

Unravelling the small-island effect through phylogenetic community ecology

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1 **Unravelling the small-island effect through phylogenetic community ecology**

2

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20 Running title: Phylogenetic diversity and the small-island effect

21

22 **Abstract**

23 **Aim:** The small-island effect (SIE) describes a different relationship between island area and
24 species richness on smaller compared to larger islands. The pattern has recently gained
25 widespread support. However, few studies have attempted to identify the actual mechanisms
26 driving the SIE. Here, we use a phylogenetic community framework to study the SIE, based
27 on the assumption that if the dominant assembly processes differ between small and large
28 islands, patterns of phylogenetic community structure should shift across the area and habitat
29 diversity gradient.

30 **Location:** The Aegean Archipelago, Greece.

31 **Methods:** We used a large dataset of 3262 vascular plant species distributed across 173
32 islands, in combination with a species-level phylogeny. The phylogenetic community
33 structure of each island was calculated using a null modelling framework and was quantified
34 using effect sizes (ES); negative values indicating phylogenetic clustering and positive values
35 overdispersion. Habitat diversity, species richness, phylogenetic diversity (PD) and ES values
36 were regressed against \log_{10} -transformed area and we tested for a SIE using piecewise
37 regression models. We also assessed differences in taxonomic and phylogenetic composition
38 between small and large islands using a beta-diversity framework.

39 **Results:** We found evidence of a SIE using species richness, PD, and phylogenetic
40 community structure (ES values). Small islands displayed low variation in habitat diversity
41 and tended to be more phylogenetically clustered, while large islands shifted from
42 phylogenetic clustering towards phylogenetic overdispersion with increasing area and habitat
43 diversity. In addition, we showed that phylogenetic composition tended to be more similar
44 between small islands than expected.

45 **Main conclusion:** Overall, our results provide an example of a SIE in the analysis of island
46 phylogenetic community structure, and point to a role of habitat diversity in driving the SIE
47 more generally.

48

49 **Keywords:** Breakpoints, island biogeography, phylogenetic diversity, small-island effect,
50 species–area relationship, beta-diversity

51

52 1. INTRODUCTION

53 The small-island effect can be broadly described as a different relationship between island
54 area and species richness (the island species–area relationship; ISAR) on smaller compared to
55 larger islands (Triantis & Sfenthourakis, 2012). That is, there is a threshold point (or at least a
56 transitional phase) in island area where the slope of the ISAR changes; either species richness
57 on small islands varies independently of area or increases / decreases at a different rate than
58 on larger islands. The first graphical representation of the pattern was provided by Niering in
59 1956 (see his Figure 32), and not by the same author in 1963 as is commonly reported.
60 Discussion of the SIE in the context of the equilibrium theory of island biogeography was
61 then later provided by MacArthur & Wilson (1967) and Whitehead & Jones (1969). Although
62 there were SIE studies in the intervening years, the pattern has undergone a resurgence in
63 interest since the start of the millennium (Lomolino & Weiser, 2001; Triantis et al., 2006;
64 Burns, McHardy, & Pledger, 2009; Dengler, 2010; Triantis & Sfenthourakis, 2012) and has
65 now been shown to be present in a variety of systems, including true islands and habitat
66 islands (Matthews, Steinbauer, Tzirkalli, Triantis, & Whittaker, 2014; Morrison, 2014; Wang,
67 Millien, & Ding, 2016), although a number of exceptions exist (Matthews et al., 2014; Wang
68 et al., 2016).

69
70 Although the SIE has become an important part of the theoretical framework of island
71 biogeography, there is still considerable debate about the mechanisms underpinning the SIE.
72 A number of explanations have been proposed and these can be broadly split into two main
73 hypotheses (Sfenthourakis & Triantis, 2009). The first hypothesis postulates that on small
74 islands extinction rates vary independently of island area due, for example, to stochastic
75 events and / or to episodic catastrophic disturbances such as storms that may result in the
76 (near) complete extirpation of species on small islands (e.g. MacArthur & Wilson, 1967). One
77 possible pattern emerging from such area-independent extinction rates on small islands is
78 higher temporal species turnover on smaller compared to larger islands (MacArthur &
79 Wilson, 1967). The second hypothesis refers to the primary role of habitat diversity and
80 niche-based factors in driving the SIE (Triantis et al., 2006; Sfenthourakis & Triantis, 2009;
81 Chisholm et al., 2016; Chen, Yang, Tan, & Wang, 2020). Here, the idea is that on small
82 islands island area and environmental heterogeneity become decoupled (Triantis, Mylonas,
83 Weiser, Lika, & Vardinoyannis, 2005; Triantis et al., 2006), and that below a threshold of
84 island area the absence of major habitat types is the main constraint on richness

85 (Sfenthourakis & Triantis, 2009; Chen et al., 2020). For example, Niering (1963) postulated
86 that the lack of mature soils on islands smaller than 3.5 acres explained the SIE pattern he
87 observed; it should be noted that Niering did not explicitly use the term SIE. Other proposed
88 mechanisms explaining the SIE include low immigration rates on small islands (Morrison,
89 2011) and species-specific area requirements (Schrader et al., 2019), both of which prevent
90 the successful establishment of species on small islands. However, despite all of these various
91 proposed hypotheses, in general, studies attempting to identify the actual mechanisms driving
92 the SIE in a given system are scarce (e.g. Morrison, 2011; Schrader et al., 2019).

93

94 In addition to the mechanisms generating the SIE, many other aspects of the SIE are still
95 debated. For instance, there have been strong disagreements about the appropriate statistical
96 approach for identifying SIEs (Dengler, 2010; Triantis & Sfenthourakis, 2012; Morrison,
97 2014; Wang et al., 2016). These disagreements include debates on whether or not to include
98 islands with no species (Morrison, 2014; Wang et al., 2016), the most effective statistical
99 model to detect a SIE (Lomolino & Weiser, 2001; Toms & Lesperance, 2003; Triantis et al.,
100 2006; Matthews et al., 2014; Chisholm, Fung, Chimalakonda, & O'Dwyer, 2016; Gao, Cao,
101 Xu, & Perry, 2019), and the best variable transformation procedure to use when fitting SIE
102 models (Burns et al., 2009; Matthews et al., 2014). Furthermore, most SIE studies have
103 focused on documenting patterns in species numbers without considering that species
104 composition may help to elucidate the mechanisms underlying the SIE. For instance, islet
105 specialists (species that exclusively occur on cliffs, rocks and coastal habitats on typically
106 small, low, uninhabited islets; Rechinger & Rechinger-Moser, 1951) are an important
107 component of the flora of small islands in the Aegean Sea (Panitsa & Tzanoudakis, 2001; see
108 Morrison, 2014, for a similar example from the flora of the Bahamas), but are largely absent
109 from the larger islands, and thus their presence will likely influence any SIE patterns in these
110 islands. In addition, SIE studies have only considered the number of species as the response
111 variable, and thus assuming that all species are evolutionarily independent and ecologically
112 equivalent. Critical information about primary community assembly mechanisms on islands
113 might thus have been ignored.

