	19	12 (10-15)	4115	617250	Estimation based on fieldwork experience in restauration actions (García et al., 2013).
		West	15		4357	653550	
<i>Adenocarpus foliolosus</i>	80	GC-Anaga	30	4 (2-5)	1811	271650	Estimation based on close species data (<i>Cytisus</i> or other Genistae species) and its shrubby growth form.
		LG	25		2024	303600	
		TF-LP	10		1847	277050	
<i>Brachypodium arbuscula</i>	38	LG	23	2 (1-4)	7225	1083750	Estimation based on its self-incompatible sexual strategy and its rhizome production.
		TF	15		7150	1072500	
<i>Canarina canariensis</i>	50	GC-Anaga	25	2 (2-5)	2578	386700	Estimation based on observations of its biennial growing habit (Caballero et al., 1992). Given its dormant stage in tuber form, the generation time can be longer (Mairal et al., 2018).
		LG	7		2459	368850	
		LP	4		2501	375150	
		Teno	7		2305	345750	
<i>Dracunculus canariensis</i>	60	GC	27	2 (2-5)	4590	688500	Estimation based on ornamental plants data stating that it flowers within 2-3 growing seasons in the best conditions, but can last till 5 years (various horticultural websites).
		West	33		4517	677550	

<i>Heberdenia excelsa</i>	23	Lau-all	16	10 (10-14)	1721	258150	Estimation based on close species data (<i>Myrsine parvula</i> ; Hermann, 2009). The relationship between <i>Heberdenia</i> and <i>Myrsine</i> genera was suggested by Appelhans et al. (2020) but is still not resolved.
		LauC	13		1633	244950	
		LauM	3		/	/	
		Ther	7		1620	243000	
<i>Luzula canariensis</i>	16	AnagaE	3	2 (1-4)	/	/	Estimation based on its rhizome production.
		AnagaW	6		120	18000	
		LG	7		136	20400	
		TF	9		142	21300	
<i>Morella faya</i>	17	All	17	5 (4-6)	1072	160800	Estimation based on observations in Hawaii where the species is invasive (Vitousek & Walker, 1989).
		Can	12		945	141750	
		Mad	5		956	143400	
<i>Persea indica</i>	25	Can	23	10 (10-15)	2640	396000	Estimation based on fieldwork experience in restoration actions (García et al., 2013).
		Mad	2		/	/	
<i>Retama rhodorhizoides</i>	54	Guimar	8	5 (4-7)	2701	405150	Estimation based on close species data (<i>Retama monospermum</i> ; Gallego-Fernández et al., 2015).
		LG	7		2569	385350	
		LP-GC	23		2889	433350	
		Teno	14		2736	410400	
<i>Streptocytisus filipes</i>	11	All	11	4 (2-5)	2635	395250	Estimation based on close species data (<i>Cytisus scoparius</i> ; Sheppard et al., 2002).

Table S2 – Genetic diversity for all species studied, at global and population levels. Genetic populations correspond to sNMF results excluding admixed individuals (>20%). sp = species name, n = number of individuals, #loci = number of loci, %NA = percentage of missing data, Ho = observed heterozygosity, Hs = expected heterozygosity, FIS = within population inbreeding, FIT = total inbreeding, FST = among population differentiation, Ar = allelic richness, %poly_loci = proportion of polymorphic loci, pi = nucleotide diversity, thetaW = Watterson's theta, Ne = population effective size. EH = El Hierro, LP = La Palma, LG = La Gomera, TF = Tenerife, GC = Gran Canaria, Mad = Madeira.

sp	population		n	#loci	%NA	Ho	Hs	FIS	FIT	FST	Ar	%poly_loci	pi	thetaW	Ne
<i>Apollonias barbujana</i>	genetic	GLOBAL	38	4628	11.5	0.067	0.096	0.317	0.441	0.181	1.095	55.3	0.089	0.203	7249777.1
		West	15		4.0	0.056	0.070	0.135	0.292		1.070	34.7	0.066	0.091	3265838.8
		East	23		16.3	0.077	0.122	0.243	0.380		1.121	75.9	0.088	0.186	6655756.3
	geographic	GLOBAL	46		16.2	0.064	0.091	0.257	0.403	0.196	1.084	28.9	0.077	0.204	7284443.0
		EH	7		3.8	0.056	0.063	0.066	0.249		1.062	20.4	0.058	0.065	2313483.5
		GC	5		33.7	0.063	0.114	0.326	0.458		1.103	25.8	0.049	0.105	3761196.0
		LG	10		4.1	0.086	0.106	0.125	0.297		1.105	42.0	0.097	0.120	4291341.4
		LP	8		4.3	0.056	0.071	0.137	0.306		1.069	25.9	0.064	0.079	2817439.1
		Mad	2		29.8	0.043	0.070	0.249	0.396		1.054	10.7	0.035	0.053	1878145.8
		TF	14		29.8	0.077	0.113	0.224	0.376		1.111	48.7	0.056	0.138	4927183.2
<i>Adenocarpus foliolosus</i>	genetic	GLOBAL	69	2120	6.9	0.039	0.052	0.228	0.326	0.128	1.051	37.9	0.051	0.172	6125855.1
		GC-Anaga	31		7.3	0.042	0.056	0.149	0.258		1.055	57.6	0.050	0.134	4784434.9
		LG	25		5.8	0.039	0.049	0.135	0.246		1.049	28.3	0.046	0.069	2462615.8
		TF-LP	13		8.0	0.036	0.050	0.166	0.272		1.049	27.6	0.045	0.079	2827668.4
	geographic	GLOBAL	95		11.9	0.038	0.053	0.270	0.343	0.100	1.052	37.2	0.043	0.176	6288905.0
		GC	35		13.6	0.040	0.055	0.173	0.256		1.055	59.8	0.041	0.128	4566817.5
		LG	27		8.9	0.039	0.050	0.153	0.238		1.050	29.0	0.040	0.065	2322962.5
		LP	5		12.9	0.038	0.051	0.160	0.244		1.049	14.9	0.038	0.055	1976407.4
		TF	28		12.4	0.037	0.054	0.204	0.284		1.054	45.2	0.041	0.102	3626694.6
<i>Brachypodium arbuscula</i>	genetic	GLOBAL	38	7546	8.1	0.077	0.102	0.239	0.412	0.228	1.101	48.9	0.106	0.187	6668630.3
		LG	23		7.6	0.074	0.098	0.163	0.353		1.097	56.7	0.092	0.146	5212204.0
		TF	15		8.8	0.080	0.106	0.175	0.363		1.104	41.2	0.097	0.119	4239201.8
	geographic	GLOBAL	38		8.1	0.077	0.102	0.239	0.412	0.228	1.101	48.9	0.106	0.187	6668630.3
		LG	23		7.6	0.074	0.098	0.163	0.353		1.097	56.7	0.092	0.146	5212204.0
		TF	15		8.8	0.080	0.106	0.175	0.363		1.104	41.2	0.097	0.119	4239201.8

<i>Canarina canariensis</i>	genetic	GLOBAL	43	2727	12.4	0.046	0.079	0.394	0.726	0.549	1.075	27.4	0.100	0.191	6821105.1
		GC-Anaga	25		9.3	0.041	0.066	0.240	0.657		1.065	40.6	0.056	0.099	3544297.6
		LG	7		15.4	0.049	0.085	0.303	0.685		1.081	24.8	0.066	0.087	3110551.6
		LP	4		14.7	0.052	0.078	0.219	0.648		1.072	18.3	0.063	0.078	2785454.2
		Teno	7		18.9	0.045	0.087	0.345	0.704		1.081	25.7	0.061	0.092	3270604.6
	geographic	GLOBAL	53		16.3	0.045	0.084	0.493	0.698	0.404	1.081	32.5	0.086	0.198	7084737.4
		GC	17		6.2	0.041	0.059	0.184	0.514		1.058	28.0	0.050	0.070	2495674.4
		LG	8		20.0	0.047	0.086	0.323	0.597		1.082	25.7	0.055	0.082	2944655.0
		LP	5		18.4	0.050	0.082	0.269	0.564		1.076	21.3	0.055	0.079	2817187.8
		TF	23		22.1	0.042	0.110	0.400	0.643		1.108	55.1	0.066	0.133	4764688.0
<i>Dracunculus canariensis</i>	genetic	GLOBAL	61	5105	7.9	0.018	0.037	0.513	0.784	0.556	1.037	49.6	0.049	0.188	6719838.3
		West	34		8.7	0.016	0.032	0.145	0.620		1.032	55.8	0.027	0.120	4277959.7
		GC	27		6.9	0.019	0.041	0.218	0.653		1.041	43.4	0.035	0.098	3488304.9
	geographic	GLOBAL	62		8.4	0.018	0.027	0.486	0.747	0.509	1.027	20.3	0.049	0.189	6745031.9
		EH	5		5.5	0.018	0.019	0.031	0.524		1.019	8.5	0.017	0.031	1094146.6
		GC	28		8.0	0.019	0.041	0.221	0.617		1.041	44.6	0.034	0.099	3542831.8
		LG	6		7.1	0.014	0.016	0.050	0.533		1.016	8.1	0.013	0.028	983311.5
		LP	5		17.1	0.021	0.025	0.084	0.550		1.024	9.3	0.017	0.035	1256926.8
		TF	18		7.8	0.016	0.034	0.202	0.608		1.033	30.8	0.028	0.076	2709406.4
<i>Heberdenia excelsa</i>	genetic	GLOBAL	23	1754	9.8	0.068	0.097	0.303	0.667	0.523	1.091	30.9	0.120	0.209	7448917.9
		The	7		11.0	0.090	0.121	0.154	0.596		1.117	41.2	0.103	0.149	5308894.7
		LauC	14		8.7	0.043	0.068	0.220	0.628		1.067	34.5	0.062	0.101	3608258.3
		LauM	2		12.8	0.071	0.104	0.142	0.590		1.089	16.8	0.092	0.097	3479125.2
	geographic	GLOBAL	26		16.2	0.062	0.094	0.472	0.610	0.261	1.088	23.5	0.103	0.209	7471796.6
		GC	2		14.9	0.098	0.115	0.022	0.277		1.107	20.4	0.097	0.118	4219707.7
		LG	6		30.3	0.040	0.060	0.224	0.427		1.057	16.0	0.030	0.066	2369234.4
		LP	3		24.4	0.048	0.064	0.125	0.353		1.059	11.9	0.038	0.065	2303934.5
		Mad	3		21.5	0.063	0.105	0.266	0.457		1.091	18.6	0.067	0.097	3451824.5
		TF	12		6.0	0.061	0.130	0.325	0.501		1.127	50.4	0.124	0.151	5391559.3

<i>Luzula canariensis</i>	genetic	GLOBAL	19	162	8.8	0.046	0.110	0.601	0.867	0.667	1.106	45.1	0.192	0.245	8740554.4
		LG	8		10.1	0.048	0.089	0.277	0.759		1.086	32.7	0.070	0.102	3651663.0
		TF	11		7.9	0.044	0.131	0.388	0.796		1.126	57.4	0.109	0.162	5791892.0
	geographic	GLOBAL	19		8.8	0.046	0.110	0.601	0.867	0.667	1.106	45.1	0.192	0.245	8740554.4
		LG	8		10.1	0.048	0.089	0.277	0.759		1.086	32.7	0.070	0.102	3651663.0
		TF	11		7.9	0.044	0.131	0.388	0.796		1.126	57.4	0.109	0.162	5791892.0
<i>Morella faya</i>	genetic	GLOBAL	17	1101	10.2	0.156	0.198	0.220	0.490	0.347	1.192	64.6	0.186	0.253	9051068.2
		Can	12		10.7	0.121	0.164	0.185	0.467		1.161	69.9	0.130	0.196	6997437.3
		Mad	5		8.8	0.191	0.232	0.094	0.408		1.222	59.4	0.198	0.214	7659203.4
	geographic	GLOBAL	17		10.2	0.141	0.175	0.192	0.421	0.283	1.159	47.6	0.186	0.253	9051068.2
		GC	3		15.5	0.106	0.132	0.089	0.347		1.123	27.7	0.098	0.124	4427356.4
		Mad	5		8.8	0.191	0.232	0.094	0.351		1.222	59.4	0.198	0.214	7659203.4
		LG	1		9.9	0.139	NA	NA	NA		1.139	NA	NA	0.139	4963314.6
		TF	8		9.1	0.124	0.156	0.136	0.380		1.153	55.7	0.129	0.174	6223919.7
<i>Persea indica</i>	genetic	GLOBAL	25	3051	6.9	0.041	0.054	0.353	0.811	0.709	1.053	29.4	0.064	0.177	6331038.9
		Can	23		6.8	0.028	0.044	0.144	0.751		1.044	47.9	0.044	0.137	4893414.5
		Mad	2		7.9	0.054	0.065	0.060	0.726		1.062	10.9	0.072	0.076	2708353.8
	geographic	GLOBAL	25		6.9	0.030	0.041	0.306	0.564	0.372	1.039	11.7	0.064	0.177	6331038.9
		EH	3		3.8	0.016	0.015	-0.025	0.357		1.016	3.6	0.015	0.021	764189.0
		GC	2		6.8	0.020	0.031	0.256	0.533		1.028	4.9	0.034	0.034	1231686.9
		LG	5		11.5	0.036	0.050	0.152	0.468		1.048	16.5	0.045	0.076	2712008.9
		LP	4		3.6	0.027	0.042	0.221	0.511		1.039	10.9	0.045	0.053	1888008.2
		Mad	2		7.9	0.054	0.065	0.060	0.410		1.062	10.9	0.072	0.076	2708353.8
		TF	9		6.7	0.029	0.044	0.163	0.475		1.043	23.5	0.043	0.087	3095952.8
<i>Retama rhodorhizoides</i>	genetic	GLOBAL	53	3132	6.9	0.058	0.073	0.178	0.415	0.288	1.072	31.3	0.079	0.188	6729566.1
		LP-GC	23		5.0	0.053	0.062	0.101	0.360		1.061	29.1	0.058	0.069	2466921.9
		LG	8		11.1	0.068	0.087	0.140	0.388		1.085	33.4	0.073	0.106	3800707.0
		Teno	14		7.1	0.064	0.081	0.134	0.384		1.080	42.3	0.070	0.114	4074041.8
		Guimar	8		8.0	0.049	0.062	0.127	0.378		1.060	20.2	0.054	0.064	2289080.8
	geographic	GLOBAL	56		7.2	0.057	0.074	0.242	0.411	0.222	1.073	33.8	0.077	0.190	6773531.2
		GC	16		5.0	0.051	0.059	0.096	0.297		1.059	23.4	0.055	0.060	2127470.6

<i>Streptococcus filipes</i>		LG	8		11.1	0.068	0.087	0.140	0.331		1.085	33.4	0.072	0.105	3738349.2
		LP	8		4.9	0.052	0.065	0.125	0.319		1.064	22.0	0.059	0.068	2438473.8
		TF	24		8.2	0.057	0.085	0.195	0.374		1.085	56.3	0.071	0.132	4709202.8
	genetic	GLOBAL	12	3027	12.2	0.131	0.205	0.226	NA	NA	1.757	100	0.151	0.280	9985890.6
	geographic	GLOBAL	12		12.2	0.127	0.170	0.257	0.400	0.193	1.160	42.5	0.151	0.280	9985890.6
		EH	3		7.0	0.135	0.171	0.107	0.279		1.161	36.8	0.146	0.164	5866124.3
		LG	5		5.8	0.148	0.186	0.116	0.287		1.180	57.9	0.165	0.208	7428332.9
		LP	4		24.1	0.098	0.153	0.229	0.378		1.138	32.9	0.086	0.138	4914812.2

Table S3 – Pairwise genetic diversity for all pairs of species populations studied. Genetic populations correspond to sNMF results excluding admixed individuals (>20%). sp = species name, population = type of grouping and pair of populations considered, FST = among population differentiation, Nei-D = Nei's genetic distance. EH = El Hierro, LP = La Palma, LG = La Gomera, TF = Tenerife, GC = Gran Canaria, Mad = Madeira.

sp	Populations			FST	Nei-D
<i>Apollonias barbujana</i>	genetic	West	East	0.1811	0.0293
	geographic	EH	GC	0.3775	0.0750
		EH	LG	0.1754	0.0293
		EH	LP	0.0902	0.0145
		EH	Mad	0.4503	0.1317
		EH	TF	0.2217	0.0392
		GC	LG	0.2015	0.0565
		GC	LP	0.3485	0.0719
		GC	Mad	0.0337	0.1000
		GC	TF	0.1134	0.0446
		LG	LP	0.1650	0.0278
		LG	Mad	0.2301	0.1177
		LG	TF	0.1181	0.0256
		LP	Mad	0.4079	0.1299
		LP	TF	0.2038	0.0359
		Mad	TF	0.1592	0.1110
<i>Adenocarpus foliolosus</i>	genetic	GC-Anaga	LG	0.1185	0.0090
		GC-Anaga	TF-LP	0.1287	0.0108
		LG	TF-LP	0.1455	0.0111
	geographic	GC	LG	0.1204	0.0092
		GC	LP	0.0890	0.0119
		GC	TF	0.0732	0.0061
		LG	LP	0.1215	0.0128
		LG	TF	0.1073	0.0082
		LP	TF	0.0437	0.0092
<i>Brachypodium arbuscula</i>	genetic	LG	TF	0.2276	0.0394
	geographic	LG	TF	0.2276	0.0394
<i>Canarina canariensis</i>	genetic	GC-Anaga	LG	0.5904	0.1395
		GC-Anaga	LP	0.6404	0.1797
		GC-Anaga	Teno	0.4635	0.0830
		LG	LP	0.4533	0.1170
		LG	Teno	0.3389	0.0799
		LP	Teno	0.5185	0.1543
	geographic	GC	LG	0.6149	0.1445
		GC	LP	0.6647	0.1825
		GC	TF	0.1638	0.0232
		LG	LP	0.4450	0.1156
		LG	TF	0.3585	0.0946
		LP	TF	0.4486	0.1453
<i>Dracunculus canariensis</i>	genetic	West	GC	0.5562	0.0508
	geographic	EH	GC	0.5609	0.0598
		EH	LG	0.3971	0.0170
		EH	LP	0.3505	0.0202

		EH	TF	0.2050	0.0144
		GC	LG	0.5769	0.0612
		GC	LP	0.5641	0.0649
		GC	TF	0.5319	0.0501
		LG	LP	0.0920	0.0088
		LG	TF	0.1463	0.0103
		LP	TF	0.1428	0.0135
<i>Heberdenia excelsa</i>	genetic	The	LauC	0.5371	0.1282
		The	LauM	0.4261	0.1692
		LauC	LauM	0.4695	0.1155
	geographic	GC	LG	0.6030	0.1873
		GC	LP	0.5360	0.1852
		GC	Mad	0.4574	0.2038
		GC	TF	0.2127	0.1110
		LG	LP	0.1547	0.0326
		LG	Mad	0.4658	0.1126
		LG	TF	0.1736	0.0440
		LP	Mad	0.4069	0.1180
		LP	TF	0.0899	0.0449
		Mad	TF	0.2694	0.1055
<i>Luzula canariensis</i>	genetic	LG	TF	0.6673	0.3200
	geographic	LG	TF	0.6673	0.3200
<i>Morella faya</i>	genetic	Can	Mad	0.3465	0.1526
	geographic	GC	Mad	0.3468	0.2131
		GC	LG	0.1722	0.1642
		GC	TF	0.1355	0.0775
		Mad	LG	0.2028	0.2463
		Mad	TF	0.3513	0.1579
		LG	TF	0.0468	0.1207
<i>Persea indica</i>	genetic	Can	Mad	0.7085	0.1581
	geographic	EH	GC	0.3111	0.0265
		EH	LG	0.1719	0.0191
		EH	LP	0.2551	0.0205
		EH	Mad	0.7788	0.1701
		EH	TF	0.1517	0.0155
		GC	LG	0.0202	0.0210
		GC	LP	0.1328	0.0261
		GC	Mad	0.6760	0.1711
		GC	TF	0.0203	0.0187
		LG	LP	0.0469	0.0120
		LG	Mad	0.6695	0.1653
		LG	TF	0.0468	0.0089
		LP	Mad	0.6734	0.1518
		LP	TF	0.0692	0.0100
		Mad	TF	0.7066	0.1634
<i>Retama rhodorhizoides</i>	genetic	LP-GC	LG	0.3368	0.0529
		LP-GC	Teno	0.2690	0.0321
		LP-GC	Guimar	0.3087	0.0368
		LG	Teno	0.2601	0.0518
		LG	Guimar	0.3546	0.0667

		Teno	Guimar	0.2287	0.0355
	geographic	GC	LG	0.3382	0.0542
		GC	LP	0.0189	0.0059
		GC	TF	0.2169	0.0261
		LG	LP	0.3042	0.0545
		LG	TF	0.2493	0.0489
		LP	TF	0.1912	0.0262
<i>Streptocytisus filipes</i>	geographic	EH	LG	0.1527	0.0895
		EH	LP	0.1854	0.1080
		LG	LP	0.2296	0.1144

Table S4 – Performance metrics for every model tested in the Species Distribution Models analyses for every species except *Luzula canariensis*, for which the number of presence points was not sufficient.

species	#occurrence	model	trans_AUC	trans_SomersD	trans_Boyce	trans_maxTSS	fit_AUC	fit_SomersD	fit_Boyce	fit_maxTSS
<i>Apollonias barbujana</i>	239	Ensemble	0.930 ± 0.008	0.860 ± 0.015	0.996 ± 0.016	0.780 ± 0.022	0.934 ± 0.003	0.869 ± 0.006	1.000 ± 0.001	0.775 ± 0.009
		GLM	0.910 ± 0.008	0.821 ± 0.017	0.997 ± 0.011	0.739 ± 0.021	0.915 ± 0.003	0.830 ± 0.007	1.000 ± 0.002	0.740 ± 0.010
		MaxNet	0.923 ± 0.008	0.846 ± 0.016	0.968 ± 0.054	0.768 ± 0.025	0.932 ± 0.004	0.864 ± 0.007	0.987 ± 0.014	0.767 ± 0.010
		RF	0.941 ± 0.008	0.881 ± 0.015	0.982 ± 0.024	0.799 ± 0.020	0.939 ± 0.004	0.878 ± 0.007	0.983 ± 0.017	0.784 ± 0.010
<i>Adenocarpus foliolosus</i>	430	Ensemble	0.927 ± 0.006	0.854 ± 0.012	0.998 ± 0.007	0.754 ± 0.018	0.929 ± 0.002	0.858 ± 0.005	1.000 ± 0.001	0.753 ± 0.007
		GLM	0.915 ± 0.006	0.831 ± 0.012	0.993 ± 0.014	0.738 ± 0.018	0.917 ± 0.003	0.834 ± 0.006	0.998 ± 0.004	0.738 ± 0.008
		MaxNet	0.922 ± 0.006	0.845 ± 0.012	0.992 ± 0.015	0.738 ± 0.018	0.928 ± 0.002	0.856 ± 0.005	0.997 ± 0.006	0.742 ± 0.008
		RF	0.930 ± 0.005	0.859 ± 0.011	0.987 ± 0.018	0.758 ± 0.018	0.928 ± 0.003	0.856 ± 0.006	0.983 ± 0.012	0.751 ± 0.010
<i>Brachypodium arbuscula</i>	139	Ensemble	0.930 ± 0.014	0.861 ± 0.028	0.976 ± 0.050	0.749 ± 0.039	0.935 ± 0.004	0.869 ± 0.009	0.998 ± 0.005	0.743 ± 0.013
		GLM	0.901 ± 0.015	0.801 ± 0.030	0.979 ± 0.043	0.686 ± 0.035	0.909 ± 0.007	0.819 ± 0.014	0.996 ± 0.012	0.684 ± 0.020
		MaxNet	0.925 ± 0.013	0.850 ± 0.026	0.961 ± 0.076	0.735 ± 0.039	0.933 ± 0.004	0.866 ± 0.009	0.994 ± 0.012	0.746 ± 0.013
		RF	0.941 ± 0.015	0.881 ± 0.030	0.988 ± 0.030	0.770 ± 0.046	0.939 ± 0.005	0.878 ± 0.011	0.998 ± 0.006	0.759 ± 0.019
<i>Canarina canariensis</i>	318	Ensemble	0.941 ± 0.007	0.882 ± 0.014	0.998 ± 0.005	0.757 ± 0.023	0.944 ± 0.002	0.888 ± 0.005	1.000 ± 0.001	0.753 ± 0.009
		GLM	0.912 ± 0.009	0.823 ± 0.018	0.976 ± 0.033	0.701 ± 0.027	0.915 ± 0.004	0.830 ± 0.008	0.989 ± 0.013	0.698 ± 0.011
		MaxNet	0.936 ± 0.007	0.872 ± 0.015	0.989 ± 0.023	0.746 ± 0.024	0.943 ± 0.003	0.887 ± 0.005	0.996 ± 0.008	0.757 ± 0.011
		RF	0.948 ± 0.006	0.896 ± 0.013	0.995 ± 0.012	0.779 ± 0.025	0.947 ± 0.003	0.894 ± 0.005	0.999 ± 0.003	0.766 ± 0.012
<i>Dracunculus canariensis</i>	110	Ensemble	0.901 ± 0.013	0.803 ± 0.026	0.972 ± 0.041	0.725 ± 0.032	0.910 ± 0.005	0.821 ± 0.009	0.994 ± 0.014	0.717 ± 0.013
		GLM	0.877 ± 0.013	0.753 ± 0.025	0.908 ± 0.076	0.693 ± 0.022	0.884 ± 0.006	0.769 ± 0.011	0.939 ± 0.027	0.700 ± 0.012
		MaxNet	0.889 ± 0.012	0.778 ± 0.025	0.905 ± 0.100	0.702 ± 0.031	0.907 ± 0.005	0.815 ± 0.009	0.975 ± 0.023	0.706 ± 0.013
		RF	0.916 ± 0.014	0.832 ± 0.028	0.988 ± 0.025	0.732 ± 0.036	0.914 ± 0.006	0.827 ± 0.013	0.991 ± 0.020	0.712 ± 0.017
<i>Heberdenia excelsa</i>	87	Ensemble	0.930 ± 0.020	0.860 ± 0.039	0.967 ± 0.057	0.760 ± 0.045	0.935 ± 0.007	0.870 ± 0.015	0.998 ± 0.007	0.751 ± 0.017
		GLM	0.870 ± 0.028	0.739 ± 0.056	0.982 ± 0.046	0.687 ± 0.055	0.883 ± 0.009	0.766 ± 0.019	0.996 ± 0.009	0.696 ± 0.029
		MaxNet	0.927 ± 0.019	0.855 ± 0.038	0.849 ± 0.169	0.742 ± 0.046	0.939 ± 0.007	0.878 ± 0.014	0.968 ± 0.039	0.744 ± 0.021
		RF	0.948 ± 0.017	0.896 ± 0.034	0.993 ± 0.023	0.801 ± 0.050	0.943 ± 0.008	0.885 ± 0.016	0.998 ± 0.008	0.767 ± 0.021
<i>Morella faya</i>	829	Ensemble	0.923 ± 0.005	0.846 ± 0.011	0.997 ± 0.005	0.745 ± 0.015	0.924 ± 0.002	0.848 ± 0.004	0.996 ± 0.005	0.746 ± 0.006
		GLM	0.906 ± 0.006	0.811 ± 0.011	0.995 ± 0.011	0.719 ± 0.015	0.907 ± 0.003	0.813 ± 0.005	0.999 ± 0.002	0.720 ± 0.007

		MaxNet	0.914 ± 0.006	0.829 ± 0.011	0.991 ± 0.014	0.719 ± 0.015	0.918 ± 0.002	0.836 ± 0.005	0.997 ± 0.005	0.722 ± 0.006
		RF	0.928 ± 0.005	0.856 ± 0.010	0.978 ± 0.013	0.774 ± 0.016	0.927 ± 0.003	0.853 ± 0.005	0.974 ± 0.010	0.772 ± 0.007
<i>Persea indica</i>	279	Ensemble	0.954 ± 0.006	0.907 ± 0.011	0.995 ± 0.013	0.816 ± 0.022	0.956 ± 0.002	0.911 ± 0.004	1.000 ± 0.001	0.811 ± 0.008
		GLM	0.939 ± 0.006	0.878 ± 0.012	0.985 ± 0.037	0.791 ± 0.018	0.942 ± 0.003	0.883 ± 0.006	0.999 ± 0.003	0.791 ± 0.008
		MaxNet	0.948 ± 0.006	0.896 ± 0.012	0.992 ± 0.015	0.795 ± 0.023	0.953 ± 0.002	0.906 ± 0.005	0.998 ± 0.005	0.797 ± 0.009
		RF	0.961 ± 0.005	0.922 ± 0.010	0.994 ± 0.023	0.841 ± 0.022	0.960 ± 0.002	0.919 ± 0.004	0.995 ± 0.011	0.831 ± 0.009
<i>Retama rhodorhizoides</i>	225	Ensemble	0.911 ± 0.012	0.823 ± 0.024	0.996 ± 0.017	0.733 ± 0.032	0.915 ± 0.005	0.830 ± 0.010	1.000 ± 0.002	0.728 ± 0.013
		GLM	0.871 ± 0.012	0.743 ± 0.024	0.991 ± 0.018	0.671 ± 0.032	0.877 ± 0.009	0.754 ± 0.018	0.994 ± 0.014	0.670 ± 0.023
		MaxNet	0.898 ± 0.013	0.795 ± 0.027	0.997 ± 0.016	0.691 ± 0.031	0.910 ± 0.005	0.820 ± 0.010	1.000 ± 0.002	0.698 ± 0.017
		RF	0.924 ± 0.010	0.848 ± 0.020	0.998 ± 0.007	0.749 ± 0.028	0.921 ± 0.005	0.843 ± 0.009	0.999 ± 0.003	0.735 ± 0.014
<i>Spartocytisus filipes</i>	141	Ensemble	0.916 ± 0.012	0.831 ± 0.025	0.971 ± 0.037	0.711 ± 0.034	0.920 ± 0.005	0.840 ± 0.010	0.993 ± 0.011	0.704 ± 0.013
		GLM	0.898 ± 0.011	0.797 ± 0.022	0.979 ± 0.035	0.711 ± 0.029	0.904 ± 0.004	0.808 ± 0.009	0.995 ± 0.011	0.718 ± 0.012
		MaxNet	0.905 ± 0.014	0.810 ± 0.028	0.904 ± 0.085	0.686 ± 0.037	0.917 ± 0.006	0.834 ± 0.011	0.963 ± 0.026	0.691 ± 0.015
		RF	0.917 ± 0.016	0.834 ± 0.032	0.980 ± 0.041	0.695 ± 0.042	0.913 ± 0.006	0.826 ± 0.013	0.996 ± 0.010	0.666 ± 0.021
all species	/	Ensemble	0.926 ± 0.015	0.853 ± 0.030	0.987 ± 0.013	0.753 ± 0.029	0.930 ± 0.014	0.860 ± 0.027	0.998 ± 0.003	0.748 ± 0.030

Figure S1 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >50% NA (below), for *Apollonias barbujana* (AB).

