

1 This is an ‘Accepted Version’ of an article published by Wiley-Blackwell in Journal of  
2 Biogeography on 26 February 2023; available online: <https://doi.org/10.1111/jbi.14580>

3 **Patterns and drivers of beta diversity across geographic scales and lineages**  
4 **in the Macaronesian flora**

5

6 **Running title: drivers of beta diversity in the Macaronesian flora**

7

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38

## 39 **Abstract**

40

41 **Aim:** To assess whether beta diversity varies with geographic scale, disentangle the contribution of  
42 historical and ecological processes to this variation across land plants, and test the hypothesis that extant  
43 ecological conditions mostly account in explaining species turnover in spore-producing lineages,  
44 whereas historical factors and geographical isolation prevail in spermatophytes.

45 **Location:** Macaronesia

46 **Taxon:** bryophytes, pteridophytes, spermatophytes

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

50 **Results:** Species turnover, but not nestedness, increased from intra- to inter-archipelago levels. This  
51 increment decreased from spermatophytes, pteridophytes, and bryophytes, wherein the median turnover  
52 was less than half that in spermatophytes. Bryophytes exhibited a significantly higher nestedness than  
53 spermatophytes, and the reverse trend was observed for species turnover. Extant climatic conditions  
54 better explained turnover in bryophytes and pteridophytes than in spermatophytes. Island age exhibited  
55 the reverse trend. Spermatophyte floras clustered by archipelago, whereas the clustering patterns in  
56 pteridophyte and bryophyte floras reflect macroclimatic conditions.

57 **Main Conclusions:** The lower increment of species turnover with spatial scale and the higher  
58 nestedness in bryophytes and pteridophytes than in spermatophytes reflect the variation in dispersal  
59 capacities and distributions ranges among land plant lineages. Accordingly, extant climatic conditions  
60 contributed more to explain turnover in bryophytes and pteridophytes than in spermatophytes, whereas

61 factors associated with dispersal limitations, including island age, geographic distance, and archipelago  
62 adscription, exhibited the reverse trend. The differences in beta diversity patterns, caused by different  
63 responses of Macaronesian land plant lineages to the main factors shaping their community  
64 composition, explain their different biogeographic affinities. These differences reflect distinct  
65 mechanisms of origin and speciation among Macaronesian land plant lineages and archipelagos.

66

67 **Keywords:** beta diversity, species turnover, nestedness, geographic scale, oceanic islands,  
68 spermatophytes, pteridophytes, bryophytes, Macaronesia, Generalized Dissimilarity Model

69

## 70 **Introduction**

71 How spatial, historical and ecological processes drive diversity patterns, and how area, elevation and  
72 isolation influence community composition, are two of the main foci of island biogeography (Patiño et  
73 al., 2017). In this context, beta diversity, the variation of biological communities across space or time,  
74 appears as a useful framework to measure changes in community composition along environmental,  
75 spatial and temporal gradients (Soininen et al., 2018). This metric can be partitioned into two process-  
76 related components: species replacement (turnover) and richness difference (nestedness) (Baselga,  
77 2010). Species turnover characterizes changes in species composition along gradients of geographical  
78 and/or ecological distance (Qian et al., 2020), whereas nestedness occurs when a set of species at one  
79 site is a subset of the species at a richer site, which has typically been interpreted in terms of ordered  
80 extinction events (Baselga, 2010).

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

89 Beta diversity also varies depending on geographic scale (Soininen et al., 2018). If an increase in species  
90 turnover with geographic scale due to the greater dispersal limitation and stronger environmental  
91 filtering over larger environmental gradients has been recurrently documented (Soininen et al., 2018;  
92 Gusmao et al., 2020; Qian et al., 2020), the relationship between nestedness and geographic scale has  
93 been more controversial. Nestedness is expected to peak at a small scale if local variations of habitat  
94 quality and availability lead to variation in species richness within habitats among sites (Gusmao et al.,

95 2020). In contrast, high nestedness at large scales is expected when extinctions vary depending on major  
96 geographic gradients (Soininen et al., 2018). Typically, nestedness should be greater for regions located  
97 at higher latitudes along latitudinal diversity gradients (Batista, de Lima & Lima, 2021; Soininen et al.,  
98 2018).

99 Oceanic islands offer an ideal framework to investigate the variation of species turnover and nestedness  
100 across geographic scales and to determine the relative contribution of contemporary climatic factors  
101 and dispersal limitations associated with geographic isolation. Oceanic islands are readily  
102 geographically circumscribed (Whittaker & Fernández-Palacios, 2007), offering naturally isolated and  
103 often replicated Operational Geographic Units (OGUs). Furthermore, because they were colonized *de*  
104 *novo*, oceanic islands accumulate species from continental or alternative insular sources at rates  
105 depending on connectivity and *in situ* speciation (Whittaker & Fernández-Palacios, 2007) that vary with  
106 geographic isolation, environmental complexity, island age and species dispersal capacities (Heaney,  
107 2000). In particular, the three northern archipelagos of the Macaronesian region (the Azores, Madeira,  
108 and Canary Islands) have long been identified as an excellent model for hypothesis testing in  
109 biogeography (Florencio et al., 2021). In fact, these archipelagos vary in terms of geographic isolation  
110 and macroclimatic conditions, so that their floras exhibit sharply different distribution patterns. In the  
111 Canarian spermatophyte flora, single-island endemics (SIEs) are much more frequent than multiple-  
112 island endemics (MIEs), whereas the reverse pattern prevails in the Azores (Carine & Schaefer, 2010).  
113 This, together with the sharper ecological gradients in the Canaries (and to some extent in Madeira),  
114 has led to the idea that speciation in the Canaries is primarily driven by ecological radiations, whereas  
115 allopatric speciation prevails in the Azores among islands that are more distant among each other and  
116 from continental sources than in the Canaries (Carine & Schaefer, 2010; Price et al., 2018). Spore-  
117 producing plants exhibit a lower proportion of SIEs and a higher proportion of Macaronesian regional  
118 endemics (i.e., taxa that are endemic to two or more Macaronesian archipelagos) than spermatophytes  
119 (Vanderpoorten et al., 2011), owing to their higher dispersal capacities, allopatric speciation modes and  
120 ecological affinities (Patiño, Carine et al., 2014). Therefore, biogeographic relationships across  
121 Macaronesia vary among major land plant groups. The assemblage of the spermatophyte flora mostly  
122 follows the structure of archipelagos (de Nicolás et al., 1989), whereas floristic analyses at the  
123 archipelago level revealed conflicting relationships among spore-producing floras (Vanderpoorten,  
124 Rumsey & Carine, 2007).

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

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

151

## 152 **Materials and Methods**

### 153 Study area

154 Macaronesia (Figure 1) is a biogeographic region located in the Atlantic Ocean between 15.8 and 40.8°  
155 N (Florencio et al., 2021). We focused here on the Azores, Madeira (including Madeira, Porto Santo,  
156 and the Desertas islands) and the Canary Island archipelagos. Within the latter, we tested the impact of  
157 the inclusion of the islets of Isla de Lobos, Montaña Clara, Alegranza, and Graciosa, whose size and  
158 elevation are, respectively, more than 95 and 6 times lower than that the main Canarian islands. The  
159 Desertas include Deserta Grande, Chão and Bugio. Due to their very small size, close proximity to each  
160 other, connection during the Last Glacial Maximum, and very low species richness, these islands are  
161 treated as a single unit in available species lists, a position that we also adopted here. We excluded Cabo  
162 Verde, whose cryptogamic flora clearly belongs to sub-Saharan Africa (Vanderpoorten et al., 2007),  
163 and the Selvagens, whose very limited flora and number of islands did not warrant inclusion in the  
164 present analyses.