114

115 Recently, ecologists and biogeographers have turned to phylogenetic and functional diversity-
116 based metrics to provide novel insights into their study systems. Phylogenetic diversity (PD)
117 incorporates the evolutionary relationships between species and provides a measure of the
118 amount of evolutionary history that is represented by the species in an assemblage (Webb,

119 Ackerly, McPeck, & Donoghue, 2002). Based on the assumption that phylogenetic
120 relatedness between species is positively correlated with functional / ecological relatedness
121 (an assumption that may not hold in all cases; Flynn, Mirotchnick, Jain, Palmer, & Naeem,
122 2011), PD provides an integrative measure encompassing the overall similarity that stems
123 from multiple traits. When used in combination with an appropriate null model, the
124 comparison of the observed PD value to the distribution of null values enables classification
125 of the observed value as being significantly larger than expected by chance (i.e.
126 overdispersed), significantly smaller than expected (i.e. clustered), or not significantly
127 different from random expectation. These different situations have been interpreted as being
128 indicative of different community assembly processes (e.g. habitat filtering resulting in
129 clustered patterns; see Münkemüller et al., 2020, for a review). PD approaches are now
130 widely utilized in community ecology, and they have provided compelling evidence for the
131 importance of integrating both ecological and evolutionary processes to test mechanisms of
132 community assembly (Emerson & Gillespie, 2008; Webb et al., 2002). However, the study of
133 PD on islands remains in its infancy (Weigelt et al., 2015), and to our knowledge PD has
134 never been applied in the study of the SIE.

135
136 The present study is based on the idea that re-approaching the SIE using a phylogenetic
137 community approach will be beneficial as it will allow for a better assessment of the
138 mechanisms driving the pattern. Based on previous work on the SIE, and on distinct studies
139 focused on PD, we can generate several predictions of how communities should assemble in
140 regard to island size and habitat diversity and how, in turn, this will result in a SIE. Overall, if
141 the dominant assembly processes differ between small and large islands, patterns of
142 phylogenetic community structure should shift across the island area gradient. More
143 specifically, it is known that smaller islands often tend to contain a limited number of
144 relatively less-complex habitats (e.g. sclerophyllous scrub vegetation in the Mediterranean)
145 (Snogerup & Snogerup, 2004; Sfenthourakis, Pafilis, Parmakelis, Poulakakis, & Triantis,
146 2018). If habitat availability is the main driver of small island richness (e.g. Triantis et al.,
147 2006; Chen et al., 2020), we would expect species occurring on small islands (in a given
148 archipelago) to be clustered in the phylogenetic tree, because only a subset of closely related
149 species (e.g. from a limited number of clades) will likely be adapted to the limited habitat
150 types on small islands. This should be reflected at the island scale with small islands being
151 less phylogenetically diverse than expected by chance (phylogenetic clustering). According to
152 this argument, and bBased on previous work (e.g. Niering, 1963), we would also predict that

153 most islands below a threshold area value will contain only limited habitat types (i.e. below
154 this point the relationship between island area and habitat diversity is decoupled). That is,
155 there will be a threshold point in area before habitat diversity and island area increase together
156 in the expected linear fashion (Triantis et al., 2006). Overall then, we predict that, if habitat
157 diversity is a primary driver of island richness, due to the decoupling of island area and
158 habitat diversity on small islands, the relationship between area and diversity (e.g. richness,
159 PD; Chen et al., ; Triantis et al.,) will differ from that on large islands (i.e. the small island
160 effect), and also that small islands are expected to support a limited subset of closely related
161 species (i.e. PD clustering). In addition, if small islands contain similar habitat types, we
162 should also expect the biota of these islands to be more phylogenetically similar (phylogenetic
163 convergence) than expected by chance (Graham & Fine,).

164

165 In contrast, larger islands should have higher habitat heterogeneity (Ricklefs & Lovette, 1999;
166 Whittaker & Fernández-Palacios, 2007; Sfenthourakis & Triantis, 2009), allowing more
167 distant lineages (that are adapted to the wider range of habitats) to establish, persist and
168 diversify, and thus the species on large islands should be more spread across the phylogenetic
169 tree than expected by chance (i.e. overdispersed). On larger islands, the biota may be either
170 more or less phylogenetically similar (phylogenetic convergence or divergence) than
171 expected, depending on, amongst other things, the level of habitat similarity between the
172 islands, and / or the prevalence of *in situ* speciation (Graham & Fine, 2008).

173

174 To test the aforementioned predictions, we used a large and well sampled dataset of 3262
175 vascular plant species distributed across 173 islands and islets of varying size in the Aegean
176 Sea (Greece). The phylogenetic community structure of each island was assessed using a
177 species-level plant phylogeny and null models were implemented to test whether islands were
178 more phylogenetically clustered or overdispersed than expected by chance. We used
179 piecewise regression models to evaluate whether there were breakpoints in the ISAR (i.e. the
180 traditional SIE), and in various types of island phylogenetic diversity–area relationships
181 (IPDAR; i.e. a SIE in phylogenetic diversity). For the purposes of this study we define a SIE
182 as a threshold point in island area where there is a statistically significant change in the slope
183 of the diversity–area relationship. We also assessed whether species turnover and
184 phylogenetic dissimilarity between islands were lower or higher than expected by chance
185 using null models, and tested whether there were differences between small and large islands.
186 Our study documents the first example of a SIE in the phylogenetic community structure of

187 islands. In addition, our findings provide evidence suggesting a role of habitat diversity in
188 driving the traditional SIE. Overall, we demonstrate how a phylogenetic community-based
189 approach can be used to provide insights into the potential mechanisms driving the SIE, and
190 community assembly on islands more generally.

