



# Patterns and drivers of beta diversity across geographic scales and lineages in the Macaronesian flora

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## Abstract

**Aim:** How spatial, historical and ecological processes drive diversity patterns remains one of the main foci of island biogeography. We determined how beta diversity varies across spatial scales and among organisms, disentangled the drivers of this variation, and examined how, consequently, biogeographic affinities within and among archipelagos vary among land plants.

**Location:** Macaronesia.

**Taxon:** Bryophytes, pteridophytes, spermatophytes.

**Methods:** Species turnover and nestedness were compared within and among archipelagos across taxonomic groups. The relationship between species turnover and nestedness, climatic, geological and geographic factors was analysed using generalized dissimilarity models.

**Results:** Species turnover, but not nestedness, increased with the geographic scale. This increment decreased from spermatophytes, pteridophytes and bryophytes, wherein the median turnover was less than half that in spermatophytes. Bryophytes exhibited a significantly higher nestedness and lower turnover than spermatophytes. Extant climatic conditions and island age contributed the most to all models but the importance of island age for bryophyte and pteridophyte turnover was marginal. Spermatophyte floras clustered by archipelago, whereas the clustering patterns in pteridophyte and bryophyte floras reflected macroclimatic conditions.

**Main Conclusions:** The lower increment of species turnover with spatial scale and the higher nestedness in bryophytes and pteridophytes than in spermatophytes reflect the variation in dispersal capacities and distribution ranges among land plants. Accordingly, extant climatic conditions contributed more to explain turnover in bryophytes and pteridophytes than in spermatophytes, whereas factors associated with dispersal limitations, including island age, geographic distance and archipelago structure, exhibited the reverse trend. The differences in beta diversity patterns, caused by different responses of Macaronesian land plant lineages to the main factors shaping their community composition, explain their different biogeographic affinities. These differences reflect a distinct origin and different mechanisms of speciation among Macaronesian land plant lineages and archipelagos.

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## 1 | INTRODUCTION

How spatial, historical and ecological processes drive diversity patterns, and how area, elevation and isolation influence community composition, are two of the main foci of island biogeography (Patiño et al., 2017). Beta diversity, the variation of biological communities through space and time, measures changes in community composition along environmental, spatial and temporal gradients (Soininen et al., 2018). This metric can be partitioned into two process-related components: species replacement (turnover) and richness difference (nestedness) (Baselga, 2010). Species turnover characterizes changes in species composition along gradients of geographical and/or ecological distance (Qian et al., 2020), whereas nestedness occurs when a set of species at one site is a subset of the species at a richer site, which has been interpreted in terms of ordered extinction events (Baselga, 2010).

Beta diversity varies depending on both extrinsic (environmental) and intrinsic (biological) factors related to species niche breadth and dispersal capacities. For instance, species turnover is expected to be inversely proportional to species dispersal capacities (Soininen et al., 2018; Varzinczak et al., 2019). In land plants, this hypothesis is in line with the steeper slope of the species-area relationship reported in spermatophytes than in pteridophytes and bryophytes explained by the production of smaller, wind-dispersed diaspores in the two latter groups (Patiño, Weigelt, et al., 2014). Furthermore, since nestedness can only arise for areas that share a common source pool, a high nestedness at large scales is expected in organisms with high dispersal capacities (Greve et al., 2005).

Beta diversity also varies depending on geographic scale (Soininen et al., 2018). If an increase in species turnover with geographic scale due to dispersal limitations and stronger environmental filtering over larger environmental gradients has been recurrently documented (Gusmao et al., 2020; Qian et al., 2020; Soininen et al., 2018), the relationship between nestedness and geographic scale has been more controversial. Nestedness is expected to peak at a small scale if local variations of habitat quality and availability lead to variation in species richness within habitats among sites (Gusmao et al., 2020). In contrast, high nestedness at large scales is expected when extinctions vary depending on major geographic gradients (Soininen et al., 2018). In particular, nestedness is expected to increase with latitude (Batista et al., 2021; Soininen et al., 2018).

Oceanic islands offer an ideal framework to investigate the variation of species turnover and nestedness across geographic scales and to determine the relative contribution of contemporary climatic factors and dispersal limitations associated with geographic

isolation. Oceanic islands are readily geographically circumscribed (Whittaker & Fernández-Palacios, 2007), offering naturally isolated and often replicated operational geographic units (OGUs). Furthermore, because they were colonized *de novo*, oceanic islands accumulate species from continental or alternative insular sources at rates depending on connectivity and *in situ* speciation (Whittaker & Fernández-Palacios, 2007) that vary with geographic isolation, environmental complexity, island age and species dispersal capacities (Heaney, 2000).

In particular, the three northern archipelagos of the Macaronesian region (the Azores, Madeira and Canary Islands) have long been identified as an excellent model for hypothesis testing in biogeography (Florencio et al., 2021). In fact, these archipelagos vary in terms of geographic isolation and macroclimatic conditions, so that their floras exhibit sharply different distribution patterns. In the Canarian spermatophyte flora, single-island endemics (SIEs) are much more frequent than multiple-island endemics (MIEs), whereas the reverse pattern prevails in the Azores (Carine & Schaefer, 2010). This, together with the sharper ecological gradients in the Canaries (and to some extent in Madeira), has led to the idea that speciation in the Canaries is primarily driven by ecological radiations, whereas allopatric speciation prevails in the Azores among islands that are more distant among each other and from continental sources than in the Canaries (Carine & Schaefer, 2010; Price et al., 2018). Spore-producing plants exhibit a lower proportion of SIEs and a higher proportion of Macaronesian regional endemics (i.e. taxa that are endemic to two or more Macaronesian archipelagos) than spermatophytes (Vanderpoorten et al., 2011), owing to their higher dispersal capacities, allopatric speciation modes and ecological affinities (Patiño, Carine, et al., 2014). Therefore, biogeographic relationships across Macaronesia vary among major land plant groups. The grouping of spermatophyte floras reflects the structure of archipelagos (de Nicolás et al., 1989), whereas floristic analyses at the archipelago level revealed conflicting relationships among spore-producing floras (Vanderpoorten et al., 2007).