165

166 Data collection and matrices

167 Lists of moss, liverwort, pteridophyte, and spermatophyte species per island were retrieved from a  
168 review of the literature and personal unpublished observations of the authors (Appendix 1). Sub-species,  
169 whose circumscription is typically associated with a restricted geographic range (Mallet, 2013), and are  
170 hence potentially informative in spatial analyses of taxonomic composition among operational  
171 geographic units (OGUs), were included. Due to the very low number of hornwort species (6), the latter  
172 were included within the liverworts, to which they are the most similar in terms of morpho-anatomy  
173 and life-history traits. Nomenclature was standardized following Hodgetts et al. (2020) for mosses and  
174 liverworts, Hassler (2018) for pteridophytes and Euro+Med (2006-) for spermatophytes. In bryophytes,  
175 *Isoetecium interludens*, *Racomitrium affine*, *Lophocolea coadunata*, and *Frullania tamarisci* agg.,  
176 which have recently been raised at species level, were not distinguished pending for a critical re-  
177 assessment of their distributions. *Bryoxiphium madeirense* was considered as a synonym of *B.*  
178 *norvegicum* based on phylogenetic evidence (Patino et al., 2016).

179 Introduced species were excluded from the analysis as they lead, at the geographic scale of entire  
180 islands, to a substantial human-induced homogenization of their floras (Otto et al., 2020). Assessing the  
181 native status of a taxon is challenging, and this status may further vary for the same taxon among  
182 archipelagos (e.g., *Clethra arborea*, Madeiran endemic invasive in the Azores), or even among islands  
183 from the same archipelago (e.g., *Echium nervosum* introduced from Madeira to Porto Santo), preventing  
184 us from defining a global list of introduced species across Macaronesia. We therefore relied on the  
185 status defined for each taxon by the most recent databases (Appendix 1) for each archipelago. As a  
186 matter of fact, however, many widespread Mediterranean species considered as native in the Canary  
187 Islands and Madeira, such as *Helminthotheca echioides*, *Hypochaeris radicata*, and *Trifolium* spp., are  
188 considered as introduced in the Azores, whereas they thrive in the same kinds of habitats across  
189 archipelagos. We thus performed a second set of analyses, wherein all species considered as introduced  
190 in the Azores, and for which unambiguous evidence of a native status was missing in the Canary Islands  
191 and Madeira is missing, were excluded.

192 Altogether, the data matrices (available at <https://figshare.com>, DOI 10.6084/m9.figshare.17099840)  
193 included 226 liverwort & hornwort species, 516 moss species, 83 pteridophytes species and 1810  
194 spermatophyte species. These matrices were employed to compute, for each of the four lineages  
195 considered, the species turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) components of Sørensen dissimilarity  
196 among all possible pairs of islands using the package betapart (Baselga et al., 2021) in R version 4.2.1.  
197 (R Core Team, 2022).

198 Environmental variables included climatic conditions (annual mean temperature, minimum annual  
199 temperature range, annual precipitation and minimum coefficient of variation in monthly precipitation),  
200 geographic distance among islands, area, elevation, distance to the closest main land, and age of each

201 island. The first nine variables were recorded from Weigelt, Jetz & Kreft (2013) while island age was  
202 obtained from Torre et al. (2019).

203

## 204 Data analysis

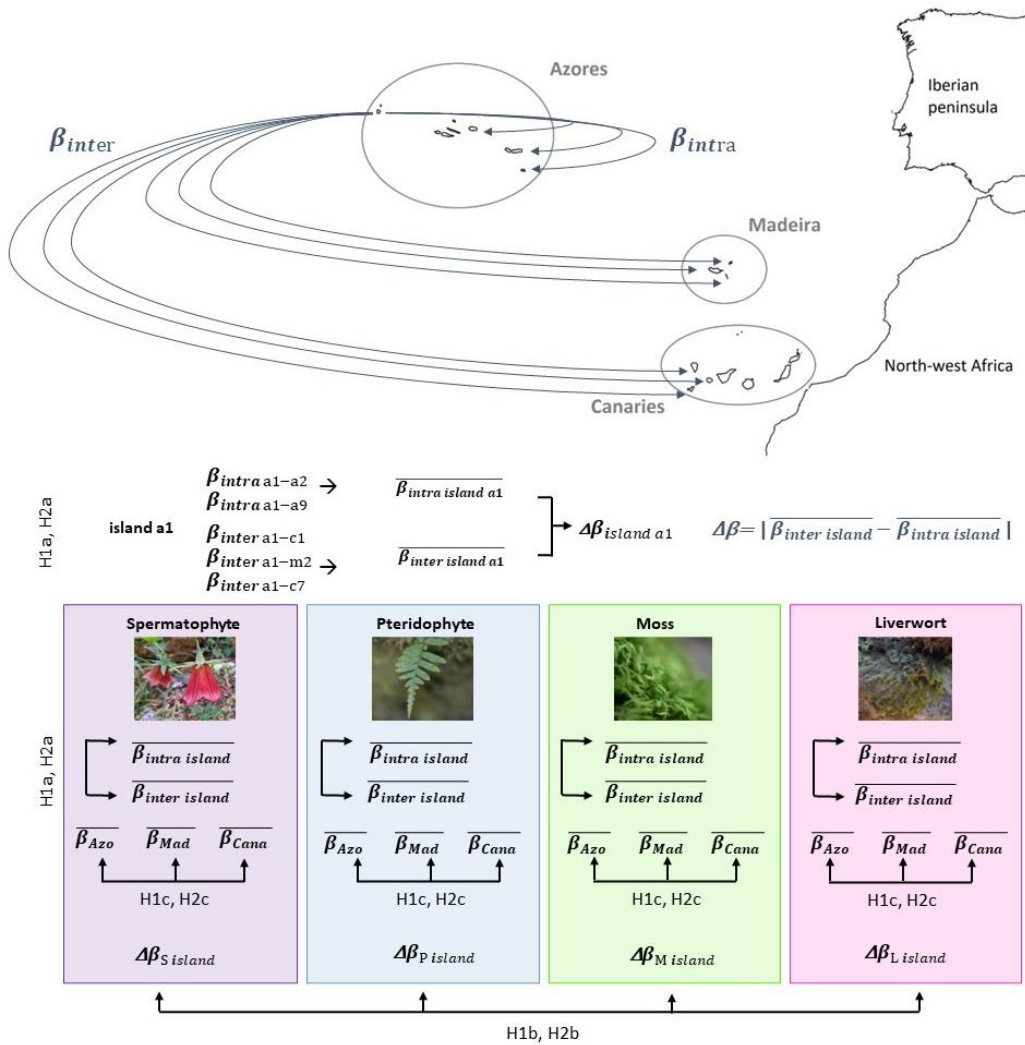
205 Comparing turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) among islands within and among archipelagos (H1a,  
206 H2a, Figure 1) involves the inclusion of the same observation multiple times (the same occurrence of a  
207 species on an island serving to compute  $\beta_{sim}$  and  $\beta_{sne}$  both within and among archipelagos), violating  
208 the assumption that the observations are independent from each other. We therefore computed, for each  
209 island, the average  $\beta_{sim}$  and  $\beta_{sne}$  values with all the other islands from the same archipelago ( $\beta_{intra}$ ,  
210 Figure 1). Then, we computed, for each island, the average  $\beta_{sim}$  and  $\beta_{sne}$  values with each island from  
211 the other archipelagos ( $\beta_{inter}$ , Figure 1). The average  $\beta$  values within archipelagos were then compared  
212 to those among archipelagos. Although the data were homoscedastic (Fisher test = 1 for all lineages),  
213 departure from normality for the turnover of spermatophytes and for the nestedness of all lineages  
214 (Shapiro test,  $p < 0.01$ ) led us to apply paired Wilcoxon rank tests.

