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3 **Declining relict plants: climate effect or seed dispersal**
4 **disruption? A landscape-scale approach**

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21 **Abstract**

22 Biodiversity loss, including the decrease of diversity of ecological interactions, is known to
23 reduce the capacity of ecosystems to cope with the effects of global change. Here we assessed
24 whether the distribution and survival of two declining relict plant species, *Daphne rodriguezii*
25 and *Cneorum tricoccon*, were affected by the mutualism disruption with their only seed-
26 disperser and by climatic and habitat conditions. Due to the lack of data on demographic rates,
27 we used an indirect approach to test these hypotheses. We used presence-absence data as
28 response variables and took two distinct sets of predictors (i.e. habitat and topoclimatic
29 conditions), which were hypothesized to be the main determinants of the demographic rates
30 under question. With these two datasets we fitted species distribution models by means of
31 MaxEnt. Such models were later used to build *Combined Species Distributions Models* (CM).
32 For each plant species, these CM allowed evaluating the role of both climatic and non-climatic
33 factors, such as the mutualism disruption. Results showed that both climate and habitat
34 conditions determined the current distribution of the two species at a landscape scale.
35 Additionally, the mutualism disruption between *C. tricoccon* and its native seed-disperser
36 affected plant distribution, moving it to areas where a new alien disperser was present. This
37 alien disperser modified the pattern of habitat selection by plants in terms of habitat quality,
38 reducing their presence in suboptimal areas, which might be the determinant for their survival.
39 Our findings highlight the need of a better understanding of the role of mutualisms within
40 natural communities in order to undertake appropriate conservation actions on threatened plant
41 populations. Furthermore, acting on key factors affecting plant-disperser disruptions (e.g.
42 controlling invasive species) might help to mitigate the effects of global change on declining
43 relict plants.

44 **Keywords:** Species distribution modelling, Maxent, mutualisms, seed dispersal interactions,
45 *Cneorum tricoccon*, *Daphne rodriguezii*

46

47 **Introduction**

48 The capacity of ecosystems to resist the effects of global change is likely to be reduced by the
49 pervasive biodiversity loss worldwide (MacDougall, McCann, Gellner & Turkington 2013).
50 Biodiversity has shown to stabilize ecological systems due to functional complementarity, as
51 different species buffer the effects of environmental changes (Barnosky, Hadly, Bascompte,
52 Berlow, Brown et al. 2012). Biodiversity loss includes not only the loss of species but also the
53 diversity of interactions (Valiente-Banuet, Aizen, Alcantara, Arroyo, Cocucci et al. 2015).
54 Besides preserving species, it is now widely accepted that it is crucial to maintain diverse
55 communities of interacting species and ecosystem functionality (Pasari, Levi, Zavaleta &
56 Tilman 2013). Mutualisms, in particular, have been shown to be essential to the survival and
57 reproduction of a multitude of organisms. They are also crucial to maintain the structure and
58 diversity of natural communities (Bronstein 2009), providing essential ecosystem services such
59 as pollination and seed dispersal. Increasing evidence shows that they are key to mitigate the
60 effects of global change as one important cause of species extinctions (Kiers, Palmer, Ives,
61 Bruno & Bronstein 2010). Therefore, understanding the role of mutualisms within natural
62 communities is not only important to predict how their decline might alter communities
63 (Christian 2001), but also to undertake associated conservation and management actions
64 (Garcia, Zamora & Amico 2010).

65 There are few documented cases where the loss of dispersal mutualisms has caused a plant
66 population to decline (Aslan, Zavaleta, Tershy & Croll 2013), many being from island
67 ecosystems (Traveset, Gonzalez-Varo & Valido 2012). In these isolated environments,
68 communities are often depauperate, with many taxonomic groups totally missing, and thus with
69 much less complex communities than in the mainland (Whittaker & Fernández-Palacios 2007).
70 Many plants are often pollinated or dispersed by just a few or a single animal species, which
71 increases the mutual dependence between interacting partners and, subsequently, they are at a
72 greater risk of mutualistic disruption (Rodríguez-Pérez, Wiegand & Santamaria 2012c). On the
73 other hand, the simplicity of island ecosystems offers a perfect scenario to carry out

74 conservation studies, and particularly on seed dispersal interactions (Hansen & Traveset 2012).
75 Island populations are especially vulnerable to introduced species (i.e. predators and
76 competitors) because they have evolved in the absence of interactions with them (Kawakami,
77 Mizusawa & Higuchi 2009). Actually, invasive species are currently considered the main threat
78 to native biodiversity on many islands (Kueffer, Daehler, Torres Santana, Lavergne, Meyer et
79 al. 2010).

