Tracking the origin of island diversity: insights from divergence with the continental pool in monocots

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Abstract

At their early age, a large proportion of island pools were a partial sampling of mainland pools whatever islands are oceanic or fragments of the mainland. Through time, colonization, diversification, extinctions, have deeply transformed insular and continental communities and therefore the degree to which they share species. We studied the relative importance of these mechanisms by looking at the shared evolutionary history between species pools on islands and continents. Indeed, most of these mechanisms are not neutral regarding phylogeny but are linked to species evolutionary relationships. We measured the phylogenetic divergence between continental and insular monocot communities through metrics of beta Mean Pairwise Distance and beta Mean Nearest Taxon Distance. We first tested the influence of spatial and environmental distance to the continent, two main factors of divergence, but whose explanatory power in a phylogenetic context was still unclear. We showed that both dispersal and enviromental filtering were important to explain divergence, although species that could pass these filters were not phylogenetically clustered. There was however a clear distinction between oceanic and continental islands: a stable climate in the latters was key to the survival of the original biota leading to a high proportion of shared lineages between the mainland and islands. But distance to the continent was only part of the story, we investigated additionnal mechanisms of phylogenetic divergence through their relation to island features and community structure. This showed that the most divergent islands occurred in the tropics and that processes of persistence of original species, diversification in remote archipelagos, neutral colonization on easy-to-reach islands, turnover, and high speciation rates may have driven phylogenetic divergence at a world scale. This study showed how phylogenetic approaches may explain how divergence, or similarity may have arisen and provide new insights in the continental origin of plant diversity on islands.

Key words: beta diversity, isolation, monocotyledon, phylogenetic divergence, world islands

Introduction

One of the main questions concerning island ecology is the extent their floras and faunas resemble those from the continents assumed to be the main source of colonisers (Patiño et al. 2017, Koenig et al. 2019). At an early stage, a large proportion of island communities are a partial sampling of mainland pools (Wallace 1880 but see Ali 2017). Continental islands already harbored a full complement of species when they separated from continents. Oceanic islands were depauperate of life at birth, and their species composition results mainly from colonization from continents. Through time, large scale factors such as geographical isolation, archipelago dynamics and island age, have shaped the arrival, settlement, diversification of species in the community. In addition, community assembly in islands may be influenced by other determinants such as habitat and resource availability that modulate population sizes or inter and intra specific interactions, driving selection, survival and speciation (Kreft et al. 2008, Kier et al. 2009, Negoita et al. 2016). All these mechanisms have deeply transformed insular and continental communities and therefore the degree to which they share species.

The theory of island biogeography (MacArthur and Wilson 1967) and empirical studies (Weigelt and Kreft 2013, Patiño et al. 2015) predict that immigration rates decrease with spatial distance. This implies that the number of species shared by islands and continents decrease with the distance between them. However, colonization is highly dependent on the abilities of species to disperse, which may be lineage specific. Consequently, some closely-related species may co-occur on spatially distant continental areas and islands, whereas other lineages may be spatially clustered and totally absent from remote places. For example, Patiño et al. (2015) demonstrated that seed plants species-richness decreased with island isolation whereas this was not the case for plants that produce spores, allowing dispersal on relatively longer distances. This dispersal filter makes that the effect of spatial distance is driven by the phylogenetic position of the species, hence blurring the expected effect of

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91 spatial distance on evolutionary history differences, *i.e.* phylogenetic divergence. Beyond

92 spatial distance, environmental distance is another factor explaining why communities may

93 share species or not (e.g. Nekola and White 1999, Tuomisto 2003, Carvajal-Endara et al.

94 2017). Different environmental conditions between ecosystems may prevent the settlement of

95 some species because they cannot form viable populations in the environment to which they

96 disperse. Again, the diversified responses of species to different environmental conditions

97 may strongly reflect their position of species in the Tree of Life. Closely related species are

98 expected to share traits and to occupy more similar niches thus co-occuring at places with

99 similar environmental conditions (Webb et al. 2002). Following this reasoning, environmental

100 distance would be a strong filter for the co-occurrence of closely related lineages and may

101 increase phylogenetic divergence between communities (Tuomisto 2003, but see Gerhold et

102 al. 2015). This may however not always be true. For instance, species from distinct lineages

103 where trait evolution is predominantly convergent, as sometimes found in islands (Gillespie

104 2007), can co-occur in similar environments, even if they are over-dispersed in the phylogeny.

105 On the contrary, very closely related species may adapt to highly diverging niches available to

106 them when they arrive on an island (Evans et al. 2014). For all these reasons, the effect of

107 spatial and environmental distance on phylogenetic divergence between islands and

108 continents is still unclear (see Carvajal-Endara et al. 2017 for a regional example). A first

109 objective of this study is thus to distinguish the contributions of spatial and environmental

110 distance to phylogenetic divergence between insular and continental species pools.

111   However, spatial and environmental distances to the continent may only be part of the

112 story explaining why species pools diverge between islands and continents and therefore why

113 some islands are more divergent than others (Koenig et al. 2019). While we acknowledge that

114 evolutionary and ecological dynamics in continents may have a role in explaining the

115 phylogenetic divergence between islands and the mainland (Cronk 1992) here we focus on

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116   processes occurring in islands. The presence or absence of lineages on islands depend on

117   ecological and evolutionary changes, resulting from colonization, diversification, extinctions

118   that have a strong phylogenetic signature (Gillespie 2007). The importance of these processes

119   in shaping island diversity may therefore be estimated by looking at the phylogenetic structure

120   of communities (Weigelt et al. 2015, Carvajal-Endara et al. 2017). Nonetheless, analyses of

121   community structure generally require the use of null models which, by randomizing species

122   between pools, are largely dependent on the scale to which these pools are defined and make

123   it difficult to detect the true community phylogenetic patterns (Graham and Fine 2008). Besides,

124   as the insular pool mostly originate from mainland lineages, subjected to diversification or

125   not, we assume here that additional processes could be revealed by looking at the

126   phylogenetic divergence between insular and continental communities. Island-mainland

127   comparison would be the "logical-way" to understand the evolution and assembly of the

128   insular biota, but there are still very few studies which have taken this approach into

129   consideration (Santos et al. 2016). Our second objective was thus to identify processes and

130   estimate their contribution to the phylogenetic divergence between islands and continents. We

131   assume that high divergence could be inferred from 1) long branches arising from

132   relictualization or/and long-term survival of species in islands providing current and past

133   refuge to plant species, 2) in situ speciation at the origin of evolutionary closely-related

134   species in islands and of the share of deep tree branches between islands and continents, 3)

135   low colonization events from the mainland so that only few branches would be shared, 4) high

136   turnover leading to a high phylogenetic divergence both at the terminal and deep-branch level.

