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2 MR CYRIL HAMMOUD (Orcid ID : 0000-0001-5367-1404)

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Past connections with the mainland structure patterns of insular species richness in a continental-shelf archipelago (Aegean Sea, Greece)

10

11 *Drowned land-bridges shaping current biodiversity.*

12

13 **Authors and affiliations**

14

15 Hammoud C.: corresponding author: cyril.hammoud@africamuseum.be | ORCiD id 0000-0001-5367-1404

16 Royal Museum for Central Africa, Invertebrate Unit, Department of Biology, 3080 Tervuren, Belgium

17 Ghent University, Limnology Unit, Department of Biology, 9000 Ghent, Belgium

18 Kougioumoutzis K.: kkougiou@aua.gr | ORCiD id 0000-0002-6938-3025

19 Department of Biology, Section of Ecology and Taxonomy, National & Kapodistrian University of Athens, 15784

20 Athens

21 Rijsdijk K.F.: K.F.Rijsdijk@uva.nl | ORCiD id 0000-0002-0943-2577

22 Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, NL-1098XH

23 Amsterdam, The Netherlands

24 Simaiakis S.: simaiakis@nhmc.uoc.gr | ORCiD id 0000-0002-0890-6814

25 Natural History Museum of Crete, University of Crete, Knossos Av., PO Box 2208, GR-71409 Irakleio, Crete, Greece

26 Norder S.J.: s.j.norder@hum.leidenuniv.nl | ORCiD id 0000-0003-4692-4543

27 Leiden University Centre for Linguistics, Leiden University, Leiden, The Netherlands

28 Foufopoulos J.: jfoufop@umich.edu | ORCiD id 0000-0002-8341-8271

29 School of Natural Resources and Environment, University of Michigan, 440 Church St. Ann Arbor, Michigan, 48109-

30 1041, U.S.A.

31 Georgopoulou E.: elsa@nhmc.uoc.gr | ORCiD id 0000-0003-3806-0386

32 Natural History Museum of Crete, University of Crete, Knossos Av., PO Box 2208, GR-71409 Irakleio, Crete, Greece

33 Van Loon E.E.: E.E.vanLoon@uva.nl | ORCiD id 0000-0002-8895-0427

34 Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, NL-1098XH

35 Amsterdam, The Netherlands

36

Abstract

Recent research in island biogeography has highlighted the important role of late Quaternary sea-level fluctuations in shaping biogeographic patterns in insular systems but focused on oceanic systems. Through this study we aim investigate how late Quaternary sea-level fluctuations shaped species richness patterns in continental shelf island systems. Focusing on the Aegean archipelago, we first compiled maps of the area's geography using published data, under three sea-level stands: 1) current; 2) median sea-level over the last nine Glacial-Interglacial cycles (MSL); 3) Last Glacial Maximum (LGM). We gathered taxon-island occurrences for multiple chorotypes of angiosperms, butterflies, centipedes and reptiles. We investigated the impact of present-day and past geographic settings on chorological groups by analysing Island Species-Area Relationships (ISARs) and using Generalized Linear Mixed Models (GLMMs) selection based on multiple metrics of goodness-of-fit. Our results confirm that the Aegean's geography has changed dramatically since the LGM, whereas the MSL only modestly differs from the present configuration. Apart for centipedes, paleogeographic changes affected both native and endemic species diversity through altering connections between land-bridge islands and the mainland. On land-bridge islands we detected over-representation of native species and under-representation of endemics. Unlike oceanic islands, sea-level driven increase of isolation and area contraction did not strongly shape patterns of species richness. Furthermore, the LGM configurations rather than the MSL configuration shaped patterns of endemic species richness. This suggests that even short episodes of increased connectivity with continental populations are sufficient to counteract the genetic differentiation of insular populations. On the other hand, the over-representation of native non-endemic species on land-bridge islands reflected MSL rather than LGM mainland connections. Our study shows that in terms of processes affecting species richness patterns, continental archipelagos differ fundamentally from oceanic systems because episodic connections with the mainland have profound effects on the biota of land-bridge islands.

Keywords: Aegean archipelago, biogeography, angiosperms, reptiles, centipedes, butterflies, Last Glacial Maximum, Pleistocene**,** land-bridge island

Introduction

Islands are dynamic entities with continuously evolving geographic settings influencing the distribution and evolution of organisms they host. At deep time scales (Ma), islands' ontogeny shapes patterns of species diversity (Whittaker et al. 2008), whereas on shorter time scales climatic processes dominate (Fernández-Palacios et al. 2015). Climate drives eustatic sea-level fluctuations causing islands to shrink and expand, fragment and merge, or even disappear and emerge (e.g., Simaiakis et al. 2017). Late-Quaternary sea-level changes have left their imprint on insular species diversity patterns (Ali and Aitchison 2014, Rijsdijk et al. 2014, Weigelt et al. 2016, Ávila et al. 2018, 2019, Norder et al. 2018, 2019). Most work, however, has focused on volcanic oceanic islands or did not make a distinction between oceanic and continental insular systems and lumped them in their analyses (Weigelt et al. 2016, Veron et al. 2019). By

73   disregarding the specifics of continental archipelagos, relevant biogeographic processes are potentially

74   overlooked (Ali 2017, Simaiakis et al. 2017, Whittaker et al. 2017).

75   Continental shelf islands (*sensu* Ali 2017) are characterized by sitting on a continental shelf and may

76   include 'land-bridge' islands that were connected to the mainland in the past when sea levels were lower

77   (Box 1). Another characteristic is the proximity to the mainland often surrounding continental islands

78   (Weigelt and Kreft 2013). The geo-spatial effects of sea-level dynamics on continental island biota have

79   been studied extensively (e.g., Diamond 1972, Cardillo et al. 2008, Itescu et al. 2020).

80   In the Mediterranean Sea, the Aegean archipelago is located between the Greek and the Anatolian

81   peninsulas and is one of the largest archipelagos on Earth (Blondel et al. 2010). Its complex geological

82   history and high environmental heterogeneity contribute to its high biodiversity and endemism, thus

83   rendering it an ideal stage for biogeographic studies (Strid 2016, Sfenthourakis and Triantis 2017).

84   Unsurprisingly, its biogeography has been studied intensively (e.g., Hausdorf and Hennig 2005, Panitsa et

85   al. 2010, Triantis et al. 2018, Itescu et al. 2020). Although these studies provide crucial biogeographic

86   insights on diversity patterns in continental island settings, it has remained an open question how species

87   diversity and chorology is influenced by continental islands that were connected during the glacial sea

88   level low stands (land-bridge islands) and continental islands that always had remained islands ('true

89   islands' *sensu* Simaiakis et al. 2017). The combined effect of area change, fragmentation and connectivity

90   driven by late-Quaternary sea-level changes on insular species diversity has never been investigated for

91   the Aegean archipelago, although such a combined analysis is crucial to interpret the relevant

92   biogeographic processes that drive species-diversity and evolutionary patterns (see Kougioumoutzis and

93   Tiniakou 2014, Norder et al. 2019). Moreover, the influence of past connections to the mainland on Island

94   Species-Area Relationships (ISARs) has never been assessed (Triantis et al. 2008, 2012; Fattorini 2017).

95   Since we have recently quantified the paleogeographic change of islands in the Aegean Sea (Simaiakis et

96   al. 2017) and its biota are well studied, this setting represents an ideal study system to investigate the

97   influence of late-Quaternary sea-level fluctuations on native and endemic species richness.

98   Our aim is to investigate the combined impact of current, as well as past, island area and connectivity on

99   the insular species diversity of four well-studied taxonomic groups (angiosperms, reptiles, butterflies and

100   centipedes) in the Aegean archipelago. Our first hypothesis (H_1) is that more native species occur per area

101   unit on land-bridge islands than on true islands (*sensu* Simaiakis et al. 2017), reflecting the higher

102   establishing rates of native species on land-bridge islands (Simaiakis et al. 2017). Our second hypothesis

103   (H_2) is that endemism is negatively influenced by past connections to the mainland, as allopatric speciation

104   is suppressed by repetitive genetic exchanges with continental populations. Our third hypothesis (H_3)

105   concerns the effect of the duration of the archipelagic configurations as a result of sea-level drop on

106   richness patterns. On oceanic islands, the median archipelago configuration largely explains richness

107   patterns of single-island endemics, rather than the extreme and short-lasting Last Glacial Maximum (LGM)

108   configuration (Norder et al. 2019). We hypothesize that on land-bridge islands too, the median geographic

109   configuration (representative of the last glacial-interglacial cycles) has largely influenced patterns of

110 species richness. In contrast, the extreme LGM configuration should not have provided the time needed

111 for speciation to occur and is therefore not expected to have significantly influenced patterns of species

112 richness. To test our two first hypotheses, we analyse the combined effects of island type (land-bridge

113 *versus* true islands) and change in area and isolation on species richness of different taxa and chorotypes.