191

192 **2. MATERIALS AND METHODS**

193 **2.1 Data collection and phylogeny construction**

194 Building on the work of Kougioumoutzis et al. (2017), we used a comprehensive database of
195 the presence-absence of plant species on 173 Aegean islands and islets (Figure 1a). We
196 compiled our dataset from an extensive and detailed database of the Aegean islands
197 (Appendix S1). Systematic research on the flora of the large Aegean Islands started in the late
198 1920s and has been undertaken continuously up to the present day. For the larger islands, the
199 dataset comprises all available records with the exception of species that have been recorded
200 only once in the distant past (i.e. their occurrence has not been confirmed with more recent
201 surveys). Study of the floristic composition of the small islands (Figure 1b-d) was undertaken
202 between 1970 and 2000. For the vast majority of these small islands, a single exhaustive plant
203 sampling trip was conducted during this period, and these data are used in the database. Island
204 species richness ranged from two (Islet East Aspronisi) to 1751 species (Crete). In total, the
205 dataset contains 3262 native vascular plant species (all non-native taxa were excluded). The
206 chorological status of the species follows Dimopoulos et al. (2013) and Strid (2016). The area
207 (km²) of each of the 173 islands and islets was sourced from the literature (Panitsa, 1997;
208 Sfenthourakis & Triantis, 2009) and ranged from 0.0006 km² for Tourleta islet to 8270 km²
209 for Crete.

210

211 Coarse-scale habitat type information for each island was calculated using the CORINE Land
212 Cover (CLC) inventory (Copernicus Land Monitoring Service, 2018). The habitat diversity of
213 each island was calculated as the total number of CLC classes present (out of a total of 44
214 classes). The CLC has a resolution of 100 m, which is relatively coarse in comparison to the
215 size of the smallest islands / islets in our dataset. As such, for these smaller islands, we used a
216 combination of satellite imagery, photographs, expert knowledge and field data from previous
217 work (e.g. Panitsa, 1997; Panitsa & Tzanoudakis, 2001; Sfenthourakis et al., 2018) to
218 compliment and ground-truth the CLC data. In all cases, only CLC classes were assigned as

219 habitat types (Appendix S2). Overall, 27 habitats were identified across the 173 islands, with
220 habitat diversity ranging from 1 (78 islands) to 23 (Evia, 3660.74 km²).

221

222 We used the dated phylogeny of vascular plants with 31,749 species (Zanne et al., 2014) as a
223 backbone tree to create a phylogeny of all species in our dataset (Figure 1e). Missing genera
224 and species were randomly grafted among tips within their respective family and genera (see
225 Appendix S3).

226

227 **2.2 Assessing island taxonomic and phylogenetic diversity**

228 Our first metric of phylogenetic diversity was Faith's phylogenetic diversity (PD; Faith,
229 1992), which is the sum of the phylogenetic branch lengths connecting all species co-
230 occurring on an island. PD captures the total amount of evolutionary history contained within
231 a given island. We included PD as a phylogenetic richness metric as, although it is usually
232 highly correlated with species richness, the corresponding island PD–area relationship
233 (IPDAR) is easily comparable with the traditional ISAR (Morlon et al., 2011).

234 To assess phylogenetic community structure on each island independently of species richness,
235 we calculated the effect size (ES) of three distinct phylogenetic community metrics (Tucker et
236 al., 2017): (1) the ES of PD (ES_{PD}); (2) the ES of mean pairwise distance (ES_{M_{PD}}), which
237 estimates the average phylogenetic distance between all pairs of species in a community; and
238 (3) the ES of mean nearest taxon distance (ES_{M_{NTD}}), which measures the mean phylogenetic
239 distance between each species and its nearest neighbour in the phylogenetic tree with which it
240 co-occurs in the community (Webb et al., 2002). While ES_{M_{PD}} provides an indication of how
241 species on an island are dispersed in the phylogenetic tree, ES_{M_{NTD}} provides a measure of
242 how densely phylogenetically packed species are on an island. The ES values were obtained
243 using the probit transformation of the probability *P* that the observed value is lower than
244 expected by chance (see further details in Appendix S4 and in Lhotsky et al., 2016). For each
245 island and each metric, we obtained the null values using a random assembly model, where
246 species names were randomly shuffled across the tree tips to create 9,999 new random
247 phylogenetic diversity values per island. This constrained randomization approach keeps the
248 island species richness, species turnover, and the spatial structure of species distributions
249 constant (Swenson et al., 2012). ES values represent a measure of departure from the null
250 expectation; values greater than zero being larger than expected (i.e. phylogenetic
251 overdispersion), and values smaller than zero being less than expected (i.e. phylogenetic

252 clustering). Values greater than 1.96 (probit of roughly 0.975) or less than -1.96 (probit of
253 roughly 0.025) were considered to be significantly greater or less than expected, respectively.
254 This calculation of effect sizes was preferred to the commonly-used standardized effect size
255 (SES) due to the non-Gaussian shape of some of our null distributions (Bernard-Verdier et al.,
256 2012).

257

258 **2.3 Detection of a small-island effect**

259 To test for a SIE, we selected two of the most widely used SIE piecewise models proposed by
260 Lomolino & Weiser (2001): the continuous one-threshold and the left-horizontal one-
261 threshold model. It has recently been demonstrated that the number of thresholds in the ISAR
262 often increases with the range in island area analysed (Gao et al., 2019). In studies that
263 contain a large range in island area (as is the case with our data), piecewise models with more
264 than one threshold should also be considered (Gao et al., 2019). As such, we also included
265 two models with two thresholds: the continuous and the left-horizontal continuous two-
266 threshold model (see Appendix S5 for a detailed description of the models). We didn't
267 include discontinuous threshold models that have been applied in previous studies (e.g.
268 Matthews et al., 2014; Gao et al., 2019) as the ecological logic of discontinuous relationships
269 in nature has been questioned (Yu et al., 2020). To test whether the relationships between
270 diversity and island area exhibited a SIE, we compared the four piecewise models with a
271 simple linear model. A model with just an intercept was also included in our analyses as a
272 null model to test for an absence of relationship between \log_{10} area and diversity.

273 We fitted our six models to the relationships between area and (1) habitat diversity, as a
274 means to evaluate any decoupling of the relationship between habitat diversity and area, and
275 (2) our five diversity metrics (species richness, PD, ES_{PD} , ES_{MNTD} and ES_{MPD}). We used a
276 semi-log transformation (\log_{10}) approach, i.e. area was log transformed but diversity was not.
277 Although semi-log transformation has been widely used in SIE studies (Morrison, 2014),
278 Matthews et al. (2014) argued that the choice of log-transformation used when fitting
279 piecewise regression models should be an integral part of the study design, and that the choice
280 of transformation depends on the aim of the study. Here, a semi-log transformation was used
281 as there is no *a priori* reason to log-transform metrics such as PD or the three ES metrics. The
282 validity of this choice was tested using a sensitivity analysis (outlined below).