137   To test these hypotheses we used measures of phylogenetic beta Mean Pairwise Distance

138   (MPD_β) - sensitive to variation at the deep branch level - and phylogenetic beta Mean Nearest

139   Taxon Distance ($MNTD_\beta$) - sensitive to variation at the terminal branch level - between

140   insular and continental pools. Both of these indices of phylogenetic divergence were then

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141 linked to the phylogenetic structure of the species pool on islands and to island biophysical

142 features, as both display traces of past mechanisms at the origin of island diversity.

143   We focused on Monocotyledons which is a very large clade, morphologically and

144 functionally diverse, representing a quarter of flowering plant diversity. Monocots are

145 distributed all across the globe and are well represented on islands. This, along with the

146 existence of a well-resolved phylogeny and with database built by experts makes that

147 Monocotyledon is a well-suited group to study the origins of phylogenetic divergence

148 between insular and continental communities.

Material and Methods

150 **Data**

151 *Islands and Continents*

152 There is a wide diversity of islands types, but common properties are that they are isolated,

153 well defined geographically and have well delimited boundaries. A total of 4,105 islands was

154 used in this study. They were delimited with the Global Island Database provided by the

155 United Nations Enviioronment Programm (UNEP) (Depraetere and Dall 2007), and restricted

156 to all isolated areas smaller than Australia occurring in oceans. Islands found within

157 continental boundaries (e.g. in lakes, estuaries, rivers) were not considered. 610 continental

158 areas were defined and delimited based one TDWG polygons at the 4th level (Brummitt et al.

159 2001).

160 *Phylogeny*

161 This study was based on a recent phylogeny of Monocots, which includes representatives of

162 the great majority of genera (Tang et al. 2016). The use of four DNA regions (*rbcL, matK, ndhF*

163 and nrITS DNA) allowed to place 1,816 genera on the phylogentic tree. The 710 genera for

164   which genetic data were missing were included as polytomies within their respective clades

165   using the most up-to-date taxonomy for each taxon (Tang et al. 2016).

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167   *Plant occurrences*

168   Data on plant occurrences were obtained from the web platform of the Global Biodiversity

169   Information Facility (GBIF). We downloaded all records, except fossil ones, and selected

170   those intersecting the islands considered in this study. Then we used e-monocot database to *i.*

171   control for synonyms and use only each species' accepted name *ii.* to exclude non-native

172   species occurrences *iii.* to control for species range by comparing occurrences from the GBIF

173   data with those from e-monocot. E-monocot is a global database on monocotyledons which

174   compiles occurrences assigned by experts to TDWG polygons. In addition, because aquatic

175   plants tend to be highly evolutionary distant from all other species and might influence our

176   estimates of phylogenetic divergence, we excluded all species belonging to the families

177   Alismataceae, Acoraceae, Aponogetonaceae, Juncaceae, Juncaginaceae, Mayacaceae,

178   Pontederiaceae, Potamogetonaceae, Ruppiaceae, Scheuchzeriaceae, Zosteraceae,

179   Posidoniaceae, Cymodoceaceae and Hydrocharitaceae.

180   The dataset resulting from these filters comprised 2,568,386 occurrences representing 16,213

181   species and 1,562 genera in 4,105 islands, and 16,571,974 occurrences of 48,140 species from

182   2,178 genera in 610 continental areas.

183   **Estimates of phylogenetic divergence between islands and surrounding continents**

184   *Metrics*

185   The phylogenetic divergence between insular and continental floras was calculated with

186   phylogenetic Mean Pairwise Distance (MPD_β) and Mean Nearest Taxon Distance ($MNTD_\beta$),

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187   using the comdist function from R package picante (Kembel et al. 2010). MPD_β is the mean

188   phylogenetic distance separating each pair of tips in two assemblages (here an insular and a

189   continental pool). MPD_β estimates phylogenetic divergence in the global composition of

190   islands and continents, and is sensitive to variation at the deep branch level (Webb et al. 2008)

191   (Webb 2000). $MNTD_\beta$ is the mean distance separating each tip in a site from its nearest

192   relative occuring in another one and is sensitive to differences at the terminal branch level (

193   Webb 2000, Webb et al. 2008). It is thus expected that these measures are complementary to

194   the assessment of different processes conducting to the share of deep or short branches

195   between islands and continents (e.g. an adaptative radiation following the settlement of a

196   genera still present on the mainland will tend to decrease the number of shared short branches

197   but will have a lesser influence on the number of shared deep branches).

198   *Effect of spatial and environmental distance on phylogenetic divergence*

199   We calculated MPD_β and $MNTD_\beta$ between each island and each of the 10 nearest continental

200   polygons. While we cannot be certain that the continental polygons defined here represent the

201   true species pool for each island, it is likely that lineages present on islands originate from

202   multiple relatively close continental regions. For example, Carvajal-Endara et al. (2017)

203   estimated that the Galapagos species could have dispersed from 9 continental countries.. To

204   test the sensitivity of the results to the number of continental polygons, we also measured

205   MPD_β and $MNTD_\beta$ between each island and each of the 5 and 20 nearest ones. We

206   distinguished between oceanic and islands connected to the mainland during the Last Glacial

207   Maximum – assumed to be a proxy for continental islands (Weigelt et al. 2013) – because

208   different mechanisms may be at stake to explain divergence in each type of island (Whittaker

209   and Fernández-Palacios 2007 but see Ali 2017).

210   As distance is assumed to be a main factor at differentiating biotas (53), we tested the

211   predictive effect of spatial and environmental distances at explaining the variations in MPD_β

212   and $MNTD_\beta$ between insular and continental communities. Spatial distance was calculated in

213   ArcGIS 10.3.1, as the distance between the centroids of an island and of a continental

214   polygon. We then used four variables from (Fick and Hijmans 2017) reflecting distances in

215   climatic conditions: differences in mean annual temperature, mean annual rainfall, mean

216   annual solar radiation, mean annual wind speed. We did not include the differences of latitude

217   and longitude due to colinearity with environmental variables, especially solar radiation and

218   temperature, but their effect was tested separately (Appendix S1). All variables (e.g.