215 To assess the variation of  $\beta$  from intra- to inter-archipelago comparisons (H1b and H2b, Figure 1), we  
216 computed, for each island, the difference ( $\Delta\beta$ ) of the average  $\beta$  between that island and all other islands  
217 from the same archipelago ( $\beta_{intra}$ ) and the average beta between that island and all other islands from  
218 different archipelagos ( $\beta_{inter}$ ) (Figure 1).  $\Delta\beta$  values were not normally distributed in the case of  
219 turnover for spermatophytes, and in the case of nestedness for mosses, ferns, and spermatophytes.  
220 Therefore, non-parametric Friedman's and post-hoc Nemenyi tests, applying Bonferroni correction on  
221 the p-value, were implemented with the package PMCMRplus (Pohlert, 2021) to search for significant  
222 differences of  $\Delta\beta$  values per island among lineages. In order to assess, for each lineage, differences of  
223 nestedness and turnover among archipelagos, we implemented Kruskal-Wallis and posthoc Dunn tests,  
224 applying Bonferroni correction for multiple comparisons, with the package PMCMRplus (Pohlert,  
225 2021).

226 To determine how beta diversity varies depending on geographic distance (both among islands and  
227 between islands and nearest continents) and variation in climatic conditions, age, area, and elevation  
228 across taxa and archipelagos (H3), Generalized Dissimilarity Model (GDM, Ferrier et al., 2007) was  
229 employed using the gdm R package (Fitzpatrick et al., 2021) for each of the four lineages independently.  
230 To control for the archipelago structure of the data, we assigned each pair of islands from the same  
231 archipelago a distance of 0, and each pair of islands from different archipelagos a distance of 1, and  
232 then treated this binary distance measure in the same manner as geographical distance (Ferrier et al.,  
233 2007). To avoid multicollinearity, we computed Pearson correlation coefficients among each pair of  
234 predictors and kept one predictor among any pair with a correlation coefficient  $> 0.75$ . As annual mean

235 temperature, annual precipitation, distance to the closest main land, distance among islands and  
 236 minimum coefficient of variation in monthly precipitation were strongly correlated, we kept only the  
 237 latter, hereafter referred to as ‘precipitation’. This approach allowed us to identify a set of six predictors,  
 238 including area, elevation, minimum annual temperature range, island age, precipitation and archipelago.  
 239 We implemented stepwise backward variable elimination as implemented in the `gdm.varImp` function  
 240 of the package `gdm` (Fitzpatrick et al., 2021) until all variables had a p-value < 0.05.

241 To address hypothesis H4, a cluster analysis of islands as a function of their taxonomic composition  
 242 was performed using Ward’s algorithm based on a total beta diversity matrix derived from Sørensen  
 243 distances. The optimal number of clusters for each lineage was determined with the `NbClust` package  
 244 (Charrad et al., 2014) using 30 indexes (i.e., all indices except GAP, Gamma, Gplus and Tau). To help  
 245 visualizing the groupings, a Classical (Metric) Multidimensional Scaling (MDS) based on the Sørensen  
 246 distance matrix was performed. All the analyses were repeated twice, with and without the Canarian  
 247 islets, to examine the impact of the latter on the explanatory power of the models and the clustering  
 248 patterns.



249



250 Figure 1 Study area and statistical framework to calculate beta diversity ( $\beta$ ) and its two components, turnover ( $\beta_{sim}$ )  
251 and nestedness ( $\beta_{sne}$ ) between islands within (intra) and between (inter) archipelagos (Azores: Azo, 9 islands labelled  
252 as a1-a9, Canary Islands: Cana, 7 islands labelled as c1-c7, and Madeira: Mad, 3 islands labelled as m1-m3) among  
253 land plant lineages (spermatophyte: S, pteridophyte: P, moss: M, and liverwort: L).

254

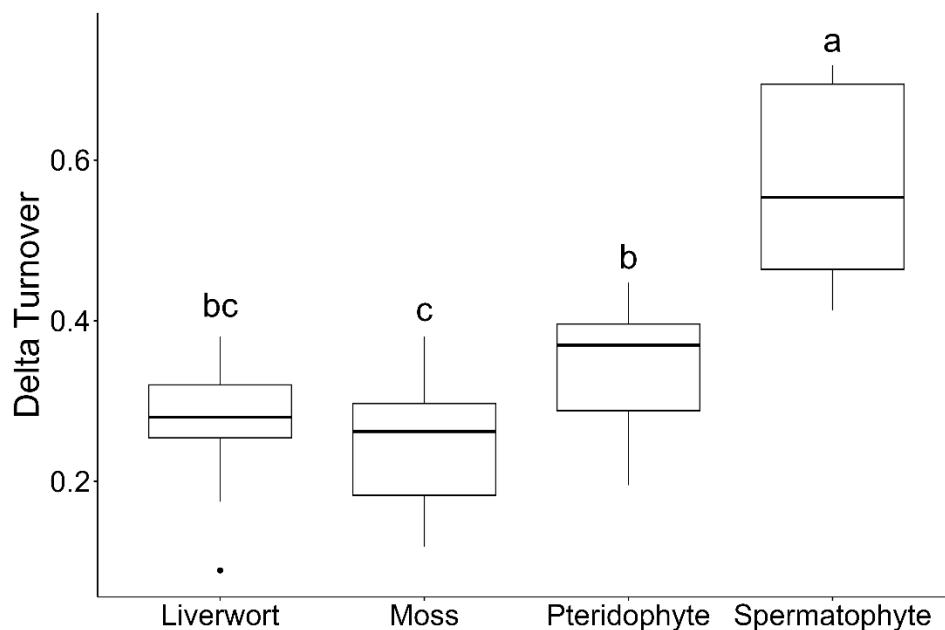
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## 256 Results

257

258 For all lineages, paired Wilcoxon tests showed a significant increase of turnover among islands from  
259 intra to inter-archipelago comparisons (Figure 2). No significant variation from intra to inter-  
260 archipelago comparisons was observed for nestedness (Table S1 in Supporting Information). The  
261 difference in turnover between intra and inter-archipelago comparisons ( $\Delta\beta_{sim}$ ) was significantly  
262 higher in spermatophytes ( $0.57 \pm 0.12$ ) than in bryophytes and pteridophytes (Friedman test, p-  
263 value  $< 0.01$ ).  $\Delta\beta_{sim}$  in pteridophytes ( $0.34 \pm 0.08$ ) was significantly higher than in mosses  
264 ( $0.25 \pm 0.08$ ) but not than in liverworts ( $0.28 \pm 0.07$ ). Among bryophytes,  $\Delta\beta_{sim}$  did not differ  
265 significantly.