114 We investigate H_3 by analysing species richness patterns in relation to three paleogeographic settings: 1)

115 current; 2) during LGM and; 3) the median sea level (MSL) during the last glacial-interglacial cycle (Figure

116 1).

117

118 **Method**

119 *The Aegean archipelago*

120 The Aegean lies at the convergence of three tectonic plates (Anatolian, African and Eurasian) and has

121 therefore developed major fault systems, resulting in the formation of the South Aegean Volcanic Arc

122 (Higgins 2009). However, even though plate tectonics have strongly shaped the paleo-evolution of the

123 Aegean archipelago, its recent history has been mainly affected by Pleistocene climatic fluctuations

124 (Sakellariou and Galanidou 2016). Compared to the magnitude of the geographic changes caused by the

125 sea-level oscillations during the last ca. 120 Ka BP (comprising the last glacial-interglacial cycle;

126 Georgopoulou et al. 2015), the importance of the tectonic changes occurring at the same time scale is

127 mostly negligible given our aim and scope (Simaiakis et al. 2017). During the LGM (26.5 – 19 Ka BP), the

128 global sea level was ~135 m lower than present and locally > 140 m lower in the Mediterranean (Lambeck

129 and Purcell 2005, Clark et al. 2009, Lambeck et al. 2014). Subsequent sea-level rise caused dramatic

130 changes in the Aegean basin with most of the marine transgression observed during 16-11 Ka BP, when

131 sea-level rise rates were 12 m/1 Ka (Simaiakis et al. 2017). This led to a major reduction of total island

132 area by ca. 70% in the Aegean basin and a rapid increase in the number of islands by fragmentation. Large

133 islands (>20 km²) were rapidly shrinking and becoming isolated during that time (Simaiakis et al. 2017).

134 Islands emerged near the coast of Turkey and Greece that were formerly peninsulas and the Cycladic

135 paleo-island fragmented into the Cyclades islands group (Figure 1).

136

137 *Species richness data*

138 We compiled datasets of species richness for angiosperms, butterflies, centipedes and reptiles from

139 published work (Supplementary Material Table A 1.1). Data matrices of angiosperms and reptiles were

140 used to investigate patterns of both native and endemic species richness as their high rate of endemism

141 allowed for such statistical analysis. Due to the paucity of data related to centipede and butterfly endemic

142 species and the low number of islands hosting them, we focused on native species for our model selection

143 analyses for these two taxa, and only considered endemics in our exploratory analyses.

144 We compiled a plant matrix for 70 Aegean islands (Figure 2, A), including a total of 3246 native angiosperm

145 taxa (species and subspecies). The angiosperms are a well-studied group in the Aegean, and we compiled

146 data on five chorotypes (native non-endemics, multiple continental Greek endemics, Aegean endemics,

phyto-region endemics, single island endemics) and two combined chorotypes (all endemics, multiple island endemics) based on an extensive bibliographical database for the Aegean archipelago (see Appendix S1 in Kougioumoutzis et al. 2017). Examples of the distribution of the 4 endemics chorotypes are presented in Figure 3. The 'native non-endemics', sometimes termed 'natives', are a widely spread taxonomic group occurring both on the Aegean islands and on the mainland across the Mediterranean (2673 taxa), ~40% of which reached the Aegean islands as a result of human action in prehistoric times (Greuter 1971; 1979, Kougioumoutzis et al. 2020, modern introductions were excluded). The 'multiple continental Greek endemics' (GE) are species exclusively occurring both on the Greek mainland and the Aegean islands (689 taxa). The 'Aegean endemics' (AE) are found on multiple islands but not on the mainland (91 taxa). The 'phyto-region endemics' (PE) are restricted to one or multiple islands located within the same Aegean phyto-geographic region *sensu* Strid and Tan (1997 - 384 taxa). Finally, the single island endemics (SIEs), are endemics occurring exclusively on one Aegean island (292 taxa). We also combined chorotypes to compare general trends of endemics with non-endemics. We combined both phyto-region and Aegean endemics to form 'multiple islands endemics' (MIEs) *sensu stricto* (450 taxa) and combined all endemic chorotypes into an "all-endemics group" (E$_{ALL}$).

We compiled a database for the distributions of reptiles on 70 islands of the Aegean archipelago (Figure 2, B). Data were gleaned from the extensive literature (Valakos et al. 2008, Poulakakis et al. 2014, Bellati et al. 2015, Marzahn et al. 2016, Kornilios et al. 2019, Spilani et al. 2019, Thanou et al. 2019). Only peer-reviewed published records, or records backed up by specimens deposited in scientific collections were used. When considering native taxa, we excluded island populations that had been likely introduced by humans in the recent past. This includes island occurrences where published information reports on very recent arrival (e.g., *Stellagama* on Karpathos, Granno et al. 2019) or where molecular phylogeographic work has demonstrated recent, likely human-assisted arrival in the region (e.g., *Hemidactylus turcicus*). As for angiosperms, we recognized endemic status both at the species and subspecies level. This was based on taxonomic information published in peer-reviewed journals, accepted over the years by the herpetological community, and ideally also supported by molecular analyses. Number of native species varies greatly between 1 (Gavdopoula) and 22 (Kos) and number of endemic species varied between 0 (numerous islands) and 5 (e.g., Milos).

A similar matrix was compiled for 56 Aegean islands (Figure 2, C) and 70 centipedes species (see Simaiakis et al. 2004, 2005). Two chorotypes were distinguished: 'native' and 'endemics' (65 and 5 species, respectively). The number of native species varies between 2 (Dragonada) and 34 (Crete), whereas most islands (82%) host no endemic species.

Finally, a total of 117 species of butterflies from 37 Aegean islands (Figure 2, D) were compiled into a matrix, based on the data published by Pamperis (2019). Distribution maps of species were georeferenced using ArcMap v.10.6 and the presence of species on the islands were recorded. Six species occur only on one Aegean island (SIE). The rest 111 species are distributed on other Aegean islands and/or (at least) in mainland Greece and Turkey.

184

Paleo-island geography

186

187   We used the work of Simaiakis et al. (2017) to estimate insular areas and distance to the mainland at MSL

188   and LGM sea level. In this earlier work, the Aegean archipelago was reconstructed based on a geophysical

189   model of relative sea-level change that uses generalized sea-level equations accounting for hydro isostatic

190   adjustments and applied on a topographic and bathymetric grid with a resolution of 30 arc-seconds

191   (Simaiakis et al. 2017). For the construction of the MSL scenario we aimed to get close to a global eustatic

192   median sea-level stand of 65 m below present for the last nine glacial-interglacial cycles, following the

193   method from Norder et al. (2019), building on the works of Tzedakis et al. (2012) and Bintanja et al. (2005).

194   We assumed that the regional geophysical effects affecting this eustatic MSL stand were minimal, and

195   therefore used the geographic setting at 11 ka BP (latest occurrence of 65 m below present sea level) as

196   estimate for MSL scenario. For the LGM setting, we based our analysis on the reconstruction at 21 Ka BP.

197   Islands smaller than the surface of a grid cell (1 km^2) were excluded from our analysis, and islands

198   separated by a distance smaller than the grid size (1 km^2) were aggregated in the paleogeographic

199   reconstruction to obtain a conservative estimate of the fragmentation dynamics occurring in the system

200   (*cf.* Rijsdijk et al. 2014). All geographic data were processed in ArcGIS 10.2.2. After aggregation, island

201   areas and Euclidean shore-to-shore distance to the mainland (without correction for satellite islets) for

202   the current, MSL (11 Ka BP) and LGM (21 Ka BP) configurations were used to calculate the difference

203   between current and past areas as well as current and past distances (Supplementary Material Table A

204   1.1), with the aim to use these variables in further inferential analysis (*cf*. method of Weigelt et al. 2016).