219   difference in mean annual temperature) were then scaled and we estimated the average

220   environmental distance as the euclidean distance among scaled variables (Tuomisto 2003).

221   Finally, to account for other environmental dimensions not examined, we tested the effect of

222   the number of different ecoregions between islands and continents (Olson et al. 2001) .

223   We first used Generalized Linear Mixed Models (GLMM) to test the effect of spatial and

224   environmental distances on MPD_β and $MNTD_\beta$ between each island and a polygon in the

225   continent. Second, we employed Boosted Regression Trees (BRT) (Elith et al. 2008) in order to

226   make an informed decision about the relative contribution of each variable to phylogenetic

227   divergence. BRT also displayed the direction of the relationship between the response and the

228   predictors and we looked for interactions with the highest contribution (Elith et al. 2008).

229   GLMM first tested the additive effects of all selected variables. We then used a second model

230   in which all variables plus interaction between variables, identified thanks to the BRT

231   method, were included. In GLMM, island's identity was held as a random variable. Yet when

232   BRT and GLMM methods led to contradictory results for a given variable, for example

233   because of residual colinearity, we performed additional models, one for each technic, in

234   which the variable in question was tested alone. Especially, this correction was needed to test

235   the effect of euclidean environmental distance.

236   **Characterisation of the minimum divergence between islands and continents**

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237 To determine the divergence of each island with the most similar surrounding continental area

238 and to further explore how mimimum divergence was distributed across the world we

239 estimated its minimum MPD_β and $MNTD_\beta$ values ($minMPD_\beta$ and $minMNTD_\beta$, respectively).

240 We measured $minMPD_\beta$ and $minMNTD_\beta$ as the minimum values of divergence between an

241 island and each of its 10 nearest continental polygons. Although insular species may have

242 settled from multiple continental pools, we could not estimate the true original pool at the

243 large scale we of our study, and we assumed that the minimum phylogenetic divergence from

244 any continental polygon allowed to compare islands between them and to study the processes

245 conducting to divergence between insular and continental pools.

Phylogenetic structure of insular communities

247 In order to explore how the phylogenetic structure of an insular community may influence

248 $minMPD_\beta$ and $minMNTD_\beta$, we calculated 7 related attributes for each island: variance in

249 pairwise diversity (VPD), mean pairwise distance (MPD_α), the average and standard deviation

250 in evolutionary distinctiveness (fair proportion index; ED), the proportion and the number of

251 genera among the 10% of the most evolutionary distinct plants, and finally the number of

252 genera in each island. Variance in pairwise diversity measures the regularity of the

253 distribution of evolutionary history (Davies and Buckley 2012, Tucker et al. 2017). Evolutionary

254 distinctiveness quantifies the number of relatives a species has and how phylogenetically

255 distant they are (Faith 1992, Forest et al. 2007). MPD_α is the pairwise phylogenetic distance

256 between the species of a given community (Webb 2000).

Abiotic correlates of phylogenetic divergence

258 Finally, we investigated which geographical, environmental, and historic factors, as well as

259 sampling effort in islands may influence the minimum phylogenetic divergence with

260 continents (Table 4). Note that these factors are intrinsic to an island, and that we did not use

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261   the difference in environmental condition between an island and the surrounding continents as

262   in the previous section. We selected variables which had low colinearity with all others (Table

263   4), i.e. excluding variables with p>0.5 (Pearson correlation test). Latitude, likely to be an

264   important factor of divergence representing a strong spatial effect, was tested independently

265   due to its high colinearity with mean annual temperature. In addition, as our results may be

266   biased by the fact that some islands were much less sampled than others, we re-ran the

267   analysis without islands with low Incidence-based Coverage Estimate (ICE) values. ICE is

268   calculated from the number of rare species in a sample and from species accumulation curves

269   We calculated ICE by defining a sub-sample within an island as a set of observations obtained

270   at a given date, and using the R function spp.est from the 'Fossil' package (Vavrek 2011). We

271   then calculated the ICEr index as the ratio of the observed number of species in an area over

272   the expected number of species estimated with ICE. The contribution and significance of

273   distance, phylogenetic structure and abiotic factors was thus tested with a dataset by

274   successively excluding islands with ICEr values lower than 0.2, 0.5 and 0.75. We found that

275   results were not affected when these islands were discarded.

276

277   *Modeling the influence of island community structure and abiotic factors on phylogenetic*

278   *divergence*

279   Using BRT and Generalized Linear Models (GLMs) we estimated the contribution and

280   significance, respectively, of community structure and abiotic factors to $minMPD_\beta$ and

281    $minMNTD_\beta$. No random variable was added in the models. Thanks to BRT we also estimated

282   the strengths of interactions. The significance of the 2 interactions with the highest

283   contributions were also tested with GLMs.

284   Exploring the relationship between abiotic features and community structure was not the main

285   aim of this paper and was documented in previous studies (Weigelt et al. 2015, Carvajal-Endara

286   et al. 2017), therefore the outcomes of this analyses is given as a supplementary material

287   (Appendix S2).

Results

289   *How spatial and environmental distance influence phylogenetic divergence between insular*

290   *and continental communities*

291   As estimated from boosted regression trees (BRT), variables with the highest importance at

292   explaining phylogenetic beta mean pairwise distance (MPD_β) were difference in solar

293   radiation and difference in spatial distance (Table 2, Appendix S3). Difference in rainfall also

294   had a high contribution in the case of oceanic islands. When accounting for island identity as

295   a random effect in generalized linear mixed models (GLMMs), MPD_β significantly increased

296   with spatial distance and rainfall, regardless if islands were continental or oceanic.

297   Differences in solar radiation and temperature had an unexpected negative relationship with

298   MPD_β, probably reflecting their non-linear relationships with the difference in latitude in the

299   tropics (Appendix S1). Indeed, when tropical islands were excluded, the effect of these two

300   variables had a significant positive relationship with MPD_β. The remaining variables (wind

301   speed, number of ecoregions and Euclidean environmental distance) had lower contributions

302   but significant positive relationship with MPD_β (Table 2 ; Appendix S3). Looking at $MNTD_\beta$,

303   variables which generally had a high contribution were the difference in annual solar

304   radiation, spatial distance and the euclidean environmental distance. However, contribution of

305   spatial distance was much lower in continental islands (Table 2, Appendix S3). When island

306   identity was integrated as a random effect in GLMMs all variables had a positive relationship

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307   with $MNTD_\beta$. Overall, the choice of number of continental polygons used to measure

308   divergence did not change the major results.