283 All models were fitted using ordinary least squares regression (OLS), and threshold values

284 were estimated using the minimum residual sum of squares (RSS) method (see electronic
285 supplementary material, Appendix S5). The functions for fitting and plotting the threshold
286 models, along with additional piecewise model functions, were integrated into the 'sars' R
287 package (Version 1.2.3; currently available on GitHub in the 'thresholds_2' branch)
288 (Matthews et al., 2019). For each diversity metric, we compared the different models using
289 the Bayesian Information Criterion (BIC; Burnham & Anderson, 2002). In each case, the best
290 model was considered to be that with the smallest BIC; however, all models with a Δ BIC
291 value < 2 were considered as having a similar degree of statistical support (Burnham &
292 Anderson, 2002). BIC was preferred to other information criteria because, as ES values tend
293 be more scattered than species richness values, spurious relationships might simply arise due
294 to random noise in the data and be incorrectly interpreted as legitimate relationships. BIC is
295 more effective in such situations due to the greater penalization in respect to the number of
296 model parameters (Link & Barker, 2006). We also tested the ability of the best model(s) to
297 account for potential spatial structure by estimating Moran's I spatial autocorrelation index
298 using the model residuals and the latitude and longitude of each island's centroid. Diagnostic
299 plots were inspected in order to detect residual deviations from normality and
300 homoscedasticity, and to identify outliers. Finally, we repeated the aforementioned model
301 fitting and model comparison analyses using habitat diversity instead of island area as the
302 predictor of the five diversity metrics.

303 **2.4 Assessing differences in species turnover and phylogenetic dissimilarity between** 304 **small and large islands**

305 We split islands into small and large using an average breakpoint calculated by averaging all
306 thresholds identified in the best models for all metrics (see results). We first estimated species
307 turnover between islands using the modified Simpson's index (β_{SIM}). β_{SIM} measures
308 compositional differences between communities independently of any species richness
309 gradients (Baselga, 2010). We investigated whether observed pairwise β_{SIM} values were larger
310 or smaller than expected under a stochastic model of community assembly. This was carried
311 out by generating 9,999 random assemblage matrices using the fixed-fixed independent swap
312 algorithm (Gotelli, 2000). The fixed-fixed independent swap algorithm keeps species
313 occurrence frequency and sample species richness constant while shuffling species presences
314 across sites. The effect size (ES) of each observed pairwise β_{SIM} value was then calculated to
315 quantify the deviation from the null expectation with ES values greater than 1.96 or less than -
316 1.96 considered to be significantly more dissimilar or dissimilar than expected, respectively.

317 Both pairwise β_{SIM} and the associated ES values were calculated using all islands and also
318 using the small and large island subsets.

319

320 Phylogenetic dissimilarity was measured in an analogous way to the measurement of
321 phylogenetic community structure. For a given pair of islands A and B, we calculated the
322 mean of all phylogenetic distances separating species occurring in A from species occurring
323 in B (MPD_{DISS}), and the average of the phylogenetic distance between each species in A and
324 its closest relative in B ($\text{MNTD}_{\text{DISS}}$). We computed the ES of MPD_{DISS} and $\text{MNTD}_{\text{DISS}}$ values
325 using the same approach as for ES_{PD} , ES_{MPD} and ES_{MNTD} .

326

327 We further tested for differences in mean β_{SIM} and ES between small and large islands using
328 Wilcoxon Rank Sum tests, and whether the distribution of ES values within small and large
329 islands significantly deviated from the null expectation (median = 0) using a one-sample
330 Wilcoxon test (Swenson & Enquist, 2009). Since islands in the Aegean are spread across a
331 large geographical region i.e. the Aegean Sea, differences in turnover and phylogenetic
332 dissimilarity between small and large islands could also be driven simply by geographical
333 distance (i.e. dispersal limitation). For example, if higher turnover is found between small
334 islands compared to large islands, this simply could be due to the fact that small islands are
335 relatively far away from each other and not because they differ in terms of the habitat types
336 they contain. β_{SIM} , $\text{ES } \beta_{\text{SIM}}$, $\text{ES } \text{MPD}_{\text{DISS}}$ and $\text{ES } \text{MNTD}_{\text{DISS}}$ dissimilarity matrices were
337 therefore correlated with the geographical distance between islands using a Mantel
338 permutation test, based on 9,999 permutations. This was implemented for all islands and for
339 small and large islands separately.

340 **2.5 Complementary analyses**

341 We undertook three complementary analyses to ensure our results were robust. First, we
342 checked the sensitivity of our results to the method used for placing unresolved genera and
343 species in the phylogeny. Second, we re-ran the above analyses on two smaller subsets of
344 islands, namely North-Eastern Aegean (83 islands and islets) and the Central Aegean (60
345 islands and islets) (Kougioumoutzis et al., 2017; Appendix S6). Third, we performed a
346 sensitivity test to ensure that we did not generate spurious small-island effects because of our
347 decisions regarding data transformation using the analytical procedure of Burns et al. (2009)
348 (Appendix S7). All analyses were undertaken using R (version 3.6; R Core Team, 2019).

349

350 3 RESULTS

351 3.1 The small-island effect: habitat diversity, the ISAR, IPDAR and phylogenetic 352 community structure

353 There was some model uncertainty regarding the relationship between habitat diversity and
354 \log_{10} Area, with the continuous and left-horizontal continuous one-threshold models and the
355 more complex continuous two-threshold models all having similar support (Figure 2a and
356 Table 1). However, all of these best models explained 94% of the variation in habitat diversity
357 and all showed at least one threshold between 3.45 and 6.28 km² (Figure 2a and Table 1). On
358 small islands there was a slow, or an absence of an, increase in habitat diversity with \log_{10}
359 Area (most of the small islands containing no more than two habitats), while for the large
360 islands a strong positive relationship was detected.

361
362 As expected, species richness and PD were highly correlated (Pearson's correlation 0.97,
363 $P < 0.001$, Figure S1). For both metrics, SIE thresholds were detected (Figure 2b, c and Table
364 1). For species richness, the left-horizontal two-threshold model was identified as the single
365 best model (Figure 2b). For PD, the continuous one-threshold model and the continuous two-
366 threshold model were identified as the best and the second-best model respectively (Figure 2c
367 and Table 1). For both the ISAR and IPDAR, the best models explained 95% of the variation
368 (Table 1).