Building on previous analyses on the drivers of the spatial variation of plant species richness (Aranda et al., 2014; Hobohm, 2000) on the one hand, and on the partitioning of beta diversity in Macaronesian vascular floras (Chiarucci et al., 2010) on the other, we examine how the components of beta diversity vary across spatial scales among the four main lineages of land plants, namely liverworts, mosses, pteridophytes and spermatophytes, and identify what are the drivers of this variation. In this framework, we address the following questions and test the following hypotheses:



- How does beta diversity vary across taxa and archipelagos? We expect that species turnover increases from intra- to inter-archipelago comparisons (H1a). We expect this increase to be significantly lower for spore-producing plants than for spermatophytes (H1b).
- Does nestedness decrease with increasing spatial scale and do the patterns differ for different groups? We test the hypothesis that nestedness decreases from intra to inter-archipelago comparisons (H2a). We expect that this decrease is stronger from spermatophytes to ferns, and then, bryophytes (H2b), due to the presumed higher dispersal capacities and, hence, higher proportion of shared species across archipelagos in spore-producing plants.
- What are the drivers of beta diversity, and how do they vary among taxa? We expect that climatic variation is more important than geographical isolation and island age in explaining species turnover for bryophytes and pteridophytes, and that geographical isolation does not correlate with bryophyte and pteridophyte nestedness, whereas we expect the reverse patterns for spermatophytes (H3).
- How do biogeographic affinities within and among archipelagos vary among land plants? Following de Nicolás et al., (1989) and del Arco Aguilar and Rodríguez Delgado (2018), we expect that islands cluster primarily by archipelago in spermatophytes, but not in spore-producing plants, wherein islands are expected to cluster depending on climatic similarity, irrespective of the archipelago in which they are found (H4).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Macaronesia (Figure 1) is a biogeographic region located in the Atlantic Ocean between 15.8 and 40.8°N (Florencio et al., 2021). We focused here on the Azores, Madeira (including Madeira, Porto Santo, and the Desertas islands) and the Canary Island archipelagos. Within the latter, we tested the impact of the inclusion of the islets of Isla de Lobos, Montaña Clara, Alegranza and Graciosa, whose size and elevation are, respectively, more than 95 and six times lower than that of the main Canarian islands. The Desertas include Deserta Grande, Chão and Bugio. Due to their very small size, close proximity to each other, connection during the Last Glacial Maximum and very low species richness, these islands are treated as a single unit in available species lists, a position that we also adopted here. We excluded Cabo Verde, whose cryptogamic flora clearly belongs to sub-Saharan Africa (Vanderpoorten et al., 2007), and the Selvagens, whose very limited flora and number of islands did not warrant inclusion in the present analyses.

### 2.2 | Data collection and matrices

Lists of moss, liverwort, pteridophyte and spermatophyte species per island were retrieved from a review of the literature and

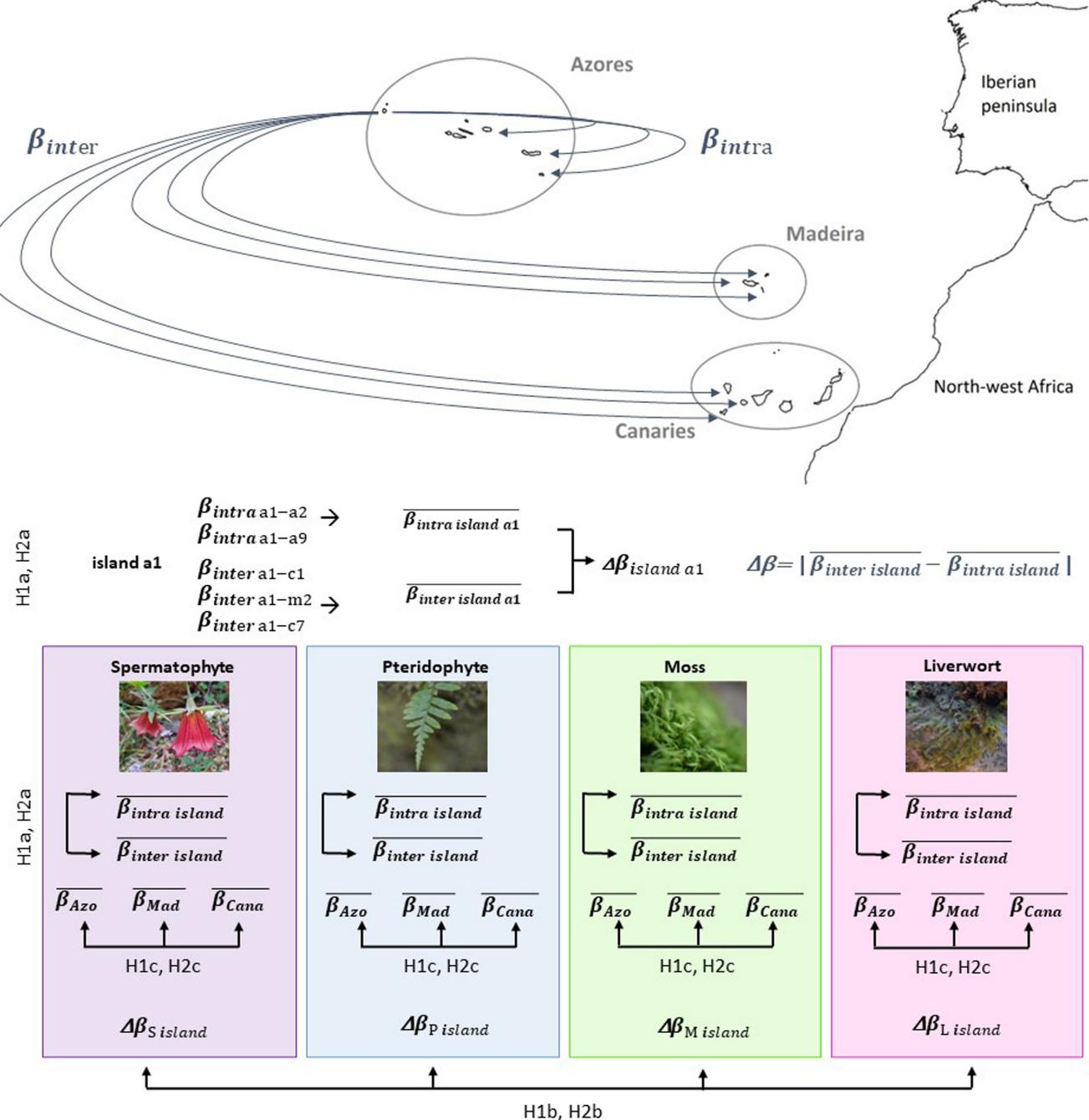
personal unpublished observations of the authors (Appendix S1). Sub-species, whose circumscription is typically associated with a restricted geographic range (Mallet, 2013), and are hence potentially informative in spatial analyses of taxonomic composition among OGUs, were included. Due to the very low number of hornwort species (6), the latter were included within liverworts, to which they are the most similar in terms of morpho-anatomy and life-history traits. Nomenclature was standardized following Hodgetts et al. (2020) for mosses and liverworts, Hassler (2018) for pteridophytes and Euro+Med (2006) for spermatophytes. In bryophytes, *Isothecium interludens*, *Racomitrium affine*, *Lophocolea coadunata* and *Frullania tamarisci* agg., which have recently been raised at species level, were not distinguished pending for a critical re-assessment of their distributions. *Bryoxiphium madeirensis* was considered as a synonym of *B. norvegicum* based on phylogenetic evidence (Patiño et al., 2016).