309   *Spatial patterns of island-continent divergence*

310   Islands with floras highly divergent from continents when using $minMPD_\beta$ were found

311   worldwide, even though $minMPD_\beta$ values tended to be the highest around the equator (figure

312   2a). Madagascar, Fiji, Indonesia and West Indies are exemples of islands with high $minMPD_\beta$

313   (figure 2a, Appendix S4).

314   Spatial patterns of $minMNTD_\beta$ roughly differed from those of $minMPD_\beta$. Especially, there

315   were relatively more islands with high $minMNTD_\beta$ in the Southern hemisphere. Yet, when

316   looking at extreme values, islands with the highest $minMNTD_\beta$ were similar to those having

317   the highest values $minMPD_\beta$. Exemples are Madagascar, Fiji, Indonesia, Cook Islands and

318   American Samoa (figure 2b, Appendix S4).

319   *Effect of phylogenetic structure on phylogenetic divergence between island and continents*

320   We found that the effect of insular community structure varied depending on whether

321    $minMNTD_\beta$ or $minMPD_\beta$ was used. The average Evolutionary Distinctiveness (ED) of insular

322   monocots had the highest contribution and a significant positive effect on $minMPD_\beta$ (table 3).

323   On the contrary, standard deviation in ED had a significant negative effect. MPD_α and genus

324   richness ranked second and fifth regarding their contribution to $minMPD_\beta$ (contributions equal

325   to 31.8% and 2.1%, repectively). Both variables displayed a significant positive relationship

326   with $minMPD_\beta$. The highest contribution to $minMNTD_\beta$ was the number of insular genera

327   (contribution = 42.3%), which had a significant negative effect. Other variables with a

328   relatively high contribution were VPD (contibution=30.6%) and MPD_α

329   (contribution=15.04%), both having a significant negative relationship with $minMNTD_\beta$.

330   *Abiotic correlates of phylogenetic divergence*

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331   Latitude was the variable with highest contribution to explain $minMPD_\beta$ and its effect was

332   significantly negative. Interaction of latitude and longitude also had a significant negative

333   effect: effect of low latitude on phylogenetic divergence between islands and continents was

334   stonger at high longitude. Other geographic variables had a low contribution to $minMPD_\beta$

335   such as the distance to the nearest continental polygon and area which had slightly significant

336   positive and negative relationships, respectively. Climatic variables generally had a moderate

337   contribution to $minMPD_\beta$. Specifically mean annual rainfall and temperature had the highest

338   contributions among all abiotic variables (Table 4a). Climatic variables all had a significant

339   effect on $minMPD_\beta$. It was positive for mean annual temperature, mean annual rainfall and

340   the number of ecosystems, but negative regarding rainfall seasonality, annual wind speed, and

341   standard deviation in vapour pressure. Although historical factors had a relatively low

342   contribution to MPD_β, we found a significant positive effect of the velocity of past climate

343   change and of the past connexion to the mainland.

344   Regarding $minMNTD_\beta$ between islands and continents, latitude (contribution=31.1%), the

345   Relative Incidence-based Coverage Estimator (ICEr; contribution=26.7%) and longitude

346   (contribution=9.7%) were important to explain $minMNTD_\beta$, with a significant negative effect

347   (Table 4b). ICE_r displayed a significant negative interaction with area, meaning that poorly

348   sampled and small islands had the highest $minMNTD_\beta$ values. Contribution of environmental

349   variables was low. Among them, mean annual temperature (contribution=4.3%; significant

350   positive effect) and standard deviation in vapour pressure (contribution=7.0%; significant

351   negative effect) had the highest importance. As for historical variables, velocity of past

352   climate change had a significant positive relationship on $minMNTD_\beta$, whereas past

353   connection to the mainland, contrary to what was observed for $minMPD_\beta$, had a significant

354   negative effect (Table 4b, Fig S2).

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Discussion

Difference in species composition between islands and continents has already been well-documented. This study goes one step further by showing that insular and continental pools also differ in their evolutionary history and that the degree to which they share phylogenetic branches depend on the phylogentic signature of the processes shaping diversity.

a. Divergence due to spatial and environmental distance

While effect of the distance to the continent is recognised to be a main driver of species richness and community composition in islands (MacArthur and Wilson 1967, Brown and Kodric-Brown 1977, Rosindell and Phillimore 2011, Cabral et al. 2014), the present study gives evidence that it is also true at the phylogenetic level. This result was expected because a difference in species composition also means that the phylogenetic branches supporting these species are distinct between pools. As spatial distance acts as a dispersal filter reducing the number of individuals exchanged between continents and islands, it also reduces the number of shared phylogenetic branches between them. More specifically, our results suggest that among the insular species and phylogenetic branches originating from the mainland, most of them are or were present on the nearest continents. One of the main benefits of using phylogenetic approaches is that it allows investigating the mechanisms of dispersal filtering that have a strong phylogenetic signature. For instance, some studies show that dispersal toward some islands is lineage specific due to phylogenetically clustered traits such as seed size. However, we found that distance had a similar influence on the co-occurrence of deep or terminal branches indicating that a dispersal filter towards species clustered in the phylogeny is not detected at a global scale.

Distance to the continent is only the first filter of species settlement, although some individuals may reach an island, only a few species may truly establish themselves due to specific niche requirements. Several studies showed the prevailance of environmental over dispersal filtering (Tuomisto 2003, Carvajal-Endara et al. 2017). However, at a global scale it was

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382   unclear which of those filters had the strongest influence on the divergence between islands

383   and continents. Strong environmental filtering is expected to generate species phylogenetic

384   clustering due to phylogenetic trait conservatism (Webb et al. 2002). Despite the fact that

385   distinct environmental conditions reduce the number of shared branches between islands and

386   continents, the genera they supported were likely not clustered the phylogeny (Table 1).

387   In the case of continental islands, increased divergence with environmental distance

388   may result from two complementary factors. On the one hand, lineages that were present at

389   the island birth and that persist nowadays may have survived thanks to the continuity of a

390   stable island climate through time (Sandel et al. 2011, Weigelt and Kreft 2013). On the

391   opposite, we showed that high velocity of past climate change result in high phylogenetic

392   divergence between continents and islands.