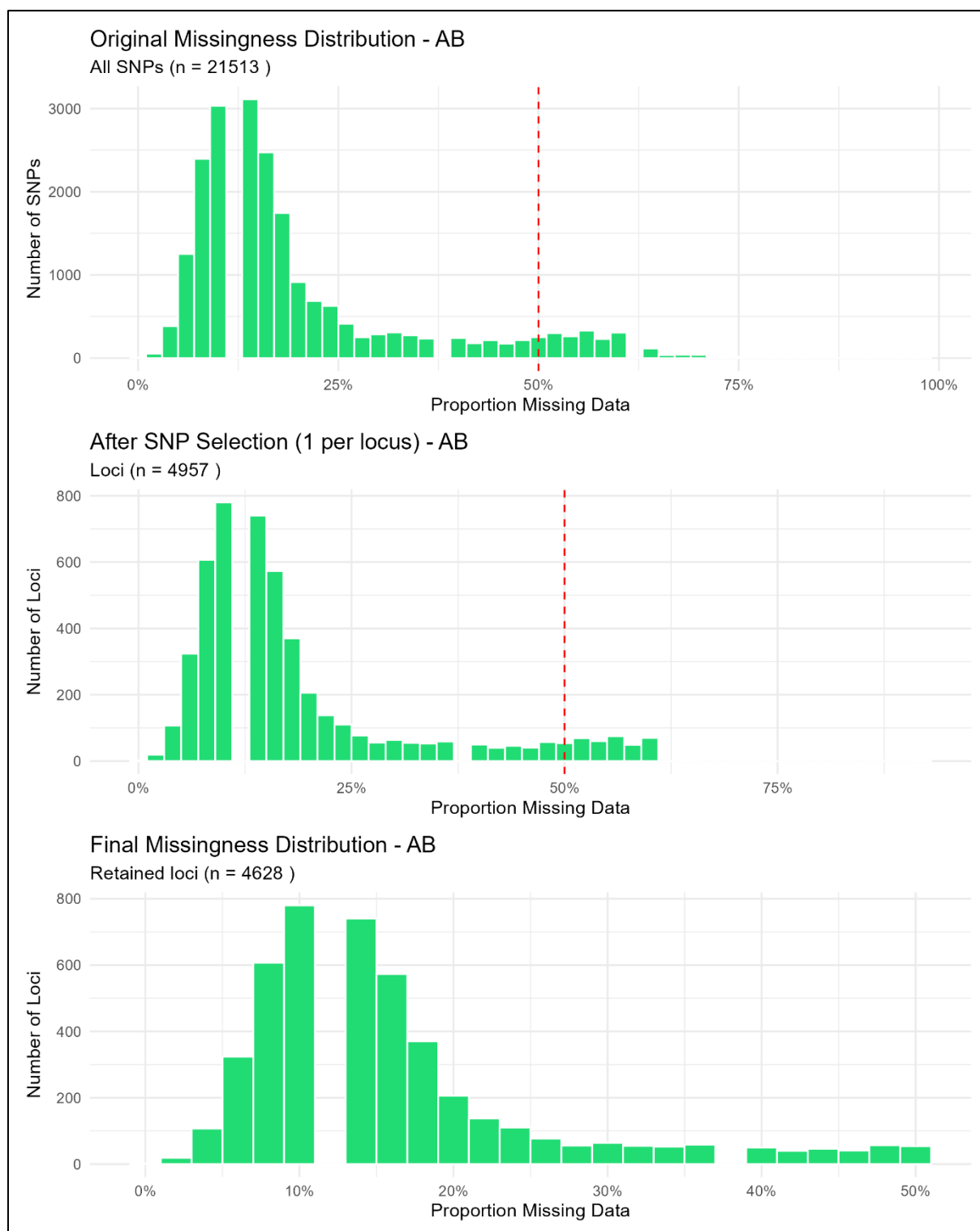


Figure S2 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >40% NA (below), for *Adenocarpus foliolosus* (AF).

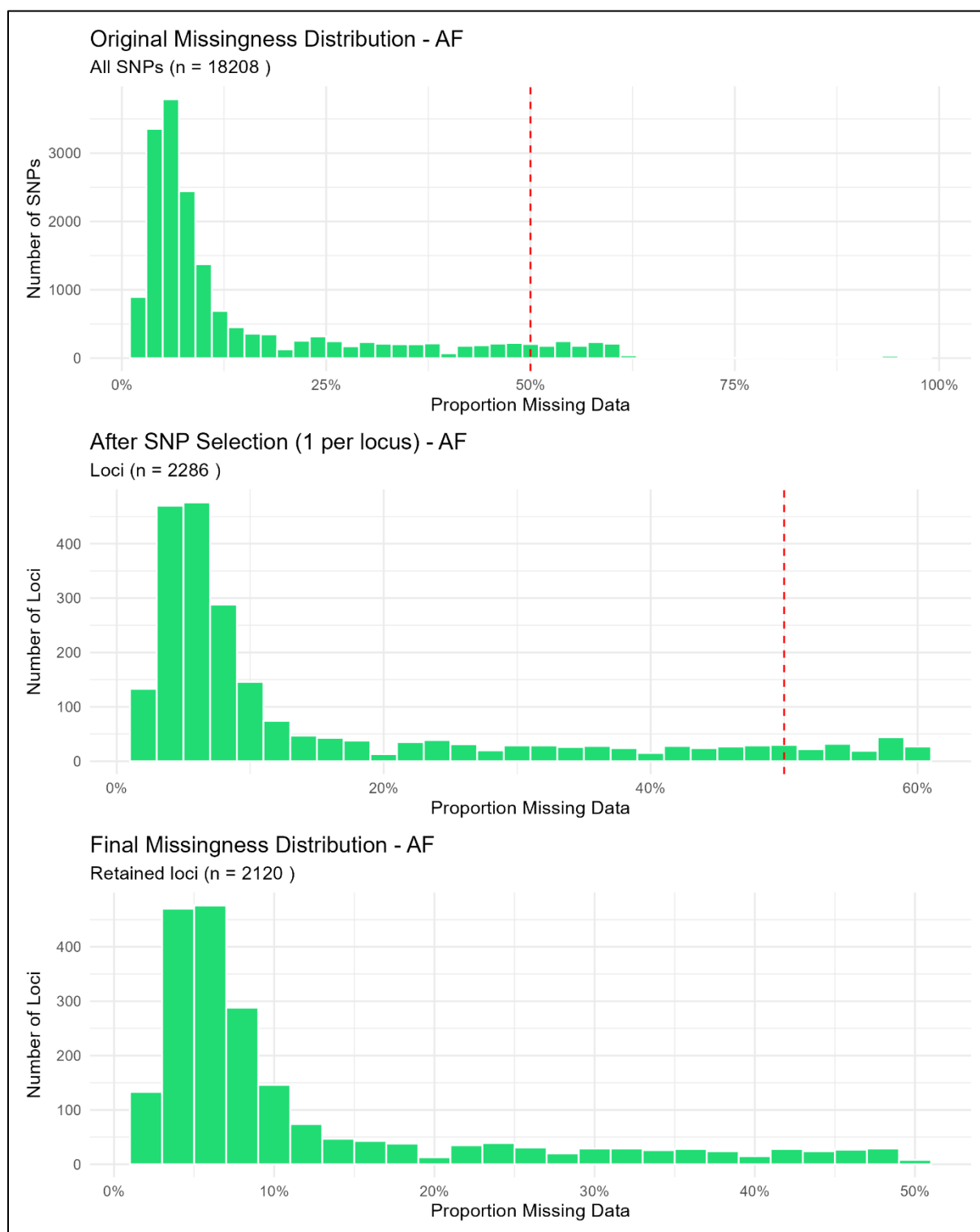


Figure S3 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >25% NA (below), for *Brachypodium arbuscula* (BA).

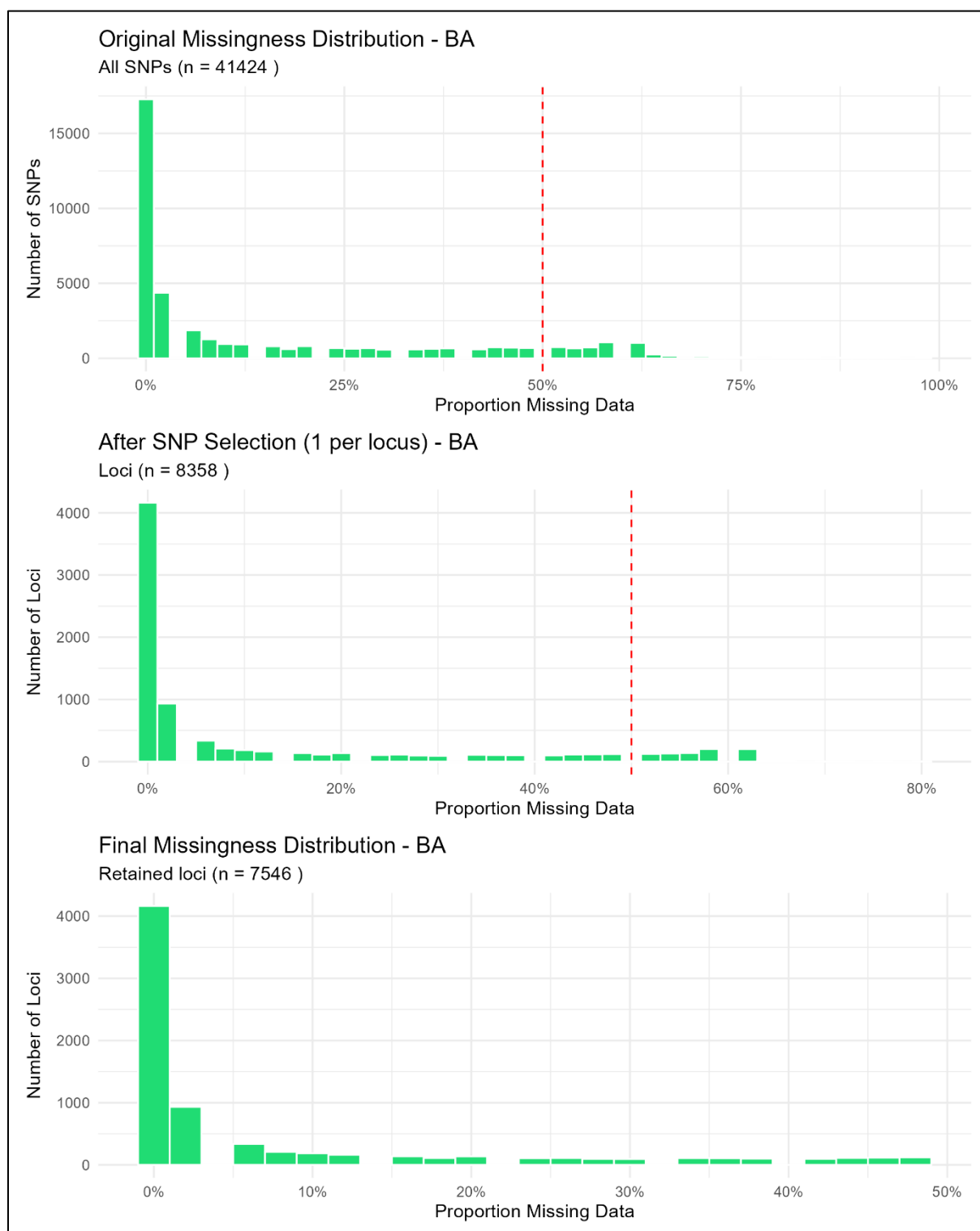


Figure S4 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >45% NA (below), for *Canarina canariensis* (CanC).

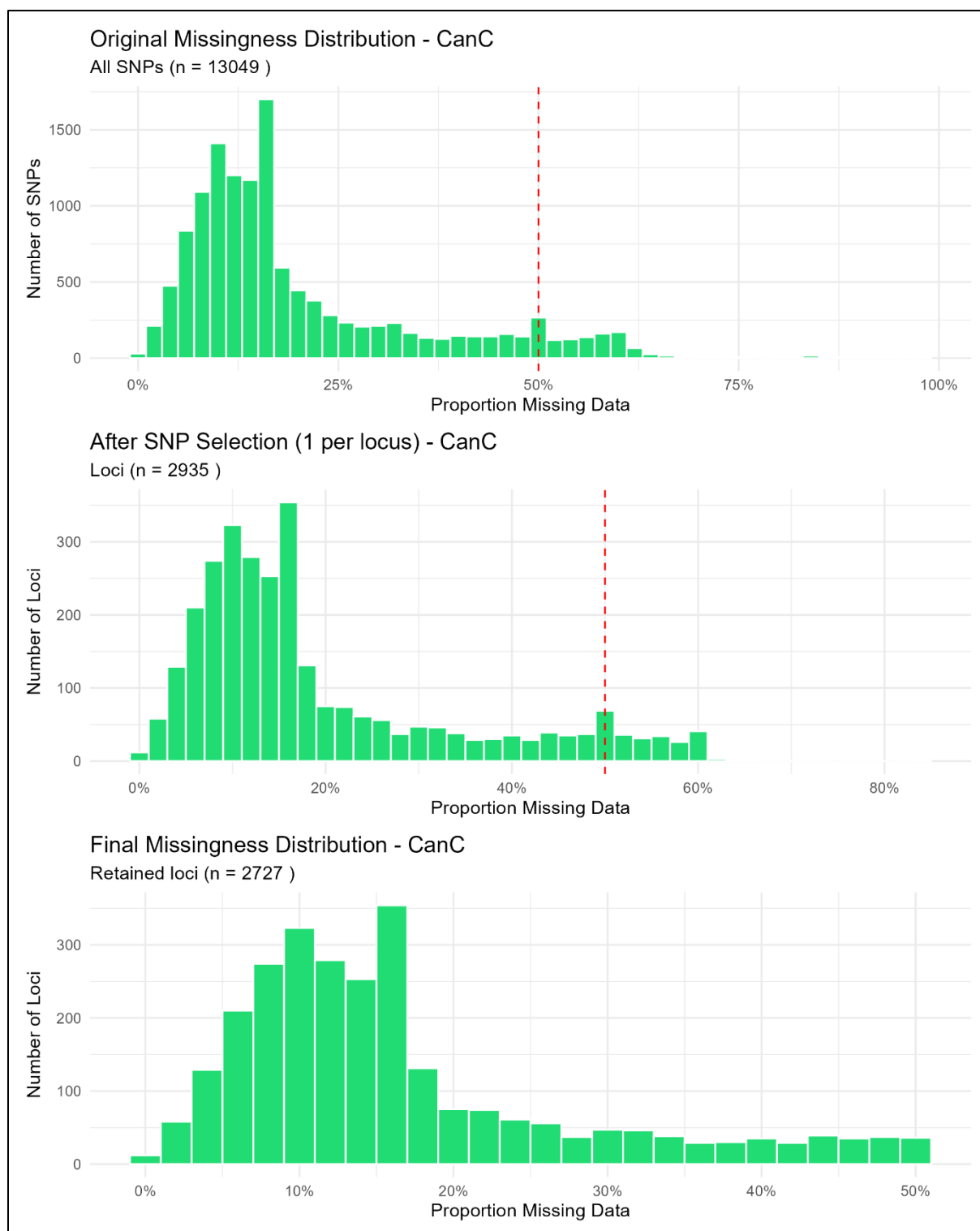


Figure S5 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >45% NA (below), for *Dracunculus canariensis* (DC).

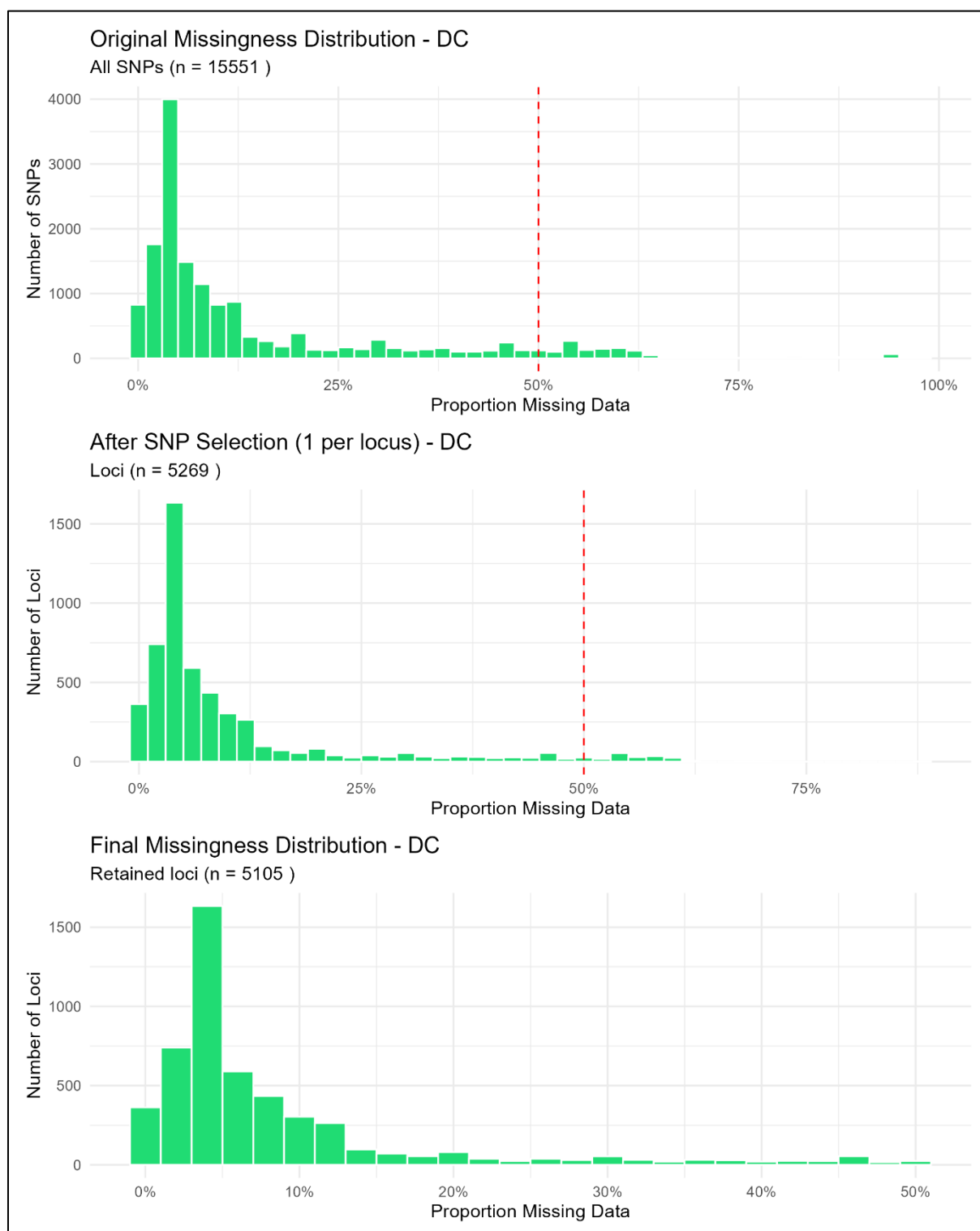


Figure S6 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >50% NA (below), for *Heberdenia excelsa* (HE).

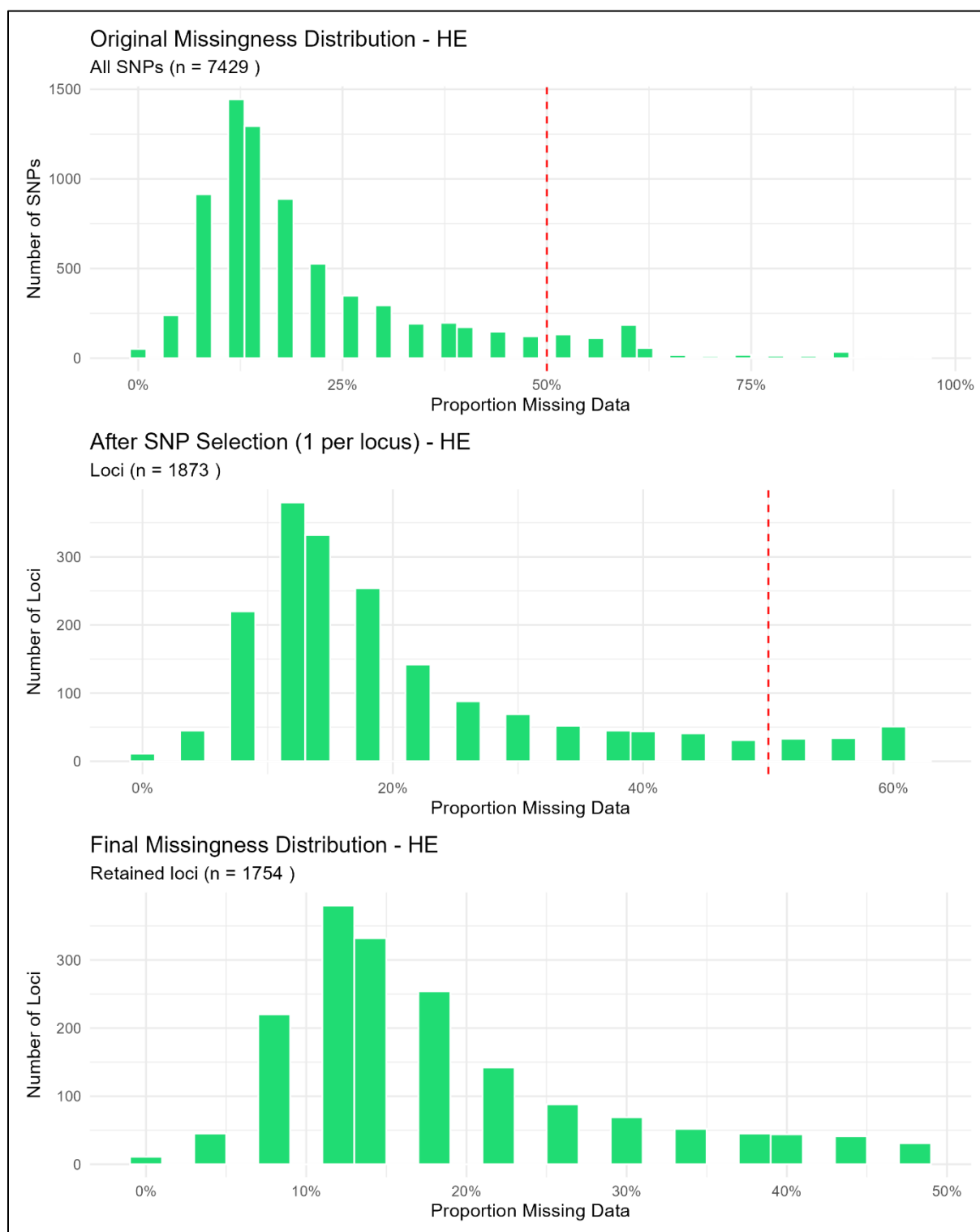


Figure S7 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >25% NA (below), for *Luzula canariensis* (LC).