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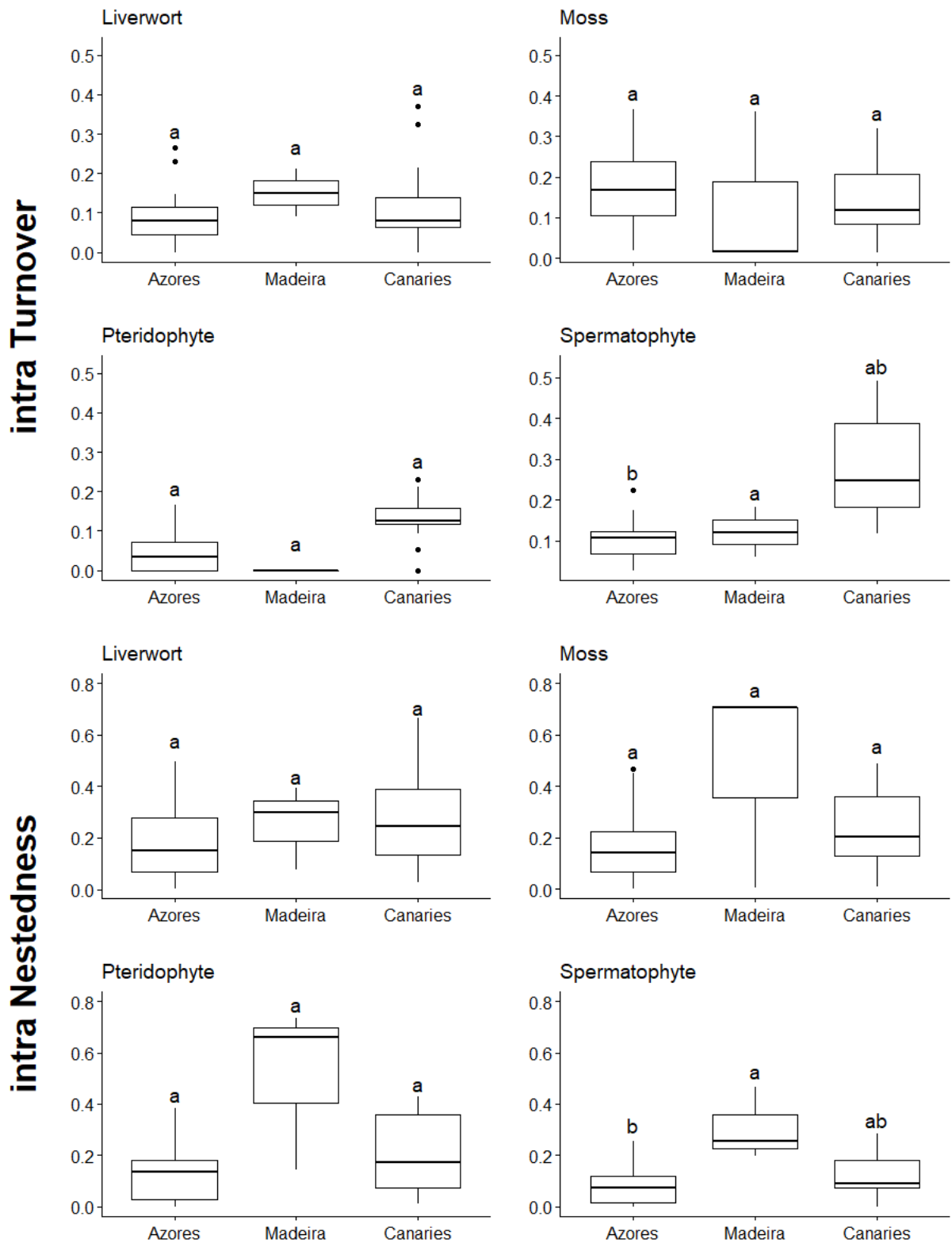


267

268 Figure 2 Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5\*  
269 interquartile range (edges of the box)) of the difference of turnover ( $\Delta\beta_{sim}$ ) of liverwort, moss, pteridophyte and  
270 spermatophyte communities among islands within (intra) and among (inter) archipelagos in Macaronesia (see Table  
271 S1 in Supporting Information for actual values). Letters above each box-plot indicate which comparisons significantly

272 differ (see Table S2 in Supporting Information for the p-values of the posthoc Friedman Nemenyi tests), identical letters  
273 being used for lineages whose turnover does not significantly differ from each other.

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



282

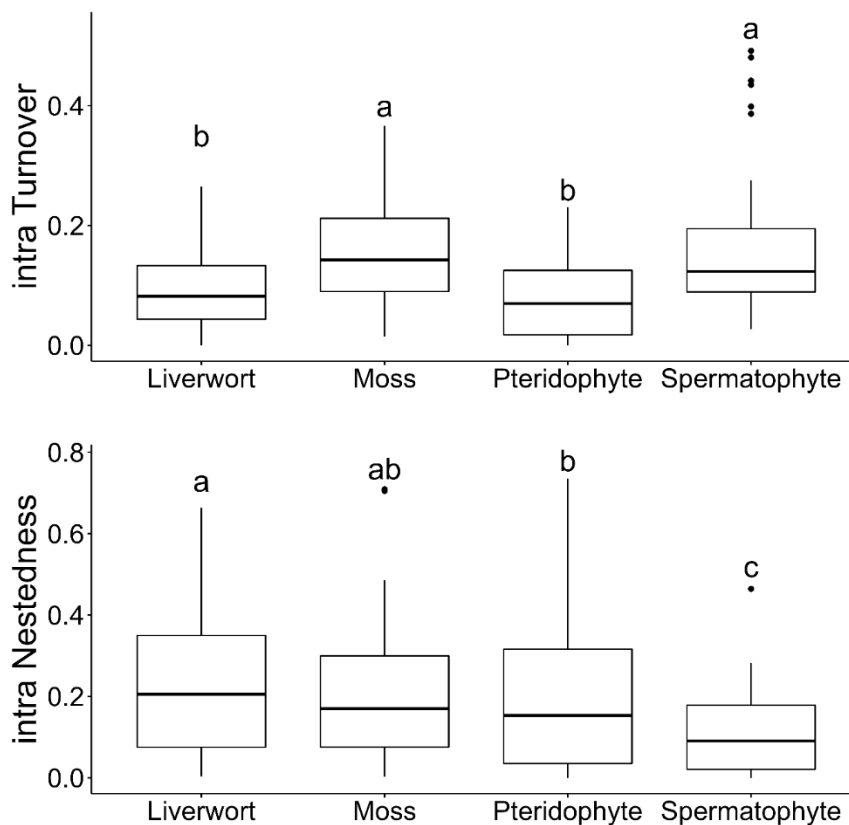
283 Figure 3 Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5\*  
 284 interquartile range (edges of the box)) of turnover and nestedness of liverwort, moss, pteridophyte and spermatophyte  
 285 communities among islands from the same archipelago in Macaronesia. Letters indicate, for each lineage, the  
 286 archipelagos among which turnover and nestedness significantly differs (see Table S3 and S4 in Supporting

287 Information for p-values of the posthoc Kruskal-Wallis Dunn tests), a same letter indicating non-significantly different  
288 average values between the archipelagos considered.

289

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

294



295

296

297 **Figure 4** Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5\*  
298 interquartile range (edges of the box)) of the turnover and nestedness of liverwort, moss, pteridophyte and  
299 spermatophyte communities among islands within archipelagos in Macaronesia. Letters indicate the lineages among  
300 which turnover significantly differs, a same letter indicating non-significantly different average values between the  
301 lineages considered.

302

303 The GDM explained 69%, 63%, 81% and 92% of the deviance of liverwort, moss, pteridophyte and  
304 spermatophyte turnover, respectively. Precipitation was the variable most contributing to the model for

305 bryophytes and pteridophytes and island age was most contributing in spermatophytes (Table 1). The  
 306 factor ‘archipelago’ was selected only in spermatophytes.