80 *Cneorum tricoccon* L and *Daphne rodriguezii* (Teixidor) are two endemic plant species to the
81 Balearic Islands regarded as pre-Pliocene relicts (Herrera 1992). Due to the introduction of alien
82 species (Pérez-Mellado 2002a; Traveset 2002), these two fleshy-fruited shrubs have suffered
83 disruptions with their native seed dispersers, two endemic lacertid lizards. Although
84 topoclimatic and habitat conditions are likely to influence the distribution of both declining
85 plant species at a landscape scale, these mutualistic disruptions might also affect their
86 distributions and maintenance, contributing to plant populations' decline and even leading them
87 to extinction. Given that no demographic data were available to test such hypothesis, we used an
88 indirect approach aimed at explaining how topoclimatic and habitat conditions influence the
89 success of two key stages of the plant's life cycle: (1) early stages of seedling recruitment and
90 (2) medium- and long-term plant survival. Thus, we used presence-absence data instead of
91 demographic rates as the response variables and include two distinct predictor sets –habitat (i.e.
92 land cover classes) and topoclimatic conditions– as predictor variables in our models. These two
93 factors are hypothesized to be the main determinants of the demographic rates under question.
94 On the one hand, the habitat determines the spatial distribution of seed-dispersers and provides
95 suitable microsites for early stages of seedling recruitment (Godínez-Alvarez & Jordano 2007;
96 Jacquemyn, Brys, Vandepitte, Honnay, Roldan-Ruiz et al. 2007; Rodríguez-Pérez, Larrinaga &
97 Santamaría 2012a; Rodríguez-Pérez et al. 2012c). On the other hand, climatic conditions are
98 one of the main drivers responsible for plant populations distributions in the medium and long
99 term (McCarty 2001, and references therein).

100 We separately modelled the habitat suitability of each plant species on the Balearic Islands by
101 means of species distribution models (SDMs). For this purpose, we used a two-dimensional
102 modelling process based on a methodology described by Naves, Wiegand, Revilla and Delibes
103 (2003). This consists of the construction of two separate SDMs, which we called Single-Models
104 (SM, hereafter). Each SM was built with one of the two predictor sets (i.e. either topoclimatic or
105 habitat). Subsequently, we combined the two SM in a "two-dimensional" SDM, which we
106 called Combined Species Distribution Model (Combined-Model or CM, hereafter). These two-
107 dimensional models are applicable when the factors that determine several demographic
108 processes differ substantially between them (Naves et al. 2003). We assumed that modelling
109 separately the plants' distribution using topoclimatic and habitat variables allowed us to evaluate
110 the influence of climatic and non-climatic factors. The latter, for instance, are those related to
111 the microhabitat or to the presence/absence and behaviour of the seed-dispersers. Hence, this
112 approach permitted us discerning between areas important for early stages of recruitment and
113 areas important for plant species survival.

114 Moreover, across the Balearic Islands, the mutualism between the two study plant species and
115 their native seed-disperser is different on each island. While in some islands the mutualism has
116 remained unaltered, in others the native seed-disperser has been replaced for an exotic new one,
117 or even, it has disappeared and the mutualism has been lost (Rodríguez-Pérez & Traveset 2010;
118 Traveset 1995; Traveset & Riera 2005). These three different situations, plus the hypothesis that
119 the effect of microhabitat on plant species was constant across the islands, allowed
120 distinguishing how each seed-disperser affected plant distributions. Additionally, it enabled us
121 to evaluate how habitat selected by plants, in terms of quality, might be affected by the
122 mutualism disruption.

123 Specifically, the goals of our study were (1) to evaluate the influence of topoclimatic and habitat
124 conditions on the distribution and maintenance of both plant species, and (2) to determine how
125 the substitution or loss of the only native seed-disperser affected the distribution and survival of
126 the two plant species at a landscape scale.

127 **Material and methods**

128 **Study area**

129 We carried out the study in the Balearic Islands, in western Mediterranean, and specifically in
130 their five largest islands (Mallorca, Menorca, Cabrera, Eivissa and Formentera; Fig. 1). The
131 numerous islets were not considered because environmental data were not available from them.
132 These five islands bear a variety of habitats, ranging from sand dunes and rocky cliffs to
133 mountain areas up to c. 1500 m in Mallorca. Forested areas consist of pine and holm oak and
134 there are also shrublands and farmland plain areas.

135 **Study plant species and their seed-dispersers**

136 *Cneorum tricoccon* L. (Cneoraceae) is a western Mediterranean endemic, whereas *Daphne*
137 *rodriguezii* Teixidor (Thymelaeaceae) –categorized as Vulnerable by the IUCN– is endemic to
138 Menorca Island and one of its islets. They are perennial evergreen shrubs and considered pre-
139 Pliocene relicts and some of their populations are in clear decline (Traveset 2002, and
140 unpublished data).

141 The native dispersers of *C. tricoccon* are two endemic lacertid lizards: *Podarcis lilfordi* Günther
142 in the Gymnesic Islands (Mallorca, Menorca, Cabrera and surrounding islets), and *Podarcis*
143 *pityusensis* Boscá in the Pythiusic Islands (Eivissa, Formentera and surrounding islets). *P.*
144 *lilfordi* is currently extinct from the two larger islands, Mallorca and Menorca. Introduced
145 mammals, mainly pine martens *Martes martes* L. (Mustelidae), are the current dispersers of the
146 two study plant species in these two islands (Celedon-Neghme, Traveset & Calvino-Cancela
147 2013; Riera, Traveset & Garcia 2002; Traveset 1995). In Menorca, however, pine martens have
148 been found to have a less frugivorous behaviour (Clevenger 1993b) and the dispersal of the
149 plant is almost zero (Riera et al. 2002; Traveset 1995). By contrast, *D. rodriguezii* is exclusively
150 dispersed by the endemic *P. lilfordi* (Rodríguez-Pérez et al. 2010; Traveset et al. 2005). Thus,

151 after the extinction of this lizard on Menorca, the lizard-plant interaction persists only on an
152 islet (Colom) offshore Menorca.