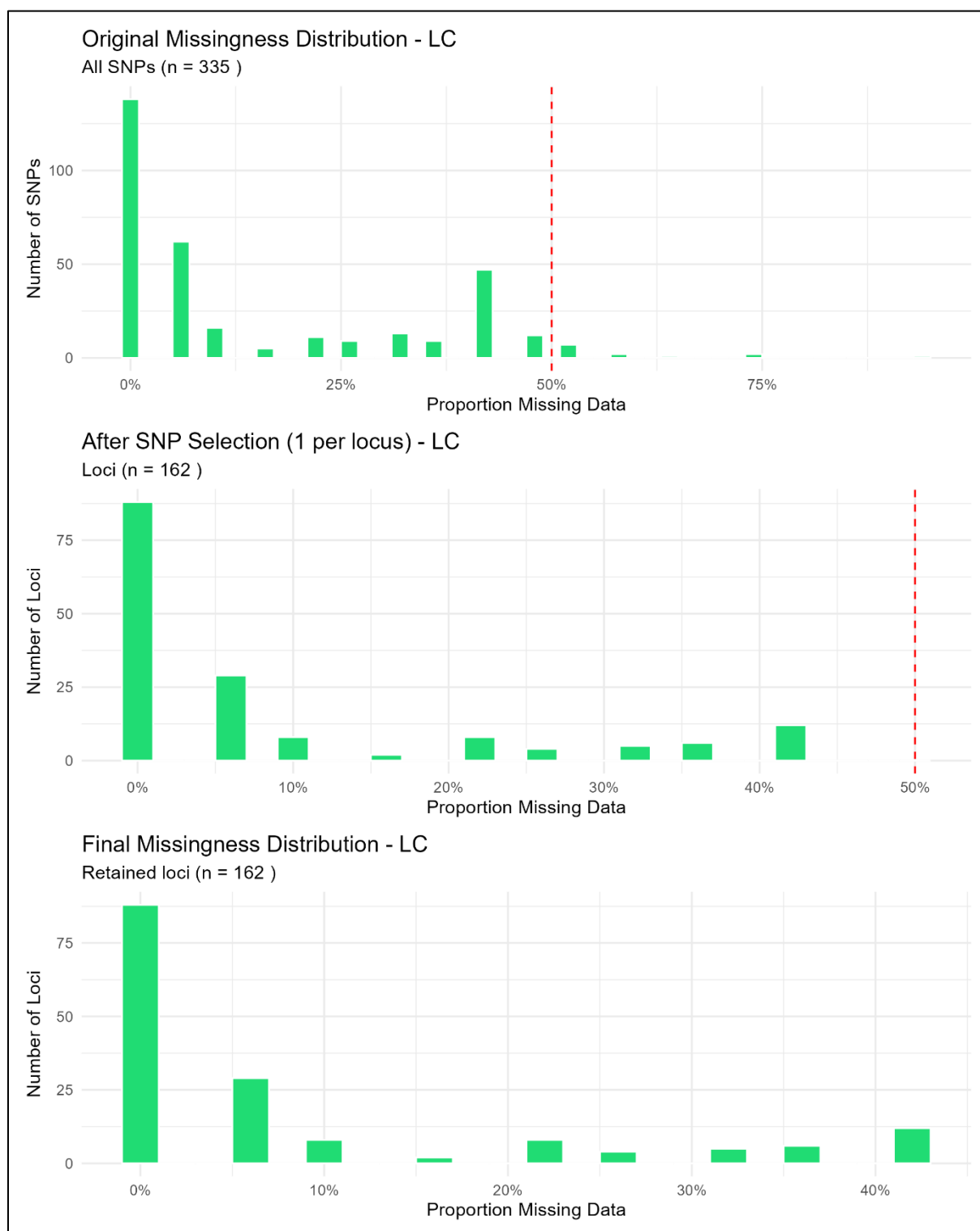


Figure S8 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >40% NA (below), for *Morella faya* (MF).

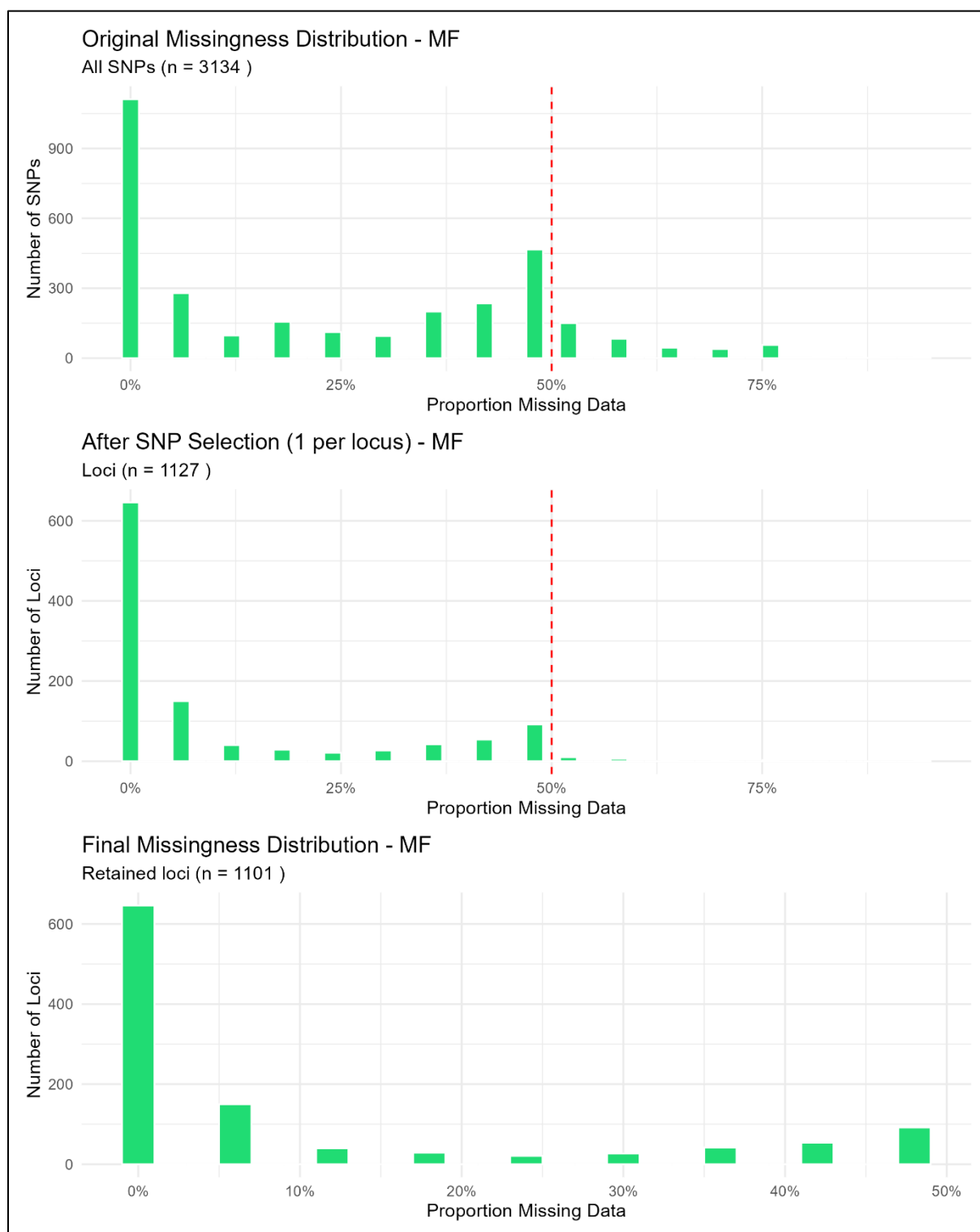


Figure S9 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >40% NA (below), for *Persea indica* (PI).

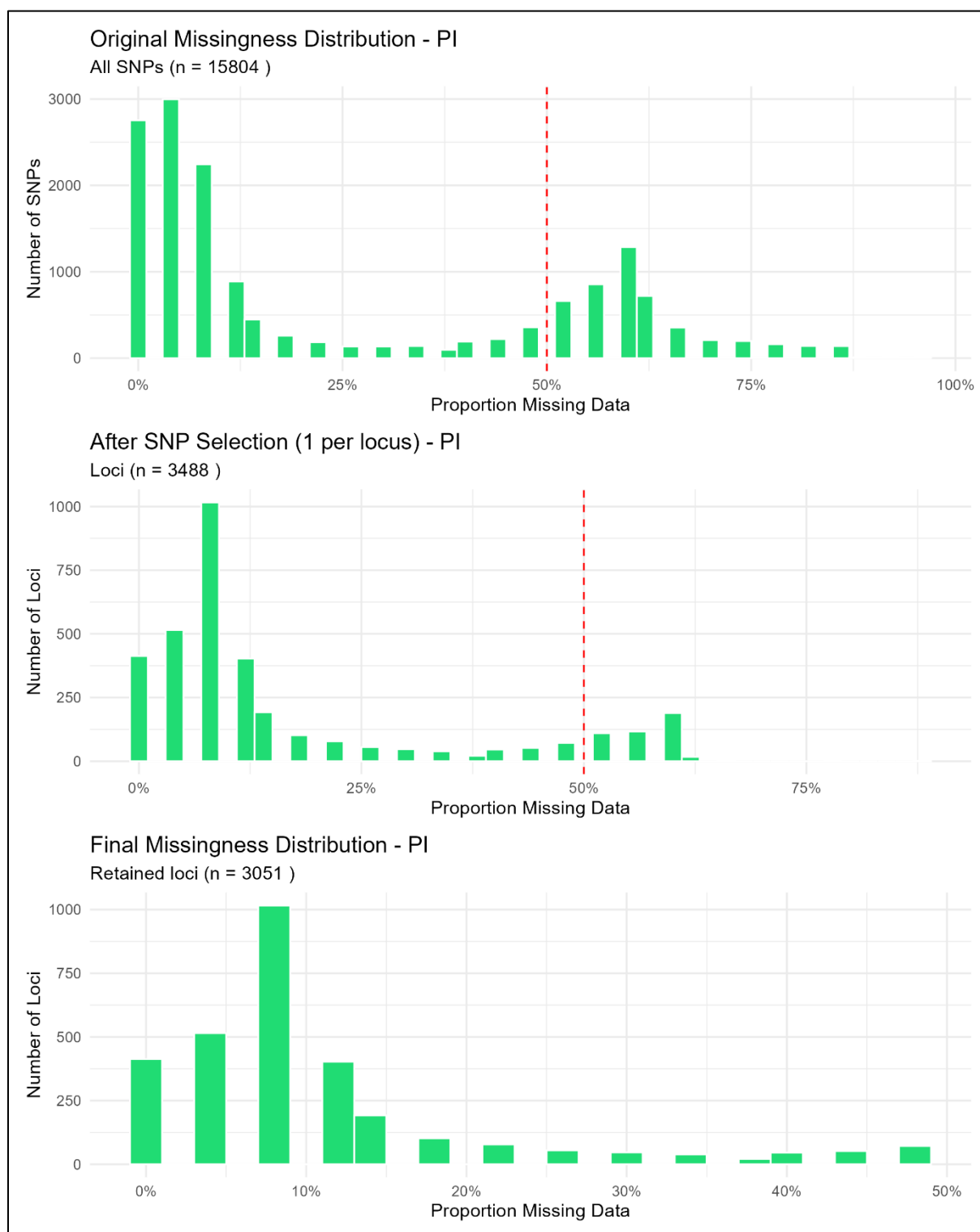


Figure S10 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >25% NA (below), for *Retama rhodorhizoides* (RR).

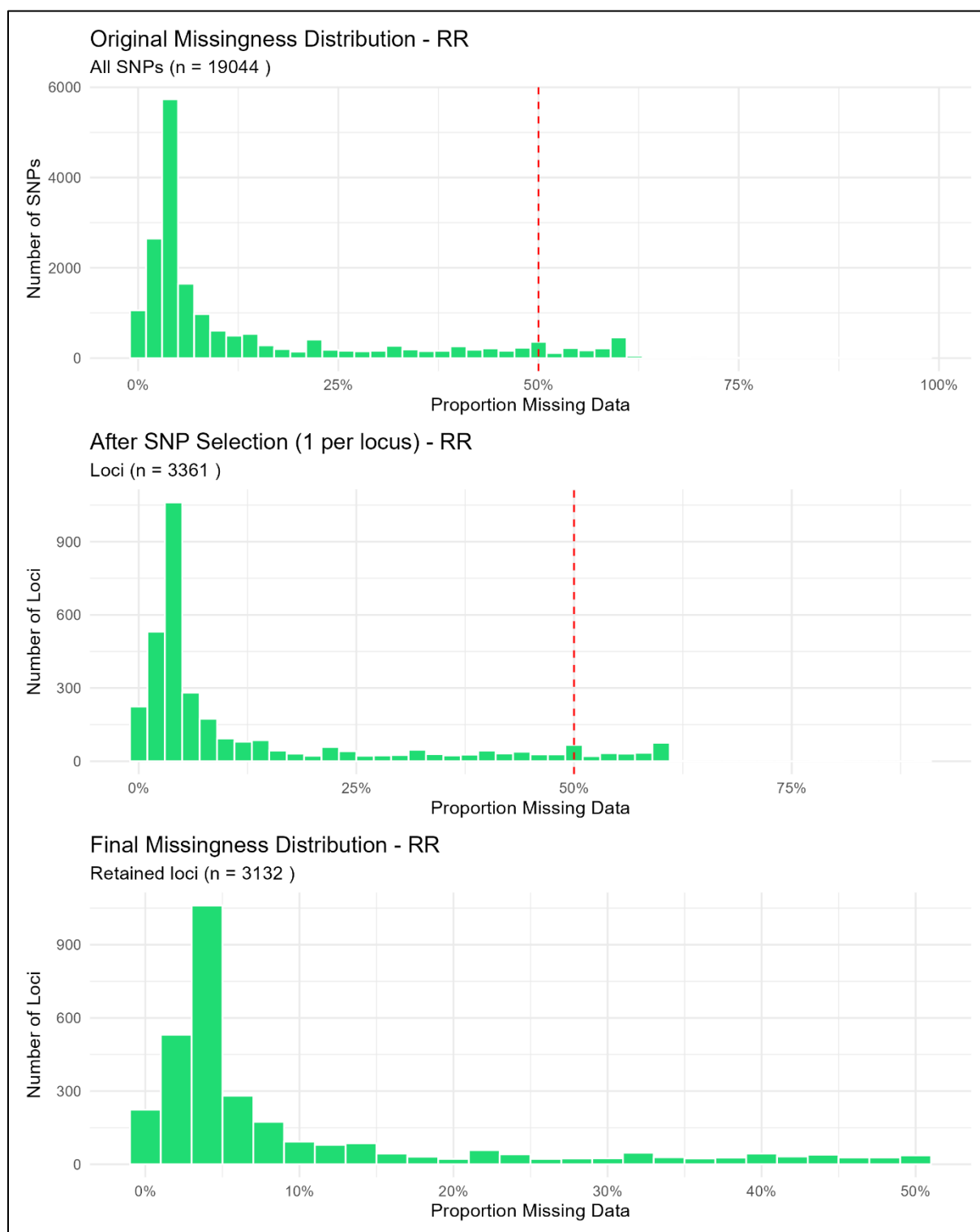


Figure S11 – Missingness proportion distribution through filtering steps from the complete dataset (above), selection of one SNP per locus (middle), removing loci >50% NA and individuals >45% NA (below), for *Streptocytisus filipes* (SS).

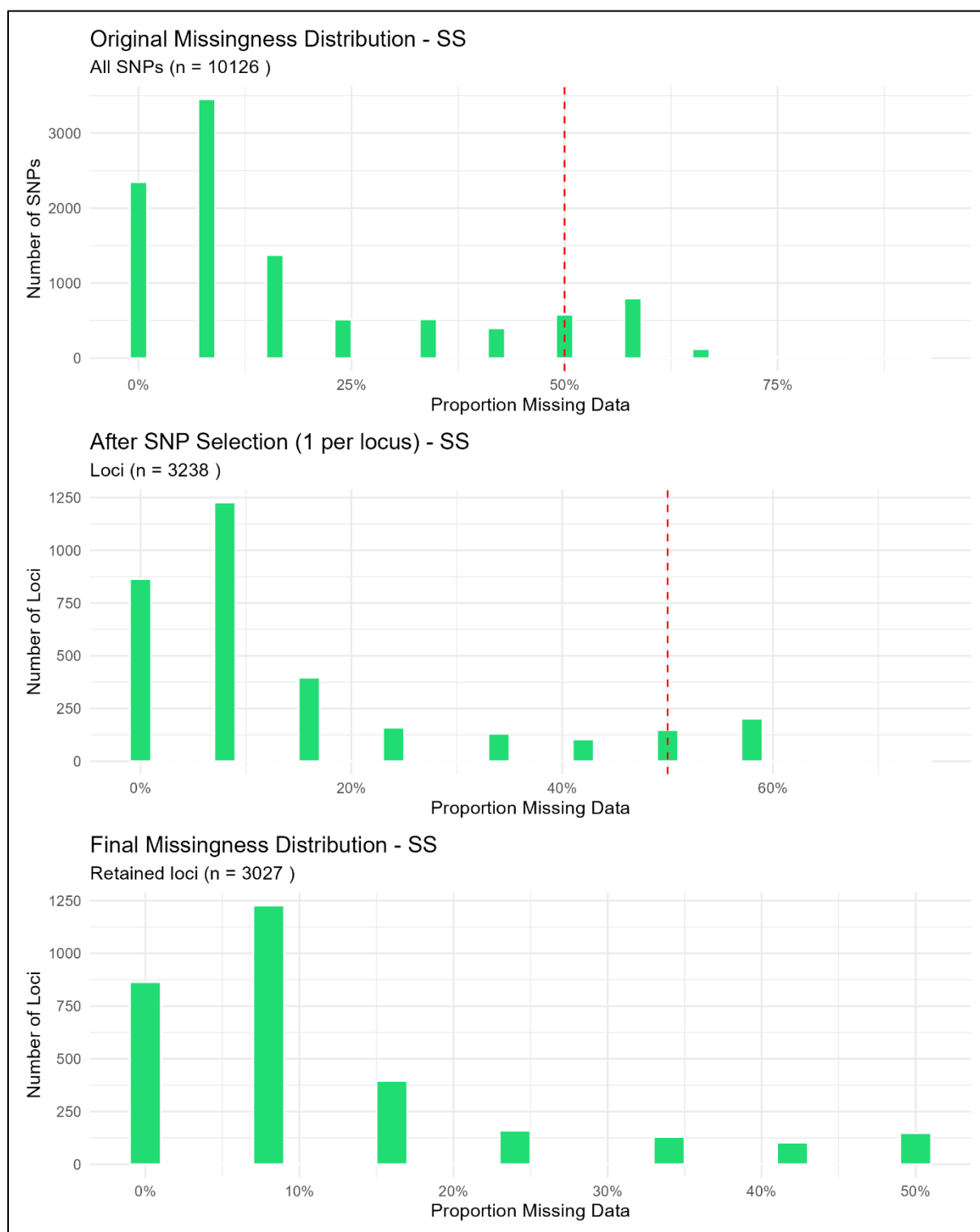


Figure S12 – sNMF results for *Apollonias barbujana*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude, with Madeira specimens on the right. K values are indicated in the title for each species.

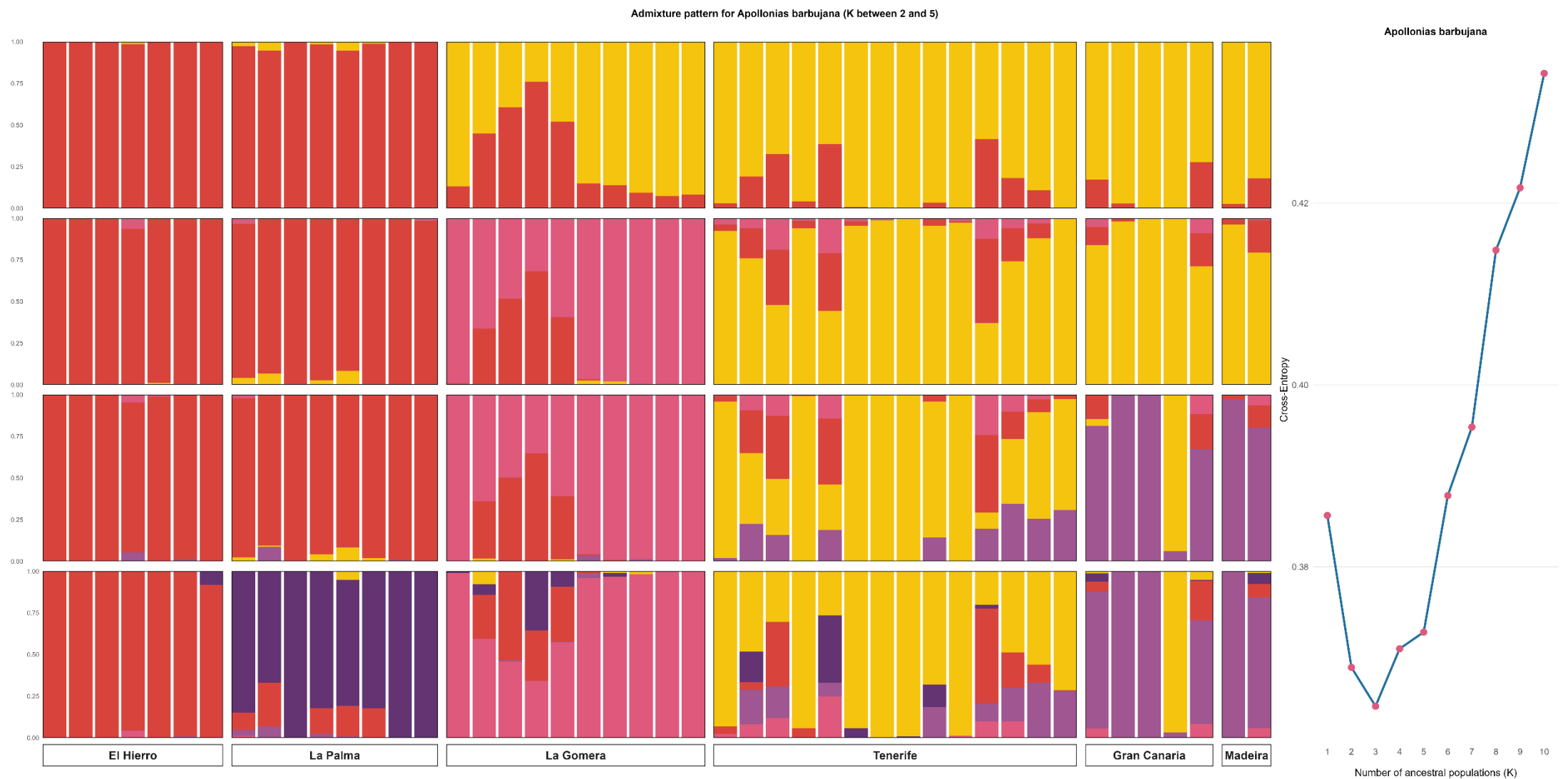


Figure S13 – sNMF results for *Adenocarpus foliolosus*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

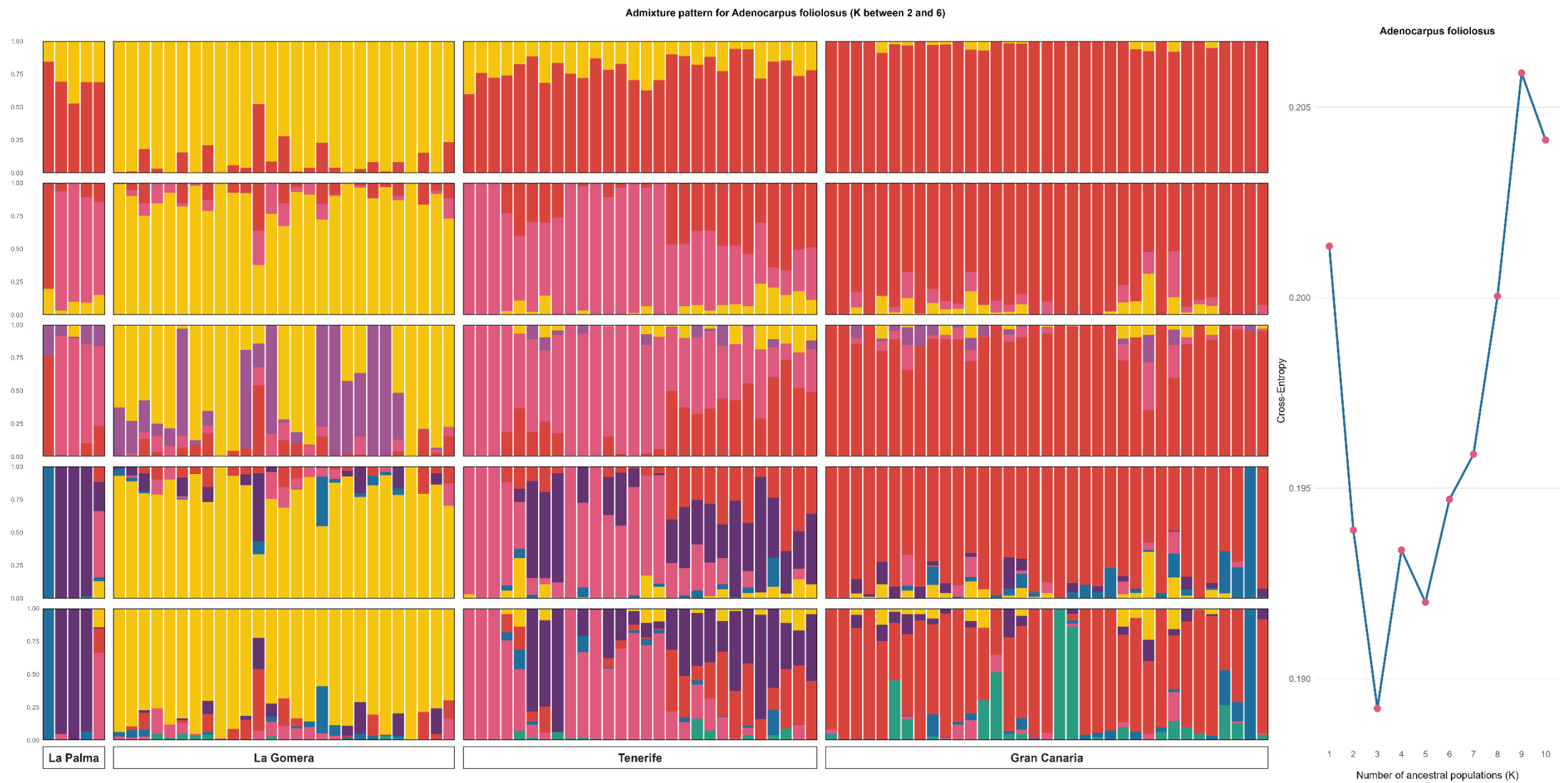


Figure S14 – sNMF results for *Brachypodium arbuscula*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

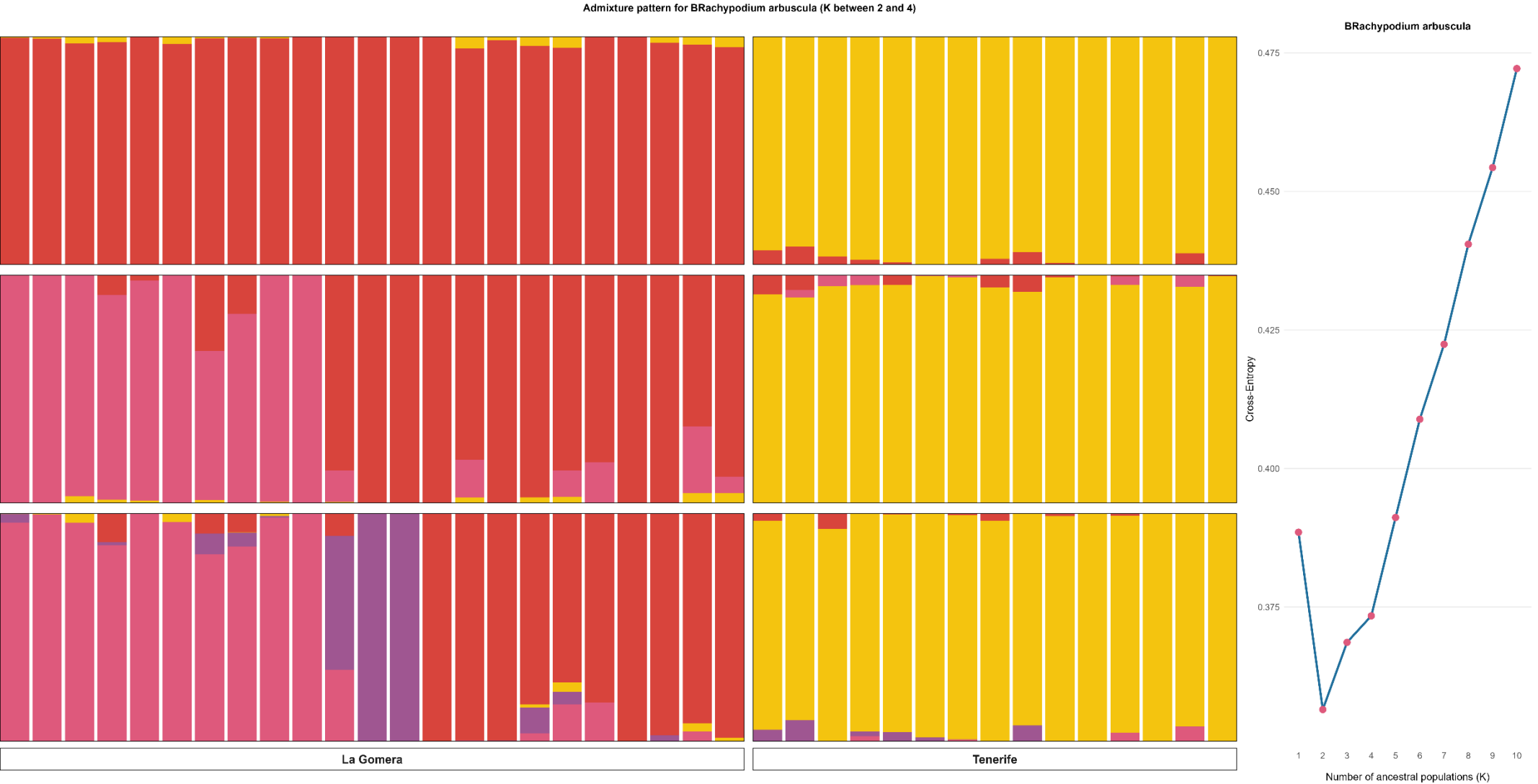


Figure S15 – sNMF results for *Canarina canariensis*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