393   This, with the complex geological history following the breakup of continental islands, the

394   presence of a complete set of species at birth and more frequent arrivals may also explain the

395   lesser importance of spatial distance on divergence when compared to oceanic islands.

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398   *b.   How island features and community structure drive phylogenetic divergence*

399   Distance is a key determinant of species arrival and establishment on islands but further

400   ecological and evolutionary processes are at the origin of divergence between islands and

401   continents. The study of phylogenetic divergence may allow distinguishing several of them.

402   Geological and climatic history of islands drive the long-term survival of species promoting

403   their evolutionary distinctiveness (ED). The monocotyledons with highest ED values, usually

404   hold long branches and have few close relatives. So, ED results either from ancient speciation

405   events that gave rise to a single of few species, or from the evolutionary isolation of a species

406   through the extinction of its nearest-relatives, i.e. relictualization (Gillespie 2007, Grandcolas

407   and Trewick 2016).   We found that the more evolutionary distinct the monocotyledon on an

408   island the more divergent from continental pools they were, but that ED had a lower

409   contribution on the divergence of the most closely-related taxa rather than on the divergence

410   beween all taxa. This is likely explained because many lineages with high ED may still be

411   present on the continent (Jetz et al. 2014). Indeed, when high ED monocotyledons are present

412   on both continents and islands, the phylogenetic distance may remain high with all other taxa,

413   but may be lower when it is estimated only from the most closely-related taxa. The present

414   results thus indicate that relictualiz:ation is likely to have been less frequent than evolutionary

415   processes in explaining the origin of ED monocotyledons. Besides, we also observed that

416   islands where mean ED is high were generally connected to the continent in the past. Insular

417   monocotyledons which are currently evolutionary distinct may have therefore probably

418   appeared on the mainland before islands became fragmented.

419   Phylogenetic divergence is not only due to ancient and isolated lineages, but also to

420   recent and clustered taxa absent on the mainland. Our results show that when phylogenetic

421   distance of the insular pool is low and regular, island and mainland flora highly diverge. At

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422   the generic level, this may correspond to islands where environmental, dispersal, or biotic

423   filters have allowed a majority of closely related monocot lineages to establish (Cadotte and

424   Tucker 2017, Koenig et al. 2019). However, as we did not find an effect of environmental

425   distance or spatial distance on the occurrence of closely-related genera on islands, additional

426   factors potentially causing such clustered phylogenetic structure should be investigated. At

427   the species level it may be expected that regular and low phylogenetic distance may cause

428   high phylogenetic divergence due to evolutionary radiations. Recent species radiations may

429   form clusters of endemic species with regular and low phylogenetic distance, conducting to

430   few terminal branches shared with the mainland. Such radiations are more likely to occur on

431   remote oceanic islands. Indeed, in these islands, immigration followed by in-situ speciation is

432   the main process at the origin of species diversity: colonization rate is so slow that the main

433   processes to fill the niche space are evolution or adaptation (Gillespie 2007, Emerson and

434   Gillespie 2008).

435   Besides diversification and extinction, colonization is likely to be another important

436   cause of phylogenetic divergence. Colonization from the continent may increase the co-

437   occurence of similar lineages between islands and continents. We found that three factors

438   related to high colonization rates increase phylogenetic similarity between island and

439   continental pools, confirming our results about the effect of dispersal filtering: small spatial

440   distance from the continent, large propotion of surrounding land mass and high wind speed.

441   Proximity to the continent, and more generally to any other land mass, facilitates exchanges

442   and thus high phylogenetic similarity at both the terminal and the deep branch levels

443   (MacArthur and Wilson 1967). It probably means that genera having established on these

444   islands are neither over-dispersed nor clustered in the phylogeny. Regarding wind speed, its

445   negative relationship with divergence highlights that monocot dispersal capacities may have a

446   critical role to explain colonization success. The importance of wind speed to divergence

18

447 tends to be stronger at deep than at terminal branch level. Genera whose representatives can

448 disperse through anemochory may consequently tend to be over-dispersed in the phylogeny

449 but functional trait analyses are needed to test this assumption. Plants may also have reached

450 islands thanks to animals, ocean currents, or human conveyance. To understand how this

451 mode of dispersal influences which lineages co-occur on islands and continents, future

452 research may look at the dispersal traits of lineages having colonized islands and at the

453 directionality and trajectories of dispersal factors (Patiño et al. 2015, Gillespie et al. 2012).

454   Other key factors of divergence between islands and continents are species turnover and

455 speciation rates. Islands with high temperature and intense but relatively regular

456 precipitations, i.e. islands with a tropical rainforest climate, were more likely to harbor a flora

457 that diverges from the mainland flora. Rainfall and temperature, but also vapour pressure, are

458 related to water and energy supply, which may increase turnover but also speciation rates,

459 conducting to divergent communities from the mainland (Hawkins et al. 2003, Beres et al. 2008).

460 While speciation are more frequent at the species level, it also occurred in monocots at the

461 generic level, especially in the tropics. This divergence was important to both deep and short

462 branches, which suggests that turnover is not clustered in the phylogeny. High energy and

463 water supply is common in the tropics and around the equator, but these are also places where

464 many processes departing from current environment, such as evolutionary, climatic and

465 geologic history, have let a strong imprint on species diversity and divergence. Mechanisms at

466 the origin of this latitudinal gradient in species diversity still fuels the debate and

467 consequences in terms of divergence between species pools remain to be investigated.

468   Finally, not only current but also past environmental conditions are important to explain

469 phylogenetic divergence, in particular on continental islands. Velocity of past climate change

470 may actually be associated to low environmental stability (Fjeldså 1994) and past species

471   extinctions of insular species (Sandel et al. 2011) but also to strong environmental filtering

472   conducting to dissimilar flora between continents and islands

473   *Directions for future research*

474   Although we reduced biases in occurrence data through different methods, working at a

475   global scale implied that the dataset can be subject to sampling biases over all islands, due to

476   varying priorities along data acquisition history. Especially, more intense sampling in some

477   less studied islands, but also the mobilisation of yet non-digitized herbarium data will

478   certainly lead to higher robustness of the results obtained here. In addition, although the use of

479   the generic level and of presence only data have been important in reducing biases in monocot

480   spatial distribution, this may have prevented from detecting the importance of some

481   mechanisms on divergence, for example adaptative radiations.