Introduced species were excluded from the analysis as they lead, at the geographic scale of entire islands, to a substantial human-induced homogenization of their floras (Otto et al., 2020). Assessing the native status of a taxon is challenging, and this status may further vary for the same taxon among archipelagos (e.g. *Clethra arborea*, Madeiran endemic invasive in the Azores), or even among islands from the same archipelago (e.g. *Echium nervosum* introduced from Madeira to Porto Santo), preventing us from defining a global list of introduced species across Macaronesia. We therefore relied on the status defined for each taxon by the most recent databases (Appendix S1) for each archipelago. Many widespread Mediterranean species considered as native in the Canary Islands and Madeira, such as *Helminthotheca echioides*, *Hypochaeris radicata* and *Trifolium* spp., are, however, considered as introduced in the Azores, whereas they thrive in the same kinds of habitats across archipelagos. We thus performed a second set of analyses, wherein all species considered as introduced in the Azores, and for which unambiguous evidence of a native status was missing in the Canary Islands and Madeira is missing (Table S16), were excluded. Species distribution matrices were employed to compute, for each of the four lineages considered, species turnover, expressed here as Simpson dissimilarity index ( $\beta_{sim}$ ) and nestedness-resultant dissimilarity ( $\beta_{sne}$ ) among all possible pairs of islands using the package 'betapart' (Baselga et al., 2021) in R 4.2.1. (R Core Team, 2020).

Environmental variables included climatic conditions (annual mean temperature, minimum annual temperature range, annual precipitation and minimum coefficient of variation in monthly precipitation), geographic distance among islands, area, elevation, distance to the closest mainland, and age of each island. The first nine variables were recorded from Weigelt et al. (2013) while island age was obtained from Torre et al. (2019).

### 2.3 | Data analysis

Comparing turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) among islands within and among archipelagos (H1a, H2a, Figure 1) involves the inclusion of the same observation multiple times (the same



**FIGURE 1** Study area and statistical framework to calculate beta diversity ( $\beta$ ) and its two components, turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) between islands within (intra) and between (inter) archipelagos (Azores: Azo, 9 islands labelled as a1-a9, Canary Islands: Cana, 7 islands labelled as c1-c7, and Madeira: Mad, 3 islands labelled as m1-m3) among land plant lineages (spermatophytes: S; pteridophytes: P; mosses: M; and liverworts: L).

occurrence of a species on an island serving to compute  $\beta_{sim}$  and  $\beta_{sne}$  both within and among archipelagos), violating the assumption that the observations are independent from each other. We therefore computed, for each island, the average  $\beta_{sim}$  and  $\beta_{sne}$  values with all the other islands from the same archipelago ( $\beta_{intra}$ , Figure 1). Then, we computed, for each island, the average  $\beta_{sim}$  and  $\beta_{sne}$  values with each island from the other archipelagos ( $\beta_{inter}$ , Figure 1). The average  $\beta$  values within archipelagos were finally compared to those among archipelagos. Although the data

were homoscedastic (Fisher test = 1 for all lineages), departure from normality for the turnover of spermatophytes and for the nestedness of all lineages (Shapiro test,  $p < 0.01$ ) led us to apply paired Wilcoxon rank tests.

To assess the variation of  $\beta$  from intra- to inter-archipelago comparisons (H1b and H2b, Figure 1), we computed, for each island, the difference ( $\Delta\beta$ ) of the average  $\beta$  between that island and all other islands from the same archipelago ( $\beta_{intra}$ ) and the average beta between that island and all other islands from different archipelagos



( $\beta_{\text{inter}}$ ) (Figure 1).  $\Delta\beta$  values were not normally distributed in the case of turnover for spermatophytes, and in the case of nestedness for mosses, ferns, and spermatophytes. Therefore, non-parametric Friedman's and post-hoc Nemenyi tests, applying Bonferroni correction on the  $p$ -value, were implemented with the package 'PMCMRplus' (Pohlert, 2021) to search for significant differences of  $\Delta\beta$  values per island among lineages. In order to assess, for each lineage, differences of nestedness and turnover among archipelagos, we implemented Kruskal-Wallis and post-hoc Dunn tests, applying Bonferroni correction for multiple comparisons, with the package 'PMCMRplus' (Pohlert, 2021).