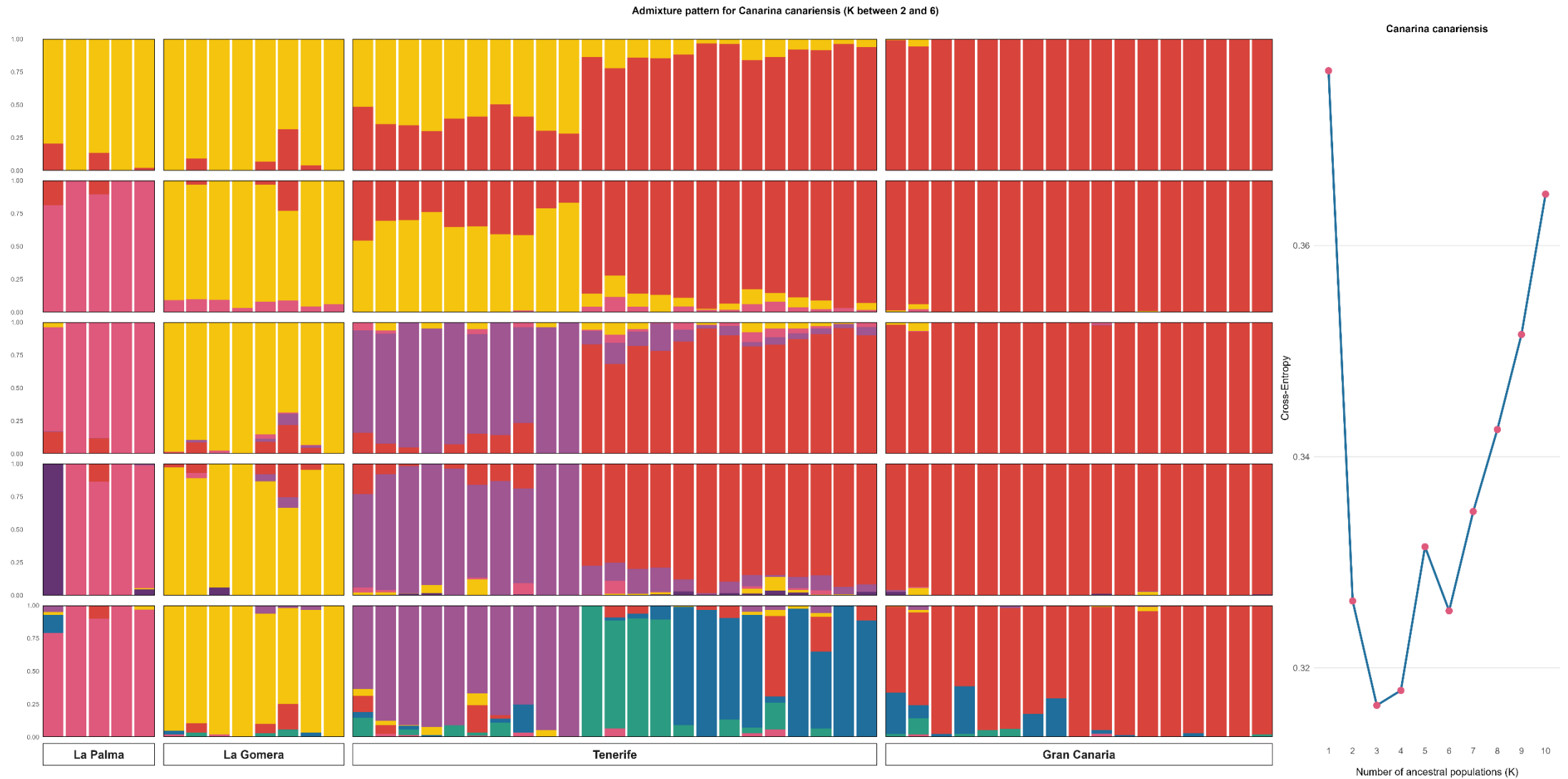


Figure S16 – sNMF results for *Dracunculus canariensis*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

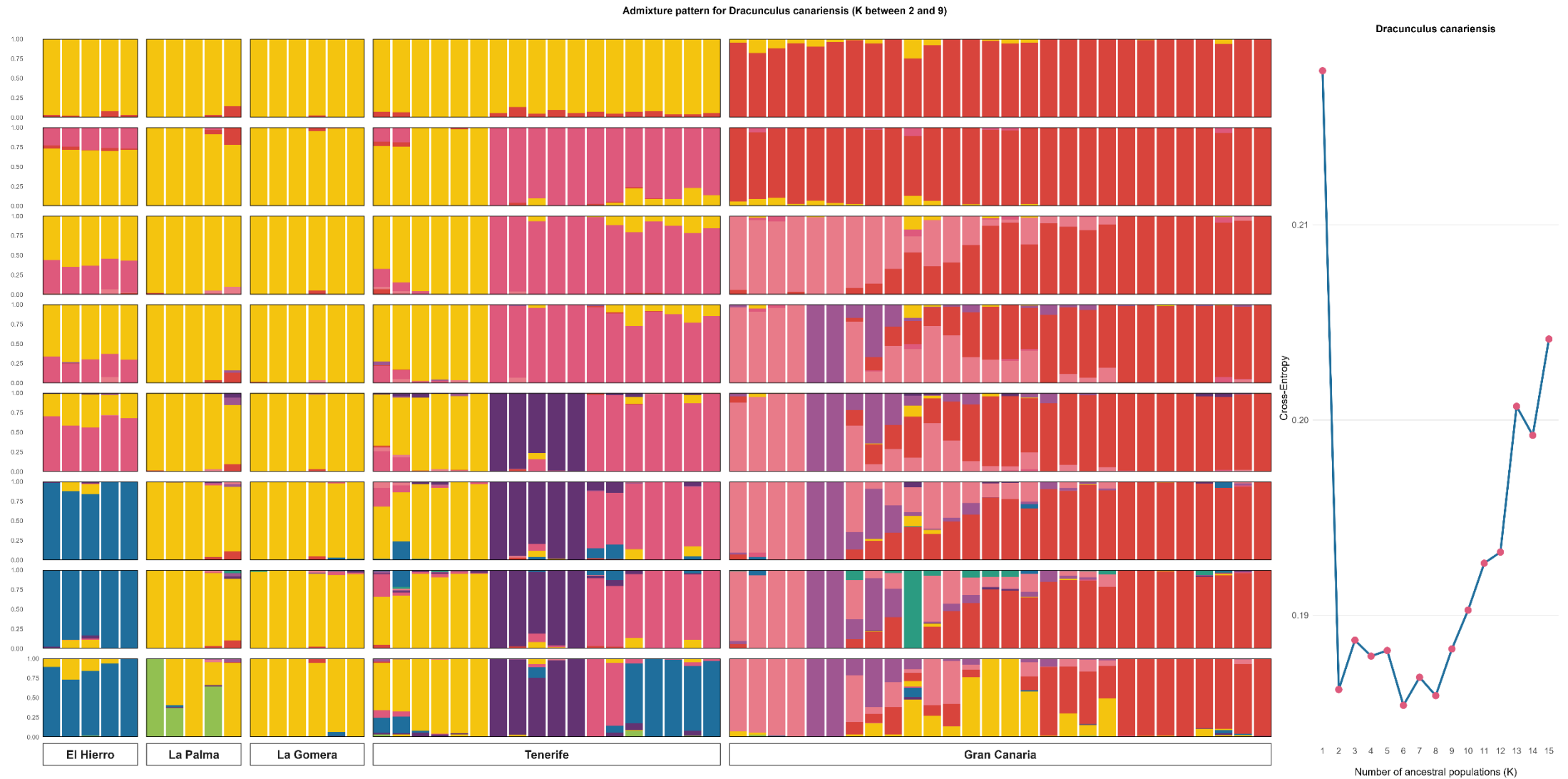


Figure S17 – sNMF results for *Heberdenia excelsa*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude, with Madeira specimens on the right. K values are indicated in the title for each species.

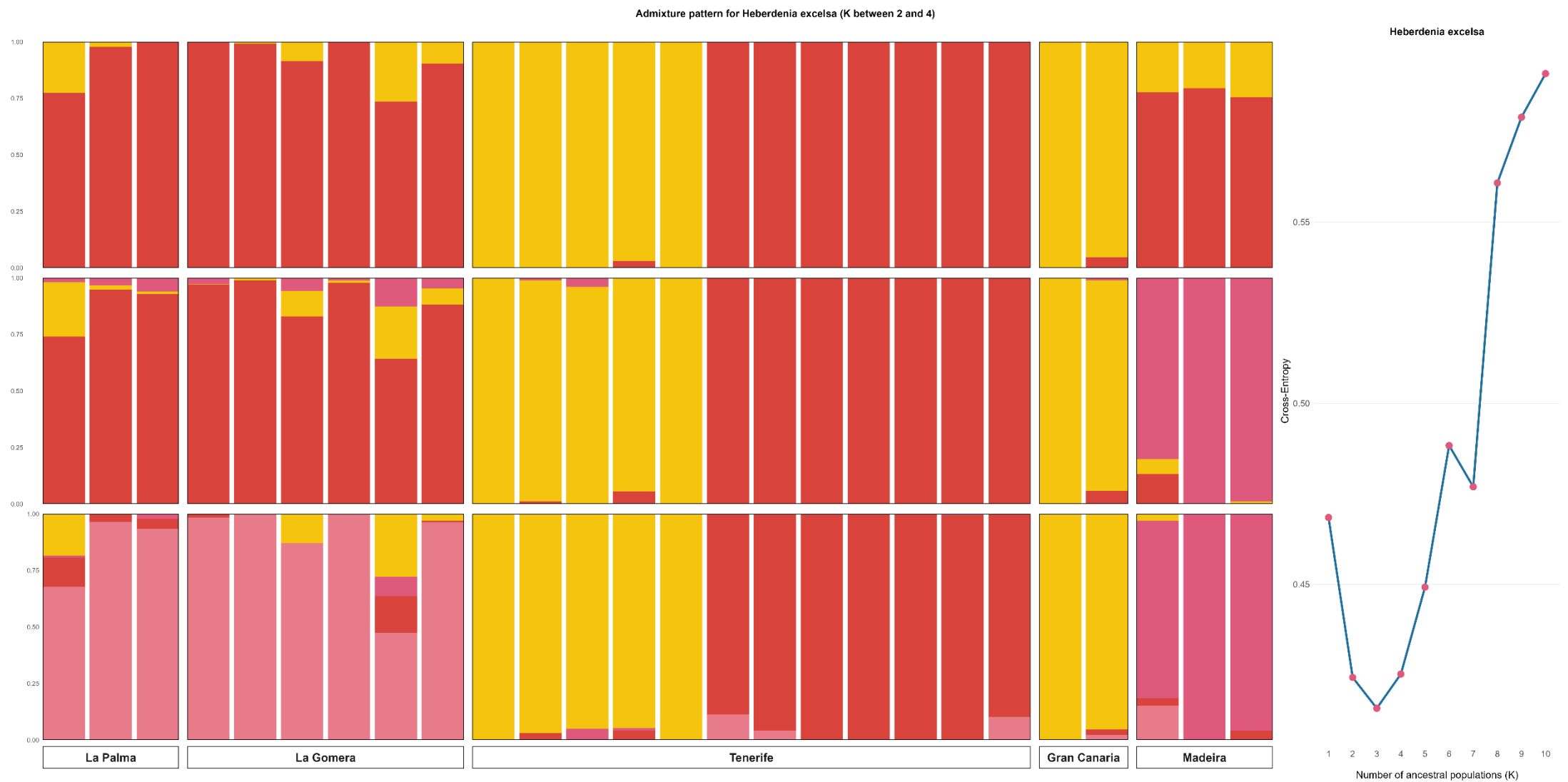


Figure S18 – sNMF results for *Luzula canariensis*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

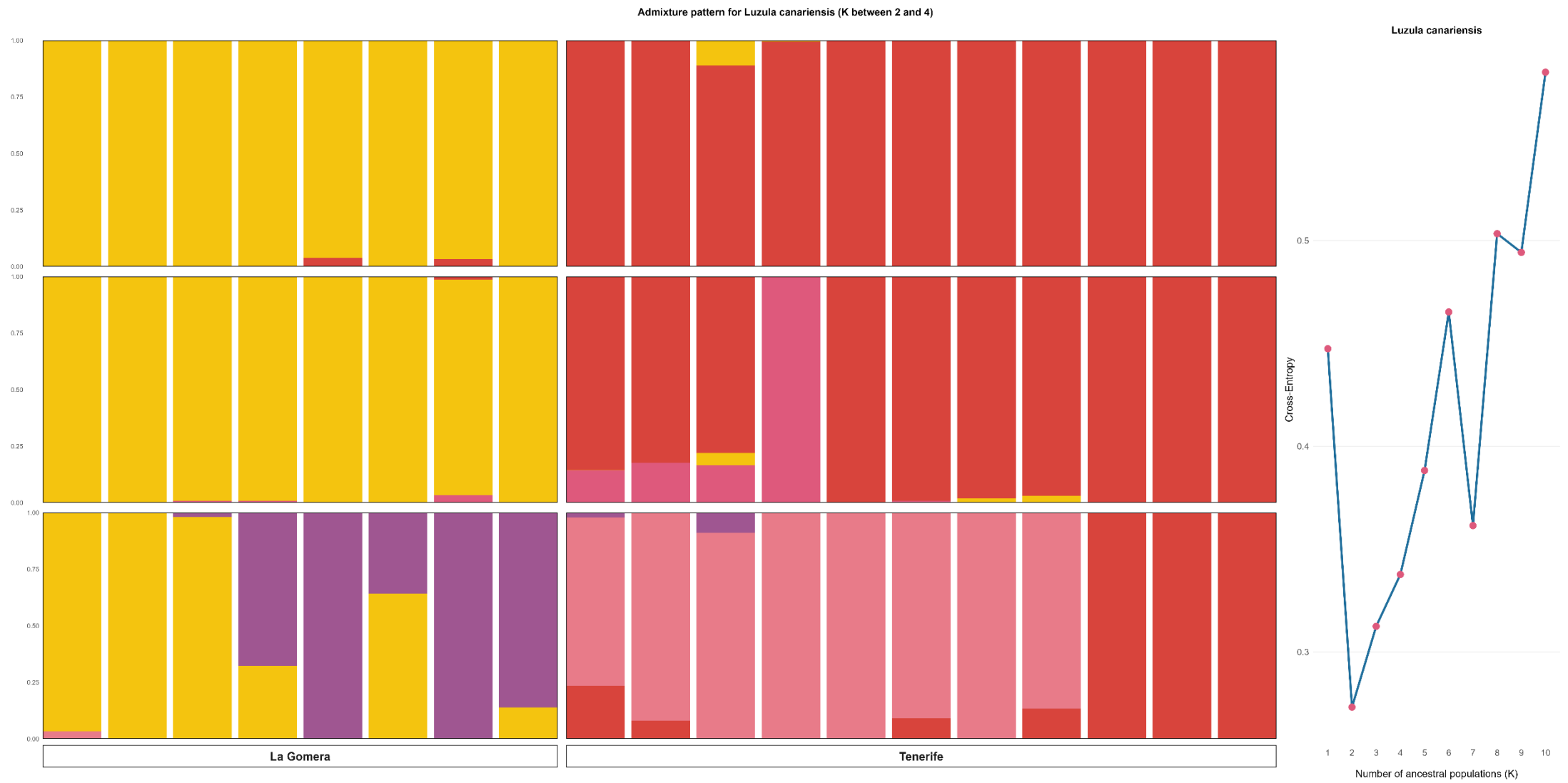


Figure S19 – sNMF results for *Morella faya*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude, with Madeira specimens on the right. K values are indicated in the title for each species.

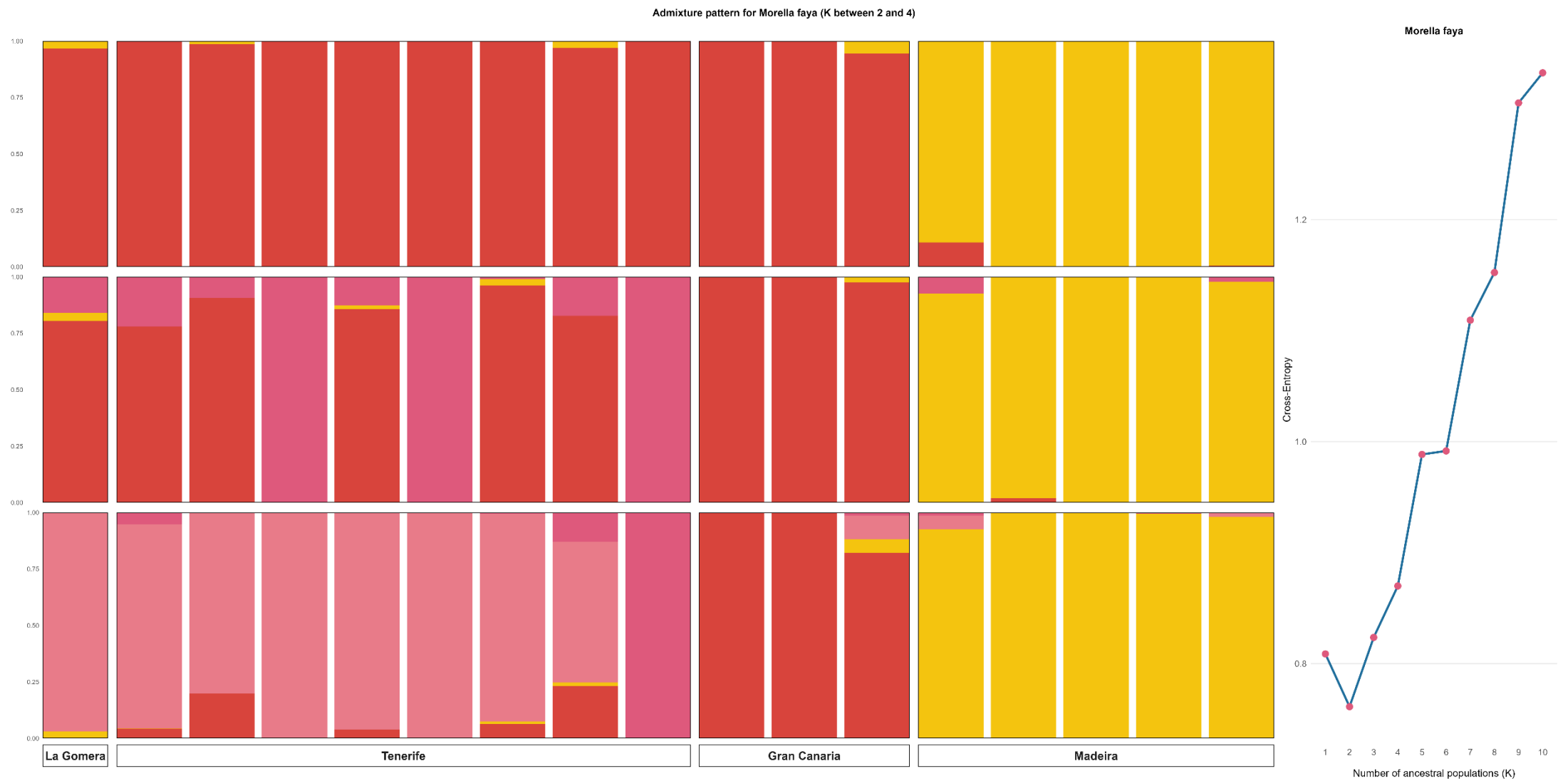


Figure S20 – sNMF results for *Persea indica*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude, with Madeira specimens on the right. K values are indicated in the title for each species.

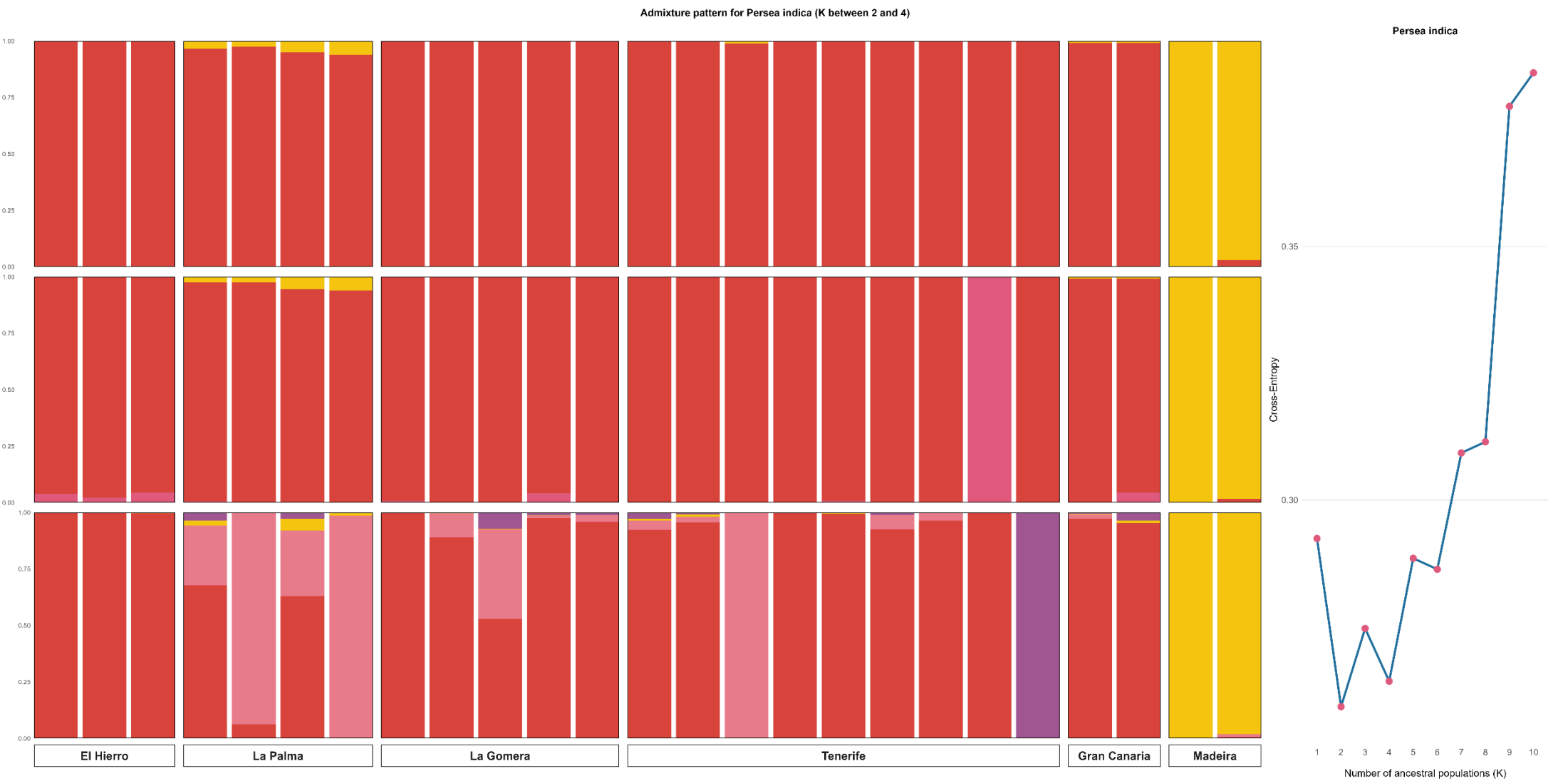


Figure S21 – sNMF results for *Ratama rhodorhizoides*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

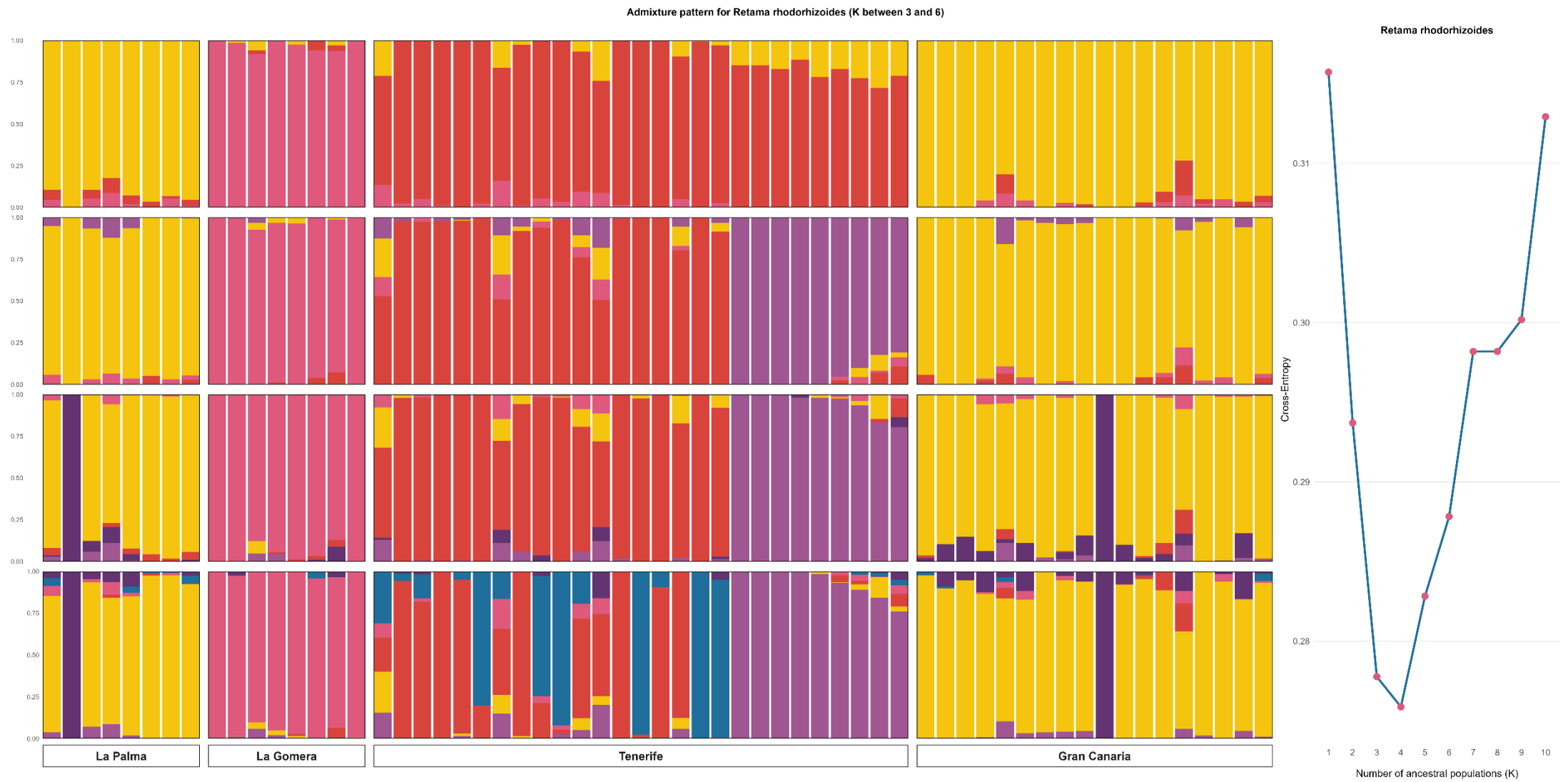


Figure S22 – sNMF results for *Streptocytisus filipes*. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude. K values are indicated in the title for each species.