153 The behaviour of each seed-disperser species is very different, especially with reference to their
154 habitat selection patterns. The European pine marten, which is usually considered a habitat
155 specialist, has been reported to mainly inhabit three mountain woodlands on Mallorca
156 (Tramuntana Mountains, Llevant Mountains and the Massif of Randa). On Menorca, pine
157 martens are more generalistic and can be found in forests, Mediterranean shrublands and cliff
158 habitats (Table1; Clevenger 1993a, b, 1994). On the other hand, lizards are not restricted to
159 specific habitats and can be found from forests and shrublands to sandy and rocky open habitats
160 (Table 1; Pérez-Mellado 2002a, b).

161 **Data compilation on plant distribution and environmental conditions**

162 We first obtained presence data of the plant species from BIOATLES (2007), a public database
163 that provides data for most of the Balearic species with up to 1 km resolution. This resolution is
164 considered adequate regarding the requirements of conservation and management planning
165 (Guralnick & Hill 2009). BIOATLES contained a total of 475 and 32 occurrence records for *C.*
166 *triccoccon* and *D. rodriguezii*, respectively. In addition, we had three *C. tricoccon* occurrence
167 records from paleontological deposits in Menorca and another one from Eivissa (Traveset et al.
168 2005). These records can be classified as extinctions because the species is no longer present in
169 these locations. Seed-disperser data were too scarce and highly biased to be used for the purpose
170 of this study.

171 A total of 30 variables were compiled as possible predictors of the distribution of both plant
172 species (see Appendix A: Methods A1 for further details). In order to reduce the excessive
173 number of predictor variables, especially for *D. rodriguezii* with low number of occurrences,
174 and also to avoid multicollinearity in the set of predictor variables, we discarded the less easily
175 interpretable variables, in terms of plant ecology, from those with a Pearson's correlation
176 coefficient higher than 0.7 (Dormann, Elith, Bacher, Buchmann, Carl et al. 2013). Thus, we

177 ended up with a total of 11 predictor variables for *C. tricocon* and 10 for *D. rodriguezii* (see
178 Appendix A: Table A1). This number of variables has been shown to perform well with
179 different modelling methods, even with fewer occurrences than those we had (Hernandez,
180 Graham, Master & Albert 2006).

181 **Modelling process and categories of suitability**

182 Spatial modelling was performed separately for each plant species in a two-step process.

183 First, we constructed two separate species distribution models with presence-only data (Single-
184 Models or SM, hereafter); one was based on topoclimatic variables (CLIM-model) and the other
185 on the five land cover classes (LAND-model). With the CLIM-models we captured favourable
186 topoclimatic conditions for plant long-term establishment. The LAND-models captured an
187 appropriate environment allowing the presence of the seed-disperser and/or good microhabitat
188 conditions for our study plants.

189 In the second step, we constructed a Combined Species Distribution Model (Combined-Model
190 or CM, hereafter) by combining every pair of Single-Models, following the methodology
191 proposed by Naves et al. (2003). With the CM we obtained four categories of suitability
192 regarding both topoclimatic and habitat conditions (see below).

193 ***Construction of Single-Models***

194 The SMs were developed with the maximum entropy algorithm of species distribution
195 modelling, MaxEnt (version 3.3.3k; Phillips, Anderson & Schapire 2006; see Appendix A:
196 Methods A1 for further details on the modelling process). MaxEnt is a widely applied tool for
197 distribution modelling with presence-only data (Elith, Phillips, Hastie, Dudik, Chee et al. 2011).
198 It was chosen because it is considered one of the strongest performers in different comparative
199 studies (Elith et al. 2011; Hernandez et al. 2006), and also because it allows using small sets of
200 data (Elith et al. 2011). MaxEnt not only builds the predictive model based on the
201 environmental variables implemented, but also provides response curves for each variable. The
202 response curves from the *C. tricocon* LAND-model were used to test the hypothesis that the

203 microhabitat affecting plant species was not variable from island to island and, thus, what
204 LAND-models captured was basically an appropriate environment allowing the presence of the
205 seed-disperser.

206 For *C. tricoccon*, we fitted two SMs (i.e. CLIM-model and LAND-model) for all the study area
207 excluding Menorca, because currently there is only one record in this island, and this could have
208 distorted the goodness-of-fit of the models (Elith et al. 2011). Thus, we used Mallorca, Eivissa,
209 Formentera and Cabrera as the areas for randomly locating background points (i.e. 10000
210 points) and, then, the two models obtained were projected to Menorca. We randomly selected
211 70% of the records to train the models and reserved the rest to test them (see Williams, Seo,
212 Thorne, Nelson, Erwin et al. (2009) for a similar methodology). We obtained two final models
213 in a logistic output format resulting from the average of 10 replicates (each replicate run with a
214 different random selection of train and test records). As a goodness-of-fit of the models we used
215 the AUC test. It is usually accepted in species distribution modelling that fair models have an
216 $AUC \geq 0.7$ (Araújo, Pearson, Thuiller & Erhard 2005, and references therein). Additionally, to
217 determine the accuracy of the model, we also used the prediction success of the test data set (i.e.
218 proportion of presences correctly predicted of the test subsample) after applying the threshold
219 that maximizes the specificity plus the sensitivity (Baldwin 2009). Likewise, we used this
220 threshold to transform the models from logistic format to binary.