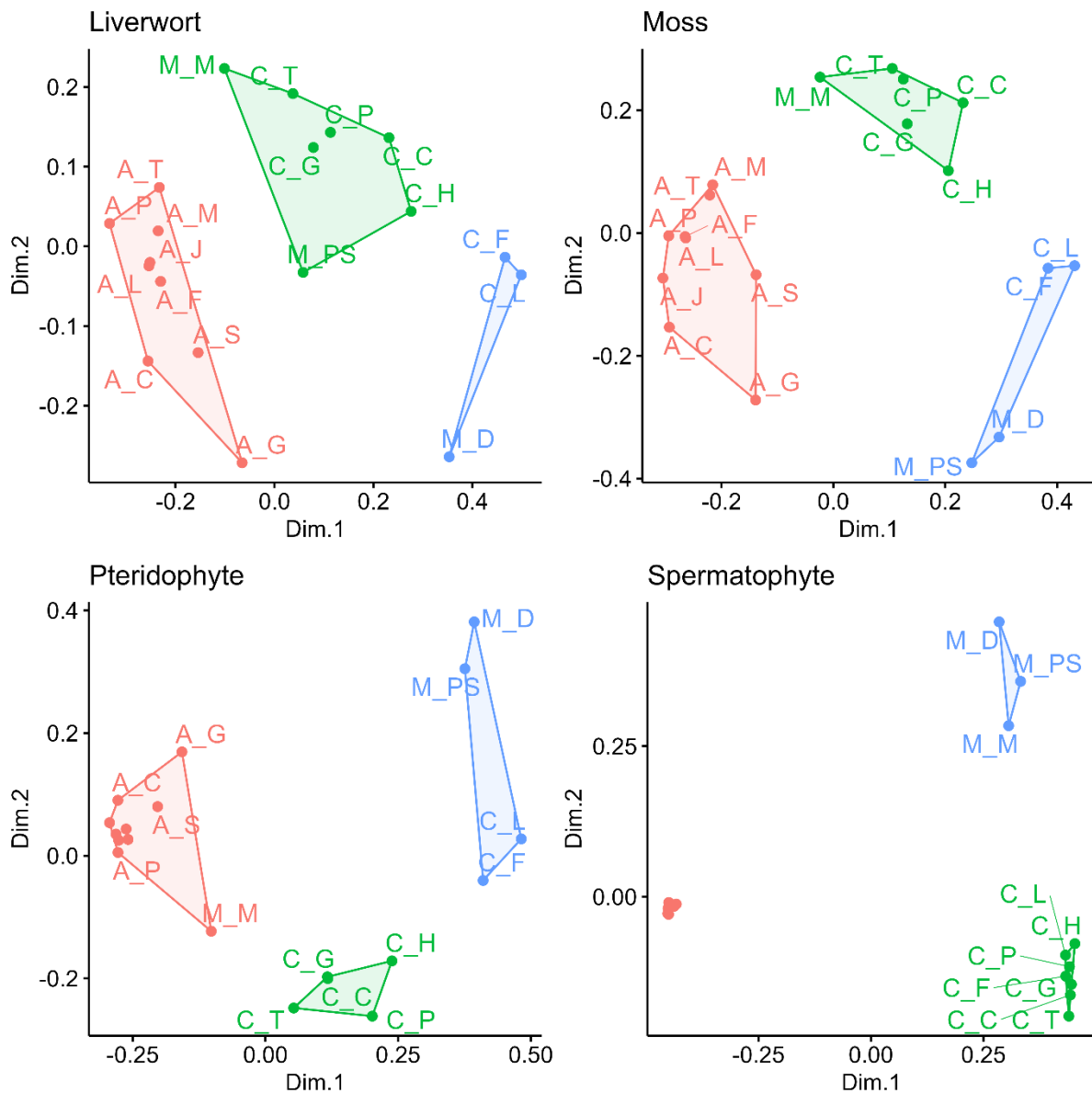
307 The GDM explained less than 50% of nestedness in liverworts, mosses and spermatophytes and 68%  
 308 in pteridophytes. Elevation and temperature were selected in all models, but the contribution of the  
 309 former was about three times higher than that of the latter. Area was selected for spermatophytes while  
 310 island age was selected for all the spore-producing plants (Table S5 in Supporting Information).

311 **Table 1 Summary statistics of the generalized dissimilarity model (GDM) used to analyse the drivers of species turnover**  
 312 **in Macaronesian land plants. Predictor importance for each variable is measured as the percent decrease in deviance**  
 313 **explained between the full model and a model wherein that variable was randomized.**

|                       | <b>Predictor importance</b> | <b>Deviance</b>             |        |
|-----------------------|-----------------------------|-----------------------------|--------|
| <b>Liverworts</b>     |                             |                             |        |
| Precipitation         | 67.71                       | NULL Deviance:              | 33.50  |
| Island age            | 7.38                        | Model Deviance:             | 11.01  |
|                       |                             | Percent Deviance Explained: | 67.15% |
| <b>Mosses</b>         |                             |                             |        |
| Precipitation         | 67.60                       | NULL Deviance:              | 30.46  |
| Island age            | 8.28                        | Model Deviance:             | 11.67  |
|                       |                             | Percent Deviance Explained: | 61.71% |
| <b>Pteridophytes</b>  |                             |                             |        |
| Precipitation         | 74.15                       | NULL Deviance:              | 39.69  |
| Island age            | 3.18                        | Model Deviance:             | 7.98   |
| Temperature           | 0.15                        | Percent Deviance Explained: | 79.91% |
| <b>Spermatophytes</b> |                             |                             |        |
| Precipitation         | 12.90                       |                             |        |
| Island age            | 5.30                        | NULL Deviance:              | 71.09  |
| Temperature           | 0.10                        | Model Deviance:             | 5.60   |
| Archipelago           | 0.04                        | Percent Deviance Explained: | 92.12% |

314

315 The groups resulting from the clustering analyses of islands as a function of their species composition  
316 in each lineage are shown on the first plane of the NMDS of islands depending on the floristic distance  
317 among them (Figure 5). The stress values, a goodness-of-fit statistic that is minimized in MDS and  
318 characterizes the extent to which the actual floristic dissimilarities among islands are well represented  
319 on the plot, were 0.032 for liverworts, 0.030 for mosses, 0.032 for pteridophytes and 0.052 for  
320 spermatophytes, indicating good to excellent fit. In spermatophytes, the three clusters identified  
321 correspond to the Azores, the Canary Islands and Madeira. In liverworts, the Azorean islands clustered  
322 together, the Canarian islands of Fuerteventura and Lanzarote, and the Desertas of Madeira archipelago,  
323 formed a second cluster, while Madeira clustered with Porto Santo and the remaining Canary Islands.  
324 The grouping observed with the moss floras was almost identical, except that Porto Santo clustered with  
325 Fuerteventura and Lanzarote and the Desertas. In pteridophytes, Madeira clustered with the Azores  
326 while Porto Santo and the Desertas (Madeira archipelago), Lanzarote and Fuerteventura (Canary  
327 Islands) formed a second cluster, and the western and central Canary Islands formed a third final cluster.



328

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

332 The results of the analyses including Isla de Lobos, Montaña Clara, La Graciosa and Alegranza in the  
 333 Canary archipelago are described in S6-S14 in Supporting Information. The most important differences  
 334 with the analyses on the main islands include (i) an increase of the average nestedness among the  
 335 Canarian islands in spermatophytes and mosses from 0.116 to 0.236 and from 0.233 to 0.564 (Table  
 336 S4, Table S9 in Supporting Information); (ii) a decrease of the deviance explained by the GDM for the  
 337 turnover in mosses (33% vs 62%) and pteridophytes (30% vs 80%), while no significant model was  
 338 obtained for liverworts nor spermatophytes (Table S12 in Supporting Information); and (iii) the  
 339 clustering of the islets independently from the main Canarian islands (Figure S14 in Supporting  
 340 Information).