205   In addition, to investigate the biogeographic effects of past fragmentation from the mainland, we

206   classified islands into two different groups (Supplementary Material Table A 1.2): those that remained

207   isolated from the mainland, referred to as 'true islands' (*sensu* Simaiakis et al. 2017) *versus* those with an

208   episodic connection to the mainland during the LGM ('LGM land-bridge islands') or under MSL scenario

209   ('MSL land-bridge islands'). For land-bridge islands (distance = 0 at Median sea level or Late Glacial

210   Maximum), the area considered is that of the island at the time step (1 Kya) preceding the connection to

211   the mainland.

212

213   *Exploratory and inferential analysis*

214   ISARs were fitted using the logarithmic transformation of the Arrhenius power model (Carey et al. 2020).

215   We compared the ISARs of different taxa/chorotypes using adjusted-R^2 values as a measure of their

216   goodness-of-fit. As the models have the same number of fitted parameters, the R^2 are directly

217   comparable, without modification (Triantis et al. 2005). We also calculated the mean area-adjusted

218   species richness (number of species divided by insular area) of true islands and land-bridge islands for the

219   native and all-endemic chorotypes of all taxa. We assessed whether the difference of mean area-adjusted

220   species richness observed between the two type of islands were significant using ANOVA.

To investigate the impact of past geographic changes on current diversity, we compared the performance of three alternative GLMMs in explaining species richness. The models were built identically for all taxa and chorotypes and corresponded to the geographic setting of the Aegean under three scenarios: present-day, LGM and MSL. The present-day model (null model) consisted of present-day area, Euclidean shore-to-shore distance to the mainland, spatial autocorrelation as fixed effect, plus phyto-geographic region as random effect to account for biogeographic affinity. The models for the paleogeographic settings (LGM or MSL) included the same predictors as the null model plus the following metrics representing the changes in insular geography compared to the present-day setting: area loss, increase of Euclidean distance to the mainland and island type ('true' *versus* 'land-bridge'). We fitted these three sets of predictors using the species richness of all aforementioned taxa and chorotypes as response variables. All models were fitted using a log-link function and Poisson distribution for the error term (lmerTest package, Kuznetsova et al. 2017). All variables with p-values > 0.1 were excluded from the models to obtain a set of "suggestive, but inconclusive" predictors (Murtaugh 2014) before refitting with the remaining variables. Multicollinearity was addressed by computing the variance inflation factors (VIF) of the predictors and removing variables with VIF > 2.5 (Dormann et al. 2013). Finally, we identified the models that provided most explanatory potential using multiple measures of goodness-of-fit: the corrected Akaike Information Criterion (AICc), Bayesian Information Criterion (BIC) and leave-one-out cross-validated (loocv) pseudo-R^2. In addition, in accordance with Nakagawa and Schielzeth (2013), we calculated the difference between conditional (R^2c, fit with random effect) and marginal (R^2m, fit without random effect) R^2 to assess how much additional variance biogeographic affinity (random factor) explained in our models (MuMIn package, Barton 2017). All analyses were performed in R version 3.4.2 (R core team 2018). Crete was diagnosed as an outlier in several GLMMs using residual plots of residuals vs. leverage (data not shown), but was still included in the analysis due to its biogeographic importance in the Aegean.

Results

Geographic changes in the Aegean

The geographic reconstructions based on Simaiakis et al. (2017) confirm that the geography of the Aegean archipelago changed dramatically throughout the last climatic cycle of the Quaternary (Figure 1). The current configuration and the LGM setting represent two extremes of the sea-level fluctuations (highest now, lowest during the LGM). The changes in areas calculated reflect this pattern: insular area loss between the LGM and the present is systematically greater compared to the difference between MSL and the present (Supplementary Material Table A 1.1). Similarly, the increase of distance between islands and mainland is greater for the LGM-present comparison compared to MSL-present (Supplementary Material Table A 1.1). Finally, fewer islands were connected to the mainland (land-bridge islands) under MSL configuration compared to the LGM (Supplementary Material Table A 1.2).

Exploratory and inferential analyses

259 The proportion of variance explained by ISARs varied greatly between taxa, chorotypes and island types;

260 adjusted-R^2 ranged -0.05 for endemic reptiles on land-bridge islands from to 0.79 for native non-endemic

261 angiosperms (Table 1). ISARs for endemic subsets were generally supported by lower adjusted-R^2

262 compared to native non-endemic subsets. Similarly, adjusted-R^2 were lower when fitting the ISARs on

263 subsets of land-bridge islands compared to true islands. ISARs slopes (z-values) also varied greatly

264 between taxa, chorotypes and island types, and ranged from -0.01 for native non-endemic reptiles to 0.37

265 for angiosperm SIEs on true islands (Table 1, Supplementary Material Figure A 2). Land-bridge islands

266 appear to host more native taxa than true islands, whereas the opposite trend was observed regarding

267 endemic taxa which were more abundant on true islands than on land-bridge islands, as indicated by the

268 comparison of the area-adjusted means of species richness (Figure 4) and the ISARs (intercept higher on

269 land-bridge islands for native non-endemics and lower for endemics - Supplementary Material Figure A

270 2).

271 The proportion of variance explained (here estimated using the loocv-R^2) by the GLMMs ranged from 14%

272 (angiosperm SIEs) to 84% (butterflies native non-endemics - Table 2) and was overall greatest for

273 butterflies, followed by angiosperms, reptiles and finally centipedes. Biogeographic affinity (accounted

274 for by the random effect and inferred from the difference between R^2c and R^2m) explained a large

275 proportion of variance for butterflies and for all angiosperm endemic categories (10-78% - Table 2), but

276 not for the native angiosperms, centipedes and reptiles (Table 2). Current area was the most important

277 predictor in almost all models (Table 2; Figure 5). Among the variables accounting for paleogeographic

278 changes, only island type was consistently selected across taxa and chorotypes, and its effect size was

279 comparable to current area. Area loss and increase of distance to the mainland were only rarely selected

280 as significant predictors of species richness, and when they were, their magnitude of effect was minor

281 compared to current area. In addition to reflecting the current area, native angiosperm species richness

282 was also influenced by MSL island type, and to a minor extent by the increase of distance to the mainland

283 compared to MSL. LGM-related variables (mostly island type) emerged as important predictors for all

284 endemic angiosperm chorotypes, except for the Greek endemics and the SIEs, for which no effect of

285 paleogeography was detected (Table 2; Figure 5). The effect of island type was opposite on native and

286 endemic chorotypes whereby land-bridge islands hosted more native species than true islands, but much

287 less endemics. GLMMs for reptile chorotypes yielded similar results; native species richness was

288 influenced by MSL island type in addition to the current geography, whereas the LGM model was clearly

289 superior for endemic species richness, also revealing a strong effect of island type (Table 2). For native

290 non-endemic centipedes, no influence of paleogeography was detected, whereas the native non-endemic

291 butterfly species richness was best explained by a combination of the current area and MSL island type,

292 with an over-representation in land-bridge islands (Table 2).

293

294 **Discussion**

295 Late Quaternary sea-level changes have left their mark on island species richness patterns (e.g., Weigelt
296 et al. 2016, Norder et al. 2019), following theoretical expectations (Fernández-Palacios et al. 2015).
297 Recently, the question arose whether LGM paleogeographic configurations or those more representative
298 of the Pleistocene better explain endemic species richness (Norder et al. 2019). On oceanic islands the
299 intermediate sea-level configuration seems to have shaped SIE diversity patterns (Norder et al. 2019). Our
300 study aimed to investigate the possibility that different patterns might be observed on continental shelf
301 island systems. Here we start by discussing whether and how past connections to the mainland – one of
302 the most distinctive features of continental islands systems compared to oceanic ones – have had an
303 impact on the diversity of native non-endemic or endemic species richness. Then, we discuss current, MSL
304 and LGM influences on the patterns of species richness observed and compare our results with those
305 obtained in oceanic settings. Finally, we complement our discussion by taxa-specific considerations on the
306 importance of biogeographic affinities.