221 To avoid the effect of spatial autocorrelation between presence points and, thus, to improve the
222 model performance (Vaclavik, Kupfer & Meentemeyer 2012), we tested the autocorrelation
223 significance of the model residuals (observed occurrence minus probability of occurrence)
224 (Marcer, Pino, Pons & Brotons 2012, and references therein) by using a Monte-Carlo simulation
225 of Mantel test (ade4 package; Dray & Dufour (2007)). As subsampling the original data matrix
226 substantially reduces the inflation effect of spatial autocorrelation (Segurado, Araujo & Kunin
227 2006), we randomly subsampled our data up to the distance between points so that the Monte
228 Carlo simulation significantly showed no spatial autocorrelation. Even with this, our models
229 might still be overestimated because of some degree of dependence of the presence records.

230 However, this is the best tool available so far and the more commonly used (Bahn & McGill
231 2013).

232 Analogously, we also constructed SMs for *D. rodriguezii*. As we had few presence records for
233 this species, it was not possible to separate data for training and testing the model. Thus, in this
234 case we used a jackknife approach to assess the significance of the model, as described by
235 Pearson, Raxworthy, Nakamura and Peterson (2007; see Appendix A: Methods A1 for further
236 details on how this methodology was implemented). Hence, we obtained two models in a
237 logistic output format and transformed them to a binary format applying the threshold that
238 maximized both specificity and sensitivity. As in *C. tricoccon* SMs, we checked the model
239 residuals for significant spatial autocorrelation by using a Monte-Carlo simulation of Mantel
240 test.

241 ***Construction of Combined-Models (CM)***

242 The second step in our modelling process was building the CM for every plant species by
243 combining the two SMs and reclassifying grid-cells into four categories depending on
244 topoclimatic and habitat suitability (Fig. 2A): (1) "Highly Suitable sites", where both
245 topoclimatic and habitat conditions were favourable (source sites, where dispersal, recruitment
246 and long-term survival of the plant were possible); (2) "Topoclimatically Suitable sites", where
247 topoclimatic conditions were good but not the habitat ones (refuge areas where plants might live
248 but where dispersion and/or recruitment was limited); (3) "Suitable by Habitat sites", where the
249 topoclimatic model predicted as unsuitable but the habitat was good (attractive sink or seed-sink
250 areas, where seeds could arrive but their long-term survival was difficult); and, finally, (4)
251 "Unsuitable sites", where both topoclimatic and habitat models predicted low suitability (sink
252 sites, which means that it would be unlikely to find the plant species there). Categories 2 and 3
253 can be collectively referred to as "Moderately Suitable sites".

254 To formally assess the accuracy of the two CM, it would have been ideal to have independent
255 presence data, and also expected dynamics such as recolonization of suitable areas (Mladenoff,

256 Sickley & Wydeven 1999) or extinctions in unsuitable areas (Naves et al. 2003). However,
257 these data were not available for any of the two plant species; thus, the categorization of the CM
258 may have some degree of arbitrariness (Falcucci, Ciucci, Maiorano, Gentile & Boitani 2009).
259 Nevertheless, all records, including those four considered extinctions, were used to calculate the
260 relative frequency of presence points in each of the four categories and to fairly validate the two
261 CMs.

262 **Results**

263 **Single-Models for *C. tricoccon***

264 We obtained one final SM based on topoclimatic variables (*Cneorum*-CLIM) and one final SM
265 based on habitats features (*Cneorum*-LAND). In a first attempt, we used the data set with all the
266 presence records, but they showed significant spatial autocorrelation. Hence, in order to restrict
267 spatial autocorrelation keeping the maximum number of presence records, we randomly
268 selected 82 points for *Cneorum*-CLIM (3 km minimum separation) and 44 points for *Cneorum*-
269 LAND (5 km minimum separation).

270 *Cneorum*-CLIM showed 90.5% and 89% prediction success for test and training records,
271 respectively, and the AUC test indicated fair performance ($AUC_{\text{test}} = 0.788 \pm 0.026$). Residuals
272 of the model showed no significant spatial autocorrelation (Mantel correlation test: -0.037; p-
273 value=0.743). In the suitability representation of the binary model (Fig. 3B), a clear pattern was
274 detected in Eivissa and Formentera, where the best conditions were given in the whole coastal
275 area, and also in Mallorca, where the main best zone coincided with the Tramuntana Mountains
276 and with the Western Coast. On the other hand, in Menorca, where the presence of *C. tricoccon*
277 is almost zero, only 3.48% of pixels were predicted as suitable (Fig. 2F), all scattered
278 throughout the island.

279 The *Cneorum*-LAND model showed worse but still acceptable levels of performance
280 ($AUC_{\text{test}} = 0.708 \pm 0.036$; 81.5% and 82.3% prediction success for test and training data,

281 respectively) and no significant residual spatial autocorrelation (Mantel correlation test: 0.021;
282 $p=0.339$). Its binary representation (Fig. 3C) did not show so clear patterns of suitable areas,
283 except that cultivated areas are the most unsuitable for *C. tricocon* (see response curves and
284 jackknife test provided by MaxEnt in Appendix A: Figure A1 and Figure A2).