To determine how beta diversity varies depending on geographic distance (both among islands and between islands and nearest continents) and variation in climatic conditions, age, area, and elevation across taxa and archipelagos (H3), Generalized Dissimilarity Model (GDM, Ferrier et al., 2007) was employed using the 'gdm' R package (Fitzpatrick et al., 2021) for each of the four lineages independently. To control for the archipelago structure of the data, we assigned each pair of islands from the same archipelago a distance of 0, and each pair of islands from different archipelagos a distance of 1, and then treated this binary distance measure in the same manner as geographical distance (Ferrier et al., 2007). To avoid multicollinearity, we computed Pearson correlation coefficients among each pair of predictors and kept one predictor among any pair with a correlation coefficient  $>0.75$ . As annual mean temperature, annual precipitation, distance to the closest mainland, distance among islands and minimum coefficient of variation in monthly precipitation were strongly correlated, we kept only the latter, hereafter referred to as 'precipitation'. This approach allowed us to identify six predictors, including area, elevation, minimum annual temperature range, island age, precipitation and archipelago. We implemented stepwise backward variable elimination as implemented in the gdm.varImp function of the package 'gdm' (Fitzpatrick et al., 2021) until all variables had a  $p < 0.05$ .

To address hypothesis H4, a cluster analysis of islands as a function of their taxonomic composition was performed using Ward's algorithm based on a total beta diversity matrix derived from Sørensen distances. The optimal number of clusters for each lineage was determined with the 'NbClust' package (Charrad et al., 2014) using 30 indexes (i.e. all indices except GAP, Gamma, Gplus and Tau). To help visualizing the groupings, a classical (Metric) multidimensional scaling (MDS) based on the Sørensen distance matrix was performed.

All the analyses were repeated without the four Canarian islets to examine the impact of the latter on the explanatory power of the models and the clustering patterns, and without 172 spermatophyte species considered as introduced in the Azores, and for which unambiguous evidence of a native status in the Canary Islands and Madeira is missing.

### 3 | RESULTS

Our species distribution matrices ([10.6084/m9.figshare.17099840](https://doi.org/10.6084/m9.figshare.17099840)) included 226 liverwort & hornwort species, 516 moss species, 83

pteridophytes species and 1810 spermatophyte species and subspecies. The proportions of endemics per lineage and archipelago are displayed in Table 1.

For all lineages, paired Wilcoxon tests showed a significant increase of turnover among islands from intra to inter-archipelago comparisons (Figure 2). No significant variation from intra- to inter-archipelago comparisons was observed for nestedness (Table S1). The difference in turnover between intra and inter-archipelago comparisons ( $\Delta\beta_{\text{sim}}$ ) was significantly higher in spermatophytes ( $0.57 \pm 0.12$ ) than in bryophytes and pteridophytes (Friedman test,  $p < 0.01$ ).  $\Delta\beta_{\text{sim}}$  in pteridophytes ( $0.34 \pm 0.08$ ) was significantly higher than in mosses ( $0.25 \pm 0.08$ ) but not than in liverworts ( $0.28 \pm 0.07$ ). Among bryophytes,  $\Delta\beta_{\text{sim}}$  did not differ significantly.

Turnover among islands within archipelagos did not significantly vary among archipelagos for mosses and liverworts (Figure 3a). Turnover was significantly higher in the Canary Islands than in the Azores and Madeira in pteridophytes. For spermatophytes, turnover in the Canary Islands was significantly higher than in the Azores. Nestedness among islands within archipelagos was consistently higher in Madeira than in the Azores and the Canary Islands across lineages (Figure 3b). Probably due to the low statistical power associated with the low number of islands in Madeira (3), the difference of turnover between Madeira and the Canaries, and of nestedness between Madeira and the Azores were, however, not significant for spermatophytes (Tables S3 and S4).

The variation in species turnover and nestedness within archipelagos among lineages is illustrated in Figure 4. Turnover was significantly higher in mosses and spermatophytes than in pteridophytes and liverworts. Mosses, liverworts and pteridophytes exhibited a significantly higher nestedness than spermatophytes.

The GDM explained 67%, 62%, 79% and 92% of the deviance of liverwort, moss, pteridophyte and spermatophyte turnover, respectively. Precipitation and island age were the variables most contributing to all models, but with different relative contributions across lineages (Table S5). Thus, the contribution of island age was about half that of precipitation in spermatophytes, but only about 1/10–1/20 in bryophytes and pteridophytes. The factor 'archipelago' was selected only in spermatophytes.

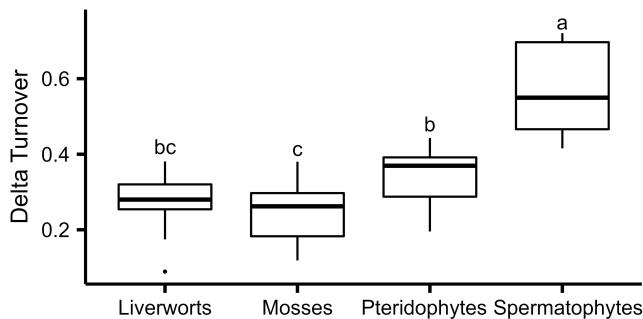
The GDM explained less than 50% of nestedness in liverworts, mosses and spermatophytes and 68% in pteridophytes. Elevation and temperature were selected in all models, but the contribution of the former was about three times higher than that of the latter. Area was selected for spermatophytes while island age was selected for all the spore-producing plants (Table S6).