307

308 *Native non-endemic species richness*

309 Our first hypothesis predicted that native non-endemic species should be more abundant on land-bridge
310 islands than on true islands because of their increased connectivity with the mainland throughout the last
311 glacial-interglacial cycle resulting in higher establishment rate of continental species. Our results
312 corroborate this hypothesis in the cases of angiosperms, reptiles and butterflies, whereas the richness of
313 native non-endemic centipedes was not influenced by past connections to the mainland (Table 2). For
314 native angiosperms, GLMMs had high predictive capacity (Table 2) which is in line with Kreft et al. (2008),
315 Kagiampaki et al. (2011), Kougioumoutzis and Tiniakou (2014) or Valli et al. (2019) (*i.e.*, 82–95%). Results
316 for this taxon group indicated that native non-endemic species richness was significantly higher on MSL
317 land-bridge islands compared to true islands, which is also apparent in the slightly higher position of the
318 ISAR curve of the land-bridge islands compared to true islands (Supplementary Material Figure A 2). In the
319 'best' GLMM, the regression coefficient of the current area was three times higher than that of island
320 type, suggesting only a modest influence of past connections to the mainland on the current richness of
321 native non-endemic angiosperm species. Native non-endemic butterfly species richness, though, was
322 strongly influenced by past mainland connections as indicated by a regression coefficient for island type
323 as high as that of current area. As for angiosperms, MSL rather than LGM island type was selected in our
324 analysis. However, we would like to point out that the butterfly dataset only included 3 MSL land-bridge
325 islands, *versus* 12 for the LGM period, so that in this specific case, the selection of the 'best' time frame
326 might be less robust than suggested by the AICc and BIC values (Table 2). Either way, our results indicate
327 that the species richness of native butterflies is strongly influenced by past connections to the mainland,
328 which directly contradicts the results of Dennis et al. (2000), according to which butterfly diversity did not
329 reflect historical influences in the Aegean. Similarly, for reptiles, the effect of island type indicated an

330 over-representation of native species on land-bridge islands and was of the same order of magnitude as
331 the current area. That effect was apparent in the higher intercept of the ISAR of land-bridge islands
332 compared to true islands. This may be explained in part by the fact that because reptiles are relatively
333 poor over-water dispersers, once isolated, species communities will undergo community relaxation
334 progressively losing species over time (Diamond 1972, Newmark 1987, Foufopoulos and Ives 1999).
335 Finally, native centipede species richness did not reflect any influence of paleogeography. Furthermore,
336 the proportion of variance explained by the current model was relatively low (37 %, Table 2), which may
337 indicate that other factors (e.g., habitat heterogeneity) are more influential than insular area or isolation
338 for this taxon (Triantis et al. 2005, Simaiakis and Martínez-Morales 2010). In summary, results show that
339 MSL land-bridge islands host proportionally more native species than true islands for all taxa except
340 centipedes.

341

342 *Endemic species richness*

343 Our second hypothesis predicted that land-bridge islands should host proportionally fewer endemic
344 species than true islands because episodic connections to the mainland would have created windows of
345 gene flow between previously isolated insular populations and their mainland relatives, thereby
346 counteracting their genetic differentiation in allopatry. The results obtained for the GLMM selection of
347 both taxa formally analysed with regards to endemics diversity (angiosperms and reptiles) strongly
348 corroborate this hypothesis, though for angiosperms the effect was chorotype dependent.

349 Except for the SIEs and the multiple continental Greek endemics, the patterns of species richness of all
350 endemic chorotypes showed strong imprints of the LGM geographic configuration through the
351 connections established to the mainland during that period of low sea-level. Indeed, island type was the
352 variable accounting for paleogeography most consistently selected in our analysis. Furthermore, its
353 regression coefficient was higher than that of the current area, indicating that the effect of LGM
354 geography was at least as influential as the current setting in shaping patterns of endemic angiosperm
355 species richness. This result is confirmed by the lower intercept of endemic angiosperm chorotypes
356 (except aforementioned) on land-bridge islands compared to true islands. A highly similar pattern was
357 observed for reptiles: land-bridge islands hosted significantly fewer endemics species than true islands,
358 as reflected in the output of both model selection and ISARs intercepts. Although the centipedes and
359 butterflies datasets were not formally analysed with regards to patterns of endemic species richness, a
360 rough examination of the distribution of the few endemic species present in the study system fits with
361 the aforementioned patterns of depletion on land-bridge islands. Indeed, none of the 9 land-bridge islands
362 included in the centipedes dataset hosted any endemic species. Similarly, only 1 out of the 12 land-bridge
363 islands of butterflies dataset hosted 1 endemic species.

364

Our third working hypothesis predicted that MSL rather than LGM insular configurations should have influenced patterns of species richness as the former is more representative of the geographic setting over the last glacial-interglacial cycle. Overall, our results validate this hypothesis for the native chorotypes of angiosperms, reptiles and butterflies, but not for the endemic chorotypes of these taxa nor for centipedes. It is noteworthy to point that GLMM selection most clearly indicates that current island geography is highly influential in determining the species richness of all taxa and chorotypes except endemic reptiles. More specifically, current area was consistently included in all models with comparatively high regression coefficients, whereas current distance to the mainland was only included in the models of a few taxa and chorotypes (Aegean and multiple island angiosperm endemics, native reptiles and native centipedes – Table 2). By comparison to the effect of current area, the respective influence of MSL and LGM-related variables was more taxon and chorotype-dependent.

The maximum, yet short-lasting connectivity achieved during the LGM (Figure 1; Sakellariou and Galanidou 2016) has negatively affected angiosperm endemic diversity (except SIEs and mainland Greek endemics), suggesting that the LGM spatial configuration of the Aegean archipelago has left its imprint on species' distribution, richness and evolutionary patterns (e.g., Poulakakis et al. 2015, Kougioumoutzis et al. 2017). The reptile endemic species richness follows a highly similar pattern, thus also pointing towards an influence of short-lasting episodes of increased connectivity with the mainland as counteracting speciation process. Finally, reptile, butterfly and angiosperm native non-endemic species richness were all affected by MSL island type. Altogether, this suggests that unlike endemic species richness, native diversity is more affected by the longer lasting geographic configuration, being partly in line with the flickering connectivity hypothesis (Flantua and Hooghiemstra 2018). The fact that angiosperm SIEs are largely unaffected by past configurations differs from observations made in oceanic insular settings, where MSL configurations were highly influential (Norder et al. 2019). We believe that, in a system of islands as highly interconnected as the Aegean, topographic complexity and environmental heterogeneity might be the main driver of SIEs diversification (e.g., Kallimanis et al. 2011; Lazarina et al. 2019; Kougioumoutzis et al. 2020; Kougioumoutzis et al. 2021). Similarly, multiple continental Greek endemics were unaffected by the variables accounting for paleogeographic changes included in the analysis, thus indicating that other processes might shape the patterns of diversity of this chorotype. As these species could have originated from the Greek mainland, we suggest that a negative longitudinal trend (reflecting the pattern of migration from the continent) could govern their distribution. Altogether, the fact that paleogeography had a heterogeneous effect on different chorotypes of the taxon highlights the importance of distinguishing between these chorotypes when addressing biogeographic questions.

398 It is noteworthy to mention that we observed that some results regarding the 'best' time frame selected

399 for island type were highly influenced by the inclusion of Crete in the analysis, as it acted as a high leverage

400 outlier. For example, removing Crete from the GLMMs selection procedure for the native angiosperm

401 resulted in selecting the LGM rather than MSL island type.

402 *Biogeographic affinity*

403 Biogeographic affinity (i.e., the random effect in our models) explained only a small fraction of the

404 variance for the native non-endemic angiosperms, non-endemic and endemic reptiles and non-endemic

405 centipedes. The high proportions of generalist species and of species with high dispersal abilities in native

406 non-endemic chorotypes might be responsible for this pattern. However, we did not investigate the issue

407 further as it goes beyond the scope of this study. For angiosperms, the lack of influence of biogeographic

408 affinity can partially be attributed to the fact that a large portion (~40%) of the present Aegean flora has

409 reached the Aegean islands due to human action in prehistoric or early historic times (Greuter 1971, 1979,

410 Kougioumoutzis et al. 2020). For reptiles, the lack of effect of biogeographic affinity could result from

411 similar levels of diversity in the various source communities 'seeding' the different islands east and west

412 of the Aegean Trench (Foufopoulos et al. 2011).

413 A large share of variance of the models of all angiosperm endemic chorotypes as well as native non-

414 endemic butterflies was explained by biogeographic affinity. For endemic angiosperms, this is in line with

415 previous studies stating that in the Aegean, bioregionalization is primarily a result of the region's complex

416 paleogeographic history (Kougioumoutzis et al. 2017, Iliadou et al. 2020). This is also due the high

417 proportion of narrowly-ranged species and consequently of high species turnover in Aegean island plant

418 communities (e.g., Iliadou et al. 2020): nearly ~45% of the endemic taxa occurring in the Aegean are SIEs,

419 the vast majority of which occur in Crete and Evvia (Panitsa et al. 2018). Other factors such as climate and

420 geodiversity probably play an important role in shaping current endemic diversity patterns throughout

421 the Aegean, as was observed for the central (Kougioumoutzis and Tiniakou 2014), eastern (Panitsa et al.