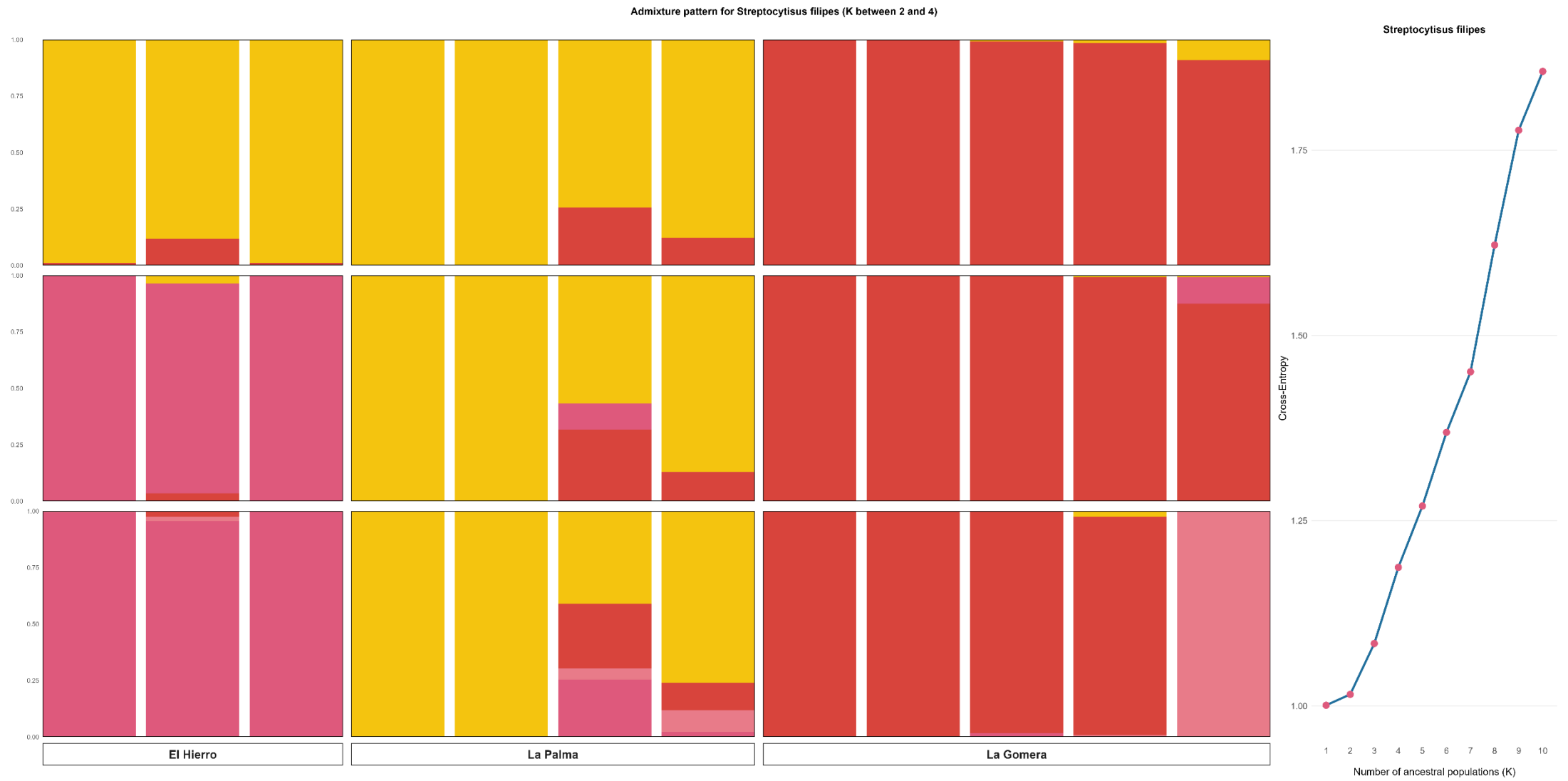


Figure S23 – Stairway plot representing the demographic history of *Apollonias barbujana* (AB) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 12 years. East = Gran Canaria + Tenerife + part of La Gomera; West = part of La Gomera + La Palma + El Hierro.

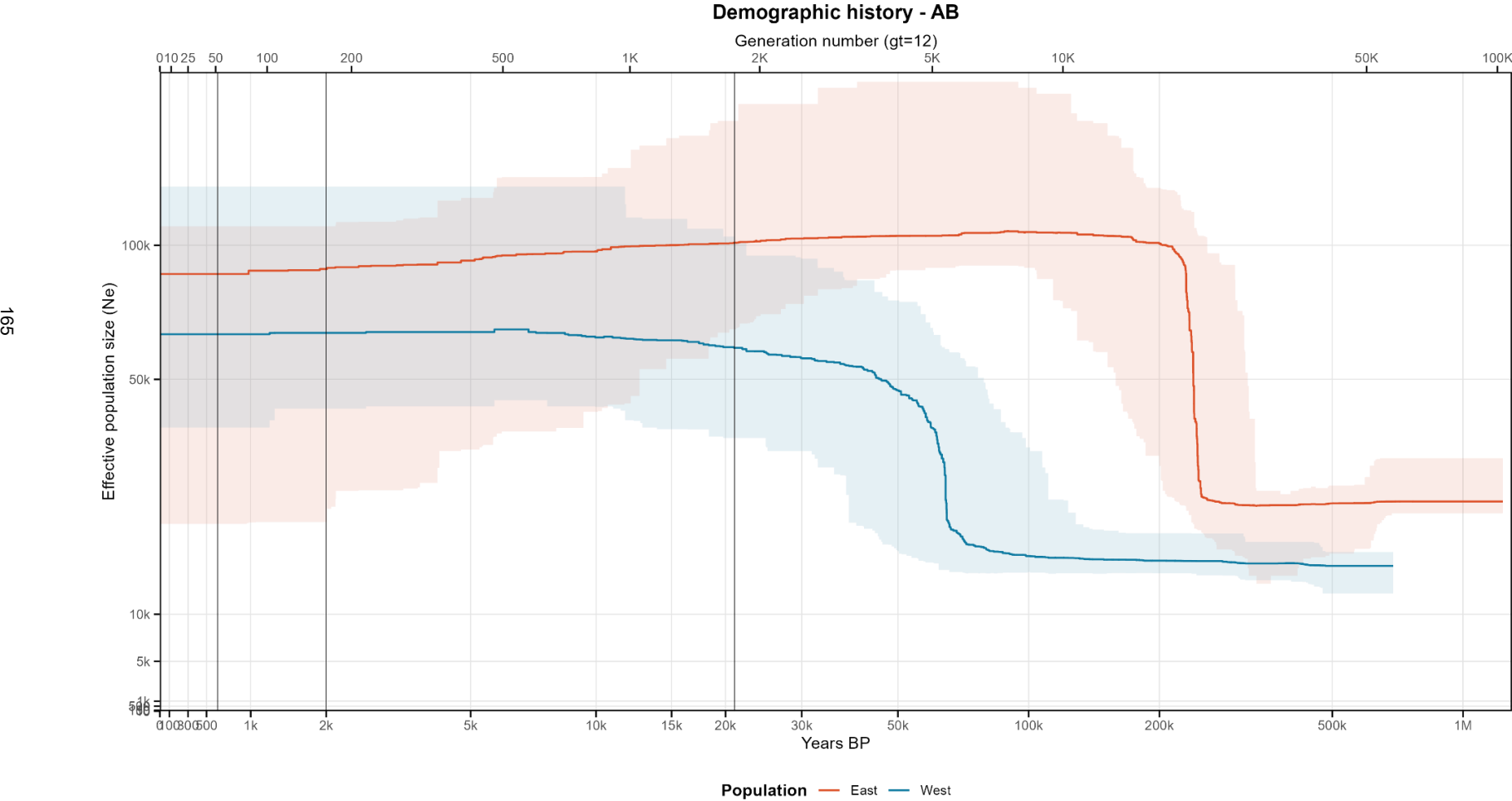


Figure S24 – Stairway plot representing the demographic history of *Adenocarpus foliolosus* (AF) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 4 years. GC-Anaga = Gran Canaria + Anaga; LG = La Gomera; TF = Tenerife except Anaga. La Palma specimens not included.

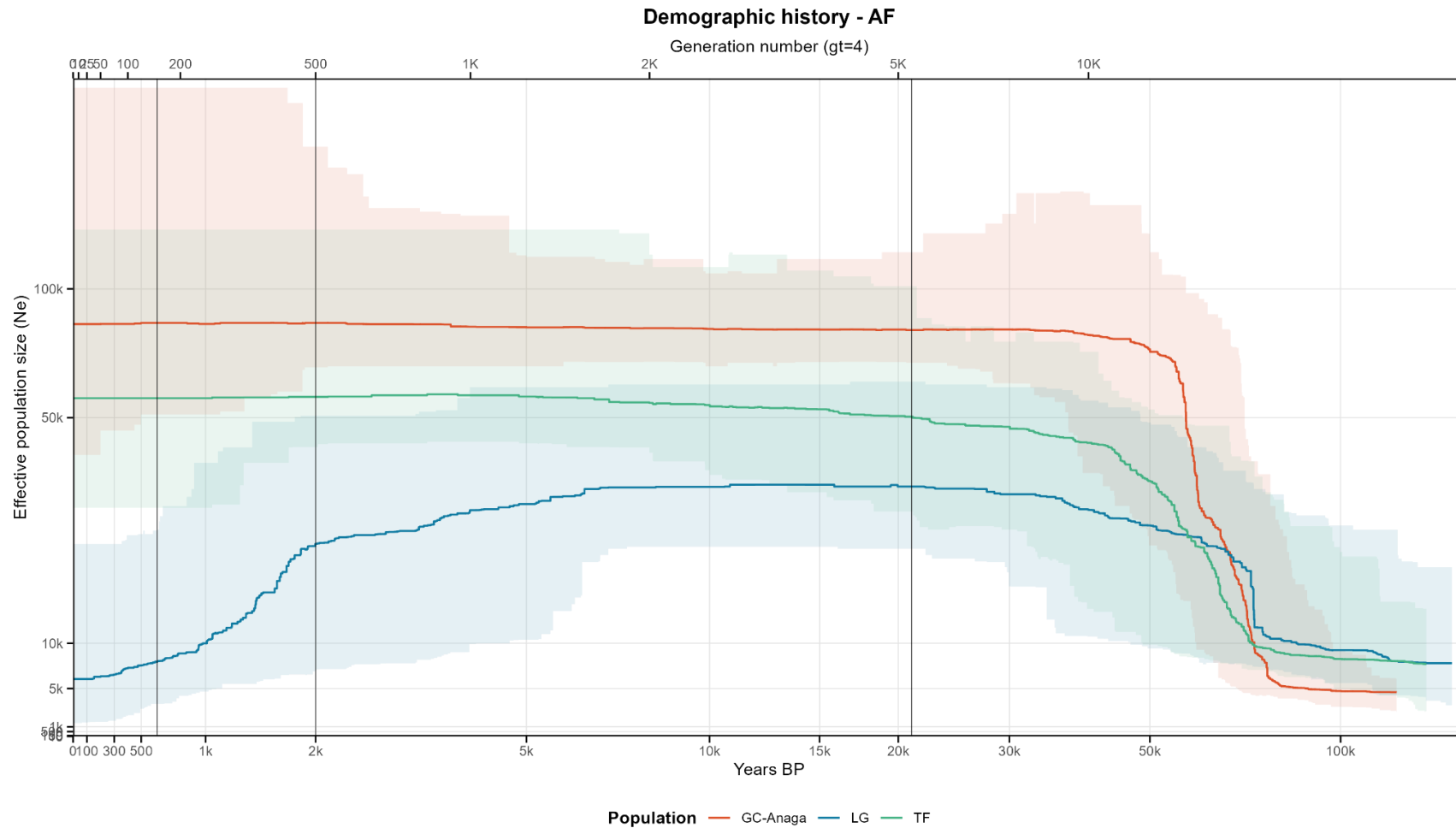


Figure S25 – Stairway plot representing the demographic history of *Brachypodium arbuscula* (BA) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 2 years. LG = La Gomera; TF = Tenerife.

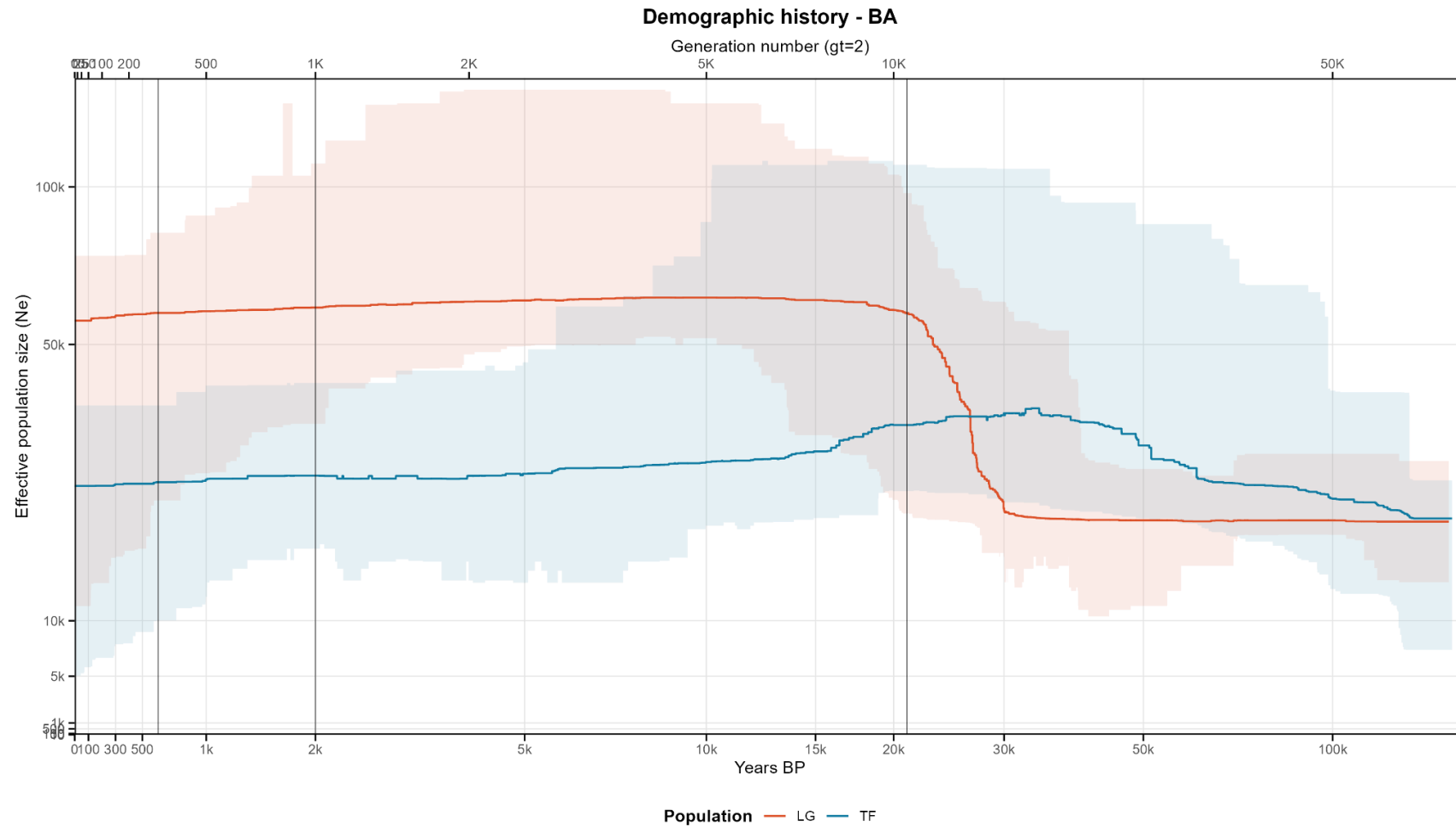


Figure S26 – Stairway plot representing the demographic history of *Canarina canariensis* (CanC) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 2 years. GC-Anaga = Gran Canaria + Anaga; LG = La Gomera; Teno = Teno; LP = La Palma.

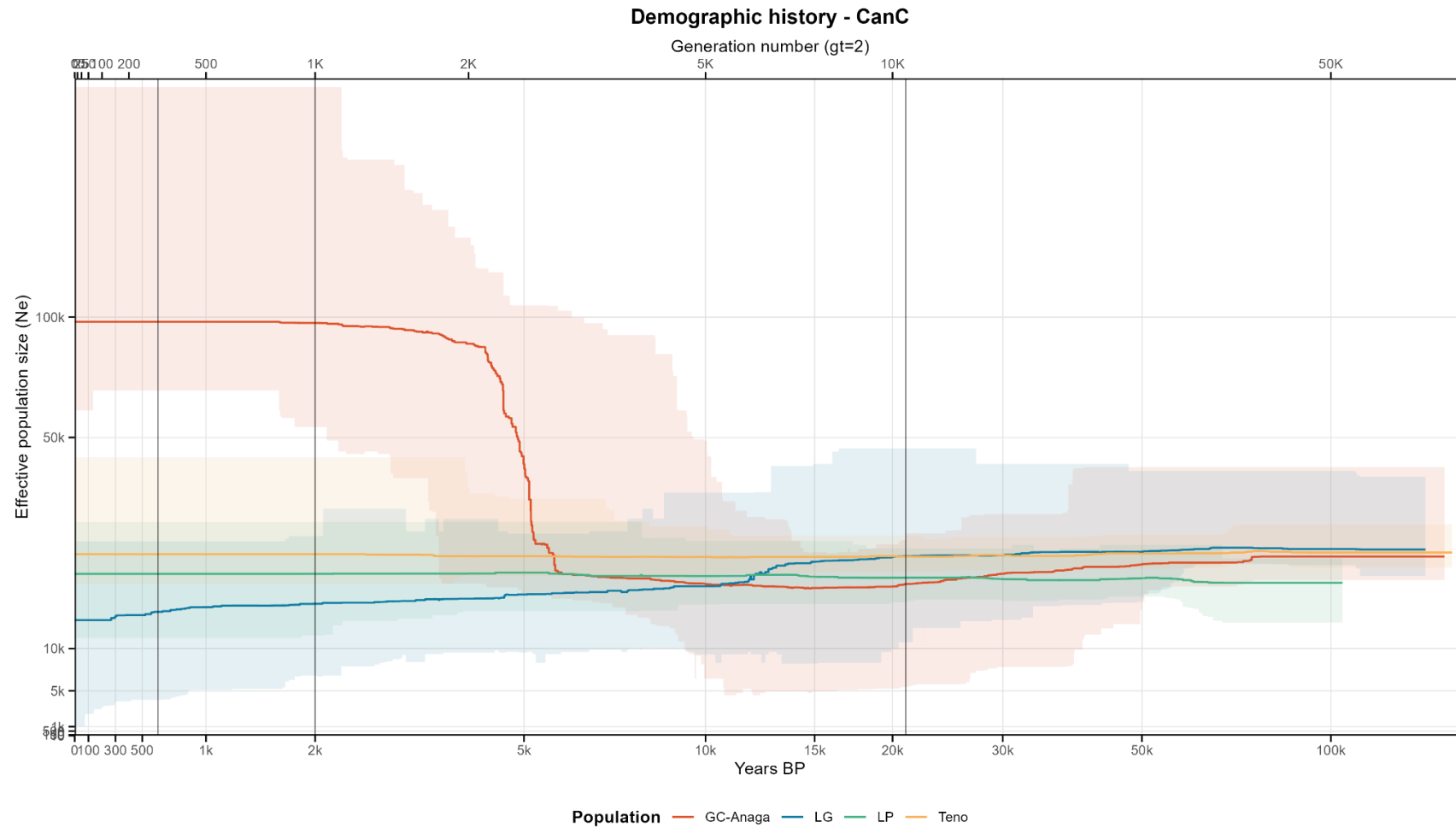


Figure S27 – Stairway plot representing the demographic history of *Dracunculus canariensis* (DC) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 2 years. GC = Gran Canaria; West = Tenerife + La Gomera + La Palma + El Hierro.

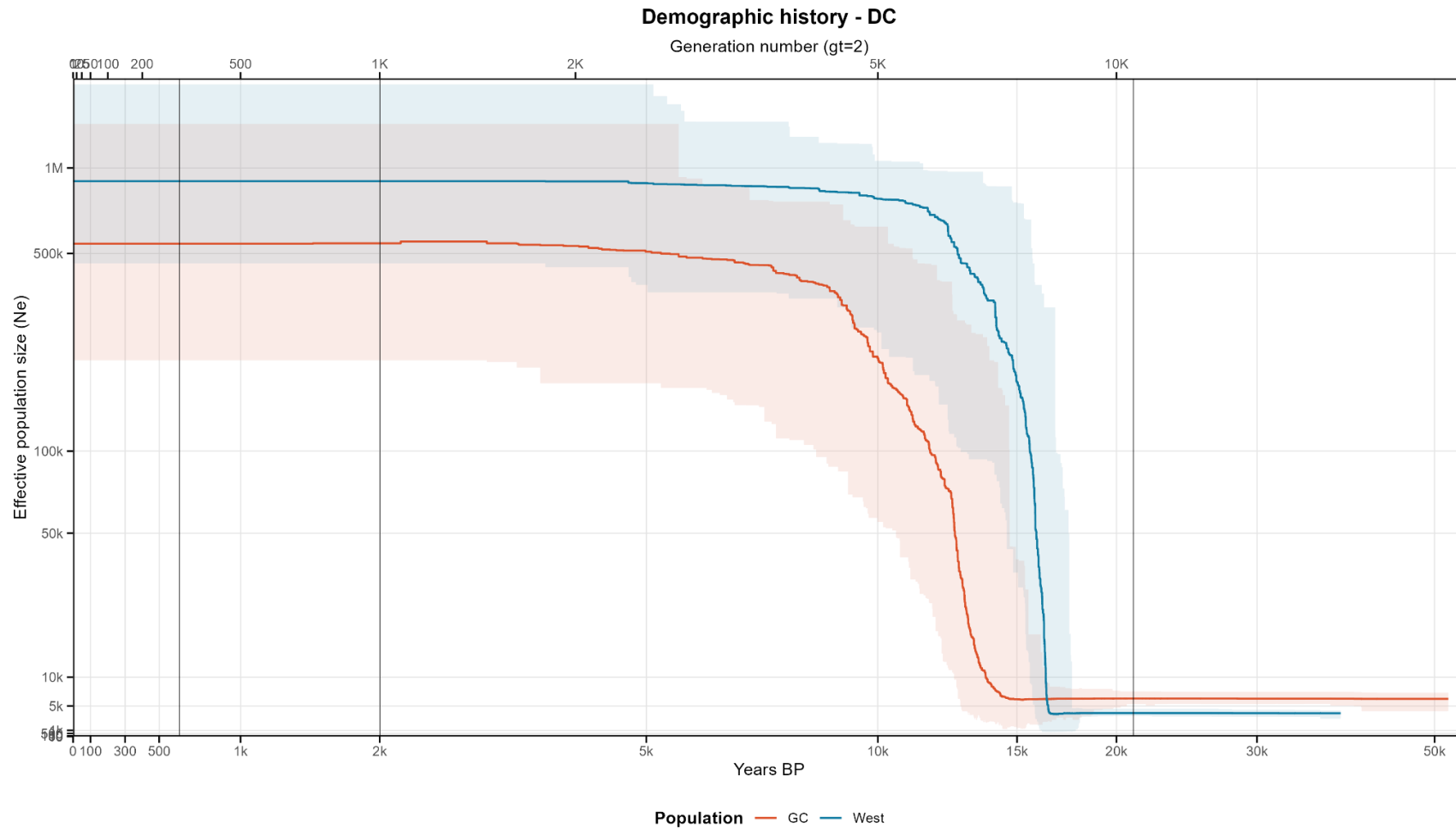


Figure S28 – Stairway plot representing the demographic history of *Heberdenia excelsa* (HE) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 10 years. Lau-all = laurel forest clade (including Madeiran samples); LauC = Canarian laurel forest clade; Ther = Canarian thermo-sclerophyllous forest clade. Madeiran specimens alone are not displayed.

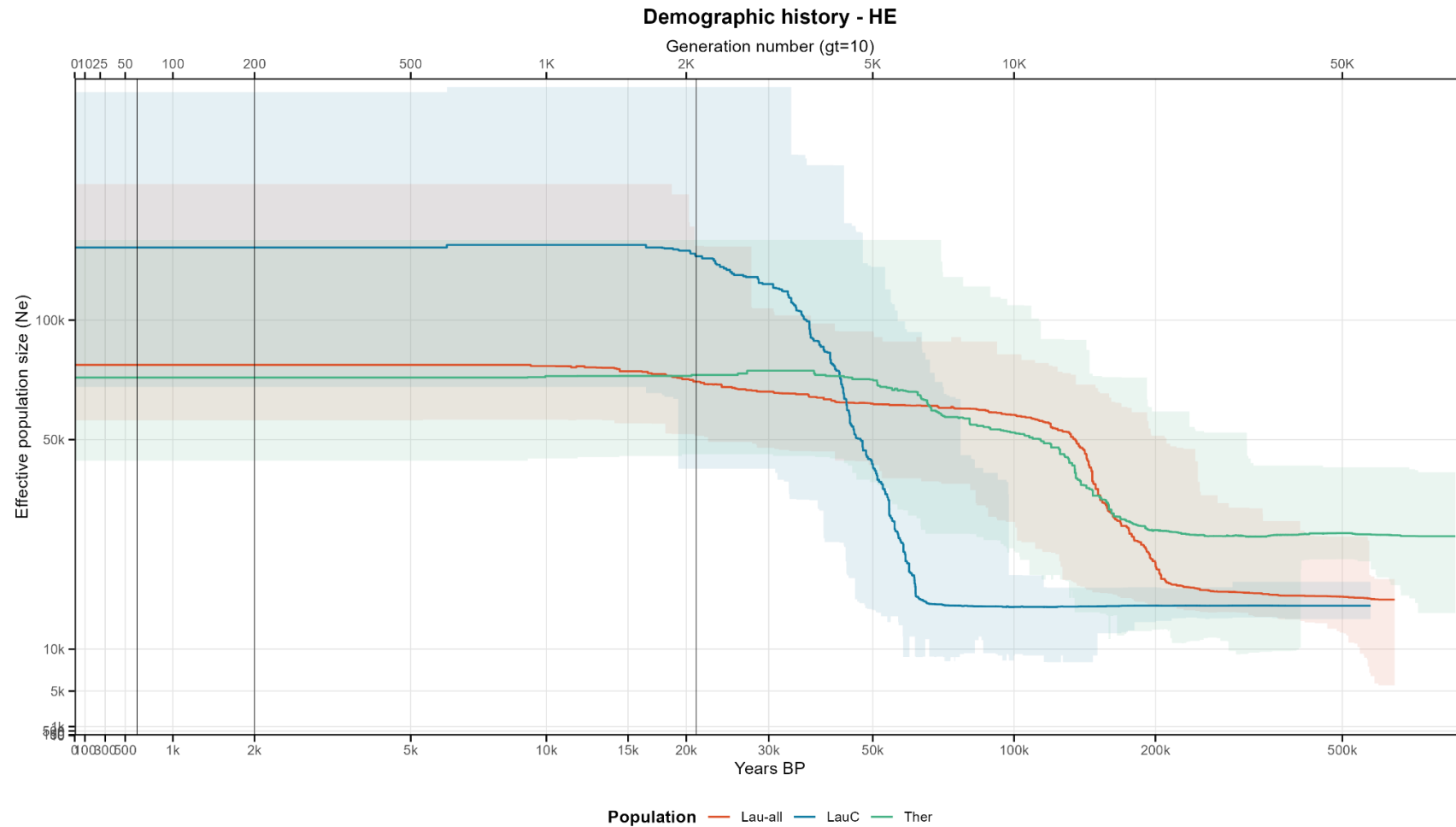


Figure S29 – Stairway plot representing the demographic history of *Luzula canariensis* (LC) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 2 years. AnagaW = West part of Anaga; LG = La Gomera; TF = all Tenerife samples together.