482   A second point that may stimulate further research is that we have only been interested in

483   abiotic factors to explain divergence between insular and continental flora. Biotic factors,

484   especially competition and interactions conducting to co-evolution, may act as a biotic filter,

485   shape the phylogenetic structure of communities and their divergence with the mainland (

486   Wilson 1969, Webb et al. 2002, Gillespie 2007, Weigelt et al. 2015). We therefore encourage to

487   direct future research on the role of biotic factors in shaping the phylogenetic structure of

488   communities and how they may explain divergence between insular and continental pools.

489   Moreover, at considering the distance from each island to the nearest continent we ignored

490   potential dispersion between islands and especially the role of island-hopping which may be

491   an important process in the composition of insular communities (Sillero et al. 2018). Insular

492   species diversity has also a strong temporal dimension: age reflects time for speciation and

493   colonization (Emerson and Gillespie 2008), area but also past distance to the continent varied

494   through geological times (Norder et al. 2018) and are expected to have a strong influence on

495   patterns of beta diversity. In addition the biological classification in a simple dichotomy, i.e.

496   oceanic versus continental islands, may be complemented by introducing other island types

497   (Ali 2017).

498

499   **Conclusion: new insights on plant community divergence between island and continents**

500   **thanks to phylogenetic approaches**

501   Phylogenetic approaches were rarely employed to understand patterns and origin of plant

502   diversity in islands (Kreft and Jetz 2007, Kreft et al. 2008, Kier et al. 2009, but see Weigelt et al.

503   2015). Here, using approaches based on phylogenetic divergence, we provided new insights

504   on the continental origin of plant diversity in islands. At a global scale spatial and

505   environmental distance act as filters to species establishment on islands although they are not

506   directed toward specific lineages. On continental islands, an unchanged climate may have

507   allowed species to persist following the isolation process. We then investigated the

508   importance of island features and phylogenetic structure in explaining deep or short branches

509   shared by islands and the mainland. This showed that reasons for phylogenetic divergence

510   were *i.* the persistence of evolutionary original species *ii.* regular and low phylogentic

511   distance among species caused by - for example - speciation in remote archipelagos *iii.*

512   colonization of non-clustered taxa *iv.* high turnover and speciation rates. We further

513   encourage future use of phylogenetic approaches in island biogeography, for example to

514   disentangle the role of age or of biotic factors on patterns of island diversity.

515

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620

Figure legends

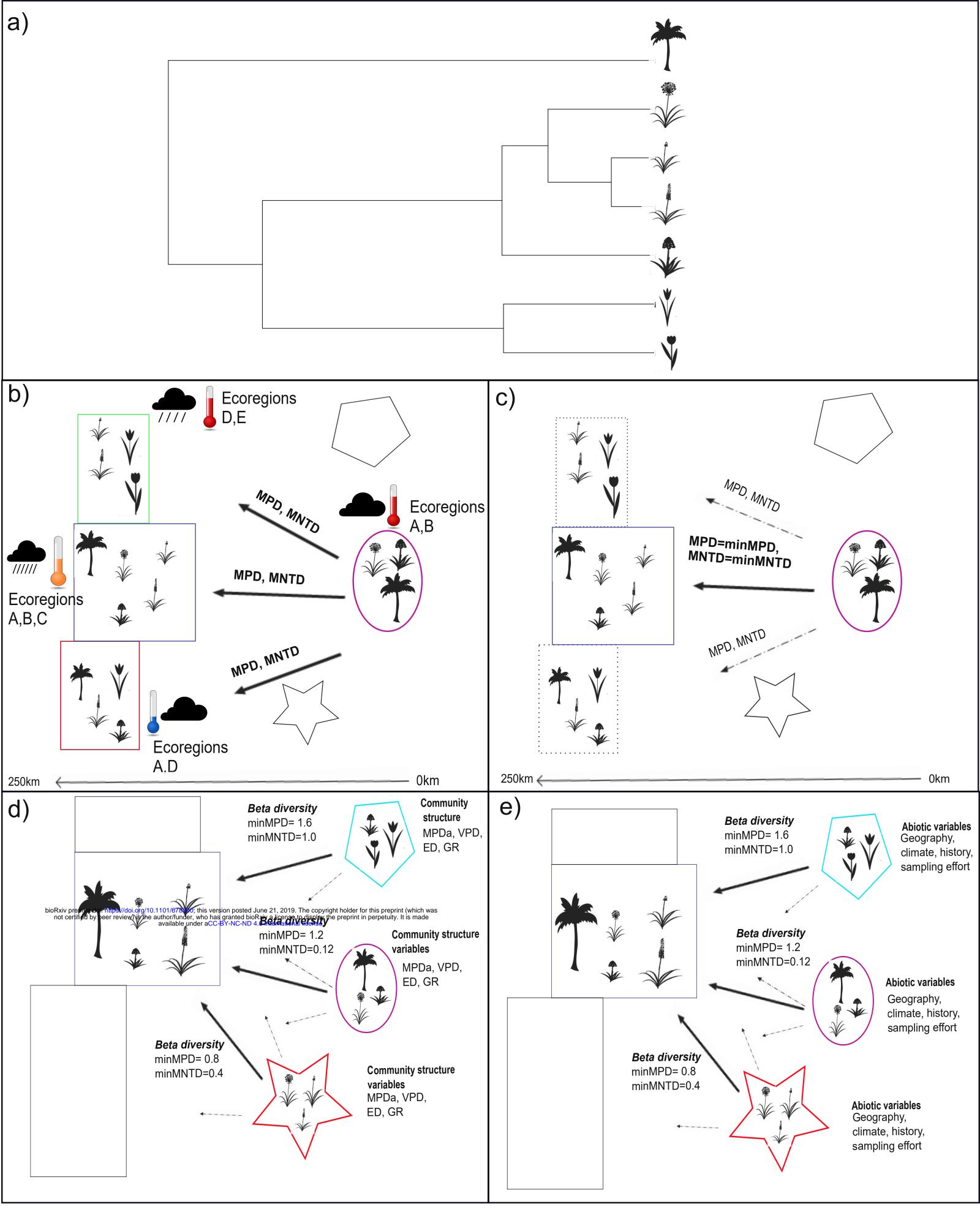622   **Figure 1.** Methodological procedure

623 **Figure 2.** Spatial distribution of the minimum phylogenetic divergence between islands and

624 the 10 nearest continental areas for a) Mean Pairwise Distance b) Mean Nearest Taxon

625 Distance.

Table legends

627 **Table 1.** The 15 abiotic variables tested and sources of data

628 **Table 2.** Effects of spatial and environmental distance on MPD_β and $MNTD_\beta$ between islands
629 and continents measured from BRT and GLM: "***" indicate $Pr(>z) <0.0001$; "**" indicate
630 $Pr(>z) <0.001$; "*" indicate $Pr(>z) <0.01$ "." indicate $Pr(>z) <0.1$; + and – indicate the
631 direction of the relationship that is positive or negative, respectively. Column A presents the
632 observed results. Column B and C represents data used as a sensitivity analysis.