341 The results of the analyses excluding the 172 species considered as introduced in the Azores and for  
342 which unambiguous evidence of a native status was missing in the Canary Islands and Madeira are  
343 described in S16-S23 in Supporting Information. The only difference which is nevertheless very futile  
344 concerns the intra-turnover. The intra-turnover of Madeira becomes greatest while the one of the Azores  
345 is similar to the Canaries once. Other than this, no other changes are noticeable.

346

## 347 **Discussion**

348 Our analyses on the spatial patterns of variation in plant beta diversity components across Macaronesia  
349 revealed that turnover, but not nestedness, significantly increased from intra to inter-archipelago  
350 comparisons. The increase of turnover with the extent of the geographic scale is in line with our  
351 hypothesis H1a, based on theoretical and empirical evidence pointing to the role of stronger dispersal  
352 limitation and environmental filtering owing to stronger environmental gradients and larger geographic  
353 distances across larger spatial scales (Soininen, Lennon & Hillebrand, 2007; Soininen et al., 2018;  
354 Menegotto, Dambros & Netto, 2019). In contrast with our second hypothesis (H2), our analyses showed  
355 no significant variation of nestedness with scale (Menegotto et al., 2019). Nestedness arises when  
356 species-poor sites represent subsets of the biota occurring in species-rich sites (Cantor et al., 2017;  
357 Baselga, 2010). In Macaronesian bryophytes and pteridophytes, species richness patterns are similar  
358 across archipelagos, so that no clear nested pattern is apparent. Differences in species richness among  
359 archipelagos are more evident in spermatophytes, with 1398, 684 and 165 native species (out of 1810  
360 in total in Macaronesia) in the Canarian, Madeiran and Azorean floras (TableS15), which is reflected  
361 by the near-significance of the difference in nestedness for within- and among- archipelago  
362 comparisons.

363 In line with our expectations H1b and H2b, the extent to which species turnover increased at large  
364 spatial scales varied, however, among lineages, being larger in spermatophytes than in pteridophytes,  
365 and then, mosses and liverworts, wherein the median turnover was less than half that in spermatophytes.  
366 In turn, nestedness was significantly higher in mosses, liverworts and pteridophytes than in  
367 spermatophytes. The progressive decrease of turnover and increase of nestedness from spermatophytes  
368 to bryophytes reflects their differences in dispersal capacities, pteridophytes producing bigger spores  
369 (30-50 $\mu$ m on average) than bryophytes (10-20 $\mu$ m on average). It also reflects major differences of  
370 speciation modes between these groups, with some spectacular radiations in the spermatophyte flora,  
371 whereas island bryophytes and ferns typically fail to radiate (Patiño, Carine et al., 2014). These  
372 differences of dispersal capacities and speciation modes are themselves reflected in differences of  
373 distribution patterns and especially, patterns of endemism. For instance, the 0.7%, 1.7% and 5% of  
374 Canarian endemic liverwort, moss and pteridophyte species, 0, 33.3% and 0 of which are SIEs, pale by



375 comparison with the 47%, Canarian endemic spermatophyte species that include 64% of SIEs (Table  
376 S15).

377 Patterns of turnover also varied among archipelagos in pteridophytes and spermatophytes, but not in  
378 bryophytes. The higher turnover observed in the Canaries for spermatophytes and pteridophytes, despite  
379 the shorter mean distance between islands than in the Azores, reflects the steeper altitudinal floristic  
380 gradients, as well as, globally, greater heterogeneity in climate, islands age and habitat types between  
381 the Canarian islands than between the Azorean islands (del Arco Aguilar & Rodríguez Delgado, 2018;  
382 Triantis et al., 2012). These differences are well reflected in the distribution of endemism among  
383 archipelagos, with the bulk of Canarian endemics being SIEs (64% of Canarian endemic  
384 spermatophytes), whereas Azorean endemics tend to be MIEs (88% of Azorean endemic  
385 spermatophytes) (Table S15), often widespread across the archipelago (Schaefer et al., 2011; Carine &  
386 Schaefer, 2010). The similarity of turnover among archipelagos in bryophyte floras is, at first sight,  
387 more striking. Indeed, large differences in bryophyte species composition would have been expected,  
388 due to poikilohydric condition of the group, between islands as different from each other as the Canary  
389 Islands. In reality, the specialized xerophytic floras of the eastern Canary Islands, characterized by low  
390 elevation and dry climates and dominated by thalloid liverworts (*Riccia spp.*) and annual mosses  
391 (especially of the family Funariaceae and Pottiaceae), can also be found at low elevation in the western  
392 Canary Islands. As a result, Canarian bryophyte communities are more nested than Canarian  
393 spermatophyte communities.

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

400 Variation in turnover and nestedness among land plant lineages depending on their dispersal capacities  
401 was paralleled by differences in their drivers. In agreement with the idea that spore-producing plants  
402 exhibit higher dispersal capacities than spermatophytes, and hence, that their distributions are better  
403 explained by extant environmental conditions than by historical factors associated with dispersal  
404 limitations (H3), extant climatic factors accounted more to bryophyte and pteridophyte turnover than to  
405 spermatophyte turnover. In contrast, island age contributed more to explain variation of turnover among  
406 islands in spermatophytes than in bryophytes and pteridophytes. Island age can be interpreted as a  
407 composite variable that accounts for time *per se*, but also, and most importantly, for the environmental  
408 heterogeneity during the life-cycle of oceanic islands, and especially, elevation and topographic  
409 complexity. Hence, island age does not necessarily reflect the amount of time available for colonisation

410 as in fact, the extant composition of the Macaronesian flora largely reflects dynamic interchanges with  
411 continental sources in both spore-producing lineages (Vanderpoorten et al., 2007) and spermatophytes  
412 (García-Verdugo et al., 2019; Hooft van Huysduynen et al., 2021). Instead, island age characterizes  
413 opportunities for speciation depending on habitat heterogeneity and availability, which peak as islands  
414 reach their highest elevation (Whittaker, Triantis & Ladle, 2008; Patiño et al., 2013). In this context,  
415 speciation plays a much more important role in the extant diversity of spermatophyte than of bryophyte  
416 and pteridophyte species, as evidenced by the striking difference in endemism rates per archipelago  
417 among lineages, of <8% in bryophytes and pteridophytes and >45% in spermatophytes. In bryophytes  
418 and pteridophytes in fact, endemic species are typically ‘isolated’ in their genus (“anagenesis”, Stuessy  
419 et al., 2006), whereas in Macaronesian spermatophytes, the ratio between the number of genera  
420 including endemic species and the number of endemic species ranges between 1.5 and 3 (Patiño et al.,  
421 2014).

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

428 In turn, area, one of the main drivers of species richness on islands due to decreased extinction rates,  
429 but most importantly, increased chances of colonization by airborne propagules (target area effect,  
430 Whittaker & Fernández-Palacios, 2007) and of speciation (Kissel & Barraclough, 2010), was never  
431 selected as a significant driver of species turnover. This was, at first sight, surprising because taxa with  
432 high dispersal capacities are expected to require larger areas to speciate than taxa with low dispersal  
433 capacities (Kissel & Barraclough, 2010), which should be reflected in higher levels of endemism on  
434 large islands, and hence, larger differences in species turnover among islands of different sizes. One of  
435 the main reasons why area did not play a role in the observed patterns of turnover is that all  
436 Macaronesian islands are much larger than the minimal area, < 10 km<sup>2</sup>, required for neutral genetic  
437 differentiation in spermatophytes (Kissel & Barraclough, 2010). In addition, Macaronesian bryophytes  
438 typically failed to speciate *in situ* (Vanderpoorten et al., 2011; Patiño, Carine et al., 2014). Even in  
439 genera that include several Macaronesian endemics, endemic species do not form a monophyletic group  
440 and each speciation event follows a long-distance dispersal event from continental sources (Patiño &  
441 Vanderpoorten, 2015). Unlike sympatric speciation, allopatric speciation depends on geographic  
442 isolation from sources, and not island size, contributing to the lack of relationship between island area  
443 and beta diversity patterns in spore-producing plants. Pteridophytes failed to radiate in Macaronesia as  
444 well. In fact, most Macaronesian ferns genera include only one endemic species that evolved by

445 allopolyploidisation (Vanderpoorten et al., 2011), a mechanism that is typically independent from area  
446 (Kissel & Barraclough, 2010).