369
370 For all three ES metrics, the continuous one-threshold model was found to be the best model
371 (Table 1) explaining overall less variation than for the ISAR and IPDAR with R^2 values
372 ranging from 37% for ES_{PD} to 22% ES_{MNTD} (Table 1). For the three ES metrics, the slope of
373 the first segment of the piecewise regression was always negative, with islands switching
374 from neutral assembly ($-1.96 < ES < 1.96$) to phylogenetic clustering ($ES < -1.96$). The slope
375 of the second segment was always positive, with islands switching from phylogenetic
376 clustering to neutral assembly and, to a lesser extent, to phylogenetic overdispersion ($ES >$
377 1.96) (Figure 2d,e,f). For ES_{MNTD} , the left-horizontal two-threshold model was found to be the
378 second best model (Figure 2f and Table 1). Overall, no spatial autocorrelation was detected in
379 the residuals of the best models (Table S1 in Appendix S8), and no specific deviations from
380 the assumptions of regression (e.g. normality, presence of outliers) were detected.

381
382 The relationship between species richness and habitat diversity was significantly positive and

383 linear, with habitat diversity explaining 93% of the variation in species richness (Table S2 and
384 Figure S2a in Appendix S8). A similar pattern was found for PD although the relationship
385 included a first phase of faster increase (Table S2 and Figure S2b). For the ES_{PD} and ES_{MPD}
386 metrics, the continuous one-threshold model was found to be the best model (Table S2 and
387 Figure S2c,d), with the slope of the first segment negative and the slope of the second
388 segment positive; the threshold being at 3.9 and 2.9 habitats respectively. For ES_{MNTD} , the
389 left-horizontal one-threshold model was found to be best with a threshold identified at 6.7
390 habitats (Table S2 and Figure S2e).

391

392 **3.2 Comparing species turnover and phylogenetic dissimilarity between small and large** 393 **islands**

394 We classified islands as small or large using a common threshold of 2.57 km^2 (\log_{10} -
395 transformed value = 0.41; corresponding to 92 small and 81 large islands), calculated by
396 averaging all thresholds identified in the best models across all metrics (range in threshold
397 values across the best models: $0.14 \text{ km}^2 - 34.52 \text{ km}^2$). Although this range of threshold values
398 was quite large (mainly due to the two-threshold models), the average resulted in quite a clear
399 split between small and large islands (see Figure S3 in Appendix S8). Overall, among the
400 3262 species recorded in our dataset, 640 occurred on small islands with three being found
401 exclusively on small islands. Differences in habitat composition between small islands was
402 very low, with most small islands containing either natural grasslands and/or sclerophyllous
403 vegetation (Appendix S2). In contrast, large islands displayed substantial differences in
404 habitat composition, with a mean habitat diversity of 8.1 (SD = 4.7) out of a total of 27
405 habitats present on large islands.

406

407 Observed species turnover (β_{SIM}) was significantly higher between small (mean $\beta_{SIM} = 0.66$)
408 than between large (mean $\beta_{SIM} = 0.24$) islands (Wilcoxon test $P < 0.001$, Figure 3a). $ES \beta_{SIM}$
409 was significantly lower between small than between large islands (mean $ES \beta_{SIM} = -0.20$ and -
410 0.09 respectively, Wilcoxon test $P < 0.001$, Figure 3b). For small and large islands, mean ES
411 β_{SIM} was significantly lower than 0 (one-sample Wilcoxon test $P < 0.001$). However, most of
412 the pairwise $ES \beta_{SIM}$ values for small islands did not show any significant deviation from
413 random (99.9% of the pairwise $ES \beta_{SIM}$ values were neutral, Figure 3), while for large islands
414 a few pairs were identified as being significantly phylogenetically convergent or divergent
415 (7.2% and 5.9% respectively, Figure 3b). For β_{SIM} , a significant and positive correlation with
416 geographical distance was found only for large islands, while for $ES \beta_{SIM}$, a significant and

417 positive correlation with geographical distance was found for all islands and for small and
418 large islands separately (Table 2).

419

420 In regard to phylogenetic composition, both small and large islands exhibited significant
421 average phylogenetic convergence for ES MPD_{DISS} (one-sample Wilcoxon test $P < 0.001$;
422 mean ES MPD_{DISS} = -0.91 and -0.87 respectively, Figure 3c), and ES MPD_{DISS} values did not
423 differ between small and large islands (Wilcoxon test $P = 0.64$). For ES MNTD_{DISS}, small
424 islands exhibited significant average convergence, while large islands exhibited significant
425 average divergence (Wilcoxon test $p < 0.001$; one-sample Wilcoxon test $P < 0.001$ for both
426 size-groups; ES MNTD_{DISS} = -0.63 and 1.54, respectively) (Figure 3d). There was no
427 significant correlation between either ES MPD_{DISS} or ES MNTD_{DISS} and geographical
428 distance, for either small or large islands (Table 2).

429

430 **3.3 Complementary analyses**

431 We found that the values of phylogenetic diversity and dissimilarity were not sensitive to the
432 method used for placing unresolved genera and species in the phylogeny (Table S3 in
433 Appendix S8). Results obtained for the North-Eastern Aegean and Central Aegean subsets are
434 given in Appendix S6 and Tables S4-S5 and Figures S4-S8 in Appendix S8. Overall, results
435 obtained for the North-Eastern Aegean and the Central Aegean were very similar to those
436 obtained using all islands; the main exception was for the Central Aegean, where no SIE was
437 detected when using the phylogenetic ES_{PD} and ES_{MNTD} metrics. Using the approach of Burns
438 et al. (2009) we found that the presence of a SIE in the relationship between island area and
439 species richness is not simply an artefact of our use of a semi-log transformation (Figure S9 in
440 Appendix S8).

441

442 **4 DISCUSSION**

443 **4.1 Phylogenetic community structure and the small-island effect**

444 We have found evidence of a SIE in the island species–area relationship, the island
445 phylogenetic diversity–area relationship and when using three phylogenetic community
446 metrics (ES_{PD}, ES_{MPD} and ES_{MNTD}). Interestingly, although there was some degree of model
447 uncertainty and the thresholds estimated from the one and two-threshold models were slightly
448 different, all thresholds (across all response variables) fall within a range of 34.38 km² (from
449 0.14 to 34.52 km²) representing no more than 0.4% of the total area range found in our data

450 (8270 km²). This suggests that the abrupt shifts in the various diversity metrics were more or
451 less synchronised, and could reflect that it is around this area range that the diversity of
452 habitats starts to increase with area in a linear fashion.