422 2010, Panitsa and Tzanoudakis 2010) and southern (Kagiampaki et al. 2011) Aegean islands. In addition,

423 favourable climatic conditions most probably permitted a relict flora to persist in the southern (i.e., Crete,

424 Karpathos, Rodos) and partly eastern (e.g., Ikaria: Christodoulakis 1996a, b) Aegean archipelago

425 (Runemark 1969, 1971). In topographically complex islands, some of the old MIEs formed neo-endemic

426 SIEs through allopatric speciation (Runemark 1969, 1971, Bittkau and Comes 2005, 2009, Comes et al.

427 2008, Jaros et al. 2018; see also Figure 7 in Kougioumoutzis et al. 2021 regarding neo-endemism centres

428 in the Aegean). Geographic isolation through sea-level oscillations may have supported the recent

429 diversification of neo-endemic species, especially in the central Aegean where several non-adaptive

430 radiations occurred (e.g. *Campanula*, *Nigella*, *Erysimum* – e.g. Comes et al. 2008, Jaros et al. 2018).

431 Specifically, episodes of high insular fragmentation occurred repetitively over the last 2 My (every glacial-

432 interglacial interval for ~20 ka), disrupting the longer lasting glacially connected state and leading to

433 cumulative genetic divergence between populations according to the flickering connectivity hypothesis
434 (Aguilée et al. 2009, Flantua and Hooghiemstra 2018). One prominent example for this is the
435 differentiation of the *Nigella arvensis* species complex due to non-adaptive radiation and random genetic
436 drift resulting from several vicariant events during the Pliocene/Pleistocene (Bittkau and Comes 2005,
437 Bittkau and Comes 2009, Jaros et al. 2018).

438 According to Dennis et al. 2000, the percentage of endemic butterflies is very low in the Aegean in
439 compliance with our findings. Also, common species live in the centre of the Aegean (i.e., the Cyclades)
440 whereas peripheral islands (close to Greek and Turkish mainland) host both rare and common species
441 (Dennis et al. 2000), which might explain the high influence of biogeographic affinities for this taxon.
442 Additionally, butterflies may largely follow the the phyto-region compartmentalization of the Aegean
443 since they are habitat and resource specialists, with many groups being food-plant specialists (Ricklefs and
444 Lovette 1999; Dennis et al. 2000).

445

446 *Continental-shelf and oceanic archipelagos*

447 The geographic setting of the LGM is an extreme configuration that was represented only sporadically and
448 for short time-periods throughout the Pleistocene, with only 2% of the last 800 Ka BP estimated to have
449 a similarly low sea level (Norder et al. 2019). Therefore, the duration of these episodes may have been
450 too short to have had a significant impact on the diversity and composition of insular biota on oceanic
451 islands (Porter 1989, Heaney et al. 2013, Norder et al. 2019). However, our results show that in a
452 continental-shelf archipelago, patterns of endemic species richness of multiple taxa (angiosperms and
453 reptiles) were strongly and negatively influenced by connections with the mainland that occurred during
454 the LGM. We explain this as the result of extreme connectivity that was achieved during the LGM between
455 the expanded Aegean true islands, land-bridge islands and the surrounding continental land mass. This
456 connectivity with the mainland, even though short-lasting, could have promoted the over-representation
457 of native butterfly (and angiosperm) species by enabling high rates of establishment on land-bridge islands
458 for species from the mainland during episodic connections. The same increased connectivity would on the
459 other hand have been detrimental to ongoing speciation processes in land-bridge islands, by enabling new
460 gene flow from populations of mainland relatives, thus resulting in the strong patterns of endemic under-
461 representation observed for angiosperms and reptiles. Alternatively, the invasion of island communities
462 by mainland taxa during LGM-like conditions, could have led to the extinction of competitively inferior
463 island endemics (Capula et al. 2002).

464 The ISAR z-values for total angiosperm richness fall into the z-value range for continental island settings.
465 On the other hand, the endemic richness z-values are much lower than those on oceanic islands, pointing
466 to reduced endemism on continental islands. We also observed that the high degree of Aegean island

fragmentation by Pleistocene sea-level oscillations led to MIEs sharing much more islands (> 5) than is observed for oceanic archipelagos. The multiple island angiosperm endemism manifested in the Aegean today is indeed largely shaped by the fragmentation of large landmasses into smaller islands by the present high sea level. It remains to be tested in how far maximum connectivity conditions are exclusively related to the lowest short-lasting sea-level stand, or whether for most biota maximum connectivity was reached earlier and lasted longer than the LGM. Clearly this depends on the geometry and depth of the basin under study, influencing the sea-level thresholds at which island area and connectedness change significantly (Norder et al. 2019). We can conclude there are two crucial differences between oceanic and continental islands: 1) in a continental setting, episodic connections with the mainland have profound effects on the biota of land-bridge islands and 2) the rate and magnitude of area loss, as well as the degree of fragmentation, is far greater in continental compared to oceanic systems. As such, metrics of area loss or distance increase such as the ones used in Weigelt et al. (2016) or Norder et al. (2019) are of little relevance when disentangling biogeographic patterns in continental island systems. Indeed, most islands included in our dataset were several times larger during the LGM than now, because they belonged to larger paleo-islands at that moment. Such large losses of area cannot be expected to be reflected in patterns of species richness the same way area contraction would be on oceanic islands and is indeed not reflected in the outputs of GLMM selection, which showed area loss and distance increase to have a minor and occasional influence on diversity patterns only.

Conclusions

Our study highlighted the importance of past sea-level changes in shaping species richness patterns in the Aegean, with MSL or LGM influences being relevant depending on the taxon and chorotype. On the one hand, LGM connections to the mainland were linked to strong endemic under-representation in land-bridge islands, a pattern which differs from previous findings according to which MSL shaped patterns of endemic species richness in oceanic systems. On the other hand, compared to true islands, MSL land-bridge islands hosted significantly more native species of all taxa except centipedes, potentially reflecting an increased rate of establishment over a long period of time on these islands. Furthermore, area loss and increase of distance to the mainland had low overall performance in model selection procedure, probably as a result of the magnitude of geographic changes endured by islands following the fragmentation of large paleo-landmasses. Continental systems thus hold ample evidence of the effect of paleogeography on the species richness, speciation and biogeographic patterns of the Aegean islands. The noted principal differences in geographic and evolutionary mechanisms between oceanic and continental islands make statistical assessments of endemic species data of combined oceanic and continental islands fundamentally problematic and studies involving both systems should explicitly incorporate their differences in statistical models.

Author's Contributions

CH, KFR, SJN and EvL designed the workflow. CH led the manuscript writing. KK compiled the plant data, SS compiled the centipede data, JF compiled the reptile data, EG compiled the butterfly data. All authors contributed equally to manuscript writing and interpretation of results.

Conflict of Interest

The authors have no conflict of interests.

Data Accessibility

GIS shapefiles of insular geography at the different time frames, as well as species richness matrixes: Dryad doi.org/10.5061/dryad.dfn2z350z.

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728 **Tables.**

729

730 Table 1. Slope and adjusted-R2 of the $\log_{10}$-transformed island species area relationship curves. NNE is

731 native non-endemic species, All-E is all endemics, PE is phyto-region endemics, AE is Aegean endemics,

732 GE is Greek island endemics, SIEs is single island endemics, MIEs is Multiple island endemic. Asterisks

733 indicate the significance level: *p-value ≤ 0.05; ** p-value ≤ 0.01; *** p-value ≤ 0.001.