447 It is worth noting that, when the four Canarian islets were included in the analysis, no significant model  
448 was obtained for liverwort and spermatophyte turnover and the percentage of explained deviance  
449 dropped of 29 and 50% in mosses and pteridophytes, respectively. Such an impact of small islands is  
450 reminiscent of the small-island effect, an anomalous pattern of the species–area relationship that  
451 predicts the existence of a threshold area, below which species richness varies independently of island  
452 area. The small-island effect is mostly driven by the decoupling of area and environmental heterogeneity  
453 on small islands (Chen et al., 2020; Matthews et al., 2020). The drop of explained deviance in our  
454 models similarly suggests that, beyond a certain threshold area, the factors affecting species  
455 composition change. As for the link between species richness and area (Yu et al., 2020), this effect  
456 varies among taxonomic groups, being most obvious in bryophytes and pteridophytes, whose floras are  
457 extremely depauperate on the Canarian islets.

458 In line with differences in beta diversity patterns among land plant lineages, caused by different  
459 responses of turnover to variation of climatic conditions and geographic distance, and with our  
460 hypothesis H4, spermatophyte floras clustered by archipelago, whereas pteridophyte and bryophyte  
461 floras did not. Fuerteventura, Lanzarote, Desertas and Porto Santo host similar cryptogamic floras of  
462 low-elevation, dry islands, whereas the western Canary Islands and Madeira, which share typical laurel  
463 forest floras, formed another cluster. In spermatophytes, this signal is erased by the predominance of  
464 the endemic element at the archipelago level (see above), so that the turnover between islands from  
465 different archipelagos is substantially higher in spermatophytes ( $0.74 \pm 0.07$ ) than in pteridophytes ( $0.41$   
466  $\pm 0.08$ ), mosses ( $0.40 \pm 0.10$ ) and liverworts ( $0.37 \pm 0.10$ ). The inclusion of the Canarian islets slightly  
467 changed the pattern, as, for all the taxonomic lineages and as previously reported (Torre et al., 2019),  
468 these islets clustered together, independently of their archipelagic adscription.

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

480

481 **Data availability**

482 The matrices of species distributions for liverworts, mosses and spermatophytes are available at  
483 <https://figshare.com>, DOI [10.6084/m9.figshare.17099840](https://doi.org/10.6084/m9.figshare.17099840).

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621

## 622 **Biosketch**

623 **Lea Mouton** is a PhD student at the University of Liège. Her research focuses on the variation of beta  
624 diversity with geographic scale.

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

628 **Acknowledgments.** J.P. is funded by the Ministerio de Ciencia e Innovación (MICINN) through the  
629 Ramón y Cajal program (RYC-2016-20506) and the grant (ASTERALIEN - PID2019-110538GA-I00)  
630 and by the Fundación BBVA (INVASION - PR19\_ECO\_0046). OH and AV are research director of  
631 the Belgian Funds for Scientific Research (FRS-FNRS).



632 Appendix 1. **Data sources**

633

634 **Azores**

635 **Bryophytes**

636 We employed the most recent databases (Borges et al., 2018; azoresbioportal.uac.pt/2019) combined  
 637 with subsequent floristic publications (Dirkse et al., 2018; Gabriel et al., 2019; Hanusch et al., 2020;  
 638 Coelho et al., 2021). The inclusion or exclusion of a series of species, for which available information  
 639 is conflictual, is justified in Table S0.

640 Table S0. Critical re-assessment of the occurrence of some bryophyte species from Azores, for which available  
 641 information is conflictual, and position adopted here.

| Species   | Comment  | Position adopted here |
|---|--|-----------------------|
| <b>Species reported from the Azores in azoresbioportal.uac.pt/2019 but considered as doubtful by Hodgetts &amp; Lockhart (2020)</b> |  |                       |
| <i>Radula complanata</i> (L.) Dumort.   | Reported from São Jorge by Claro (2008) but impossible to tell apart morphologically from <i>R. lindenbergiana</i> when sterile. All specimens from this group from Macaronesia in the molecular phylogeography of Laenen et al. (2011) belong to <i>R. lindenbergiana</i> | Excluded              |
| <i>Lepidozia reptans</i> (L.) Dumort.   | Several records of this species for the Azores by R. Gabriel, some of which were identified by the late R. Schumacker ( <a href="https://herbarium.nrm.se/specimens/B16236">https://herbarium.nrm.se/specimens/B16236</a> )  | Included              |
| <i>Rhynchostegiella curviseta</i> (Brid.) Limpr.  | All Azorean <i>Rhynchostegiella</i> specimens sequenced to date belong to <i>R. azorica</i> , which is morphologically extremely difficult to separate from other species (Patino et al., 2017).   | Excluded              |
| <i>Serpoleskea confervoides</i> (Brid.) Loeske  | Reported by Gonzalez-Mancebo et al. (1991) and Coelho et al. (2021)  | Included              |

|  |  |          |
|--|--|----------|
| <i>Thamnobryum maderense</i> (Kindb.) Hedenäs                  | A species of doubtful taxonomic status (Olsson et al., 2009), but confirmed in the Azores (Hedenäs, 1992a).  | Included |
| <i>Rhynchostegiella litorea</i> (De Not.) Limpr.               | All Azorean <i>Rhynchostegiella</i> specimens sequenced to date belong to <i>R. azorica</i> , which is morphologically extremely difficult to separate from other species (Patino et al., 2017).                                 | Excluded |
| <i>Entosthodon fascicularis</i> (Hedw.) Müll.Hal.              | Reported from the Azores by Dias (1986) but subsequently considered as doubtful  | Excluded |
| <i>Entosthodon muhlenbergii</i> (Turner) Fife                  | Reported from the Azores by Armitage (1931), Allorge & Allorge (1952) and von Hübschmann (1974). Re-examination of the material collected by Allorge suggests that this material was wrongly identified (C. Sérgio, pers. comm.) | Excluded |
| <i>Exsertotheca crista</i> (Hedw.) S.Olsson, Enroth & D.Quandt | All Macaronesian material, except for one collection from Madeira, belongs to other species (Hedenäs, 1992b)   | Excluded |
| <i>Grimmia incurva</i> Schwägr.                                | Old records (Allorge & Allorge, 1946, 1952) not subsequently confirmed despite recent intensive field surveys  | Excluded |
| <i>Grimmia montana</i> Bruch & Schimp.                         | Old records (Barros 1958) not subsequently confirmed   | Excluded |
| <i>Hygroamblystegium humile</i> (P.Beauv.) Vanderp.,           | Old records (Allorge & Allorge, 1948) not subsequently confirmed   | Excluded |