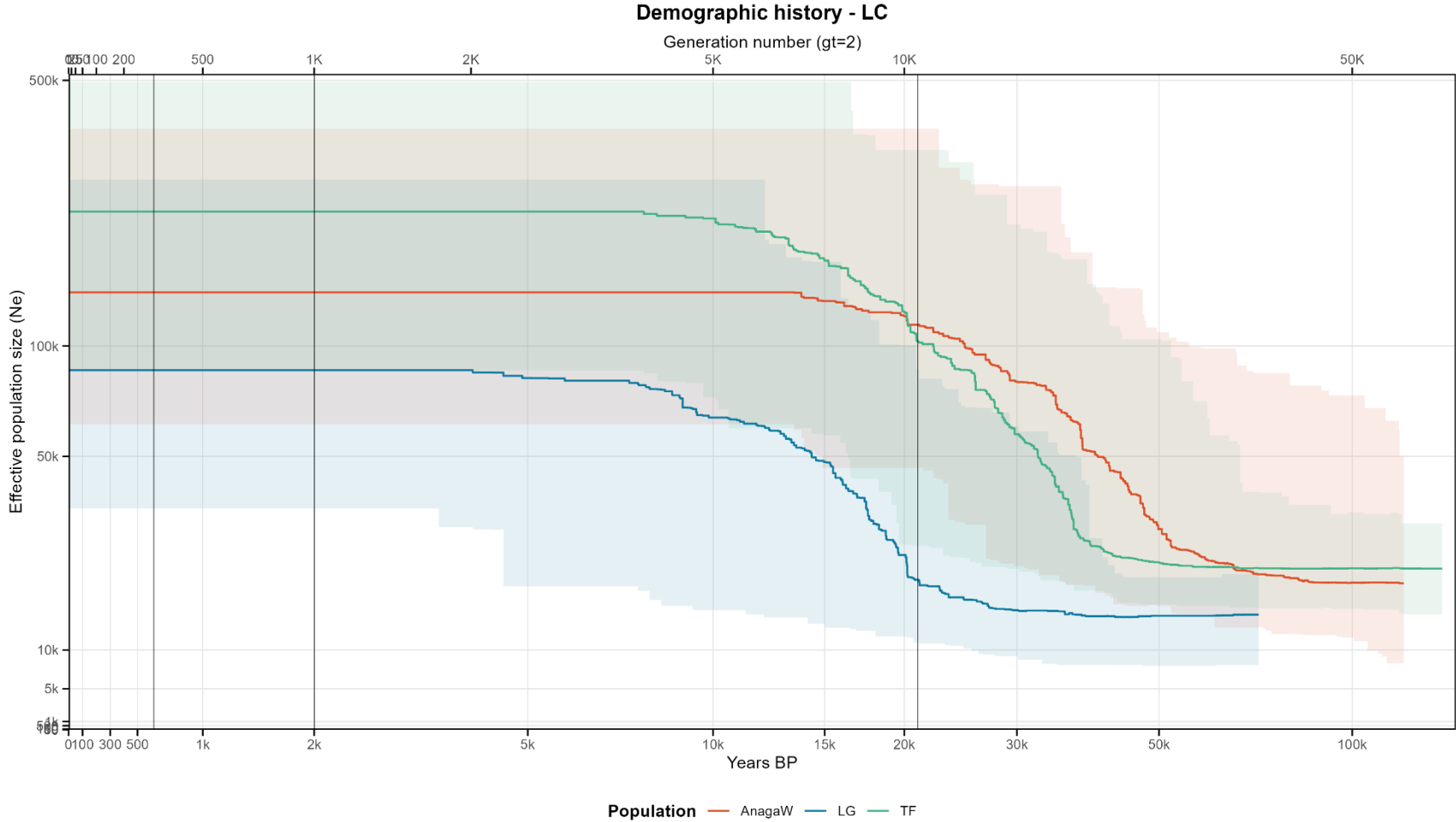


Figure S30 – Stairway plot representing the demographic history of *Morella faya* (MF) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 5 years. all = all specimens together; Can = Canarian specimens; Mad = Madeiran specimens.

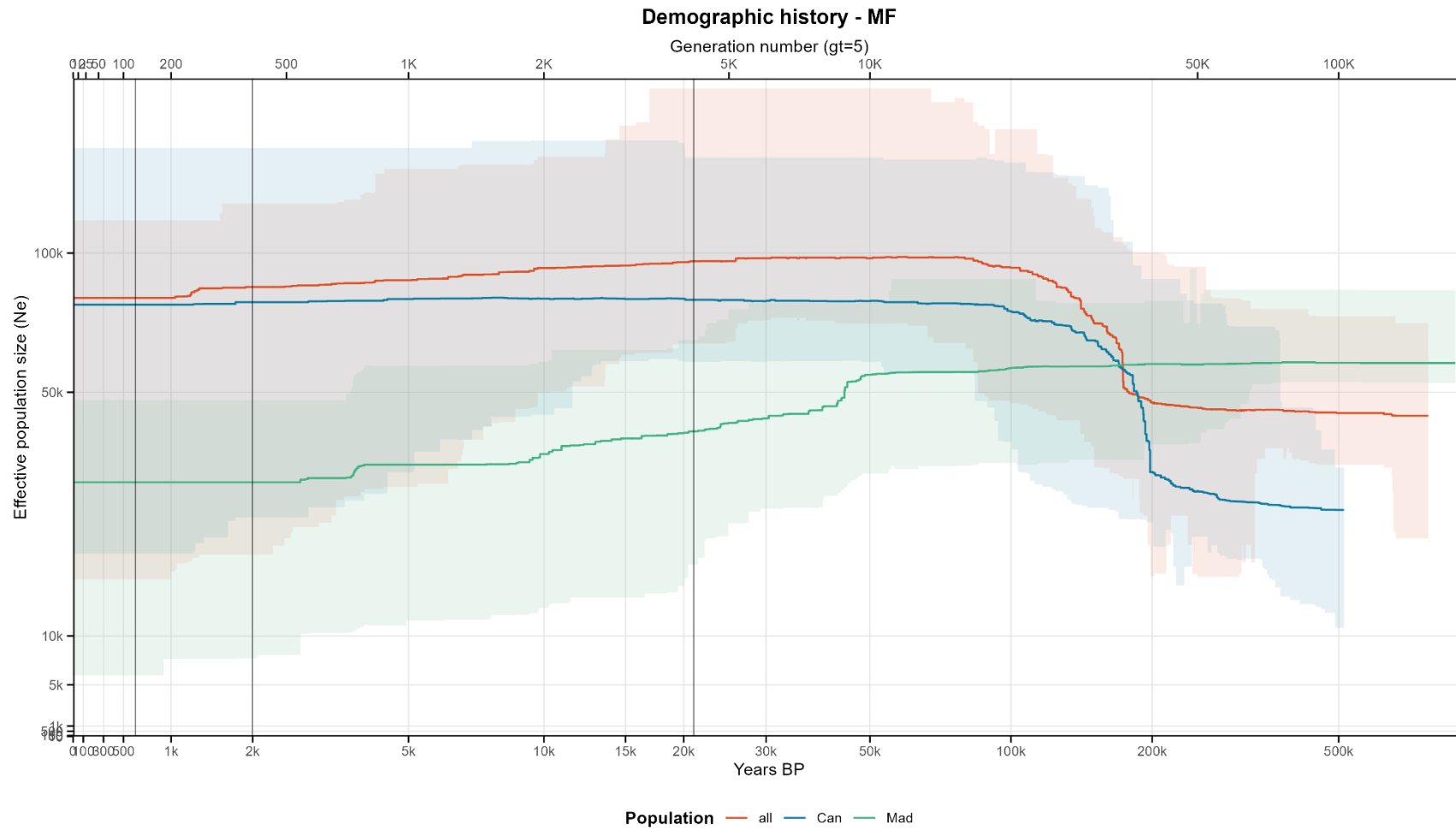


Figure S31 – Stairway plot representing the demographic history of *Persea indica* (PI) population through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 10 years. The only population represents Canarian specimens. Madeira specimens not included.

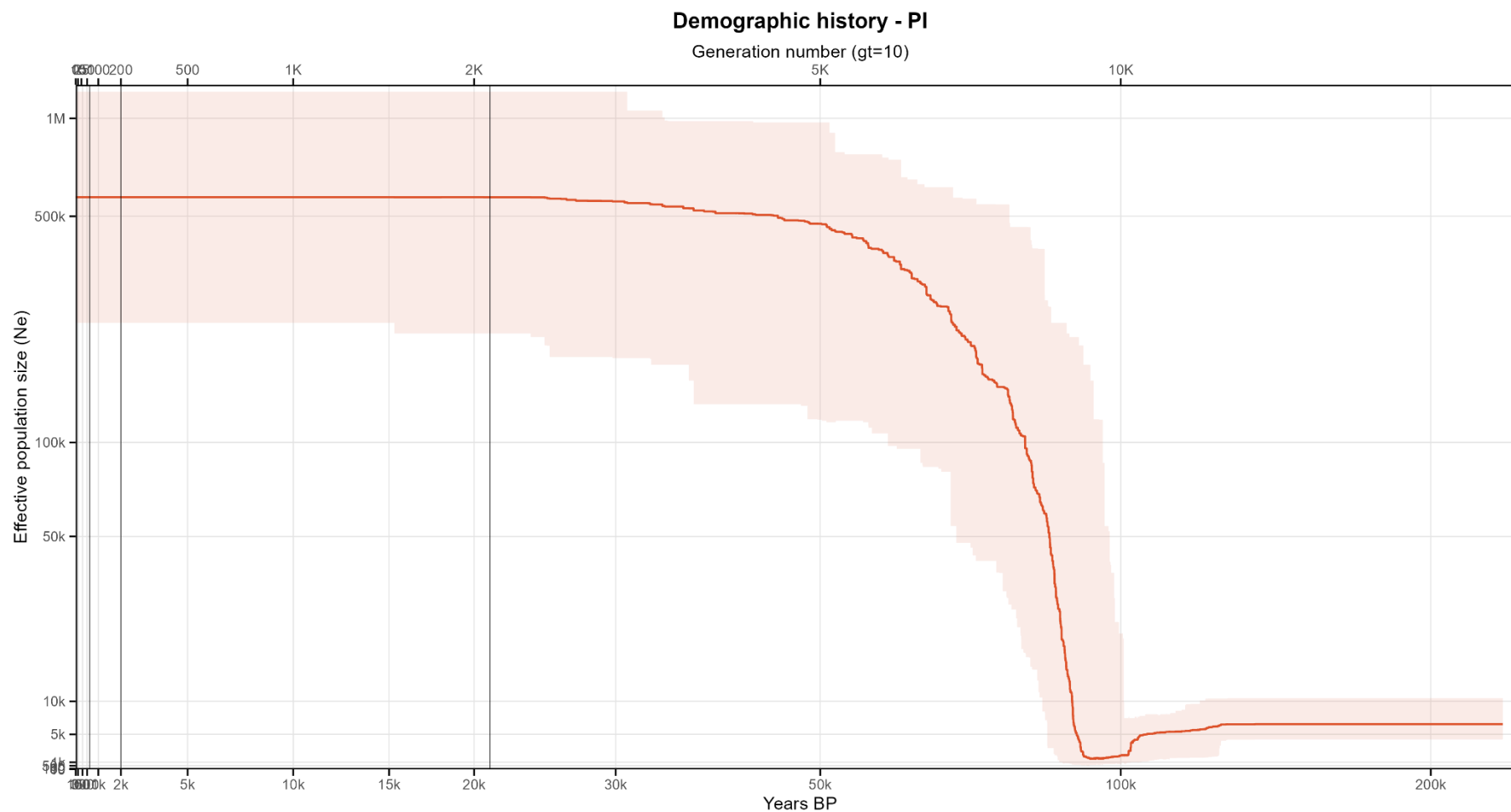


Figure S32 – Stairway plot representing the demographic history of *Retama rhodorhizoides* (RR) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 5 years. Guimar = Güímar; LG = La Gomera; LP-GC = La Palma + Gran Canaria; Teno = Teno.

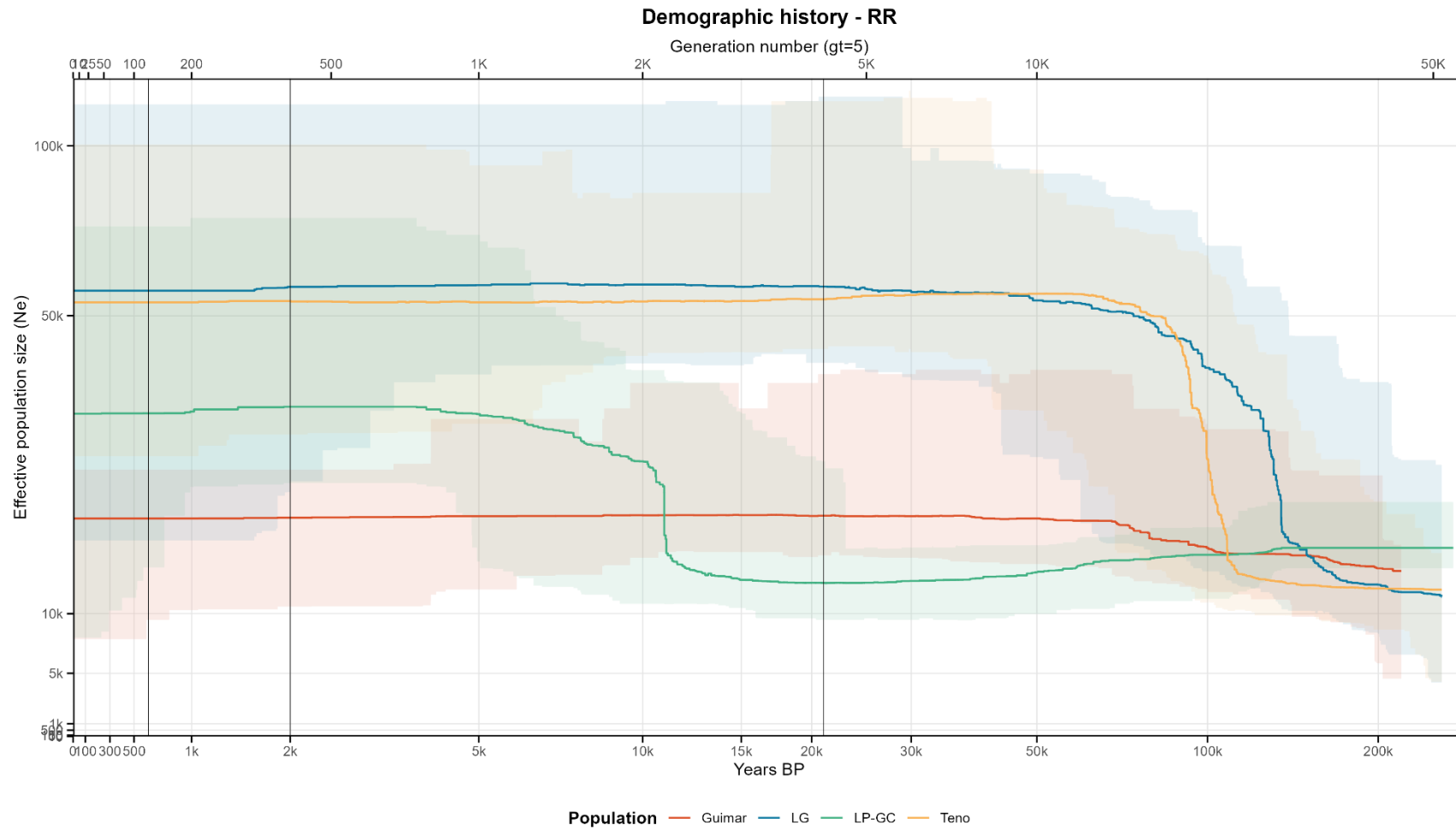
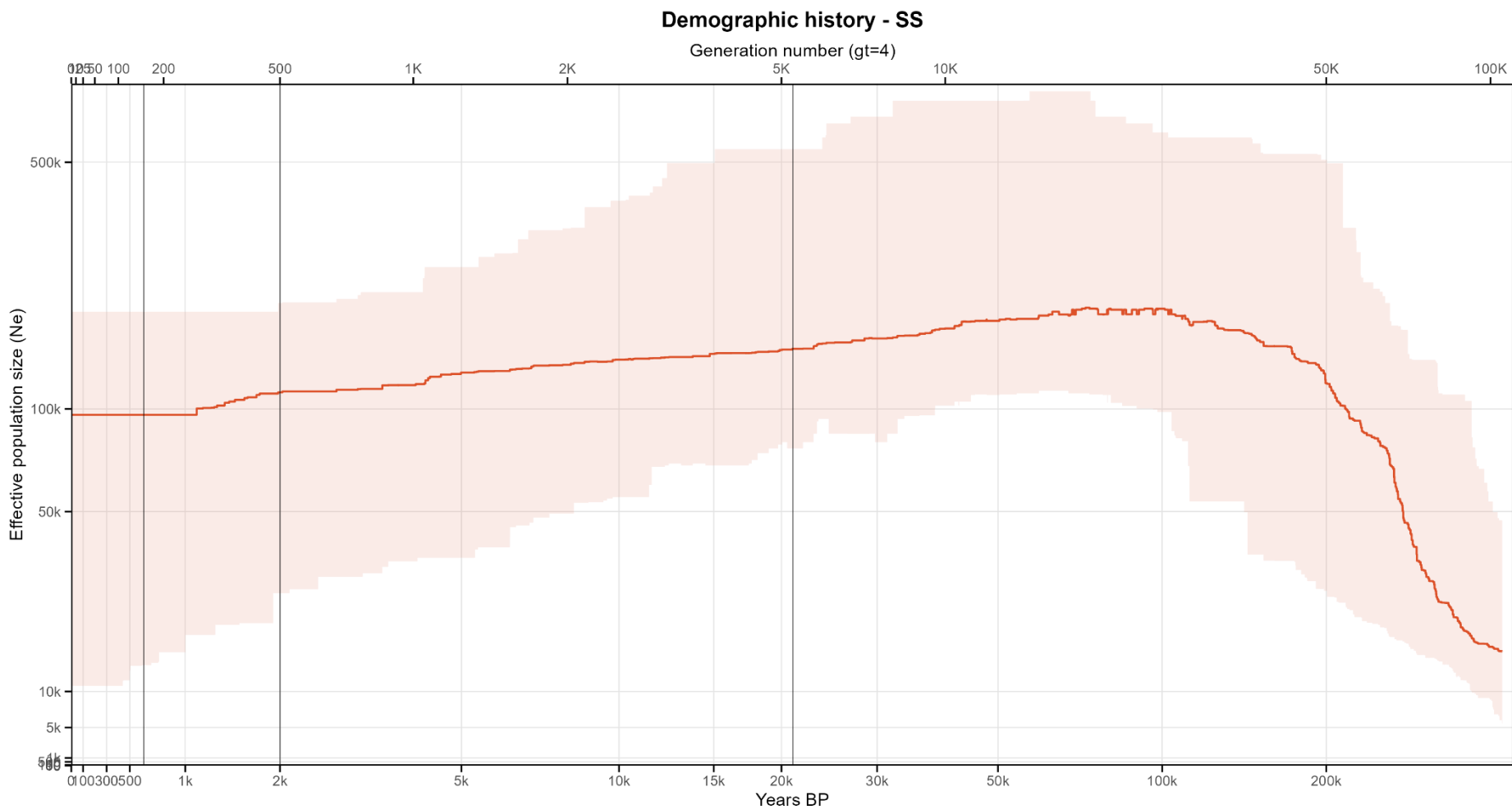
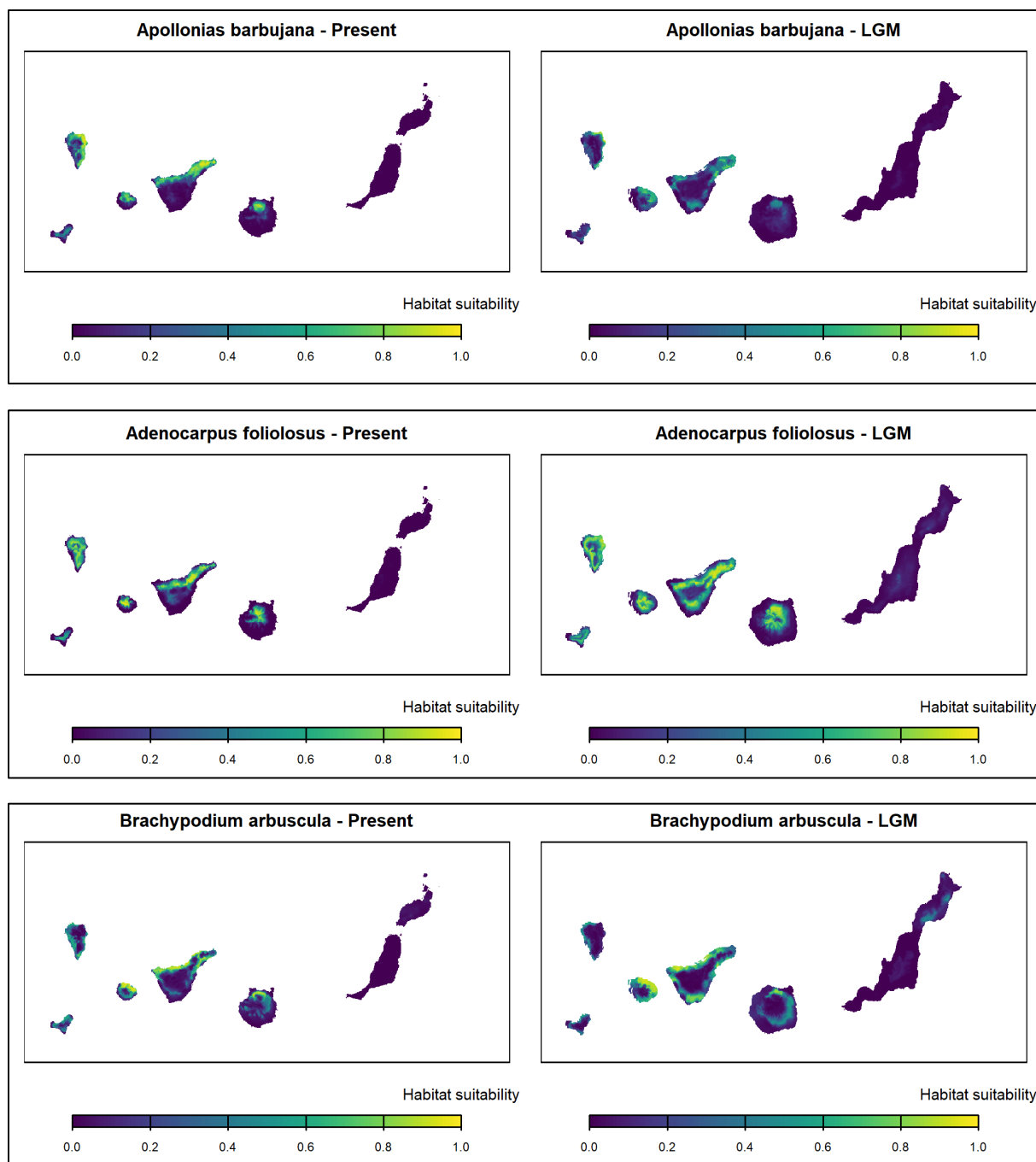
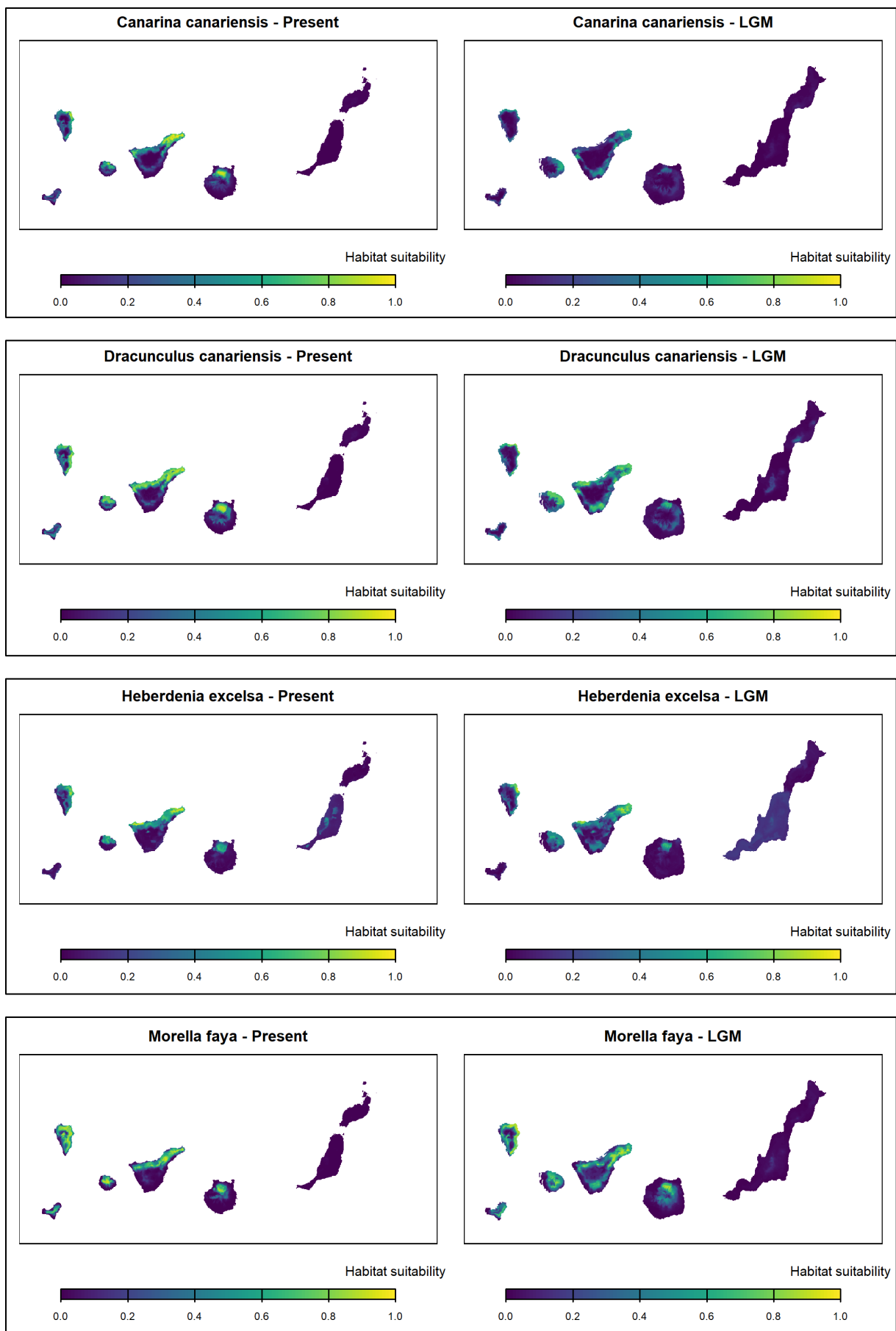