285 **Combined-model for *C. tricocon***

286 After reclassifying the CM for *C. tricocon* (*Cneorum*-CM), its graphical representation (Fig.
287 3A) showed different spatial patterns on each island. In Mallorca, Highly Suitable area tended
288 to be in the Tramuntana Mountains and in some cores in the eastern (Llevant Mountains) and
289 western coasts. A large part of the island, however, was predicted as Unsuitable (56.2%; Fig.
290 2F), mainly the central and southern areas. In Eivissa, Formentera and Cabrera, the pattern was
291 less clear and only 10.2% was predicted as Unsuitable. On the other hand, in Menorca only 2%
292 of surface was classified as Highly Suitable due mainly to the low topoclimatic suitability.

293 Comparing the predictions of the *Cneorum*-CM with the full set of observed presences (Fig.
294 2D), we found that most of them were located in Highly Suitable (73.6%) and Moderately
295 Suitable (23.8%) sites. Only 2.6% of presence records were predicted as Unsuitable sites.
296 Furthermore, there was a larger proportion of observed records in Topoclimatically Suitable
297 sites than in the Suitable by Habitat category (16.2% vs. 7.6%, respectively). Additionally, three
298 of the four extinction records were located in suboptimal predictions (Fig. 2E).

299 When considering the results separately by islands or group of islands, depending on the
300 identity and behaviour of the *C. tricocon* seed-disperser (Fig. 2D), we found diverse results.
301 On the one hand, the highest proportion of *C. tricocon* records (79.7%) in Mallorca, where
302 dispersers are pine martens, was predicted as Highly Suitable sites by the model. Presences
303 predicted as Topoclimatically Suitable and Suitable by Habitat were 11% and 7.2%,
304 respectively. Tolerance to unsuitable topoclimatic conditions (presences predicted as Suitable
305 by Habitat plus Unsuitable) was 9.3% whereas tolerance to unsuitable habitat conditions
306 (presences predicted as Topoclimatically Suitable plus Unsuitable) was 13.1%. On the other

307 hand, on the islands where lizards are the main dispersers, the trend was not so clear: the largest
308 proportion was for Moderately Suitable predictions (54.3% for Topoclimatically Suitable sites
309 and 8.7% for Suitable by Habitat), whereas Highly Suitable sites obtained 30.4% of presence
310 records. Tolerance to unsuitable topoclimatic conditions was 15.3% whereas tolerance to
311 unsuitable habitat conditions was 60.9%. Finally, in Menorca, where dispersal of *C. tricoccon*
312 seeds is almost zero, the only presence record for this species was predicted for a Suitable by
313 Habitat site.

314 **Single-Models for *D. rodriguezii***

315 We obtained one final SM based on topoclimatic variables (*Daphne*-CLIM; $AUC_{train} = 0.862$)
316 and one final SM based on habitats features (*Daphne*-LAND; $AUC_{train} = 0.746$), both based on 8
317 random records at least 3 km apart. Success ratio was 0.625 (p-value = 0.002) for *Daphne*-
318 CLIM and 0.75 (p-value = 0.014) for *Daphne*-LAND. Neither of them showed significant
319 spatial autocorrelation (*Daphne*-CLIM Mantel's test: -0.162, $p = 0.599$; *Daphne*-LAND
320 Mantel's test: 0.245; $p = 0.143$). The *Daphne*-CLIM graphical display (Fig. 4B) showed a clear
321 pattern of suitable area at the northeastern coast and some small centres at the southern coast.
322 By contrast, *Daphne*-LAND (Fig. 4C) showed scattered small cores throughout Menorca, only
323 slightly related with no cultivated areas (see response curves and jackknife test provided by
324 MaxEnt in Appendix A: Figure A3 and Figure A4). Nevertheless, a small proportion of the
325 study area was predicted as suitable, both for topoclimatic and habitat conditions (10.5% and
326 12%, respectively; Fig. 2C).

327 **Combined-model for *D. rodriguezii***

328 The graphic representation of the CM for *D. rodriguezii* (*Daphne*-CM; Fig. 4A) showed a clear
329 spatial pattern of suitability in Menorca Island. The best area predicted was in the eastern coast,
330 with some small cores in northern and southern coasts. The main part of the study area for this
331 species was predicted as unsuitable (71.5%; Fig. 2C).

332 Most presence records of this species were predicted as Highly Suitable by the model (60.7%;
333 Fig. 2B). Comparing records predicted as Moderately Suitable, the proportion of sites predicted
334 as Topoclimatically Suitable was higher than those predicted as Suitable by Habitat (21,4% vs.
335 3.6%), whereas 14.3% were predicted as Unsuitable. Finally, tolerance to unsuitable
336 topoclimatic conditions was 17.9% whereas tolerance to unsuitable habitat conditions was
337 35.7%.