453

454 In relation to ES_{PD}, ES_{MPD} and the ES_{MNTD}, we found that, for the smaller islands (i.e. those to
455 the left of the breakpoint), island communities tended to be more phylogenetic clustered as
456 area increased (i.e. a negative slope – discussed in the next paragraph, Figure 2d,e,f). We also
457 observed that within the SIE range, area and habitat diversity are decoupled (see also Triantis
458 et al., 2006), with habitat diversity being almost stable throughout the SIE range. If habitat
459 diversity is the main driver of diversity rather than area per se, one possible explanation for
460 our observation of phylogenetic clustering on smaller islands is greater habitat filtering, where
461 only species being able to establish in the limited habitat types accumulate, leading to
462 phylogenetic redundancy (species drawn from a limited array of clades) within the species
463 assemblages. It is worth noting that small islands mostly contain one or both of natural
464 grasslands and sclerophyllous vegetation as land-cover classes (Appendix S2). This result
465 corroborates an earlier study assessing the habitats of a number of small islets in the Aegean
466 (including various islands included in our dataset) where it was found that many major habitat
467 types, such as mature forest and freshwater, were missing (Snogerup & Snogerup, 2004; see
468 also Panitsa, 1997; Sfenthourakis et al., 2018). However, these findings were not discussed in
469 the context of the ISAR or the SIE (Snogerup & Snogerup, 2004).

470

471 Interestingly, we did not identify phylogenetic clustering when focusing just on the very small
472 islands (i.e. the smallest of the islands we have classified here as small) (see Figure 2d,e,f).
473 The above habitat filtering explanation may explain this observation. However, this could
474 also be due to the species present on the smallest islands being adapted (i.e. possessing salt
475 tolerance) to littoral habitats, that are prevalent on very small islands (Snogerup & Snogerup,
476 2004). If salt tolerance is distributed across several families, this would explain the random
477 patterns observed in the phylogenetic structure of these islets (Flowers, Galal, & Bromham,
478 2010). As small island area increases, ‘phrygana’ communities primarily comprising annual
479 grasses and members of few other families start to dominate, leading to phylogenetic
480 clustering. In addition, it could be that on the very smallest islets natural disturbance (e.g.
481 intense storms and/or waves) has more of an impact (Whittaker & Fernández-Palacios, 2007),
482 driving community assembly to be essentially random with regard to phylogenetic structure.
483 Alternatively, it could be that, for the small islands, another variable co-varies with area, such

484 as human disturbance. For example, the smallest islets may be unsuitable for human activities
485 (e.g. tourism or land for grazing), meaning that there is in fact a greater amount of certain
486 types of disturbance (and reduction in habitat heterogeneity) on the larger of the smaller
487 islands, leading to the patterns observed.

488 As island area increased, we observed a gradual shift from phylogenetic clustering toward
489 phylogenetic overdispersion on individual islands, which mirrored a clear increase in habitat
490 diversity. One interpretation of this finding is that, on larger islands, the greater range of
491 habitats, such as freshwater systems, sub-alpine ecosystems and mature forest, enables a
492 much wider variety of functional forms drawn from a broader range of clades to persist. This
493 will result in greater phylogenetic diversity (and its ES) on the larger islands.

494

495 **4.2 Differences in species and phylogenetic composition between small and large islands**

496 A shortcoming of previous SIE studies has been the focus on species numbers, without any
497 consideration of species composition (Morrison, 2014). We found striking differences
498 between small and large islands in regard to species turnover: species spatial turnover
499 between small islands was high (Figure 3a) and mostly random (ES β_{SIM} , Figure 3b). The
500 strong correlation between ES β_{SIM} and geographical distance also suggests that neutral
501 processes such as dispersal limitation might have played an important role in shaping species
502 composition on small islands in the Aegean (see Runemark, 1971). In contrast, phylogenetic
503 composition tended to be, on average, more similar on small islands than expected by chance,
504 and independent of geographical distance, supporting our hypothesis of possible deterministic
505 convergence regarding the main plant clades present on small islands. This is also reinforced
506 by the small differences in habitat composition between the small islands, with almost all
507 small islands containing only natural grasslands and/or sclerophyllous vegetation. Altogether,
508 this indicates that, while only certain clades are able to establish and survive on the smaller
509 islands, the identity of these taxa (i.e. the identity of the taxa within these clades) is more
510 randomly distributed. This is likely due, at least in part, to stochastic extinction / immigration
511 and / or dispersal. That is, both neutral and niche-based processes might operate in
512 combination in this system to drive the SIE.

513

514 On the larger islands, much lower spatial turnover was observed, implying that species
515 composition on the larger islands was more ordered. Patterns of phylogenetic composition on
516 the large islands were more complex, with our two metrics showing opposite results: ES

517 MPD_{DISS} identifying mostly convergence and ES MNTD_{DISS} mostly divergence. ES MPD_{DISS}
518 is a measure of phylogenetic dissimilarity that captures variation associated with basal nodes
519 (e.g. substitutions of a given order or even higher taxonomic ranks; Kembel et al., 2010) and
520 thus showed an overall similarity between large islands due to the fact most of the higher
521 taxonomic groups represented in the regional island species pool occur on most of the large
522 islands. In contrast, ES MNTD_{DISS} focuses on variation associated with terminal nodes and is
523 more sensitive to lower-level taxonomic substitutions (i.e. changes in representation of
524 families/genera) among communities (Kembel et al., 2010). Therefore, the divergence
525 reported between large islands with ES MNTD_{DISS} could be due to differences in the source
526 pools (Kougioumoutzis et al., 2017), or *in-situ* speciation.

527

528 **4.3 Caveats and future directions**

529 This study is not the first to find breakpoints in the ISAR (Matthews et al., 2014; Niering,
530 1963; Wang et al., 2016), or to postulate that the mechanisms driving the ISAR (and SIE)
531 may change across breakpoints in the relationship (e.g. see Triantis et al. 2006 and Losos &
532 Parent, 2010, for a discussion on the speciation–area relationship). However, to our
533 knowledge this is the first assessment of the SIE undertaken through the lens of phylogenetic
534 community ecology, and the approach has proven useful for shining light on the potential
535 mechanisms driving the SIE. However, as always, in the absence of controlled experiments
536 and trait data (discussed below) and more explicit fine-scale measurements of habitat
537 diversity, it is impossible to be certain that habitat availability is the primary driver of the SIE
538 in this system. Nonetheless, based on our results we would argue that the approach applied
539 here (i.e. combining evaluation of the ISAR, IPDAR and species and phylogenetic
540 composition) represents a useful framework for analysing the SIE and the underlying
541 mechanisms, and assembly processes on islands more generally.