633 **Table 3.** Contribution, direction and significance of variables of phylogenetic structure to a)
634 minimum MPD_β and b) minimum $MNTD_\beta$ between islands and continents.

635 **Table 4:** Contribution, direction and significance of abiotic variables to a) minimum MPD_β
636 between islands and continents and b) minimum $MNTD_\beta$ betweeen islands and continents.

Appendix legends

638 **Appendix S1**. Analysis of the relationship between solar radiation, latitude and phylogenetic
639 divergence

640 **Appendix S2**. Effect of island features on phylogenetic structure of insular pools

641 **Appendix S3**. Boosted Regression Tree contributions of spatial and environmental distance to
642 phylogenetic divergence

Data

644 Data will be made available on the Dryad repository

Declarations

649

650 Author contributions – The first author is the major contributor to this study. The last co-
651 author is the leading co-author of this work

652

653

a) Figure of a phylogenetic tree

b) Beta diversity between an islands and the surrounding continents. MPD and MNTD were estimated from the 5, 10, 20 closest continental areas to each island as well as from all continents belonging to a similar biome as each island. Relationships between MPD and MNTD with spatial and environmental distances

c) Identification of minimum beta diversity values for each island and each index (MPDmin and MNTDmin).

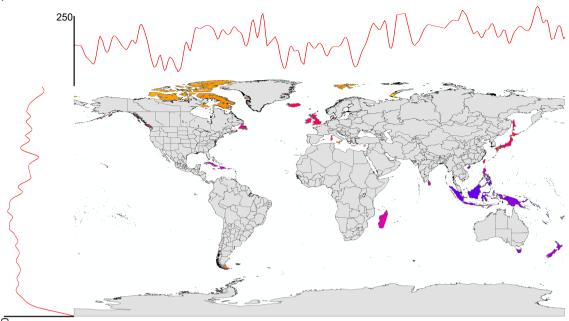d) Relationships minimum between beta diversity and community structure measures (see also table 2).

MPDa= alpha Mean pairwise Distance; VPD= Variance in Pairwise Distance
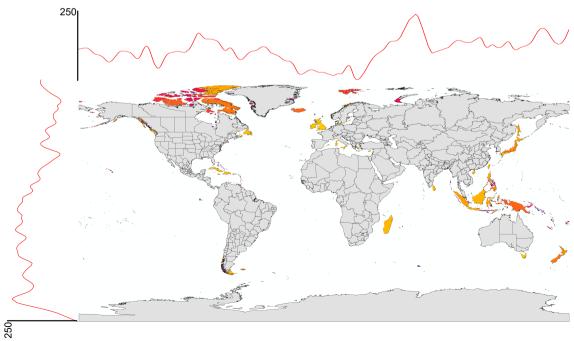
ED= Evolutionary Distinctiveness; GR= Genus Richness

e) Relationships between minimum beta diversity and abiotic factors (see also table 3)

a) minMPDbéta

b) minMNTDbéta

Phylogenetic divergence

Table 1: The 15 abiotic variables tested and sources of data

Variable	Unit	Source
Geographical variables		
Latitude	Decimal degrees	Depraetere & Dall (2007)
Longitude	Decimal degrees	Depraetere & Dall (2007)
Minimum distance to continent	km	Depraetere & Dall (2007)
Proportion of surrounding land mass (SLMP)		Weigelt et al. (2013)
Area	km²	Depraetere & Dall (2007)
Elevation	m	Weigelt et al. (2013), Depraetere & Dall (2007)
Climate		
Number of ecosystems		Olson et al. (2001)
Mean annual temperature	°C	Fick & Hijmans, (2017)
Mean annual rainfall	mm	Fick & Hijmans, (2017)
Rainfall seasonality	mm	Fick & Hijmans, (2017)
Mean annual wind speed	m.s^{-1}	Fick & Hijmans, (2017)
Standard deviation of vapor pressure	kPa	Fick & Hijmans, (2017)
Historical factors		
Connection to the mainland during the LGM (GMMC)		Weigelt et al. (2013)
Velocity of past climate change	y.m^{-1}	Sandel et al. (2011)
Sampling effort		
ICE_r		Lee & Chao (1994)

Table 2: Effects of spatial and environmental distance on MPD_β and $MNTD_\beta$ between islands and continents measured from BRT and GLM: "***" indicate Pr(>z) <0.0001; "**" indicate Pr(>z) <0.001; "*" indicate Pr(>z) <0.01 "." indicate Pr(>z) <0.1; + and – indicate the direction of the relationship that is positive or negative, respectively. Column A presents the observed results. Column B and C represents data used as a sensitivity analysis.