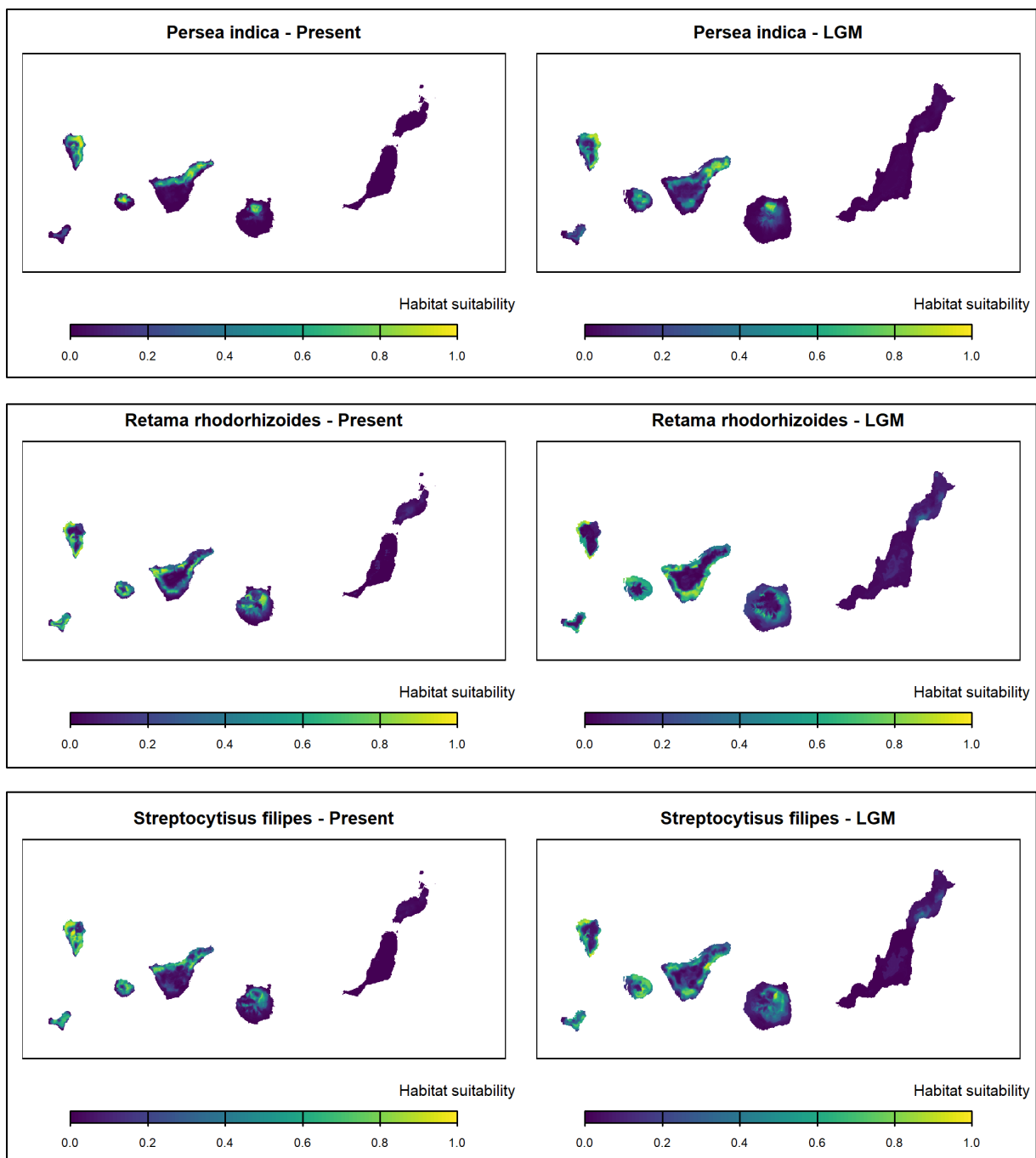
Figure S33 – Stairway plot representing the demographic history of *Streptocytisus filipes* (SS) populations through time. Both axes were log-transformed and displayed in pseudo-log scale, with the present on the left side going backward in time to the right. The thick colored line represents the median, the colored zone represents the 95% confidence interval, and the thick vertical grey lines represent major historical events (European colonization, Guanche colonization, Last Glacial Maximum). The generation time was set at 4 years. The only population represents specimens from El Hierro + La Palma + La Gomera.



Figures S34 – Suitable area for each species according to the Species Distribution Models computed in the present analyses for both the present and the LGM. *Luzula canariensis* is not represented as this species didn't have enough presence points to allow classical SDM computation.









G

lobal Discussion

The present thesis was articulated around two main questions regarding the biogeographic history of the Macaronesian flora, namely:

Q1: what have been the mechanisms through which the evolution of bryophytes and spermatophytes led to so contrasting patterns of endemism (Figure 4)? More precisely, we aimed at (i) disentangling the mechanisms responsible for the lower endemism rate in bryophytes compared to spermatophytes through a review of available evidence and re-analyses of published data, and (ii) better understanding the role of oceanic islands as refugia or stepping-stones for continental diversity.

Q2: to what extent have human disturbance and natural climatic cycles impacted species demographic history?

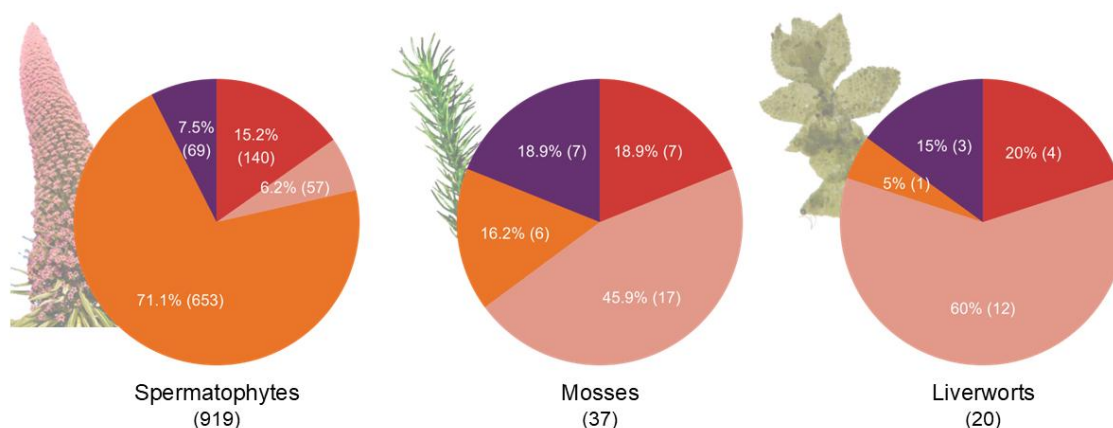


Figure 4 – Proportions of single and multiple archipelago endemic species in spermatophytes, mosses and liverworts (no Macaronesian hornworts are endemic). Numbers and percentage of endemic species are shown in each slice of the pie diagram, with the total number of endemic species in each group indicated below the charts. Orange = Canary Islands; purple = Azores; red = Madeira; pink = multiple archipelagos.

The answers to those questions are extensively discussed below. Furthermore, the data and results generated during these four and a half years are not limited to the present thesis. These results pave the way for further research on various topics, including taxonomy and conservation genetics. Those aspects are also discussed, including future perspectives on what could be done following the present work.

5.1 Why are there so few island bryophyte endemic species?

Bryophytes exhibit the lowest rates of island endemism across land plants (Chapter 1, Figure 1). In liverworts, species endemism rates are of 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). As discussed in Chapter 1, three main processes may account for these patterns:

- (1) a low evolutionary capacity intrinsic to the group;
- (2) low speciation rates on islands associated with either (2a) a high connectivity between island and mainland populations or (2b) differences in the speciation mode, and in particular, (2c) hybrid speciation following secondary contact among lineages previously isolated on the mainland;
- (3) the loss of endemic status due to (3a) extinctions and/or (3b) subsequent continental (back-) colonization.

5.1.1 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 equally old as the latter and would have remained unchanged for tens of million years (see Vanderpoorten et al., 2010, 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 constant for long periods of time (Patiño & Vanderpoorten, 2018). Although overall estimates of net species diversification in bryophytes are approximately 30% 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 more recently gained support through two lines of evidence. First, rates of molecular evolution, which, in plants, correlate with species diversity (Barraclough & Savolainen, 2001) 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 the 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 quickly fixed in the population, altogether 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 (Linde et al., 2021; Szövényi et al., 2013), calls for alternative explanations for the low levels of endemism in bryophytes.

5.1.2 The lower speciation rate hypothesis

5.1.2a 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 (Chapter 1, Figure 3, Table S2), indicating that migration does not completely erode genetic differentiation by drift. Limited gene flow was further evidenced by the presence of a significant phylogeographical signal ($N_{ST} > G_{ST}$) in 7 of the 19 species for which DNA sequence data were available (Chapter 1, Figure 3). A significant phylogeographical signal in the data involves a higher mutation than dispersal rate, evidencing that island populations have evolved in isolation for long enough to generate related endemic genotypes (Demenou et al., 2020; Heuertz et al., 2014; Ley et al., 2014). A significant phylogeographical signal is hence indicative of incipient speciation (Dauby et al., 2010). In Macaronesian spermatophytes, such a 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 Macaronesia 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 unexpected high proportion of bryophyte species with a significant island/mainland phylogeographic signal points to an active diversification process.

Furthermore, our results also 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 in Chapter 2. This suggests that the high ability for long-distance dispersal does not necessarily

translate into high migration rates. 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 transoceanic dispersal rate.

Overall, the idea that frequent migrations in island bryophytes necessarily prevent genetic divergence and, hence, incipient speciation, 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 phylogeographical signal is more likely to occur between distant (Macaronesian vs extra-European populations) than closer (Macaronesian vs European) populations. A meta-analysis of spatial genetic structures in bryophytes revealed that, beyond the limits of short-distance dispersal (<100m from the source), a decay of the isolation-by-distance signal occurs (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. Beyond such distances, i.e., at distances between Macaronesia and extra-European mainland, increasing genetic divergence among populations occurs, marking the limits of regional dispersal, beyond which an increasingly smaller proportion of spore travel. Altogether, these observations suggest that speciation more likely occurs in island bryophytes at sufficient distances from the mainland for genetic divergence to take place.

5.1.2b The speciation mode hypothesis

Species-level phylogenies on the origin of Macaronesian endemic species 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 (Chapter 1, Figure 4 right). In spermatophytes in 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 in all but one of the 31 genera (out of 39) including Macaronesian endemic bryophytes investigated here. In spermatophytes, a colonization:speciation ratio of 1 was reported in 44 out of a total of 90 genera analysed, but the almost equal number of radiations (46 genera) disproportionally contributes to 88% of the endemic species reviewed here (56% of the total number of endemic Macaronesian species).

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, wherein single-island endemics prevail (Carine & Schaefer, 2010), the vast majority of Macaronesian endemic bryophytes are multiple-island and multiple-archipelago endemics (see above Chapter 1, Figure 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 further diversify (Chapter 1, Table S3), challenging the application of the niche pre-emption hypothesis in bryophytes. This hypothesis is further weakened in bryophytes as its main driver, namely competition, plays a marginal role in bryophyte communities (Ma et al., 2024 and references therein). In particular, none of the Macaronesian endemic bryophyte species is annual, a strategy that would be expected if competition was a limiting factor for *in situ* speciation.

Third, certain traits, termed as key innovations, have been proposed as leading to adaptive radiations by permitting shifts into previously inaccessible ecological niches (Miller et al., 2023). In island plants, one of the most striking innovations is the evolution of woodiness (Nürk et al., 2019). In bryophytes, the shift toward pleurocarpy is assumed to have triggered the radiation of Hypnales (Shaw et al., 2003), while shifts towards bisexuality significantly correlate in liverworts with increased diversification rates (Laenen et al., 2016). 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 capacities, and hence, over-representation on islands than in-situ shifts towards bisexuality (Patiño et al., 2013). Thus, there is to date no evidence for the evolution of key innovations in island

bryophytes that would have triggered their 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 (see Patiño & Vanderpoorten, 2018, for review), thereby offering an explanation for their failure to adaptively radiate. Mounting evidence for local adaptation from genome-wide analyses (Wu et al., 2025; Xing et al. 2024, 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 locally adapt and diversify, but because of their preference for habitats that are not prone to trigger radiations. In particular, Patiño et al., (2014) attributed the lack of radiation in Macaronesian bryophytes to their strong association with the laurel forest, which harbours 16 out of 20 endemic liverworts and 22 out of 36 endemic mosses. The composition of the laurel forest might have experienced faster composition shifts than previously thought (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 (Santana et al., 2025; Castilla-Beltrán et al., 2021; de Nascimento et al., 2020). An evergreen forest habitat, the laurel forest has, however, been characterized by buffered microclimatic conditions throughout its paleoclimatic 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., 2014). In fact, none of the major radiations of Macaronesian spermatophytes have been inferred to occur within, or even 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).

5.1.2c Opportunities for hybrid speciation

The Surfing Syngameon Hypothesis (SSH, 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 such a hypothesis, genetic diversity in bryophytes was similar in island and mainland population (Chapter 1, Figure 6). In contrast to

spermatophytes (Rincón-Barrado et al., 2024; Caujapé-Castells et al. 2017; Curto et al., 2017), however, high levels of genetic diversity in Macaronesian bryophytes did not trigger diversification, with a colonization:speciation ratio virtually equal to one in bryophytes (Chapter 1, Table S4).

A key feature of the SSH is the crucial role played by introgression. In bryophytes, allopolyploidization has been recurrently reported (e.g., Nieto-Lugilde et al., 2018; Barbulescu et al., 2017; Karlin & Smouse, 2017), but the role of homoploid hybridization has long been questioned (Sawangproh & Cronberg, 2021; Natcheva & Cronberg, 2004). 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 & Hedenäs, 2024; Draper et al., 2007).

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., 2016), sexual reproduction is hampered as the sexes need to be in close sympatry due to the very short distance that sperm cells can travel to reach the archegonia (typically much less than 1m but up to 20m 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 et al., 2012), and although sperm release in the air was reported in the liverwort genus *Conocephalum* (Shimamura et al., 2008), sperm dispersal most commonly takes place through a continuous film of water, and thus strongly depends on environmental conditions (Hedenäs & Bisang, 2019; Sundberg, 2002).

Unisexual bryophytes populations are further characterized by large numbers of individuals that do not express sexual organs and by strongly biased sex-ratios with female dominance (see Bisang et al., 2025, for review). 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 et al., 2009). In bisexual species, intragametophytic selfing largely prevails (Eppley et al., 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., 2013). Out of 10 bryophyte species investigated in the present study, seven exhibited significant linkage

disequilibrium among loci (Chapter 1, Table S6). In contrast to our hypothesis, which posits that higher rates of selfing in island populations and/or clonality prevent admixture, however, significant linkage disequilibrium was twice as frequent in continental populations compared to island ones. Previous evidence 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 of 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.

More globally, it has been suggested that the role of homoploid hybridization in bryophytes has been largely underestimated (Sawangproh & Cronberg, 2021; Natcheva & Cronberg, 2004). 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 hybrid 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 for molecular signatures of hybridization and indeed increasingly revealed evidence for interspecific recombination in the nuclear genome (Klink et al., 2024; Sawangproh & Cronberg, 2021, and references therein). Altogether, there is thus no reason that would explain why, like in spermatophytes, the SSH would not apply to island bryophytes, calling for further research on the actual role played by hybridization in the latter.

5.1.3 Extinctions and (back-) colonizations

5.1.3a Extinctions

Island vegetations are characterized by fast rates of turnover after human invasion (Nogué et al., 2021), which may have triggered high extinction rates and accounted for the observed low rates of endemism in island bryophytes. The history of Macaronesia has, in fact, been shaped by extensive deforestation, which started in the Canary Islands about 2000 years BP with the colonization by Berber/Amazigh people and peaked across all Macaronesian archipelagos from the 16th century upon Castilian arrival (Elias et al., 2022; Castilla-Beltrán et al., 2021). In the Canary Islands, well-preserved laurel forests cover about 12 % of their potential distribution range

(Betzin et al., 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 in the course of 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 massively introduced (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 were documented (*Nobregaea latinervis* and *Fissidens microstictus*) (Sim-Sim et al., 2014). In spermatophytes, 13 cases of extinctions were, by comparison, 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 rates in bryophytes would, however, need to be extremely biased as compared to spermatophytes to account for the substantial variations of the rates of endemism between the two groups. Furthermore, although exotic trees were introduced in Macaronesia from the late 18th century, thus post-dating the original destruction of the laurel forest that took place upon 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 *Pittosporum* and *Cryptomeria* in the Azores (Gabriel & Bates, 2005). As a result, the degradation of the laurel forest may not necessarily translate into effective extinctions.

5.1.3b (Back-) colonization

Alternatively, endemic Macaronesian species may have lost their endemism due to subsequent emigration. Evidence for a Macaronesian origin was found in 22 bryophyte species (about 2.7% of Macaronesian flora) distributed across Macaronesian and mainland areas, including results from both chapter 1 and 2 (see Chapter 1, Table 3 and Chapter 2, Figure 2). 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 can have subsequently expanded 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., 2015). In agreement with our hypothesis, the low rates of island endemics in bryophytes thus at least partly reflect the loss of their endemic status due to subsequent back or *de novo* colonization of continental areas. In fact, adding those 22 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 in pteridophytes (Vanderpoorten et al., 2011).

Continental (back-) colonization may have been facilitated by two processes. First, wind connectivity is currently higher from Southwestern Europe and western North Africa toward the archipelagos than the reverse (Hutsemékers et al., 2011), but was inverted during the last glaciations, during which the Westerlies wind regime prevailed (Wang et al., 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 capacities of bryophytes, stepping-stones may play a relevant role in their distribution patterns. Although bryophyte spores are efficiently dispersed by air, genetic structure increases with geographic distance beyond the regional range, marking the limits of regional dispersal (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 the role of Macaronesia as a stepping-stone for the dispersal of trans-oceanic migrants on their ‘colonization road’ to a new continental environment (Patiño et al., 2015). Stepping-stones may in particular play an important role in species that fail to reproduce sexually, and wherein a stepping-stone colonization process among forest patches was reported (Percel et al., 2024).

(Back-) colonization from Macaronesia to the continent has also been recurrently reported in spermatophytes (Chapter 1, Table 3), raising the question of whether the prevalence of this pattern in bryophytes would offer an explanation of the striking difference of Macaronesian endemism rates between bryophytes and spermatophytes. To further investigate this question, we performed phylogeographic analyses of amphi-Atlantic bryophyte species (Chapter 2). We show that, even within the pool of Macaronesian amphi-Atlantic species shared with Europe and other mainland areas, 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. 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 (Chapter 1, Supplementary data), this would lead to an estimation that slightly less than 50% of the bryophyte species of Macaronesia have an extra-European origin. 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 (Chapter 1, Table S5). These

patterns serve to illustrate the extent to which high long-distance dispersal capacities of bryophytes shape their distribution patterns.

Despite the substantially larger number of phylogeographic studies in Macaronesian spermatophytes than bryophytes (Chapter 1, Tables S5-S4, respectively), evidence of actual (back-) colonization in spermatophytes was reported in only 9 genera (about 0.7% of the Macaronesian flora) (Chapter 1, 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 (Figure 4 and Chapter 1, Table 2) pales by comparison with the spermatophyte flora (Mouton et al., 2023), being, respectively, of 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%) (Figure 4).

In spermatophytes, furthermore, speciation of the migrants of Macaronesian origin took place in seven out of the 9 genera, wherein continental back-colonization was reported (Chapter 1, Table 3), leaving the endemic status to the ancestral insular lineage. In bryophytes conversely, speciation of migrants of insular origin on continents was reported only in 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 endemism 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 endemism in island bryophytes therefore does not accurately reflect their actual speciation rate. While, in spermatophytes, island endemism rates thus provide an easy way to assess one of the most fundamental parameters in evolutionary biology, that is, speciation rates (Weigelt et al., 2016; Emerson & Kolm, 2005), this is not the case in bryophytes.

5.2 Human impact on endemism

This thesis evidenced substantial variations of effective population size (N_e), but the timing of the major shifts in population size occurred well-before the human colonization of the Canarian archipelago, ruling-out the hypothesis that human disturbance over the past 2000 years left a clear signature in extant patterns of genetic diversity. The only exception was a reduction of the population of *Adenocarpus foliolosus* from La Gomera ~2000BP, concomitant with the colonization of the island by human populations of Amazigh origin (Santana et al., 2024) and the increase of the fire regime (Castilla-Beltrán et al., 2021; Nogué et al., 2013). An anthropogenic interpretation of this pattern is, however, at odds with the fact that, although La Gomera has the best-preserved laurel forest ecosystem across the archipelago, with ~70% of its potential natural area remaining (del Arco Aguilar et al., 2010). Although it does not necessarily mean that the forest remained intact during 2000 years, no recent bottleneck was evidenced in the populations of other islands, where the extent of laurel forest is much more reduced and the conservation status of this ecosystem much more degraded.

The lack of imprints of recent human disturbance on patterns of genetic structure and diversity was unexpected because mounting evidence points to a global loss of genetic diversity due to human activity, both by direct actions like changes in land use or habitat fragmentation, or by indirect consequences from species introductions, pollution, or climate change, sometimes linked to population extinctions (Shaw et al., 2025; Exposito-Alonso et al., 2022; Almeida-Rocha et al., 2020; Leroy et al., 2018). The impact of ancient civilizations on current patterns of genetic diversity and structure has also been previously reported (Goudie, 2018; Hofman et al., 2015). On islands, the link between genetic loss and human perturbation is even more visible as they are seen as model systems (Whittaker et al., 2017), where colonization happened quite recently and has been shown to have impacted plant communities (Nogué et al., 2021) and their genetic diversity (e.g., Seersholm et al., 2018 in New Zealand; Bourgeois et al., 2024 in La Réunion).

There might be several explanations for the lack of a signature of human disturbance in extant patterns of genetic diversity. A limitation due to the number of markers available is unlikely as in many instances, genetic analyses based on similar genomic data (e.g., Xie et al., 2026; Vintsek et al., 2022), and even datasets yielding lower numbers of markers such as microsatellites (Gonzalez et al., 2014), revealed genetic signatures of recent demographic events (e.g., Bourgeois et al., 2024; Qin et al., 2024; Wang et al., 2023; Liu et al., 2020). With SNP matrices from RAD sequencing comparable in size to the ones generated here, *STAIRWAYPLOT2* analyses proved very efficient in

recovering recent demographic events in non-model species (e.g., Wang et al., 2023; Liu et al., 2020).

One interpretation of the lack of any signature of recent anthropic disturbance in the present data is that genetic responses are delayed or result from a genetic extinction debt, a parallel concept to the classic extinction debt that represents the delayed loss of species following habitat deterioration (Tilman et al., 1994; Essl et al., 2015), which has already been found in the Canary Islands, including for vascular plants (Otto et al., 2017). In fact, a genetic extinction debt, i.e., the time lag between disturbing events and genetic responses at the population scale, is an increasingly recognized pattern. Habitat disturbance affects species fitness and survival, and results in genetic drift through the loss or change in frequency of genetic variants. This genetic signature of habitat perturbations can be detected only after a number of generations, as moderately high levels of genetic diversity are preserved through persisting individuals that hold genetic legacies of their ancestors (see Gargiulo et al., 2025, and references therein). In species with short generation times, such as *Canarina canariensis* (estimated at between 2 and 5 years, see Chapter 3, Table S1), we would have expected a recent anthropic period signal from 2000BP onward (~400 generations). The failure of our analyses to retrieve the signal of demographic events dating back to 2000ya may reflect the low impact of people from Amazigh origin on the demography of this species, while the European settlement, dating back to only ~100 generations, may have been too recent to leave a detectable imprint in the genome.

The prevalence of ancient vs recent demographic events reported in the present analyses is in line with the results obtained in Afrotropical species on the continent. Little to no demographic signal was found in phylogeographic analyses across various plant species of the African tropical forest. The absence of any recent demographic signal, despite substantial fragmentation during the last glacial/interglacial cycles, was interpreted by Hardy et al. (2021) and Ernst et al. (2025) in the context of Maley's refuge hypothesis (Maley, 1996). This hypothesis posits that repeated Quaternary cold and dry periods contracted and fragmented Afrotropical forests into isolated refugium patches, before expansion phases and populations secondary contacts took place during wet periods. Genetic evidence, however, points toward a more nuanced and species-specific response, wherein species distribution ranges were fragmented, according to a pattern that varied depending on differences in life-history traits and ecological preferences (see reviews by Hardy et al., 2021 and Ernst et al., 2025), in a much similar way as the patterns reported here in species with short (*Canarina canariensis*, *Dracunculus canariensis*) or long (*Apollonias barbuja*, *Persea indica*) generation times. In Afrotropical ecosystems, contrasted demographic histories were recovered for long-lived, shade-tolerant species and pioneer, sun-loving species

with different dispersal capacities. In long-lived, shade-tolerant species with limited dispersal capacities, i.e., species with non-assisted seed dispersal, deep signals of demographic shifts dated back to Pleistocene events. In pioneer, sun-loving species with high long-distance dispersal capacities, i.e., with wind dispersed seeds, more recent signals of demographic shifts dating to the LGM and post-LGM period were identified (Piñeiro et al., 2021). Indeed, high dispersal capacities allow for a better genetic mixing, “overwriting” the signature of old demographic variations by more recent events in the genome, whereas low dispersal capacities prevent homogenization of allele frequencies, contributing to maintain genetic structures for longer periods. This same pattern was also visible in meta-analyses, showing that habitat fragmentation and degradation have lower or delayed effects on the genetic diversity of long-lived species, proportionally to the number of generations since the disturbance event (González et al., 2020; Vranckx et al., 2012; Aguilar et al., 2008).