338 Discussion

339 The introduction of invasive mammals in some of the Balearic Islands, together with the
340 behaviour of such newcomer species, caused different degrees of mutualism disruption: (1)
341 extinction of the native seed-disperser without replacement on Menorca; (2) replacement of the
342 seed-disperser on Mallorca; and (3) survival of the native seed-disperser on Eivissa, Formentera
343 and Cabrera. On the other hand, the habitat suitability of our combined distribution models
344 (CM) implied favourable topoclimatic conditions for the plants (captured by CLIM-models), but
345 also an appropriate environment providing favourable microhabitat conditions and/or the
346 presence of seed-disperser (captured by LAND-models). However, the response curves of the
347 LAND-models showed that the microhabitat (i.e. the environment given by the surrounding
348 land cover) affected the plants uniformly on the islands. Thus, what mainly captured the LAND-
349 models was the seed-disperser effect on plant distributions. These findings allowed us to discern
350 between the different degrees of influence exerted by both topoclimatic conditions and the
351 dispersal pattern on the plant species distributions. Nevertheless, it must be noted that some
352 degree of bias might be introduced into the models by potentially dissimilar factors on each
353 island (e.g. secondary seed-dispersers or micro-scale effects). In this sense, the European genet
354 (*Genetta genetta*), ants and gulls have been suggested as possible or occasional dispersers of *C.*
355 *triccoccon* seeds (Traveset et al. 2012, and references therein). It has also been reported that *D.*
356 *rodriguezii*'s seedling survival is related to the presence of nurse-plant species (Rodríguez-Pérez
357 & Traveset 2012b, and references therein). The local distribution of *D. rodriguezii* and how it is
358 influenced by the interaction with its seed disperser had previously been studied, using a similar

359 "two-dimensional" approach, by Rodríguez-Pérez et al. (2012c) on an islet offshore Menorca.
360 These authors found that both lizard activity and local habitat features determine the spatial
361 distribution of the plant.

362 Overall, we found that both topoclimatic conditions and habitat determined plant distributions at
363 the landscape scale. Moreover, we also found that the plant-disperser interaction was able not
364 only to influence these distributions but also to modify the pattern of habitat selection by plants
365 in terms of habitat quality (i.e. optimal, suboptimal, unsuitable), which might be the determinant
366 for their survival.

367 **What happens when the disperser is replaced? The case of *C. tricocon* on** 368 **Mallorca**

369 Based on fossil records, *P. lilfordi* presumably lived below 500 m a.s.l., until its extinction after
370 250 A.D. (Alcover, Moyà-Solà & Pons-Moyà 1981). Given that such a lizard was likely the sole
371 disperser before the arrival of pine martens in Mallorca (Alcover et al. 1981), the altitudinal
372 distribution of *C. tricocon* would have been limited to the lower central and eastern parts of the
373 island (Riera et al. 2002). Nevertheless, nowadays its distribution has mainly moved to higher
374 areas in Tramuntana Mountains, where most pine martens are found (Clevenger 1993b). On
375 Mallorca, *C. tricocon* mostly occupies Highly Suitable areas according to the CM. In contrast,
376 on Eivissa, Formentera and Cabrera, where lizards are more widely distributed, the plant species
377 is also widespread with regard to categories of suitability: it can be present in Highly Suitable
378 areas, but most occurrences are in Moderately Suitable areas. Therefore, at a landscape scale,
379 pine martens seem not only able to change the distribution of this relict plant, but also appear to
380 have moved it to areas with suboptimal conditions.

381 Novel mutualistic relationships with introduced species can compensate for the loss of native
382 mutualist extinctions, but not without long-term consequences (Kiers et al. 2010; Traveset &
383 Richardson 2014). *C. tricocon* is an example of that. It has compensated the loss of its only
384 former seed-disperser with the appearance of a new one, which is, paradoxically, partly

385 responsible for its extinction (as pine martens prey upon lizards). The long-term consequence of
386 such change has been the new distribution of the plant species and its increasing dependence on
387 the optimal conditions to live.

388 **What happens when the disperser disappears? The case of *D. rodriguezii* and *C.***
389 ***tricocon* on Menorca**

390 On Menorca Island there are two different situations: (1) that of *C. tricocon*, which has almost
391 gone extinct (there is only one small population in a suboptimal area, according to *Cneorum-*
392 *CM*), and (2) that of *D. rodriguezii*, which, despite the disperser loss, is present in optimal and
393 suboptimal areas (Fig 4A).

394 According to *Cneorum*-CLIM (Fig. 3B), in Menorca there was a small and highly scattered
395 topoclimatically suitable surface. Considering that much of the extinction records were in
396 topoclimatically unsuitable sites, we could argue that the island is climatically evolving to a less
397 suitable zone for *C. tricocon*. This is probably the reason why it is in sharp decline and it has
398 been able to persist only in a site of favourable habitat quality. Nevertheless, if there had been
399 lizards, not constrained by habitat, the plant might have been able to colonize new areas
400 environmentally suitable, as it is the case of *D. rodriguezii* in the islet where the mutualism
401 remained (Rodríguez-Pérez et al. 2012b). This would show that the habitat, by itself, bears some
402 importance on plant species maintenance; however, without any disperser, its chances of
403 survival decrease dramatically.

404 *D. rodriguezii* kept its distribution in Highly Suitable areas, but also in Moderately Suitable, and
405 Unsuitable ones (Fig. 2B), presumably as a legacy of its extinct native seed-disperser and
406 because persisting in these suboptimal refuges might allow it to avoid competition and/or
407 predation. The fact that it remains in better conditions than *C. tricocon* on Menorca, even
408 though our results showed only a slight effect caused by the surrounding vegetation, might be
409 due to some other micro-scale effects, since *D. rodriguezii* depends on the shelter by nurse-
410 plants (Rodríguez-Pérez et al. 2012b; Rodríguez-Pérez et al. 2012c).