|  |   |  |
|--|---|--|
| Goffinet & Hedenäs                               |   |  |
| <i>Leucodon canariensis</i> (Brid.) Schwägr.     | Doubtful occurrence in the Azores (Hedenäs, 1992b; Ros et al., 2013; Gonzalez-Mancebo et al., 2009)                     | Excluded   |
| <i>Plagiothecium succulentum</i> (Wilson) Lindb. | Reported from São Jorge by Claro (2008)   | Tentatively excluded pending from publication of the results |
| <i>Pleuroidium subulatum</i> (Hedw.) Rabenh.     | Old records (Silveira Moniz, 1937; Allorge & Allorge, 1952) not subsequently confirmed                                  | Excluded   |
| <i>Pohlia andalusica</i> (Höhn.) Broth.          | Old records (Allorge & Allorge, 1952) not subsequently confirmed  | Excluded   |
| <i>Pohlia cruda</i> (Hedw.) Lindb.               | Old records (Richards, 1936; Allorge & Allorge, 1952) not subsequently confirmed despite recent intensive field surveys | Excluded   |
| <i>Schistidium agassizii</i> Sull. & Lesq.       | Reported from Pico (Sjögren, 2005) and Flores (Allorge & Persson, 1938).  | Included   |
| <i>Schistidium rivulare</i> (Brid.) Podp.        | Reported from Pico (Sjögren, 2005) and Flores (Allorge & Persson, 1938).  | Included   |

642

|   |   |          |
|---|---|----------|
| <b>Species reported from the Azores by Hodgetts &amp; Lockhart (2020) but not included in azoresbioportal.uac.pt/2019</b> |   |          |
| <i>Entosthodon convexus</i> (Spruce) Brugués  | Reported from the Azores by Allorge & Allorge (1952) and von Hübschmann (1974) but subsequently excluded by Sjögren (2001). Re-examination of the material collected by Allorge suggests that this material was wrongly identified (C. Sérgio, pers. comm.) | Excluded |

643

| <b>Species reported from the Azores by Hodgetts &amp; Lockhart (2020), included in azoresbioportal.uac.pt/2019, but without any distribution data</b> |   |  |
|---|---|--|
| <i>Atrichum androgynum</i><br>(Müll.Hal.) A.Jaeger  | Reported from São Jorge by Sérgio et al. (2010),  | Included (São Jorge)   |
| <i>Fissidens monguillonii</i><br>Thér.  | Reported from Santa Maria by Allorge & Allorge (1952)   | Included (Santa Maria)                                       |
| <i>Grimmia hartmanii</i><br>Schimp.   | Reported from São Jorge by Claro (2008)   | Tentatively excluded pending from publication of the results |
| <i>Grimmia meridionalis</i><br>(Müll.Hal.) E.Maier  | Tentatively included in the Azores by Ros et al. (2013) but possible confusion with <i>G. lisae</i> | Excluded   |
| <i>Hydrogonium bolleanum</i> (Müll.Hal.)<br>A.Jaeger  | Reported from São Miguel by Frahm (2011),   | Included (São Miguel)  |
| <i>Hygroamblystegium fluviatile</i> (Hedw.)<br>Loeske   | Reported from Flores by Blockeel et al. (2009)  | Included (Flores)  |
| <i>Ptychostomum kunzei</i><br>(Hornsch.) J.R. Spence  | Reported from Flores by Allorge & Allorge (1946, 1952)  | Included (Flores)  |
| <i>Tortella fragilis</i><br>(Drumm.) Limpr.   | Reported from São Jorge (Claro, 2008).  | Tentatively excluded pending from publication of the results |
| <i>Tortella inflexa</i> (Bruch)<br>Broth.   | Reported from São Jorge (Claro, 2008).  | Tentatively excluded pending from publication of the results |

|  |   |   |
|--|---|---|
| <i>Tortella tortuosa</i><br>(Schrad. ex Hedw.)<br>Limpr. | Reported from São Jorge (Claro, 2008).  | Tentatively<br>excluded<br>pending from<br>publication of<br>the results                  |
| <i>Zygodon rupestris</i><br>Schimp. ex Lorentz           | This species was mentioned from several islands by<br>different authors including Allorge, Schwab and<br>Sjögren. | Tentatively<br>excluded<br>pending actual<br>evidence based<br>on specimen<br>examination |

644

| <b>Species reported from the Azores in azoresbioportal.uac.pt/2019 but not by Hodgetts &amp; Lockhart (2020)</b> |   |  |
|--|---|--|
| <i>Bryum gemmiferum</i><br>R. Wilczeck & Demaret   | Reported from Terceira (Aranda et al., 2015) as 'record<br>to be confirmed'   | Excluded   |
| <i>Dicranella varia</i><br>(Hedw.) Schimp.   | Reported from São Jorge (Claro, 2008).  | Tentatively<br>excluded<br>pending from<br>publication of<br>the results |
| <i>Neckera pumila</i> Hedw.  | This species was included in the Moss Register of the<br>Swedish Museum of Natural History (2006) based on<br>collections by H. Persson (1937). | Included   |
| <i>Philonotis tomentella</i><br>Molendo  | Reported from São Jorge (Claro, 2008).  | Tentatively<br>excluded<br>pending from<br>publication of<br>the results |

645

| <b>Species reported from the Azores in azoresbioportal.uac.pt/2019 and Hodgetts &amp; Lockhart (2020) but requiring revision</b> |
|--|
|  |

|   |  |          |
|---|--|----------|
| <i>Homalothecium sericeum</i> (Hedw.) Schimp. | According to Hedenäs et al. (2014), <i>H. mandonii</i> , and not <i>H. sericeum</i> , occurs in the Azores | Excluded |
|---|--|----------|

646

647 **Pteridophytes**

648 Borges et al. (2005, 2018)

649 **Spermatophytes**

650 Borges et al. (2005, 2018), with updates and amendments from Schäfer (2003), Bateman, Rudall &  
651 Moura (2013), Hay et al. (2014), Moura et al. (2015a, b), Banasiak et al. (2016), Durán et al. (2020),  
652 Galán de Mera et al. (2017), Fontinha, Andrade & Pinheiro de Carvalho (2020), Uotila (2020),  
653 Frankiewicz (2021), Míguez et al. (2021) and Schäfer (2021) and authors personal observations.

654 **Madeira**

655 **Bryophytes**

656 Borges et al. (2008) with updates and amendments from Dirkse et al. (2018), Ellis et al. (2011, 2014,  
657 2017, 2018), Fontinha et al. (2020), Hanusch et al. (2020), Hodgetts & Lockhart (2020), Kürschner et  
658 al. (2008a, b), Lobo (2008), Luis et al. (2008, 2010), Patiño et al. (2017), Sim-Sim et al. (2010, 2017).

659 **Pteridophytes and Spermatophytes**

660 Borges et al. (2008) with updates and amendments from Menezes de Sequeira et al. (2011), Galán de  
661 Mera, Linares Perea & Vicente-Orellana (2017), Matzke-Hajek, Gonçalves Silva & Paz Fontinha  
662 (2017), Andrade & Pinheiro De Carvalho (2020), Hernández (2020), Jardim & Menezes de Sequeira,  
663 2020.

664 **Canary Islands**

665 **Bryophytes**

666 Canary Island Biodiversity Database (<https://www.biodiversidadcanarias.es/>, last access on  
667 03/03/2021).

668 **Pteridophytes and Spermatophytes**

669 Canary Island Biodiversity Database (<https://www.biodiversidadcanarias.es/>, last access on  
670 03/03/2021) with updates and amendments from Izquierdo et al. (2001), Caujapé-Castells et al. (2008),  
671 Banasiak et al. (2016), Galán de Mera, Linares-Perea & Vicente-Orellana (2017), García-Aloy et al.

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