A. Oceanic islands

	A. 10 nearest continental areas		B. 5 nearest continental areas		C. 20 nearest continental areas	
a) MPD_β	Contribution estimated from BRT	Pr(>z) estimated from GLMM	Contribution estimated from BRT	Pr(>z) estimated from GLMM	Contribution estimated from BRT	Pr(>z) estimated from GLMM
Spatial distance	15.4%	+***	12.8%	+***	16.2%	+***
Temp. difference	12.2%	+.	12.7%	+.	11.3%	-***
Rainfall difference	19%		17.6%		22%	+**
Solar radiation difference	28.4%	-***	32.3%	-***	23.5%	-***
Wind speed difference	10%	+***	9.7%	+***	12%	+**
Euclidean environmental distance	9.7%	+***	8.2%	+***	10.4%	+***
Number of different ecoregions	5.3%	+***	6.7%	+***	4.6%	+***
b) $MNTD_\beta$						
Spatial distance	23.8%	+***	24%	+***	20.8%	+***
Temp. difference	12.2%	+***	10.8%	+***	11%	+***
Rainfall difference	15.4%	+**	15.6%	+**	13.3%	+***
Solar radiation difference	17.5%	+***	20.6%	+***	15.6%	+***
Wind speed difference	11.6%	+***	11.3%	+***	12.1%	+***
Euclidean environmental distance	13.9%	+***	11.7%	+***	22.7%	+***
Number of different ecoregions	5.7%	+***	6%	+***	4.3%	+***

B. Continental islands

	A. 10 nearest continental areas		B. 5 nearest continental areas		C. 20 nearest continental areas	
a) MPD$_\beta$	Contribution estimated from BRT	Pr(>z) estimated from GLMM	Contribution estimated from BRT	Pr(>z) estimated from GLMM	Contribution estimated from BRT	Pr(>z) estimated from GLMM
Spatial distance	13%	+***	12.7%	+***	13.6%	+**
Temp. difference	12.5%	-	13.6%	+***	12.6%	+***
Rainfall difference	12.8%	+***	13%	+*	13.2%	+***
Solar radiation difference	32%	+	31.1%	-***	29.5%	-***
Wind speed difference	13.9%	+***	12.6%	-***	15.6%	-*
Euclidean environmental distance	9.3%	+***	11.1%	+	8.8%	-***
Number of different ecoregions	6.5%	+***	5.9%	+***	6.8%	+***
b) MNTD$_\beta$						
Spatial distance	10.8%	+***	10.6%	+***	9.7%	+***
Temp. difference	15.4%	.	14.3%	+***	16.4%	+***
Rainfall difference	12%		13.6%	+***	11.4%	+***
Solar radiation difference	31.9%	+***	28.9%	+***	28.9%	+***
Wind speed difference	10.5%	+***	10%	+***	10.4%	+***
Euclidean environmental distance	9.5%	+***	10.6%	+***	13%	+***
Number of different ecoregions	9.8%	+***	11.8%	+***	10.2%	+***

Table 3: Contribution, direction and significance of variables of phylogenetic structure to minimum MPD_β and $MNTD_\beta$ between islands and continents.

	Contribution	Estimate	Standard error	Pr(>z)
A. $minMPD_\beta$				
MPD_α	31.8% (2/7)	6.2	0.55	***
Mean ED	43.6% (1/7)	15.1	0.73	***
Sd ED	14.4% (3/7)	7.9	0.47	***
Nb top 10 ED species	0.22% (7/7)	-0.63	0.43	
Proportion of top ED species	1.36% (6/7)	11.2	0.97	***
VPD	6.3% (4/7)	-1.94	0.37	***
Genus richness	2.1% (5/7)	2.6	0.41	***
B. $minMNTD_\beta$				
MPD_α	15.04% (3/7)	-0.17	0.0034	***
Mean ED	9.3% (4/7)	0.22	0.0044	***
Sd ED	3.1% (5/7)	-0.14	0.007	***
Nb top10 ED species	0.005% (7/7)	0.23	0.0039	***
Proportion of top ED species	0.07% (6/7)	-0.034	0.066	***
VPD	30.6% (2/7)	-0.006	0.002	***
Genus richness	42.3% (1/7)	-0.60	0.0048	***

Table 4. Contribution, direction and significance of abiotic variables to A) minimum MPD_β between islands and continents and B) minimum $MNTD_\beta$ between islands and continents.

A. $minMPD_\beta$

		Contribution to $minMPD_\beta$	*Estimate*	*Standard error*	*Pr(>z)*
Geographic variables	Area	1.6% (11/15)	-1.2	0.58	*
	SLMP	1.5% (12/15)	1.1	0.86	
	Elevation	0.9% (13/15)	-0.17	0.68	
	Minimum distance to continents	5.8% (8/15)	1.2	0.54	*
	Latitude	35.5% (1/15)	-7.9	0.87	***
	Longitude	9.8% (3/15)	0.17	0.55	
Climatic variables	Number of ecosystems	0.2% (15/15)	1.8	0.56	**
	Mean annual temperature	9.1% (4/15)	7.3	0.94	***
	Mean annual rainfall	10.7% (2/15)	5.06	0.68	***
	Rainfall seasonality	7.7% (5/15)	-6.3	0.65	***
	Mean annual wind speed	6.3% (6/15)	-5.0	0.75	***
	Standard deviation in vapour pressure	5.9% (7/15)	-3.6	0.63	***
Historical variables	Velocity of past climate change	4.5% (9/15)	4.9	0.72	***
	GMMC	0.2% (14/15)	7.7	1.62	***
Sampling effort	ICE*r*	1.7% (10/15)	-0.31	0.48	
Interactions	Latitude:Longitude		-6.5	0.53	***
	Longitude:Temperature		2.6	0.54	***

B. $minMNTD_\beta$

		Contribution to $minMNTD_\beta$	*Estimate*	*Standard error*	*Pr(>z)*
Geographic variables	Area	4.3% (6/15)	0.034	0.003	***
	SLMP	2.6% (9/15)	-0.098	0.004	***
	Elevation	1.6% (13/15)	-0.12	0.0039	***

	Minimum distance to continent	1.8% (10/15)	0.045	0.0032	***
	Latitude	31.1% (1/15)	-0.22	0.004	***
	Longitude	9.7% (3/15)	-0.07	0.0029	***
Climatic variables	Number of ecosystems	0.8% (14/15)	-0.063	0.0037	***
	Mean annual temperature	4.3% (5/15)	0.017	0.0049	***
	Mean annual rainfall	3.1% (7/15)	0.066	0.0033	***
	Rainfall seasonality	1.7% (11/15)	0.037	0.0035	***
	Mean annual wind speed	1.6% (12/15)	-0.08	0.0039	***
	Standard deviation in vapour pressure	7.0% (4/15)	-0.004	0.00é	.
Historical variables	Velocity of past climate change	2.7% (8/15)	0.07	0.0036	***
	GMMC	0.03% (15/15)	-0.058	0.009	***
Sampling effort	ICE*r*	26.7% (2/15)	-0.10	0.0031	***
Interactions	Latitude:Longitude		-0.14	0.0023	***
	ICE:Area		-0.036	0.0027	***