Taxon	Chorotype	z-values			Adjusted R^2		
		Land-bridge islands	True Islands	Both	Land-bridge islands	True Islands	Both
Angiosperms	NNE	0.30***	0.33***	0.33***	0.73	0.78	0.79
	All-E	0.35*	0.32***	0.26***	0.26	0.51	0.25
	PE	0.25*	0.21***	0.14*	0.16	0.18	0.05
	AE	0.13	0.25***	0.14*	-0.01	0.33	0.06
	GE	0.38*	0.33***	0.30***	0.22	0.52	0.33
	SIEs	0.30*	0.37***	0.34***	0.20	0.45	0.39
	MIEs	0.19	0.25***	0.14*	0.03	0.29	0.05
Reptiles	NNE	0.30***	0.29***	0.33***	0.57	0.51	0.56
	All-E	0.02	0.10**	-0.01	-0.05	0.14	-0.01
Centipedes	NNE	-0.03	0.18***	0.15***	-0.11	0.37	0.26
Butterflies	NNE	0.29*	0.31***	0.35***	0.42	0.52	0.48

735 Table 2: Selected Generalized Linear Mixed Model (GLMM) models for each chorotype with overall best
736 performance in bold. Model performance was assessed based on corrected Akaike Information Criterion
737 (AICc), Bayesian Information Criterion (BIC) and leave-one-out cross-validated (loocv) pseudo-R^2. The
738 difference between conditional and marginal R^2 (R^2c and R^2m respectively) was used to assess the impact
739 of the random effect of the models (phyto-geographic region to which the island belongs). In each of these
740 models, variables with p-values higher than 0.1 or Variance Inflation Factor (VIF) higher than 2.5 were
741 removed. Meaning of acronyms: MSL = Median Sea Level; LGM = Last Glacial Maximum; *S-A* = spatial
742 autocorrelation; *prov* = phyto-geographic region; *logApr* = logarithm of current area; *Dpr* = current
743 shortest distance to the mainland; *dDmed* = increase in distance to the mainland compared to median sea
744 level; *dAmed* = insular area loss compared to median sea level; *typemed* = island type (land-bridge island
745 or true island) based on median sea level; *dDlgm* = increase in distance to the mainland compared to LGM
746 sea level; *dAlgm* = insular area loss compared to LGM sea level; *typelgm* = island type based on LGM sea
747 level. Sample size information is provided in the first column (Taxon), and it remains the same for all sub-
748 models within this group.

Taxon	Chorotype	Sea-level	Model (m.)	Model (predictors: p-value ≤ 0.1 | VIF ≤ 2.5)	AICc	BIC	loocv-R^2	R^2c - R^2m
Angiosperms (n = 70)	Native non endemic	Present	1	logApr - Dpr + S-A + prov	2377	2387	0,75	0,03
		MSL	**2**	**0.46 logApr - 0.01 dDmed + 0.15 typemed (P) + S-A + prov**	**2298**	**2310**	**0,75**	**0,03**
		LGM	3	logApr - Dpr + typelgm (P) - 0.01 S-A + prov	2332	2344	0,75	0,02
	All endemics	Present	4	logApr + Dpr + S-A + prov	647	657	0,38	0,45
		MSL	5	logApr + Dpr + dDmed + typemed + S-A + prov	651	664	0,39	0,43
		LGM	**6**	**0.55 logApr + 0.08 dDlgm - 0.49 typelgm (P) + S-A + prov**	**629**	**641**	**0,43**	0,36
	Phyto-region endemics	Present	7	logApr + Dpr + S-A + prov	351	361	0,48	0,84
		MSL	8	logApr + typemed + S-A + prov	344	355	0,47	0,83
		LGM	**9**	**0.39 logApr - 0.58 typelgm (P) - S-A + prov**	**340**	**351**	**0,50**	0,78
	Aegean endemics	Present	10	logApr + S-A + prov	490	498	0,42	0,71
		MSL	11	logApr + dDmed + typemed + S-A + prov	465	477	0,43	0,68
		LGM	**12**	**0.50 logApr + 0.13 Dpr - 0.14 dAlgm - 0.57 typelgm (P) + S-A + prov**	**464**	478	**0,46**	0,55
	Multiple continental Greek endemics	**Present**	**13**	**0.63 logApr - S-A + prov**	**368**	**376**	**0,60**	0,44
		MSL	14	logApr + S-A + prov	368	376	0,60	0,44
		LGM	15	logApr + S-A + prov	368	376	0,60	0,44
	Single island endemics	**Present**	**16**	**1.51 logApr + 0.35 Dpr + S-A + prov**	**228**	**239**	**0,14**	0,10
		MSL	17	logApr + Dpr + S-A + prov	228	239	0,14	0,10
		LGM	18	logApr + S-A + prov	228	239	0,14	0,10
	Multiple island endemics	Present	19	logApr + Dpr + S-A + prov	571	581	0,45	0,79
		MSL	20	logApr + dDmed - typemed (P) + S-A + prov	552	564	0,45	0,77
		LGM	**21**	**0.49 logApr + 0.13 Dpr - 0.10 dAlgm - 0.58 typelgm (P) + S-A + prov**	**537**	**551**	**0,48**	0,68
Reptiles (n = 70)	Native non endemics	Present	22	logApr - Dpr + S-A + prov	323	333	0,57	0,00
		MSL	**23**	**0.35 logApr - 0.29 Dpr + 0.30 typemed (P) + S-A + prov**	**321**	**333**	**0,61**	0,00
		LGM	24	logApr - Dpr + S-A + prov	323	333	0,57	0,00
	All endemics	Present	25	logApr + S-A + prov	217	225	0,55	0,26

		MSL	26	logApr + S-A + prov	217	225	0,55	0,26
		LGM	**27**	**0.22 logApr - 2.3 typelgm (P) + S-A + prov**	**197**	**207**	**0,60**	**0,00**
Centipedes (n = 56)	Native non endemics	**Present**	**28**	**0.22 logApr - 0.23 Dpr + S-A + prov**	**297**	**306**	**0,37**	0,01
		MSL	29	logApr - Dpr + S-A + prov	297	306	0,37	0,01
		LGM	30	logApr - Dpr + S-A + prov	297	306	0,37	0,01
Butterflies (n = 37)	Native non endemics	Present	31	logApr - Dpr + S-A + prov	287	293	0.62	0,32
		MSL	**32**	**0.41 logApr + 0.41 typemed (P) + S-A + prov**	**270**	**277**	**0.84**	0,35
		LGM	33	logApr -Dpr + typelgm (P) + S-A + prov	280	287	0.68	0,17

Figure captions.

Figure 1: Map of the current geography of the Aegean archipelago with estimated land surfaces at median sea level (MSL, black) and during the Late Glacial Maximum (LGM, grey).

Figure 2: Maps of the islands used for the analysis of the four taxa included in this study. A = angiosperms; B = reptiles; C = centipedes; D = butterflies.

Figure 3: Map of the islands cited in the text, the phyto-geographic regions of the Aegean and the distribution of the four angiosperm species in the Aegean archipelago, illustrating the characteristics of their respective chorotypes. NAe = North Aegean; WAe = West Aegean; EAe = East Aegean; StE = Sterea Ellas; Kik = Cyclades; KK = Crete.

Figure 4: Bar plot of the averaged, area-adjusted insular species richness (species richness / log10 of insular area) for the two island types studied for the Last Glacial Maximum (LGM) and Median Sea Level (MSL). Error bars report standard error on the mean. NNE = Native non-endemics; E-All = All endemics. Significance was addressed using ANOVA tests. **: p-value < 0.01, ***: p-value < 0.001

Figure 5: Value and sign of the regression coefficients of the predictors of the best models selected (see Table 1) for the different taxa and some of the chorotypes analysed. The colours are used to assist in finding corresponding variables in the different subplots. Note the different ranges on the x-axis for the different subplots. NNE = Native non-endemics; E-All = All endemics.