542

543 Going forward it would be interesting to expand this approach to include functional diversity
544 (e.g. see Schrader et al., 2020, for an interesting start in this direction). An assumption of the
545 use of phylogenetic diversity in these types of studies is that there is a correlation between
546 phylogenetic diversity and functional diversity. However, while a correlation between
547 phylogenetic diversity and functional diversity may exist in many systems, it is unlikely ever
548 to be a perfect association (Flynn et al., 2011). While many traits have been shown to have
549 strong phylogenetic signal, such that related species have similar traits, some have not
550 (Srivastava et al., 2012), and arguably functional trait data are better than phylogenetic data in

551 community ecology studies of this nature (Paine, Deasey, Duthie, & Thompson, 2018). Thus,
552 the expansion of the framework presented here to include functional diversity will no doubt
553 increase our understanding of the SIE.

554

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559

560 **DATA ACCESSIBILITY**

561 The data are provided in the Supporting information.

562

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714

715 BIOSKETCHES

716 **Tom Matthews** is a macroecologist and biogeographer at the University of Birmingham, UK.
717 He is interested in the application of macroecological methods to global environmental
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720

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723

724 **Author contributions:** KAT, TJM, and FR designed the analytical study. KK and PT
725 collected the data. FR and TJM wrote the code, and FR analyzed the data. TJM and FR wrote
726 the first draft of the manuscript. All authors contributed to the final manuscript.

727 **Table 1.** Summary of the BIC-based model selection for habitat diversity, species richness, PD and the three effect sizes ES_{PD} , ES_{MPD} and
728 ES_{MNTD} (with \log_{10} Area as the predictor). Only results for the best model(s) are given. For each best model and each metric, the likelihood (LL),
729 number of parameters (k), BIC value, ΔBIC , BIC weight (w_i), R^2 and the area threshold T_1 and, for the two breakpoint cases, T_2 , are given. All
730 best models were significant ($P < 0.001$).

Metrics	Best models	LL	k	BIC	ΔBIC	w_i	R^2	T_1 (km ²)	T_2 (km ²)
Habitat diversity									
	Continuous one-threshold	-267.24	5	560.25	0	0.31	0.94	6.28	-
	Left-horizontal continuous one-threshold	-269.87	4	560.35	0.10	0.29	0.94	4.55	-
	Left-horizontal continuous two-thresholds	-264.88	6	560.68	0.43	0.25	0.94	3.45	143.88
	Continuous two-thresholds	-262.83	7	561.74	1.49	0.15	0.94	4.55	150.66
Species richness									
	Left-horizontal continuous two-thresholds	-1004.01	6	2038.94	0	0.77	0.95	0.67	34.52
PD									
	Continuous one-threshold	-1499.69	5	3025.14	0	0.53	0.95	2.28	-
	Continuous two-thresholds	-1494.76	7	3025.60	0.46	0.42	0.95	0.66	17.30
ES_{PD}									
	Continuous one-threshold	-250.28	5	526.39	0	0.89	0.38	13.43	-
ES_{MPD}									
	Continuous one-threshold	-223.54	5	472.85	0	0.91	0.34	6.14	-
ES_{MNTD}									
	Continuous one-threshold	-222.07	5	469.91	0	0.62	0.22	3.22	-
	Left-horizontal continuous two-thresholds	-220.24	6	471.39	1.48	0.30	0.24	0.14	0.74

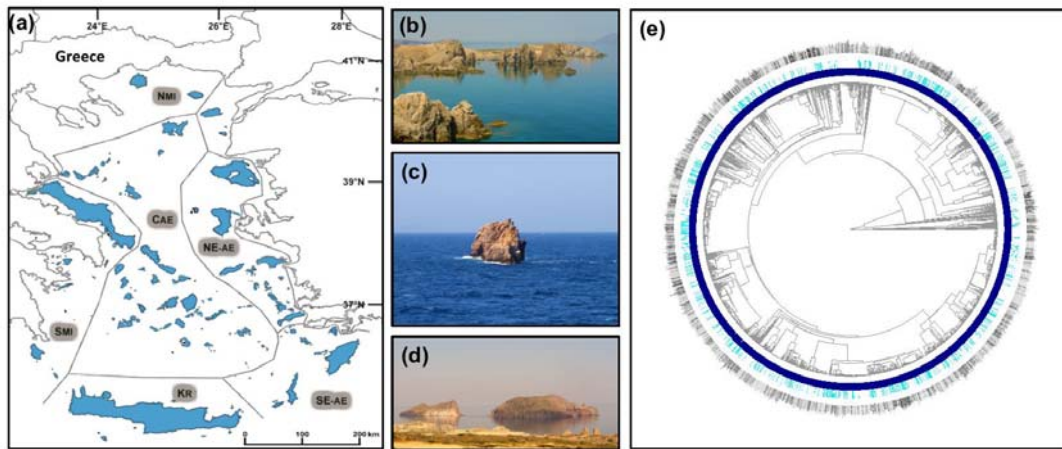
732 **Table 2.** Results of the Mantel permutation tests implemented between the β_{SIM} , ES β_{SIM} , ES
733 MPD_{DISS} and ES $\text{MNTD}_{\text{DISS}}$ dissimilarity matrices and the geographical distances between
734 islands. The analysis was implemented using all islands and for small and large islands
735 separately. The Pearson's correlation coefficients (r) and associated P-values (P) are given.
736 Significant results are highlighted in bold.

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Dissimilarity	All islands		Small islands		Large islands	
	r	P	r	P	r	P
β_{SIM}	-0.132	0.997	-0.012	0.427	0.310	<0.001
ES β_{SIM}	0.442	<0.001	0.303	<0.001	0.615	<0.001
ES MPD_{DISS}	0.018	0.368	-0.075	0.809	0.099	0.097
ES $\text{MNTD}_{\text{DISS}}$	0.190	<0.001	-0.055	0.834	0.052	0.140