411 **Conclusions**

412 Seed dispersal seems to be determinant for the long-term persistence of many plant species. In
413 this study we have shown that seed-dispersers importantly contribute to determine the
414 distribution of two relict plant species. We have also evidenced that an alien disperser might
415 raise the dependence of these plants on their optimal conditions (regarding habitat and climate)
416 to survive. Thus, it could be argued that preserving native dispersers might help to mitigate the
417 effects of global change on such plants.

418 The introduction of alien species can generate a gradual cascading effect leading to the loss of
419 mutualistic interactions. These processes, although can be slow, need early conservation actions.
420 In the case of *C. tricocon* and *D. rodriguezii* in Menorca, with no longer seed-dispersal, the
421 only future for these plants involves active actions conducted by conservationists and
422 stakeholders.

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431

432 **Appendix A. Supplementary Data**

433 Supplementary data associated with this article can be found, in the online version, at XXXXX.

434

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582 **Figures**

583 Fig. 1. Study area. The Balearic Islands (the five biggest islands) with current distribution and
584 extinctions of *Cneorum tricoccon* (black points and grey stars, respectively) and current
585 distribution of *Daphne rodriguezii* (grey triangles)

586

587 Fig. 2. Conceptual framework (A) for classifying Combined Species Distribution Model grid-
588 cells into four categories, depending on topoclimatic suitability (horizontal axis) and on habitat
589 suitability (vertical axis). Abundances of *D. rodriguezii* (B) and *C. tricoccon* (D) presence
590 records and *C. tricoccon* extinctions (E) predicted by the CM in each of the four categories of
591 suitability on each island or group of islands related to its plant-disperser pattern. Proportion of
592 surface predicted by the CM in each of the four categories of suitability on each island or group
593 of islands related to its plant-disperser pattern for *D. rodriguezii* (C) and *C. tricoccon* (F)

594

595 Fig. 3. Graphical representation of the Combined Species Distribution Model (A), and the two
596 binary single models, one based on topoclimatic variables (B) and the other one based on
597 habitat features (C), for *Cneorum tricoccon* on the Balearic Islands

598

599 Fig. 4. Graphical representation of the Combined Species Distribution Model (A), and the two
600 binary Single-Models, one based on topoclimatic variables (B) and the other one based on
601 habitats features (C), for *Daphne rodriguezii* on Menorca Island. The different levels of
602 suitability predicted by the models are indicated

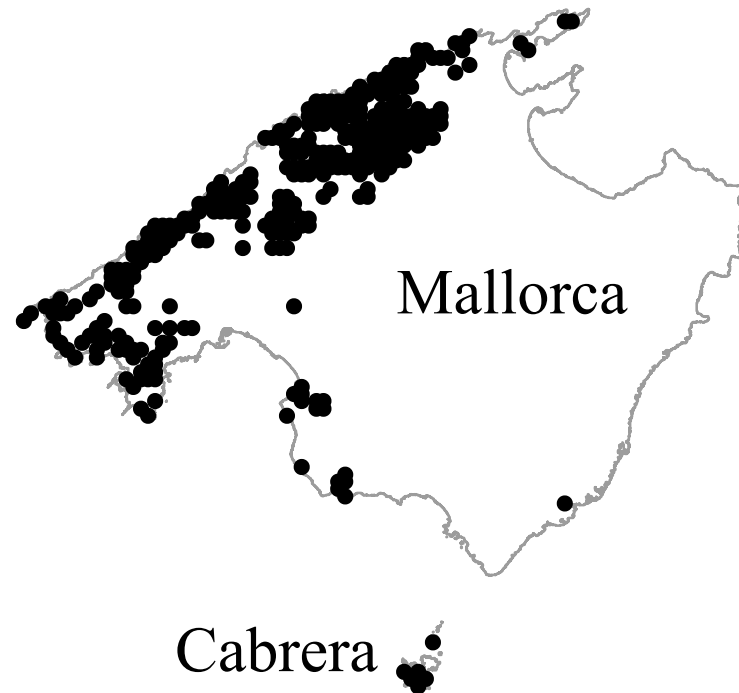
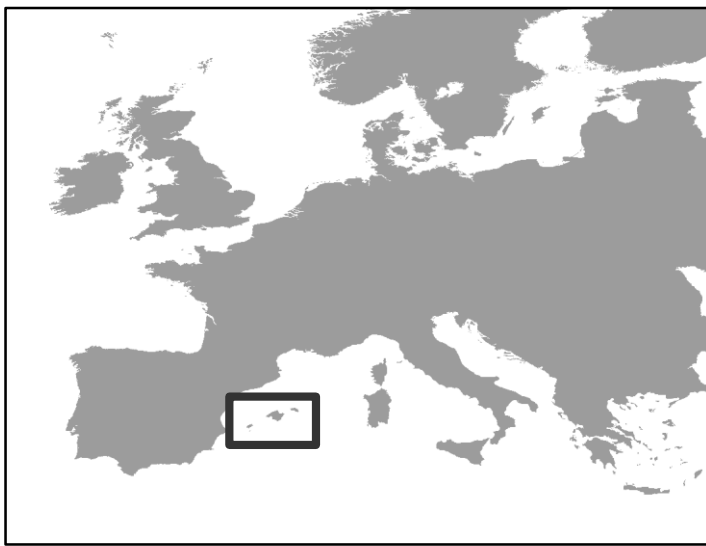
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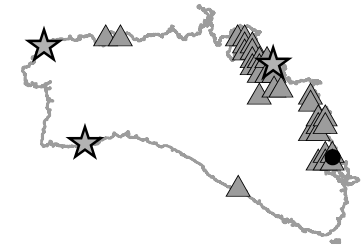
Table 1. Main occupied habitats by the seed-dispersers on each island.