The groups resulting from the clustering analyses of islands as a function of their species composition in each lineage are shown on the first plane of the NMDS of islands depending on the floristic distance among them (Figure 5). The stress values, a goodness-of-fit statistic that is minimized in MDS and characterizes the extent to which the actual floristic dissimilarities among islands are well represented on the plot, were 0.032 for liverworts, 0.030 for mosses, 0.031 for pteridophytes and 0.042 for spermatophytes, indicating good to excellent fit. In spermatophytes, the



	Azores	Madeira	Canaries	Macaronesia
<b>Liverworts</b>				
Endemic/total/%	3/156/2	4/182/2	1/148/0.7	12/226/5
SIE/% SIE	0/0	2/1	0/0	—
MIE/% MIE	3/2	2/1	1/0.7	12/4
<b>Mosses</b>				
Endemic/total/%	7/295/2	8/359/2	6/359/1.7	16/516/3
SIE/% SIE	3/1	7/1.95	2/0.7	—
MIE/% MIE	4/1	1/0.5	4/1	16/1
<b>Pteridophytes</b>				
Endemic/total/%	4/53/8	5/59/8	3/58/5	7/83/8
SIE/% SIE	0/0	05 August	0/0	—
MIE/% MIE	4/8	0/0	3/5	7/8
<b>Spermatophytes</b>				
Endemic/total/%	69/167/41	141/683/21	653/1398/47	57/1810/3
SIE/% SIE	8/5	97/14	416/30	—
MIE/% MIE	61/36	44/6	237/17	57/3

Abbreviations: MIE, %MIE: number and proportion of multiple islands endemic species and subspecies; SIE, %SIE: number and proportion of single island endemic species and subspecies.



**FIGURE 2** Box-plots (showing the first and third quartiles (upper and lower bounds), second quartile (centre), 1.5× interquartile range (whiskers) and minima-maxima beyond the whiskers) of the difference of turnover ( $\Delta\beta_{sim}$ ) of liverwort, moss, pteridophyte and spermatophyte communities among islands within (intra) and among (inter) archipelagos in Macaronesia (see Table S1 for actual values). Letters above each box-plot indicate, which comparisons significantly differ (see Table S2 for the *p*-values of the post-hoc Friedman Nemenyi tests), identical letters being used for lineages whose turnover does not significantly differ from each other.

three clusters identified correspond to the Azores, the Canary Islands and Madeira. In liverworts, the Azorean islands clustered together, the Canarian islands of Fuerteventura and Lanzarote, and the Desertas of Madeira archipelago, formed a second cluster, while Madeira clustered with Porto Santo and the remaining Canary Islands. The grouping observed with the moss floras was almost identical, except that Porto Santo clustered with Fuerteventura and Lanzarote and the Desertas. In pteridophytes, Madeira clustered with the Azores while Porto Santo and the Desertas (Madeira archipelago), Lanzarote and Fuerteventura

**TABLE 1** Numbers of native and endemic species and subspecies of liverworts, mosses, pteridophytes and spermatophytes in the Azores, Canary Islands, Madeira archipelago and Macaronesia (Macaronesian endemics corresponding to species or subspecies restricted to Macaronesia but distributed across at least two archipelagos).

(Canary Islands) formed a second cluster, and the western and central Canary Islands formed a third final cluster.

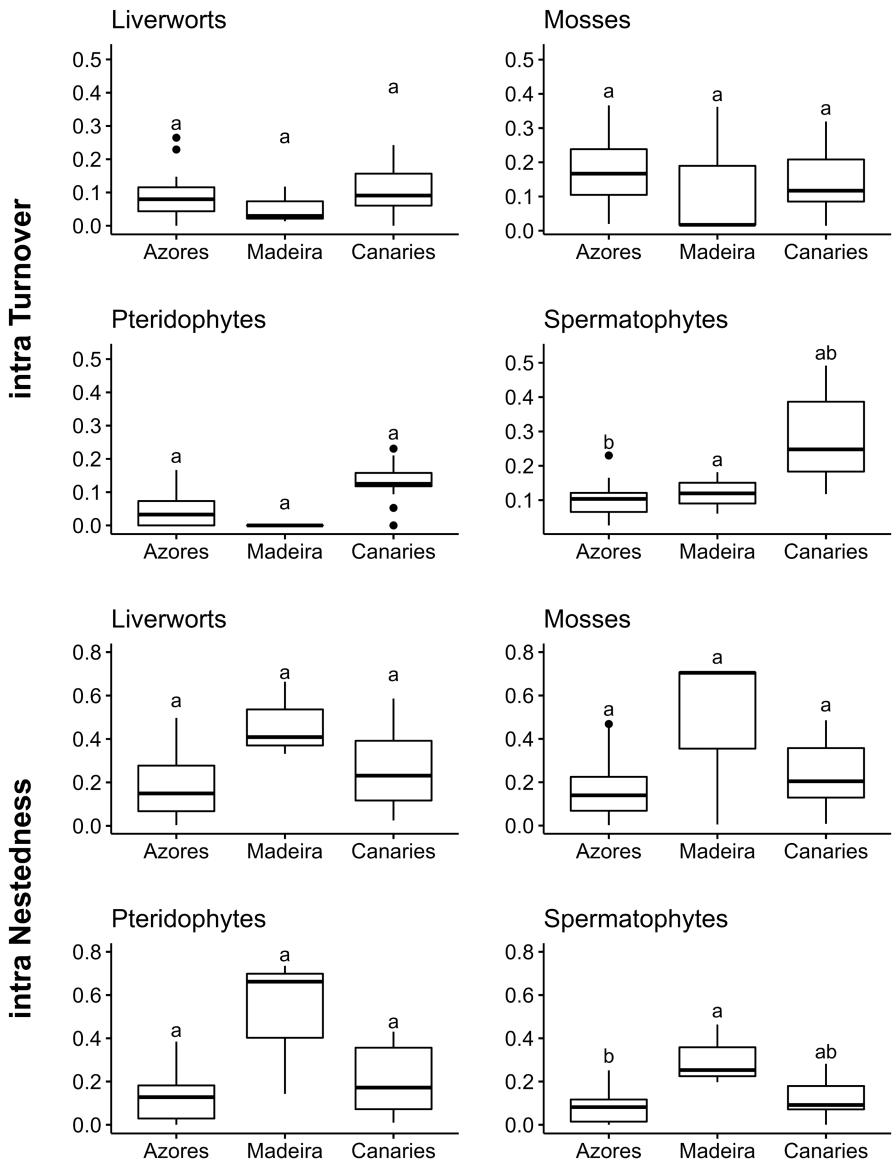
The results of the analyses including Isla de Lobos, Montaña Clara, La Graciosa and Alegranza in the Canary archipelago are described in S7–S15. The most important differences with the analyses on the main islands include (i) an increase of the average nestedness among the Canarian islands in spermatophytes and mosses from 0.116 to 0.236 and from 0.233 to 0.564 (Tables S4 and Table S10); (ii) a decrease of the deviance explained by the GDM for the turnover in mosses (33% vs 62%) and pteridophytes (30% vs 80%), while no significant model was obtained for liverworts nor spermatophytes (Table S13); and (iii) the clustering of the islets independently from the main Canarian islands (Figure S15).