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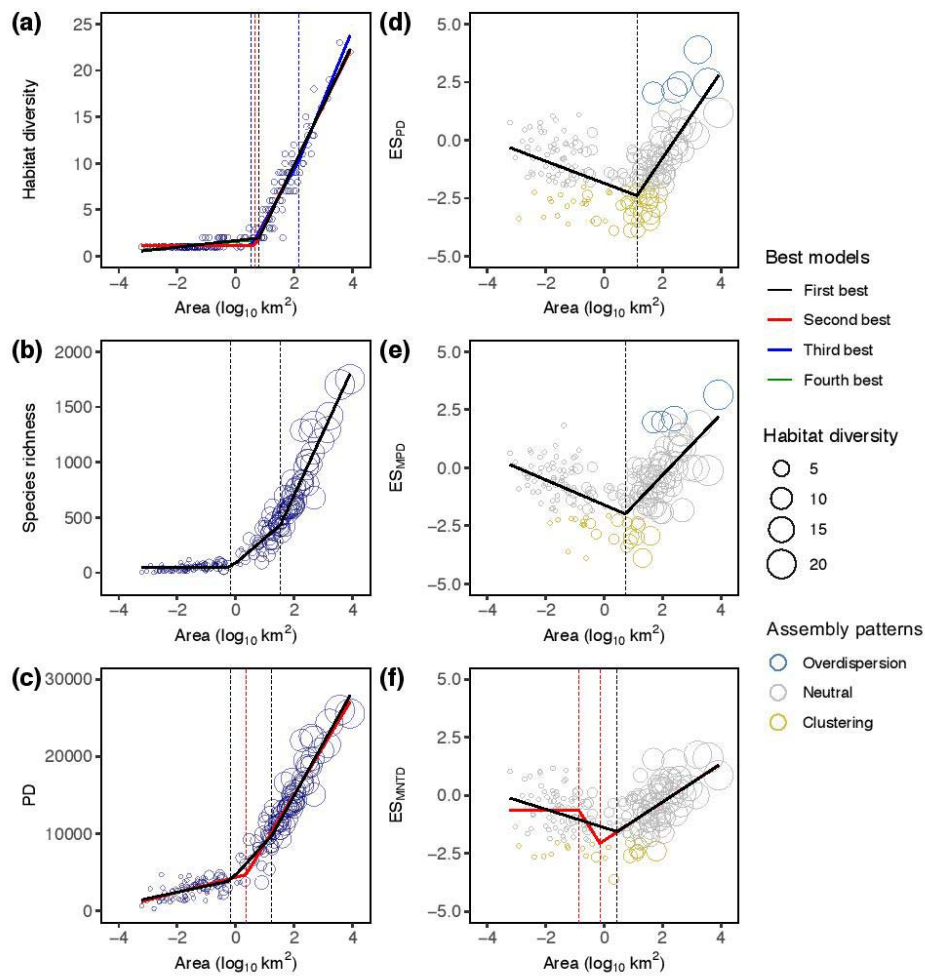
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741 **FIGURE 1** (a) Map of the Aegean Sea islands. Major island groups are highlighted: NMI =
 742 North Islands; CAE = Central Aegean; NE-AE = North East Aegean; SMI = South Islands;
 743 KR = Kriti; and SE-AE = South Eastern Aegean. (b) Kampanes, Milos, (c) Portes, Paros, and
 744 (d) Akradies, Milos. (e) Community phylogeny of the vascular plants of the 173 Aegean
 745 Islands in our dataset. The occurrence of each species in large and small islands is indicated
 746 by colours along the tips: light blue for small islands and dark blue for large islands. Tip
 747 labels coloured black highlight species grafted randomly on the tree.

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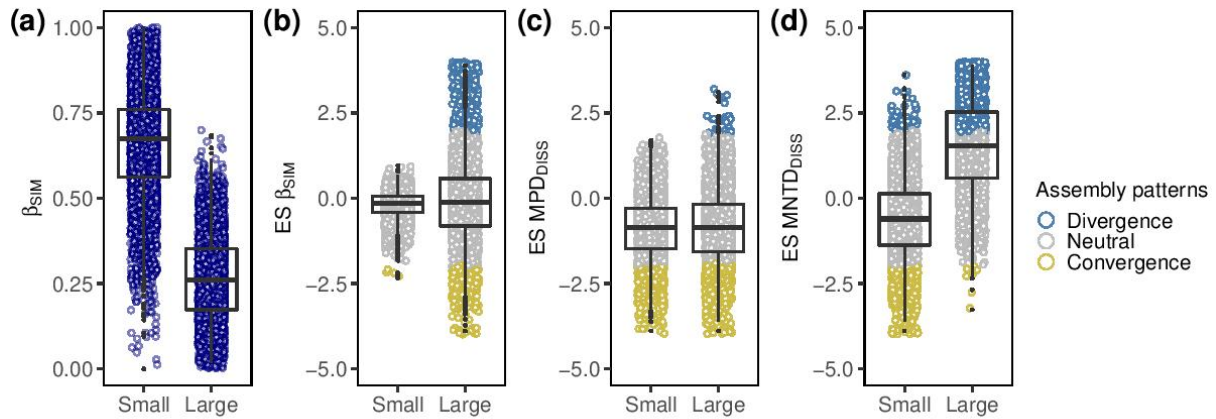
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751 **FIGURE 2** Relationships between \log_{10} Area and habitat diversity (a), species richness (b),
 752 PD (c), ES_{PD} (d), ES_{MPD} (e) and ES_{MNTD} (f). Coloured circles indicate islands. Thick solid
 753 lines represent the predicted values of the best model(s) and dashed vertical lines represent the
 754 threshold(s) of the best model(s). Best models were selected using BIC-based model selection
 755 comparing four SIE piecewise models, a simple linear model and a null model. To illustrate
 756 the link between \log_{10} Area and habitat diversity (HD) and the diversity relationships (b to f),
 757 the size of the dots were made proportional to the number of habitats. For the ES metrics,
 758 overdispersion indicates that values are significantly higher than expected by chance ($ES > 1.96$)
 759 and clustering indicates that phylogenetic diversity values are significantly lower than
 760 expected by chance ($ES < -1.96$). Neutral indicates that values are neither lower nor higher
 761 than expected by chance ($-1.96 < ES < 1.96$).

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767 **FIGURE 3** Differences in species turnover (a, b) and phylogenetic dissimilarity (c, d)
 768 between small and large islands. Islands were split into small and large using a breakpoint
 769 value of 2.57 km², calculated by averaging all breakpoints identified in the best models across
 770 all diversity metrics (see Figure 2b-f). Dots indicate the dissimilarity between pairs of islands.
 771 Species turnover was calculated using the index β_{SIM} (a) as well as its effect size $ES \beta_{SIM}$ (b).
 772 Phylogenetic dissimilarity was calculated using $ES MPD_{DISS}$ (c) and $ES MNTD_{DISS}$ (d).
 773 Convergence indicates that species turnover / phylogenetic dissimilarity values are
 774 significantly lower than expected by chance ($ES < -1.96$), and divergence indicates values that
 775 are significantly higher than expected by chance ($ES > 1.96$). Neutral indicates values that are
 776 neither lower nor higher than expected by chance ($-1.96 < ES < 1.96$).