Box caption

Box 1: A land-bridge island is an island that was connected to a nearby mainland during an episode of lower sea-level (e.g., the Last Glacial Maximum). Island formation occurs with the drowning of the land-bridge connecting the landmass to the mainland. The timing of separation from the mainland may differ among land-bridge islands of the same archipelago, depending on the topography of the peninsula and local heterogeneities in the dynamics of sea-level rise. With continuing sea-level rise, the isolation of the island is followed by a progressive decline of its area. Because insular area is a major determinant of species richness, variations in the magnitudes and rates of area loss are expected to drive varying rates of species loss. Here we considered 3 hypothetical islands with the same initial area and undergoing the change of sea-level to illustrate how the magnitude of species richness loss might differ depending on an island's topography (Box 1.A: I, II and III). Area loss of the first hypothetical island is gentle (Box 1.B: I), initially slow then fast for the second island (Box 1.B: II), and fast then slow for the third one (Box 1.B: III.). Species richness loss follows a similar trend though it occurs in a delayed fashion after area loss (Box 1.C:
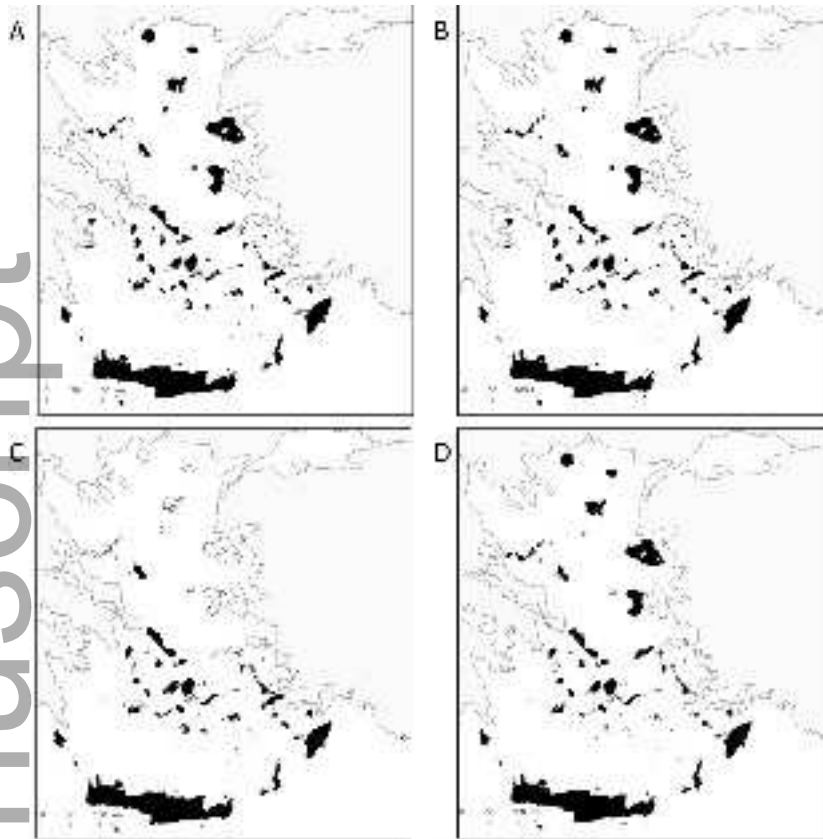
787   S0 to SP). Due to its larger remaining area, island I now hosts a larger richness of species than island II and

788   III. Furthermore, species richness is expected to be at equilibrium in island I and III but not island II, as it
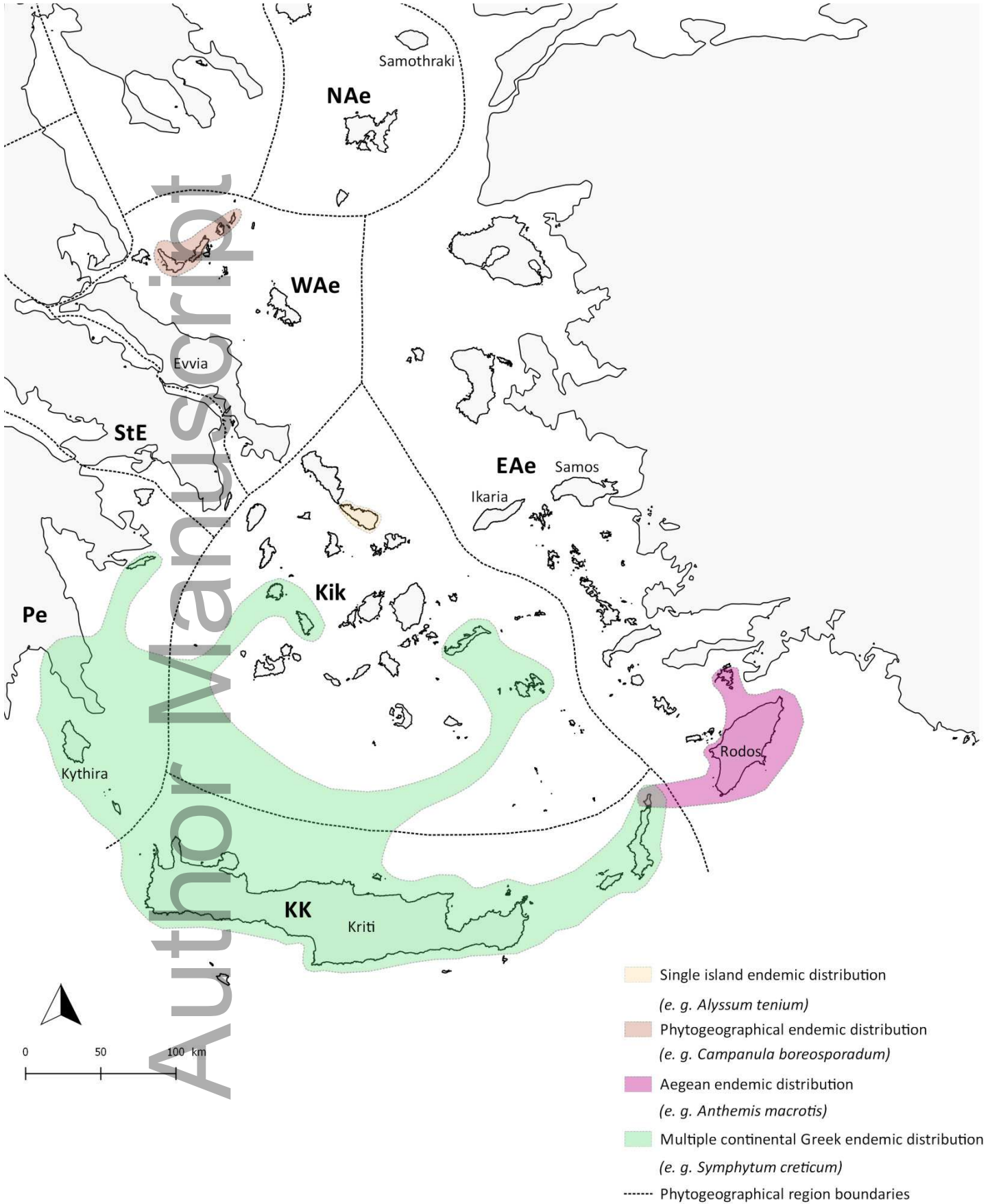
789   lost a large share of its area recently.