Analyses excluding 172 species (listed in Table S16) considered as introduced in the Azores, and for which unambiguous evidence of a native status was missing in the Canary Islands and Madeira (S17–S24), yielded similar results to those of the complete dataset.

## 4 | DISCUSSION

Our analyses on the spatial patterns of variation in plant beta diversity components across Macaronesia revealed that turnover, but not nestedness, significantly increased from intra to inter-archipelago comparisons. The increase of turnover with the extent of the geographic scale is in line with our hypothesis H1a, based on theoretical and empirical evidence pointing to the role of stronger dispersal limitation and environmental filtering owing to stronger environmental gradients and larger geographic distances across larger spatial scales (Menegotto et al., 2019; Soininen et al., 2007, 2018). In contrast with our second hypothesis (H2), our analyses

**FIGURE 3** Box-plots (showing the first and third quartiles (upper and lower bounds), second quartile (centre), 1.5 × interquartile range (whiskers) and minima–maxima beyond the whiskers) of turnover and nestedness of liverwort, moss, pteridophyte and spermatophyte communities among islands from the same archipelago in Macaronesia. Letters indicate, for each lineage, the archipelagos among which turnover and nestedness significantly differs (see Tables S3 and S4 for *p*-values of the posthoc Kruskal–Wallis Dunn tests), a same letter indicating non-significantly different average values between the archipelagos considered. The y-axis represents the values of the species turnover (based on Simpson index of dissimilarity) and nestedness components of beta diversity among islands of the same archipelago.

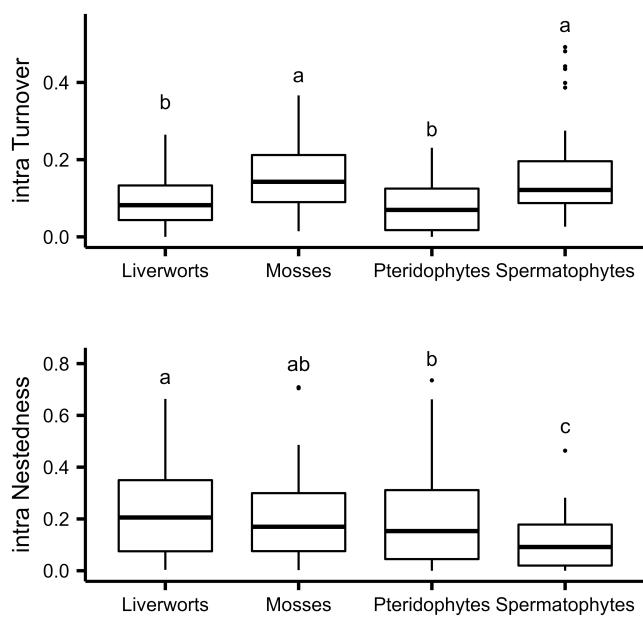


showed no significant variation of nestedness with scale (Menegotto et al., 2019). Nestedness arises when species-poor sites represent subsets of the biota occurring in species-rich sites (Baselga, 2010; Cantor et al., 2017). In Macaronesian bryophytes and pteridophytes, species richness patterns are similar across archipelagos, so that no clear nested pattern is apparent. Differences in species richness among archipelagos are more evident in spermatophytes, with 1398, 683 and 167 native species and subspecies (out of 1810 in total in Macaronesia) in the Canarian, Madeiran and Azorean floras, which is reflected by the near-significance of the difference in nestedness for within-and among-archipelago comparisons.

In line with our expectations H1b and H2b, the extent to which species turnover increased at large spatial scales varied, however, among lineages, being larger in spermatophytes than in pteridophytes, and then, mosses and liverworts, wherein the median turnover was less than half that in spermatophytes. In turn, nestedness was significantly higher in mosses, liverworts and pteridophytes than in spermatophytes. The progressive decrease of turnover and

increase of nestedness from spermatophytes to bryophytes reflects their differences in dispersal capacities, pteridophytes producing bigger spores (30–50 µm on average) than bryophytes (10–20 µm on average). It also reflects major differences of speciation modes between these groups, with some spectacular radiations in the spermatophyte flora, whereas island bryophytes and ferns typically fail to radiate (Patiño, Carine, et al., 2014). These differences of dispersal capacities and speciation modes are themselves reflected in differences of distribution patterns and especially, patterns of endemism. For instance, the 0.7%, 1.7% and 5% of Canarian endemic liverwort, moss and pteridophyte species, 0, 33.3% and 0 of which are SIEs, pale by comparison with the 47%, Canarian endemic spermatophyte species species and subspecies that include 64% of SIEs.