In line with those results, species with short generation times growing in humid conditions like *Canarina canariensis*, *Dracunculus canariensis* or *Luzula canariensis* showed important increases in population size after the LGM and during the African Humid Period (AHP) (see Chapter 3, Figure 5 for a summary of demographic events across all species, or Chapter 3, supplementary Figure S23 to S33 for detailed results by species). In contrast, species with short generation time, but growing in more arid conditions, like the grass species *Brachypodium arbuscula* or the bush species *Retama rhodorhizoides*, showed different signals. A slow, steady N_e decrease was found for *B. arbuscula* (Tenerife population) since the LGM period, and 95% IC tends to suggest the La Gomera population also underwent a genetic bottleneck during the AHP (see Figure S25). In *R. rhodorhizoides* (La Palma + Gran Canaria cluster) conversely, a sharp increase in effective population size was identified during the AHP. These patterns can be linked to a West African Monsoon northward limit reaching the Canarian latitude at peak of humid periods during the AHP (Pausata et al., 2016; von Suchodoletz et al., 2010), but also to intrinsic dispersal capacities as *B. arbuscula* has short-distance dispersal capacities, whereas the seeds of *R. rhodorhizoides* are dispersed through endozoochory (Chapter 3, Table 1), i.e., long-distance dispersal capacities. A vegetation turnover identified in the pollen record (Nogué et al., 2013; Castillan-Beltrán et al., 2021) further emphasized the importance of the AHP for shaping the Canarian ecosystems, with a rapid decrease in abundance of hygrophilous taxa like *Salix canariensis* or *Phoenix canariensis* around 6000-5500BP in La Gomera, concomitant with an increase in common laurel forest taxa. This palynological pattern was also recorded in continental Africa sediments (Lézine et al., 2025, 2019, 2005), showing important modifications of species

distribution during the AHP along strong decreases in freshwater discharges between 7100 and 5500BP (Lézine et al., 2025).

More ancient demographic shifts were inferred for species with longer generation time, which aligns with findings in Afrotropical continental species according to which the inherent inertia associated with long generation time species prevents to detect demographic signatures of relatively recent events such as the LGM in the genome (see reviews by Hardy et al., 2021 and Ernst et al., 2025 on Afrotropical species, and Gargiulo et al., 2025 on genetic response delay). Furthermore, old strong genetic structuring signals were shown to persist even after major population disruptions like habitat reduction and fragmentation, making it possible to date the habitat disruption through this strong signal decline (Sgarlata et al., 2025). Our results show a strong signal of N_e increase during the Last Glacial Period or sometimes even before the last interglacial period (Eemian). This period corresponds to a climatic shift from tropical to Mediterranean like, thus promoting species exchanges between islands and mainland (Caujapé-Castells et al., 2022; García-Verdugo et al., 2019; Fernández-Palacios et al., 2011). This old signal could also represent a complete isolation of the species after the extinction of the taxon on mainland, as has been hypothesized as the “late Pleistocene endemism increase hypothesis” (Caujapé-Castells et al., 2022).

In fact, the signal for ancient demographic events reported here could also reflect departures of our data from the assumptions of the *STAIRWAYPLOT2* analyses. Stairway plots results are recovered from coalescent estimates and according to all hypotheses going along this theory, e.g., a unique panmictic isolated unstructured population (Liu & Fu, 2020). Different recent theories (Rodríguez et al., 2018; Mazet et al., 2016) show that very similar effective population size demographic histories (or curve trajectories) can arise from various processes like connectivity between populations, population and subpopulation sizes and number, different sampling strategies, etc. (Fedorca et al., 2024; Mazet & Noûs, 2023; Boitard et al., 2022; Chikhi et al., 2018). In an archipelago context, an expansion signal can represent a real population size increase through range expansion, but also an increase in the connectivity between islands during the last glacial period and associated lower sea level (Fernández-Palacios et al., 2016), or a founder event and associated genetic drift.

5.3 Implications for taxonomy and conservation

5.3.1 Taxonomical applications

The phylogeographic analyses implemented in the present thesis led to the discovery of two hitherto undescribed species in the leafy liverwort genus *Plagiochila* and in the tree genus *Heberdenia*, while also suggesting possible hitherto undescribed differentiation in the tree genus *Persea*.

5.3.1a *Plagiochila* sp. nov.

During the analyses of ancestral range estimation in Chapter 1, I computed the phylogeny of the liverwort genus *Plagiochila* sect. *rutilans* that contains a Macaronesian endemic species (*P. maderensis*). In an unexpected way, the continental (Ireland) and Madeiran accessions of *Plagiochila exigua* (Taylor) Taylor did not cluster together in the Bayesian phylogeny (Figure 5). *P. exigua* is a liverwort species with a wide distribution area including the Macaronesian region, growing on all continents except Oceania. We decided to study this species in more details across its entire distribution range to determine if there are various cryptic species hiding within this complex. Herbarium specimens were retrieved for most regions where the species occur (see Table 3). We received Norwegian specimens from the Museum of Archaeology and Natural History of Trondheim (TRH), South American specimens from the Muséum National d'Histoire Naturelle de Paris (PC), Central American specimens from the Universidad Nacional Autónoma de México (MEXU), North American specimens from the Cryptogamic Herbarium of Duke University (DUKE), Chinese specimens from the Guangxi Institute of Botany (IBK), East African specimens from the Herbarium of Eszterházy Károly University (EGR) and Meise Botanic Garden (BR). We also have fresh material from Madeira (2023) and Canary Islands (2024), along with herbarium specimens from all Macaronesia including the Azores held in Université de Liège Herbarium (LG). Our Portuguese collaborator, Manuela Sim-Sim, also investigated morphological features from different specimens from Madeira and diverse locations from the Royal Botanic Garden Edinburgh Herbarium (E).

In March 2024, I secured 500€ in funding from the Fondation VAN BENEDEN (ULiège Fondations) to launch the project. We plan to sequence 48 individuals for two genes (*ITS* and *rps4*). Initially, we will test a direct PCR approach using a standard Taq polymerase. If unsuccessful, we will proceed with specialized direct PCR kits until we obtain sequences covering the species' full distribution range.

Table 3 – Geographic distribution of the *Plagiochila exigua* (Taylor) Taylor specimens currently available in the framework of our project.

Region	Number of individuals	Collection date
North America	2	2022
Central America	2	2009-2010
South America	5	2008-2011
Europe	33	1899-2018
East Africa	18	1972-2022
Asia	2	2021
Macaronesia	49	1982-2024

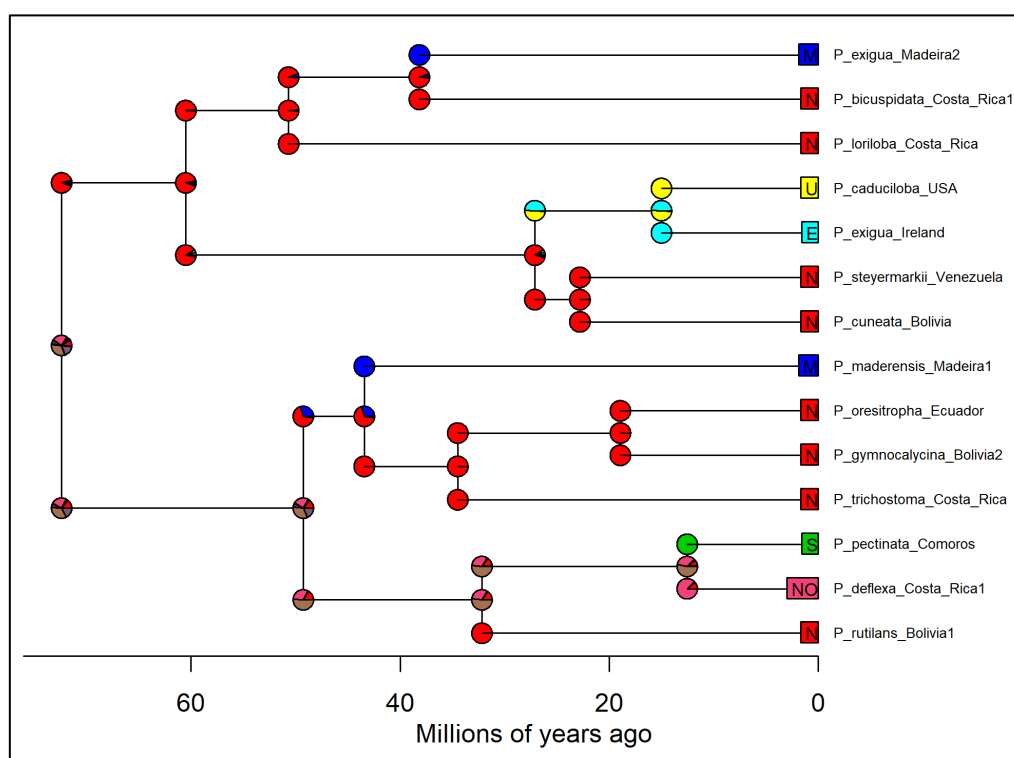


Figure 5 – Ancestral range estimation of the genus *Plagiochila* sect. *rutilans* on a dated Bayesian phylogeny. The two specimens of *P. exigua* are visible at the top in dark blue (Madeira) and the 5th line in light blue (Ireland). M = Macaronesia; E = Europe and the Mediterranean; U = North America; N = South America; O = Others. Each colour represents a region or a unique combination of regions.

5.3.1b *Heberdenia*

Heberdenia excelsa (Aiton) Banks ex A.DC. was already considered a complex of two cryptic species based on molecular and morphological evidence and habitat preference (thermo-sclerophyllous woodland vs laurel forest) (Alfredo Reyes-Betancort, personal communication). When working on the genetic data of the present thesis, the two species were also resolved as two distinct groups, but a third group including only Madeiran specimens was further resolved in the genetic clustering analysis. The pairwise F_{ST} between the two Canarian species (0.54) on the one hand, and between the putative new Madeiran species and the two Canarian species (0.47 and 0.43), are similar, supporting the notion that the Madeiran clade deserves taxonomic recognition at the same level as the two Canarian species. Investigators from both archipelagos were contacted in order to start a collaboration with the aim of describing the three cryptic taxa together, both from a morphological and genetic point of view. Currently, a preliminary analysis of morphological features from herbarium specimens was conducted by Alfredo Reyes-Betancort (director of El Jardín de Aclimatación de La Orotava, Puerto de la Cruz, Tenerife) and Miguel Menezes de Sequeira (director of the Jardim Botânico da Madeira, Funchal, Madeira), but further investigation needs to be done regarding flower and fruit characterization.

Phylogenies computed for this side-project (Figure 6) showed the same pattern of three well separated groups, with a shorter phylogenetic distance between the Madeiran cluster and the Canarian laurel forest clade than with the Canarian thermo-sclerophyllous clade. A plausible hypothesis could be that the ecological preferences evolved first, with laurel forest specialists on one side, and thermo-sclerophyllous woodland specialists on the other. Later, dispersal from the Canary Islands to Madeira (or vice versa) of the laurel clade could have led to the isolation of a new Madeiran lineage.

In this thesis, we limited the sampling in Madeira to one population per species, but it would be interesting to investigate more populations both in Madeira and the Canary Islands, focusing on ecological preferences, but also by adding individuals from El Hierro where this species is very rare and difficult to access. On the Madeiran side, doubts exist regarding the individuals growing on Porto Santo island as they might be different from the ones growing on Madeira Island. Furthermore, the thermo-sclerophyllous clade was only sampled from Teno on Tenerife, with two individuals from Gran Canaria probably originating from a restoration initiative with plant material coming from Teno as well. This taxon is also known to grow on La Gomera, and a more exhaustive sampling could lead to interesting new findings.

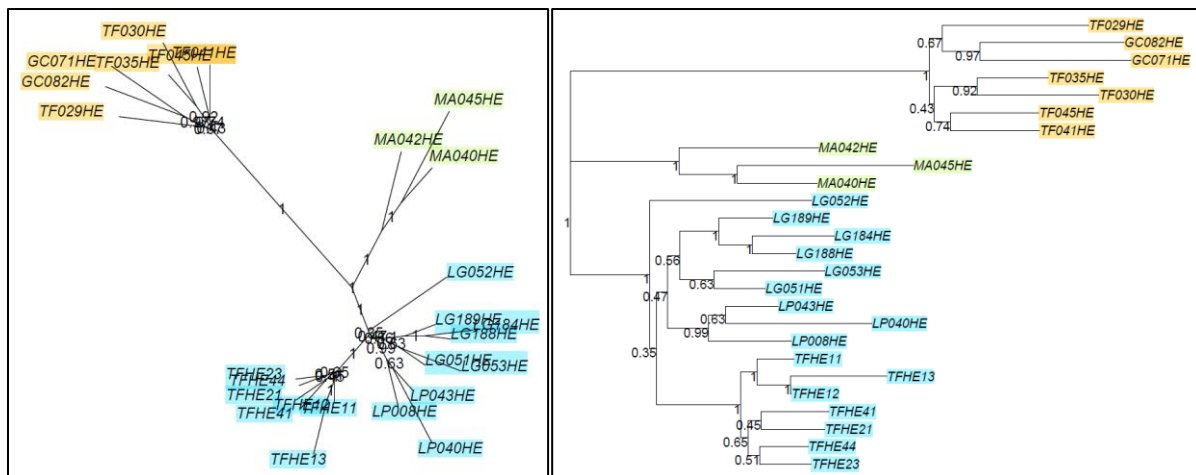


Figure 6 – *Heberdenia excelsa* (Aiton) Banks ex A.DC. Maximum Likelihood phylogeny, with bootstrap proportions indicated at each node. Individuals from Madeira are colored in green, Canarian individuals are in blue for the laurel forest clade and yellow for thermo-sclerophyllous woodland clade. Left = unrooted phylogeny, right = empirically rooted phylogeny.

5.3.1c *Persea* sp. nov.

When working on the genetic diversity data in Chapter 3, and more specifically on *Persea indica* (L.) Spreng., we found a pairwise F_{ST} value of 0.71 between the populations from the Canary Islands and Madeira, which was strikingly higher than any other F_{ST} value in the remaining of the investigated species. There are suspicions of cryptic differentiation within this species (Miguel Menezes de Sequeira, personal communication) and, based on the genetic clustering showing almost no shared ancestry in the investigated samples (Figure 7), the PCA, the neighbour-joining and maximum likelihood phylogenies (not shown), our results support this interpretation.

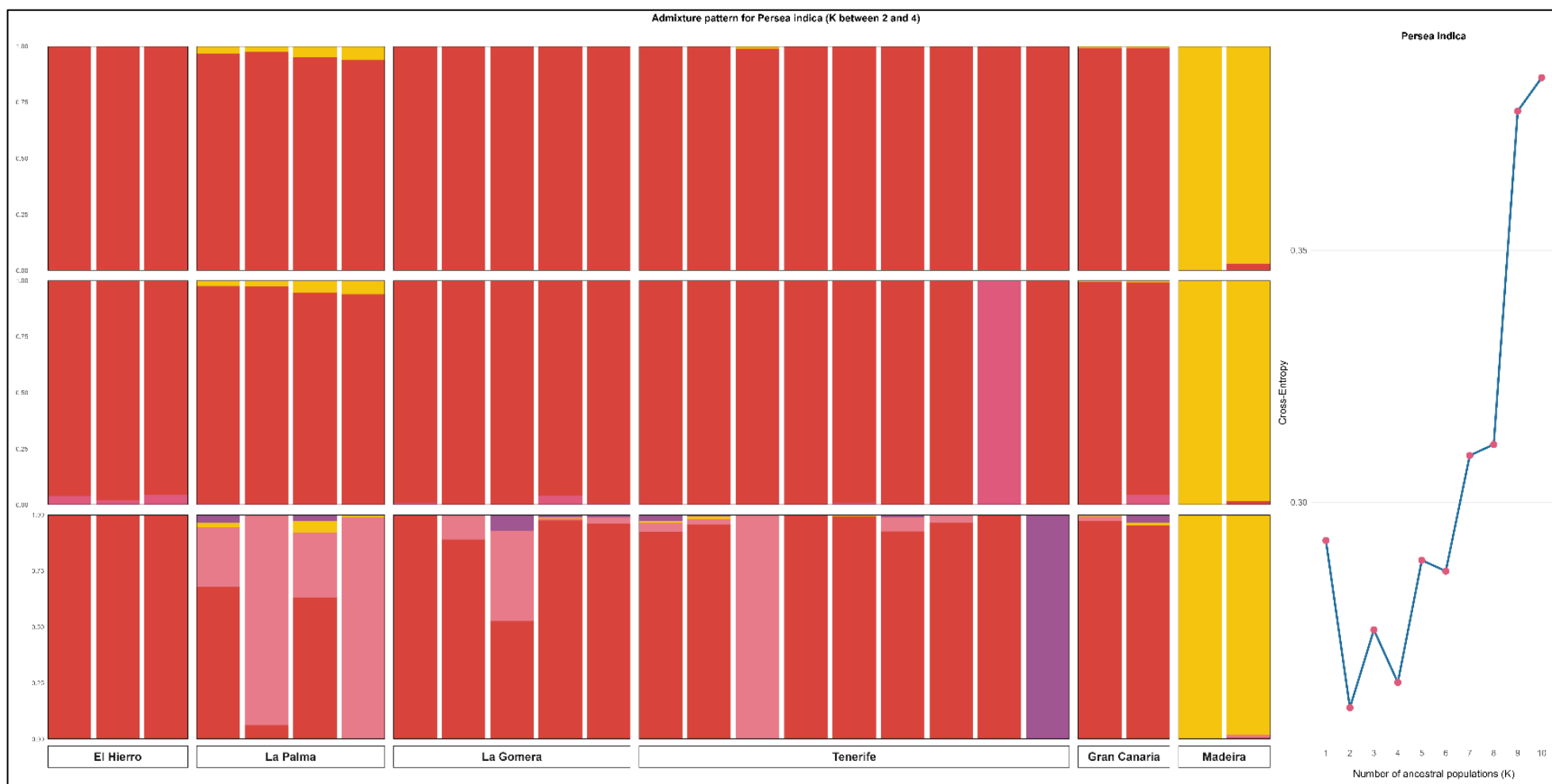


Figure 7 – genetic clustering results for *Persea indica* (L.) Spreng. Admixture patterns (left) according to lowest values of cross-entropy for K populations (right), with the lower K above, increasing toward the bottom. Individuals are grouped by islands and ordered according to longitude, with Madeira specimens on the right. K values are indicated in the title.

5.3.2 Conservation applications

Beyond species extinctions and the local decrease in species richness, the loss of genetic diversity is a huge contemporary issue, as emphasized in the Convention on Biological Diversity's Kunming-Montreal Global Biodiversity Framework (www.cbd.int/convention/text/). Conservation actions, and in particular, population translocation to boost the genetic diversity of a decreasing population or to re-introduce a species where it went extinct due to human disturbance, can mitigate the problem, but need to be undertaken within an explicit phylogeographic framework. In fact, failure to take the population genetic structure of a species into account may lead to the decrease or even extinction of a local strain or taxon due to the introduction of an allochthonous strain, eventually accelerating the loss of local, endemic genetic diversity (Shaw et al., 2025).

While analyzing the genetic structure of *Apollonias barbujana*, we found that some individuals from La Gomera show mixed ancestry between the eastern (native strains from La Gomera) and western (La Palma and El Hierro) genetic clusters. The existence of individuals admixed at 50-50% or 25-75% suggests that individuals from La Palma and El Hierro were introduced in La Gomera, where they hybridized with the local strain.

Another intriguing pattern found in our genetic structure analyses was the inclusion of individuals from an island within the genetic cluster otherwise endemic to another island. For example, an *A. barbujana* specimen from Gran Canaria was more closely related to the Tenerife cluster than to the Gran Canaria cluster, and young individuals of *Heberdenia excelsa* from the thermo-sclerophyllous woodland clade of Tenerife were found in the Finca de Osorio laurel forest on Gran Canaria. Although natural dispersal cannot completely be discarded, these results likely point to translocations of specimens from one island to another in the framework of restoration initiatives taking place during the 1970s or before. No real archives exist regarding restoration actions in the Canary Islands prior to the 70s, and even more recent documentation is scarce and difficult to access. First-hand accounts from the Environment Department (*Medio Ambiente*) staff in Gran Canaria explained that population reinforcement took place throughout the island from populations originating from other islands. Furthermore, Ángel Fernández Lopez, former director of the Garajonay National Park on the island of La Gomera, told me that many specimens from a wide range of species were grown in their plant nurseries and shipped to other islands at the end of the 20th century. In particular:

- *Apollonias barbujana*, and probably *Persea indica* from La Gomera and Tenerife were planted in the periphery of Los Tiles de Moya Rural Park (Gran Canaria).

- *Heberdenia excelsa* was planted in Finca de Osorio and Barranco de las Ánimas (Gran Canaria) using specimens from other islands.
- Specimens of *Persea indica*, *Laurus novocanariensis*, *Apollonias barbujana* from Garajonay National Park were shipped to other islands. Specifically, all specimens of *Persea indica* from El Hierro come from Garajonay National Park.

To discriminate natural dispersal events from human-mediated introductions, analyses aiming at dating introgression events among populations are currently implemented. Preliminary results from analyses with the software *DILS* (Fraïsse et al., 2021) have already shown that the genetic clusters in *A. barbujana* have been isolated for thousands of generations, implying that the recently admixed individuals are probably not the result of naturally occurring colonization processes. Further analyses are on their way using more powerful software programs such as *dadi* (Gutenkunst et al., 2009) and its extension *moments* (Jouganous et al., 2017), in order to evaluate in more details the past connections between genetic clusters. We will also investigate the potential of a range of analyses to study the observed admixture patterns: R packages such as *hybriddetective* (Wringe et al., 2017a), *admixr* (*admixtools* software suite on R; Petr et al., 2019) and *parallelnewhybrid* (*NewHybrid* software on R; Wringe et al., 2017b), software such as *AdmixtureBayes* (Nielsen et al., 2023). An interesting implementation would also be to model projections of the current genetic diversity, including the translocated individuals, under future climatic conditions. This approach has been described in the literature (Henry, 2025), and could be really important in the context of the Canary Islands as native species will almost all lose climatically suitable areas with climate change (Hanz et al., 2023). For instance, the software *SLiM* would be used as it is widely used in conservation genetics studies (Haller et al., 2026).

5.4 CONCLUSION AND PERSPECTIVES

The present thesis opens the door to two main axes of research in island and historical biogeography.

Insular bryophyte distribution patterns

In island biogeography, a well-known pattern is ‘Island Disharmony’, i.e., the different proportions of some taxonomic groups between insular and mainland regions assumed to be their geographic source origin (Carlquist 1966, 1974). A possible perspective to our results would be to explicitly test the disharmony pattern using liverworts in the modelling context developed by König et al. (2023). Their work aimed at finding clues to what makes islands more prone to show over- or under- representation of certain clades compared to their mainland source regions, and to find out which clades show the highest levels of disharmony among oceanic floras worldwide. Here, I propose to follow the same approach using liverworts as a model to quantify the levels of island disharmony in the group and investigate the underlying mechanisms. Liverworts appear as a suitable model for addressing the question of island disharmony because a complete database of species distribution across the world is already available (Söderström et al., 2016). Second, a phylogeny of all liverwort genera is available (Bechteler et al., 2023), which may allow us to include phylogenetic distances as an explanatory variable, and see if niche conservatism within closely related species plays a role in the disharmonic pattern. Third, different databases exist regarding functional traits of liverwort species (Van Zuijlen et al., 2023), including their micro-habitat preferences (pH, humidity, life mode...) and architectural conformations (septum orientation, spore size, sporophyte length...), that will allow us to see the role of functional diversity in shaping the disharmonic pattern as well.

GUACAMOL: next steps

Our demographic reconstructions gave us information about the general trends in species effective population size through time, but this descriptive approach lacks an explicit framework to test specific hypotheses. In particular, model selection approaches using coalescence simulations in an Approximate Bayesian Computation framework (e.g. Xie et al., 2026; Kastally et al., 2025; Gibert et al., 2024) would be particularly relevant. In the framework of our study on anthropic impact on the genetic diversity of Macaronesian and Canarian endemic plant species, our results could be complemented by directly testing this impact. Using the software *fastsimcoal2* (Excoffier et al., 2021), we will test four competing scenarios per genetic cluster: with or without anthropic impact, with or without climatic impact during the Last Glacial Maximum. This same approach could also be used to test different scenarios of colonization

routes to see how our species reached their current distribution area, thus making it possible to interpret our stairway plots in a migration context.

Furthermore, the extinction debt found in the Canary Islands (Otto et al., 2017) could be formally tested based on the genetic data produced here. Each island has its own features and was subjected to different amounts of disturbance: their size, altitude, environmental complexity, climate, distance to continent, human population density, agriculture intensity, percentage of natural vegetation remnants, etc. Using information similar to Norder et al. (2020), a simple model could be used to explain nucleotide diversity (π) according to these variables as explaining factors, and the island could be used as random factor. We could also test this methodology by implementing a single model with all the species together, the species identity being implemented as random factor along with the island.

Finally, we could also implement network analyses. A shortcoming of the simple model approach is that many explaining factors will more than probably be correlated with each other, such as the population density and the island size and proximity to continent. The network analysis would be able to draw connections between the different factors and the genetic diversity in order to describe the whole picture, and quantify the links between factors.

Ancient DNA analyses

No ancient DNA study was, to my knowledge, conducted on native plant species in the Canary Islands. Working with remains of plant materials (seeds, stems, leaves...) preserved in archeological sites or within sediments (sedaDNA) would allow a direct comparison of the past genetic diversity with our results. Our DNA extraction protocol did not permit exploitation of *Visnea mocanera* samples (80 individuals across the whole distribution range including Madeira), but this species in particular would be interesting to study at different periods of time as it was widely used by Guanches and other people of the Canary Islands as food source. Furthermore, seeds of this species have been recovered from old granaries archeological sites from at least three of the seven islands (Morales & Gil, 2014).

The ultimate Guanche legacy

Guanche funeral rituals involved that dead bodies were washed, emptied and refilled with ointments prepared from various plants and minerals. Plant remains found within mummies could be used to investigate the taxonomic composition, but also the allelic structure and diversity of land plants that composed the Canarian landscape 2000 years ago. In particular, moss material was found in 1991 in a Guanche mummy preserved in Montréal (Horne & Ireland, 1991), implying that it is probably also available from other mummies. Recent investigations of plant remains found in this context showed that this unexpected source of information can be used to discover, for instance, new endemic species that went extinct (Marrero-Rodríguez et al., 2023). Through their mysterious mummies prepared following a formula that went lost in the course of time, the Guanches have left an entire library of life representative of the biodiversity that surrounded their civilization, which fast developing ancient DNA techniques will hopefully shortly allow us to read more than 2000 years later.

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Spatial resolution impacts projected plant responses to climate change on topographically complex islands

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Abstract

Aim: Understanding how grain size affects our ability to characterize species responses to ongoing climate change is of crucial importance in the context of an increasing awareness for the substantial difference that exists between coarse spatial resolution macroclimatic data sets and the microclimate actually experienced by organisms. Climate change impacts on biodiversity are expected to peak in mountain areas, wherein the differences between macro and microclimates are precisely the largest. Based on a newly generated fine-scale environmental data for the Canary Islands, we assessed whether data at 100m resolution is able to provide more accurate predictions than available data at 1 km resolution. We also analysed how future climate suitability predictions of island endemic bryophytes differ depending on the grain size of grids.

Location: Canary Islands.

Time period: Present (1979–2013) and late-century (2071–2100).

Taxa: Bryophytes.

Methods: We compared the accuracy and spatial predictions using ensemble of small models for 14 Macaronesian endemic bryophyte species. We used two climate data sets: CHELSA v1.2 (~1 km) and CanaryClim v1.0 (100m), a downscaled version of the latter utilizing data from local weather stations. CanaryClim also encompasses future climate data from five individual model intercomparison projects for three warming shared socio-economic pathways.

Results: Species distribution models generated from CHELSA and CanaryClim exhibited a similar accuracy, but CanaryClim predicted buffered warming trends in mid-elevation ridges. CanaryClim consistently returned higher proportions of newly suitable pixels (8%–28%) than CHELSA models (0%–3%). Consequently, the proportion of species predicted to occupy pixels of uncertain suitability was higher with CHELSA (3–8 species) than with CanaryClim (0–2 species).

Jairo Patiño and Flavien Collart have contributed equally to this work.

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