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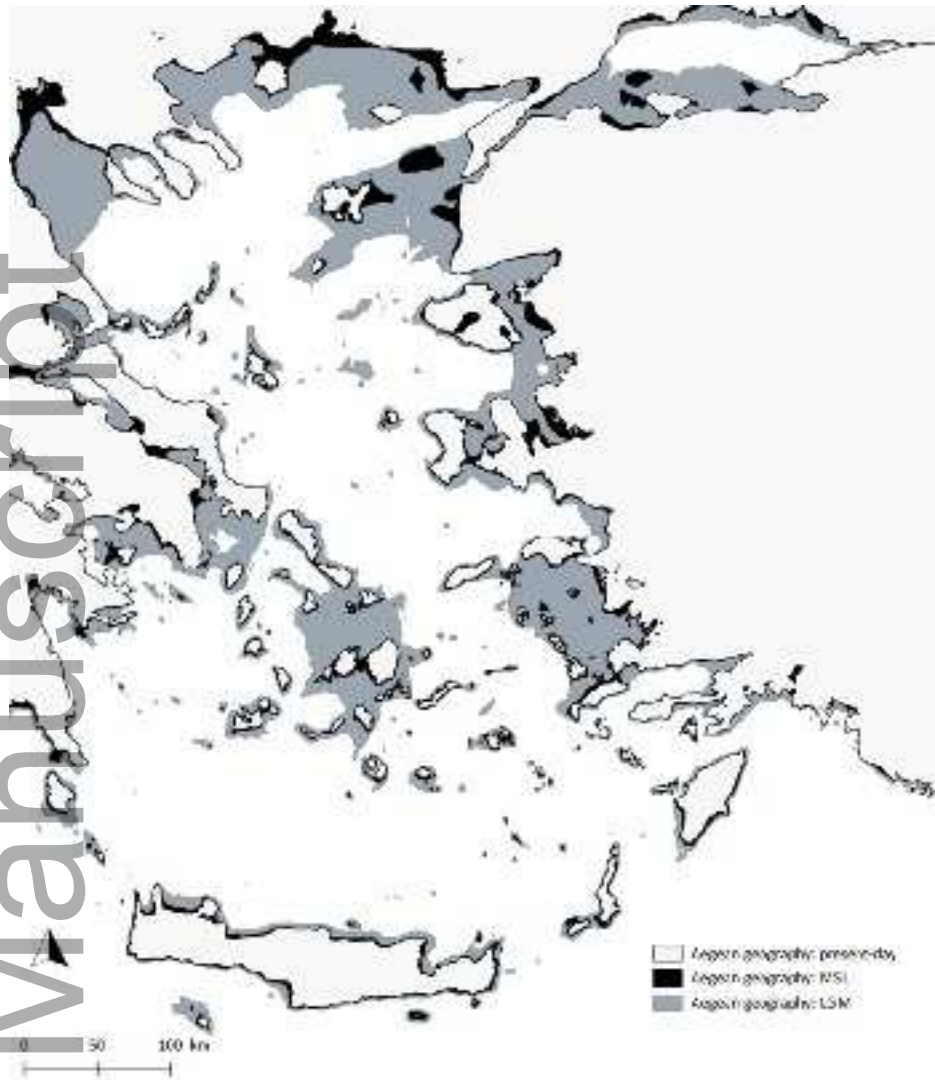
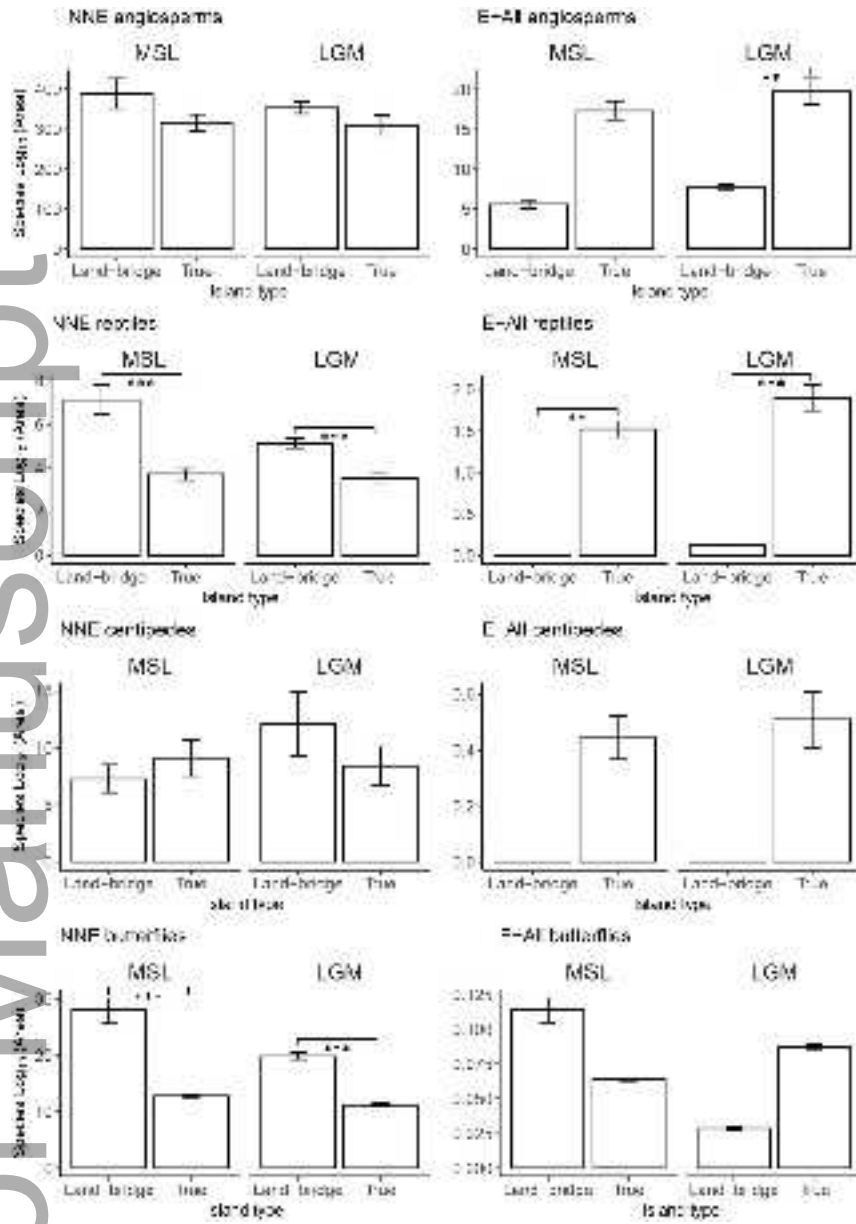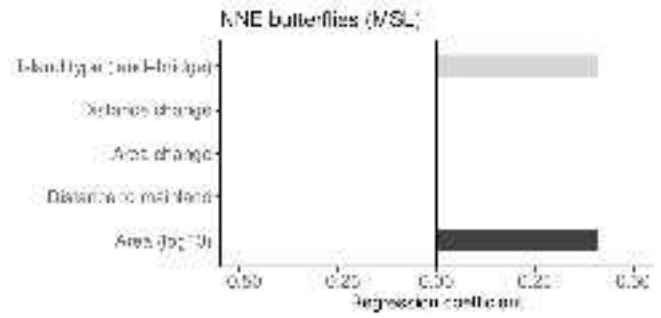ece3_7438_f1.jpeg

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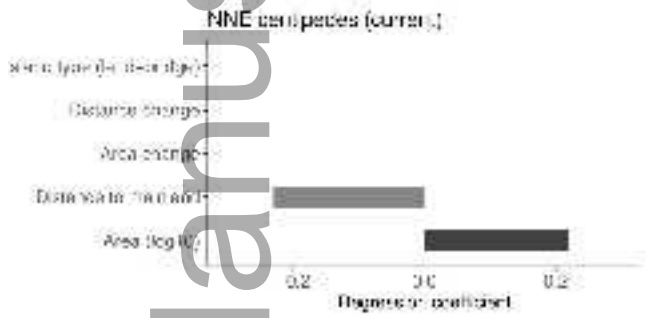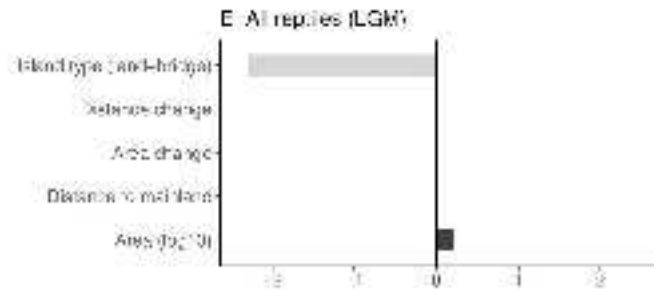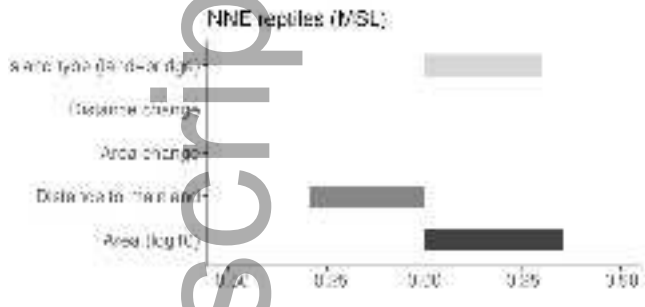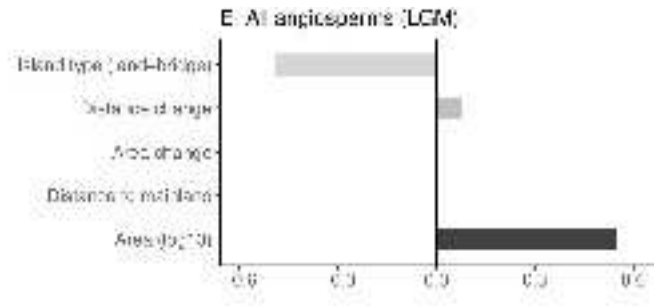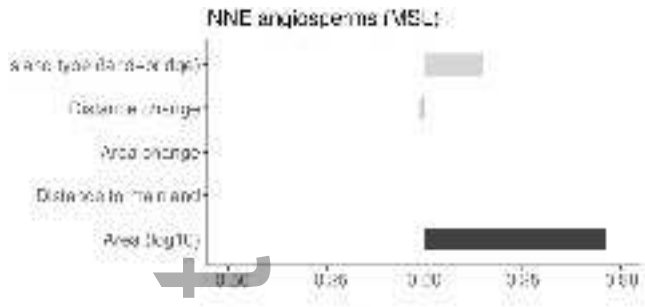
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