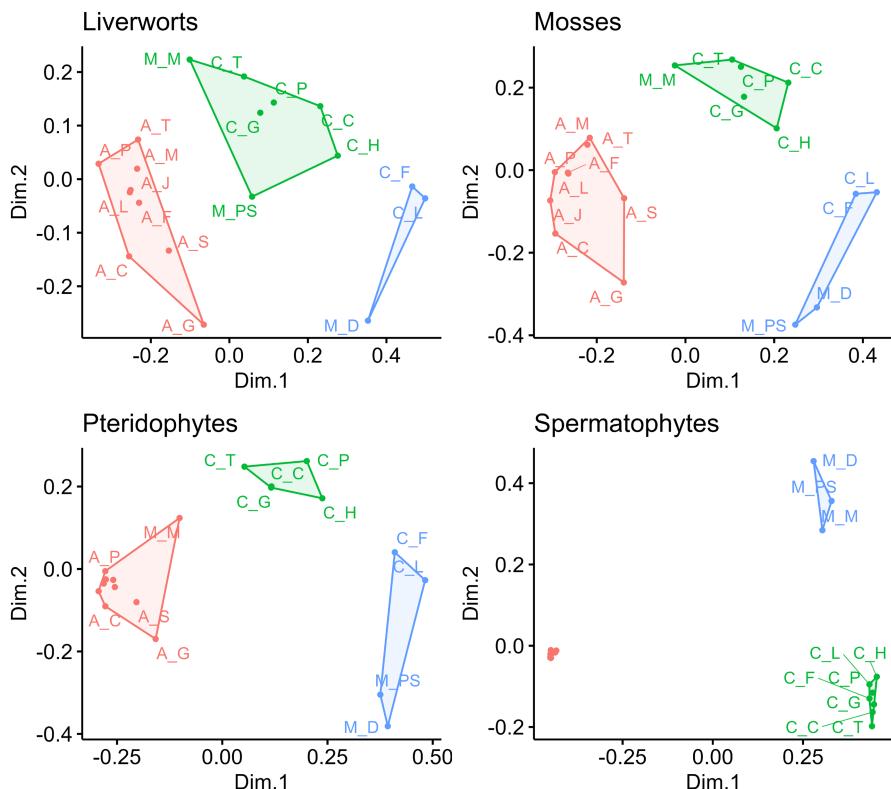
Patterns of turnover also varied among archipelagos in pteridophytes and spermatophytes, but not in bryophytes. The higher turnover observed in the Canaries for spermatophytes and pteridophytes, despite the shorter mean distance between islands than in the Azores, reflects the steeper altitudinal floristic gradients, as well



**FIGURE 4** Box-plots (showing the first and third quartiles (upper and lower bounds), second quartile (centre),  $1.5 \times$  interquartile range (whiskers) and minima-maxima beyond the whiskers) of the turnover and nestedness of liverwort, moss, pteridophyte and spermatophyte communities among islands within archipelagos in Macaronesia. Letters indicate the lineages among which turnover significantly differs, a same letter indicating non-significantly different average values between the lineages considered. The y-axis represents the values of the species turnover (based on Simpson index of dissimilarity) and nestedness components of beta diversity among islands of the same archipelago.

as, globally, greater heterogeneity in climate, islands age and habitat types between the Canarian islands than between the Azorean islands (del Arco Aguilar & Rodríguez Delgado, 2018; Triantis et al., 2012). These differences are well reflected in the distribution of endemism among archipelagos, with the bulk of Canarian endemics being SIEs (64% of Canarian endemic spermatophytes), whereas Azorean endemics tend to be MIEs (88% of Azorean endemic spermatophytes), often widespread across the archipelago (Carine & Schaefer, 2010; Schaefer et al., 2011). The similarity of turnover among archipelagos in bryophyte floras is, at first sight, more striking. Indeed, large differences in bryophyte species composition would have been expected, due to poikilohydric condition of the group, between islands as different from each other as the Canary Islands. In reality, the specialized xerophytic floras of the eastern Canary Islands, characterized by low elevation and dry climates and dominated by thalloid liverworts (*Riccia* spp.) and annual mosses (especially of the family Funariaceae and Pottiaceae), can also be found at low elevation in the western Canary Islands. As a result, Canarian bryophyte communities are more nested than Canarian spermatophyte communities.

Differences of nestedness among archipelagos revealed a recurrent pattern across lineages, according to which nestedness in Madeira was higher than in other archipelagos. The archipelago of Madeira was represented in our analyses by Madeira, Porto Santo and the Desertas. The latter two exhibit much lower elevation, and much drier climates than Madeira, so that their species richness is comprised of the most drought-tolerant elements of the Madeiran flora, resulting in a strong nested pattern that correlates with variation in climatic conditions.



**FIGURE 5** MDS ordination of the Macaronesian islands depending on their floristic composition (spermatophytes, pteridophytes, mosses and liverworts), based on Sørensen dissimilarity. Colours represent the clusters identified using Ward's clustering algorithm and correspond to the optimal number of clusters obtained by the consensus of 30 indexes.



Variation in turnover and nestedness among land plant lineages depending on their dispersal capacities was paralleled by differences in their drivers. In agreement with the idea that spore-producing plants exhibit higher dispersal capacities than spermatophytes, and hence, that their distributions are better explained by extant environmental conditions than by historical factors associated with dispersal limitations (H3), extant climatic factors accounted more to bryophyte and pteridophyte turnover than to spermatophyte turnover. In contrast, island age contributed more to explain variation of turnover among islands in spermatophytes than in bryophytes and pteridophytes. Island age can be interpreted as a composite variable that accounts for time per se, but also, and most importantly, for the environmental heterogeneity during the life-cycle of oceanic islands, and especially, elevation and topographic complexity. Hence, island age does not necessarily reflect the amount of time available for colonization as in fact, the extant composition of the Macaronesian flora largely reflects dynamic interchanges with continental sources in both spore-producing lineages (Vanderpoorten et al., 2007) and spermatophytes (García-Verdugo et al., 2019; Hooft van Huysduyzen et al., 2021). Instead, island age characterizes opportunities for speciation depending on habitat heterogeneity and availability, which peak as islands reach their highest elevation (Patiño et al., 2013; Whittaker et al., 2008). In this context, speciation plays a much more important role in the extant diversity of spermatophyte than of bryophyte and pteridophyte species, as evidenced by the striking difference in endemism rates per archipelago among lineages, of <8% in bryophytes and pteridophytes and >45% in spermatophytes. In bryophytes and pteridophytes in fact, endemic species are typically 'isolated' in their genus ("anagenesis", Stuessy et al., 2006), whereas in Macaronesian spermatophytes, the ratio between the number of genera including endemic species and the number of endemic species ranges between 1.5 and 3 (Patiño, Carine, et al., 2014; Patiño, Weigelt, et al., 2014).

Differences in dispersal capacities, and hence, endemism patterns among the mainland plant lineages, were further evidenced by the selection of the factor 'archipelago structure' in the model for species turnover in spermatophytes, but not in bryophytes and pteridophytes. The relevance of archipelago structure in spermatophytes, but not spore-producing plants, again mirrors patterns of endemism among those groups, with 0.7%–2%, 1.7%–2%, 5%–8% and 21%–47% of archipelago endemics in liverworts, mosses, pteridophytes, and spermatophytes, respectively.

In turn, area, one of the main drivers of species richness on islands due to decreased extinction rates, but most importantly, increased chances of colonization by airborne propagules (target area effect, Whittaker & Fernández-Palacios, 2007) and of speciation (Kissel & Barraclough, 2010), was never selected as a significant driver of species turnover. This was, at first sight, surprising because taxa with high dispersal capacities are expected to require larger areas to speciate than taxa with low dispersal capacities

(Kissel & Barraclough, 2010), which should be reflected in higher levels of endemism on large islands, and hence, larger differences in species turnover among islands of different sizes. One of the main reasons why area did not play a role in the observed patterns of turnover is that all Macaronesian islands are much larger than the minimal area,  $<10\text{ km}^2$ , required for neutral genetic differentiation in spermatophytes (Kissel & Barraclough, 2010). In addition, Macaronesian bryophytes typically failed to speciate *in situ* (Patiño, Carine, et al., 2014; Vanderpoorten et al., 2011). Even in genera that include several Macaronesian endemics, endemic species do not form a monophyletic group and each speciation event follows a long-distance dispersal event from continental sources (Patiño & Vanderpoorten, 2015). Unlike sympatric speciation, allopatric speciation depends on geographic isolation from sources, and not island size, contributing to the lack of relationship between island area and beta diversity patterns in spore-producing plants. Pteridophytes failed to radiate in Macaronesia as well. In fact, most Macaronesian ferns genera include only one endemic species that evolved by allopolyploidisation (Vanderpoorten et al., 2011), a mechanism that is typically independent from area (Kissel & Barraclough, 2010).

It is worth noting that, when the four Canarian islets were included in the analysis, no significant model was obtained for liverwort and spermatophyte turnover and the percentage of explained deviance dropped of 32 and 50% in mosses and pteridophytes, respectively. Such an impact of small islands is reminiscent of the small-island effect, an anomalous pattern of the species-area relationship that predicts the existence of a threshold area, below which species richness varies independently of island area. The small-island effect is mostly driven by the decoupling of area and environmental heterogeneity on small islands (Chen et al., 2020; Matthews et al., 2020). The drop of explained deviance in our models similarly suggests that, beyond a certain threshold area, the factors affecting species composition change. As for the link between species richness and area (Yu et al., 2020), this effect varies among taxonomic groups, being most obvious in bryophytes and pteridophytes, whose floras are extremely depauperate on the Canarian islets.

In line with differences in beta diversity patterns among land plant lineages, caused by different responses of turnover to variation of climatic conditions and geographic distance, and with our hypothesis H4, spermatophyte floras clustered by archipelago, whereas pteridophyte and bryophyte floras did not. Fuerteventura, Lanzarote, Desertas and Porto Santo host similar cryptogrammic floras of low-elevation, dry islands, whereas the western Canary Islands and Madeira, which share typical laurel forest floras, formed another cluster. In spermatophytes, this signal is erased by the predominance of the endemic element at the archipelago level (see above), so that the turnover between islands from different archipelagos is substantially higher in spermatophytes ( $0.74 \pm 0.07$ ) than in pteridophytes ( $0.41 \pm 0.08$ ), mosses ( $0.40 \pm 0.10$ ) and liverworts ( $0.37 \pm 0.10$ ). The inclusion of the Canarian islets slightly changed the



pattern, as, for all the taxonomic lineages and as previously reported (Torre et al., 2019), these islets clustered together, independently of their archipelagic adscription.

The differences of beta diversity patterns among Macaronesian land plant lineages illustrate two major evolutionary differences among those groups depending on their dispersal capacities. First, spermatophytes speciate *in situ* at much faster rates than spore-producing plants, wherein allopatric speciation following long-distance dispersal is the rule (Patiño, Carine, et al., 2014; Patiño, Weigelt, et al., 2014). Second, the higher dispersal capacities of spore-producing plants explains the striking tropical affinities of Macaronesian endemic spore-producing plants (Vanderpoorten et al., 2011), which contrasts with the predominantly Mediterranean origin of Macaronesian endemic spermatophytes (Carine et al., 2004). Combined with the differences in beta diversity reported here, these observations point to different assemblage mechanisms in terms of origin, timing and mode of colonization among Macaronesian land plant lineages. These differences in the mechanisms of assembly among land plant in Macaronesia call for a comparative analysis of the geographic origin of these floras in an explicit time-frame.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The matrices of species distributions for liverworts, mosses and spermatophytes are available at <https://figshare.com>. doi: 10.6084/m9.figshare.17099840.

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## BIOSKETCH

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**Author contributions:** AV and LM conceived the project; LM, MC, FR, JP, MMS, JMGM, RMAG, MSS, JARB, AV collected the data; LM, FC and OJH analysed the data; and LM and AV led the writing with assistance from all co-authors.

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