Disperser	Island	Main habitat (reference)
<i>Podarcis pityusensis</i>	Eivissa	All kinds (Pérez-Mellado 2002b)
<i>Podarcis pityusensis</i>	Formentera	All kinds (Pérez-Mellado 2002b)
<i>Podarcis lilfordi</i>	Cabrera	All kinds (Pérez-Mellado 2002a)
<i>Martes martes</i>	Mallorca	Mountain woodlands (Clevenger 1993a)
<i>Martes martes minoricensis</i>	Menorca	Forests, Mediterranean shrublands and cliffs (Clevenger 1993b, 1994)

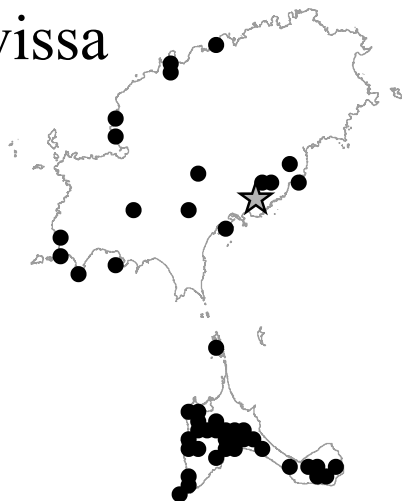
Figure 1



Menorca



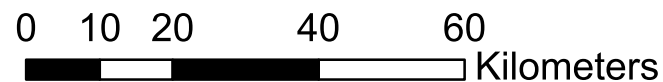
Eivissa

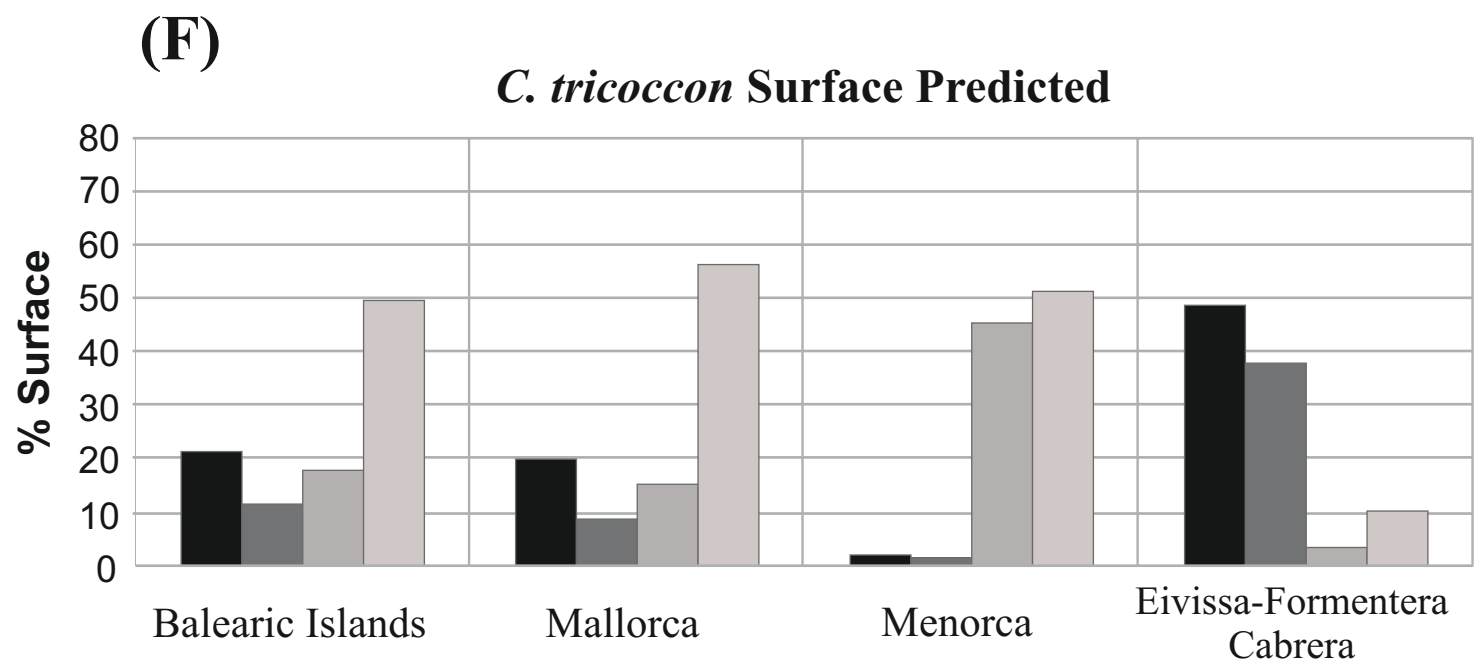
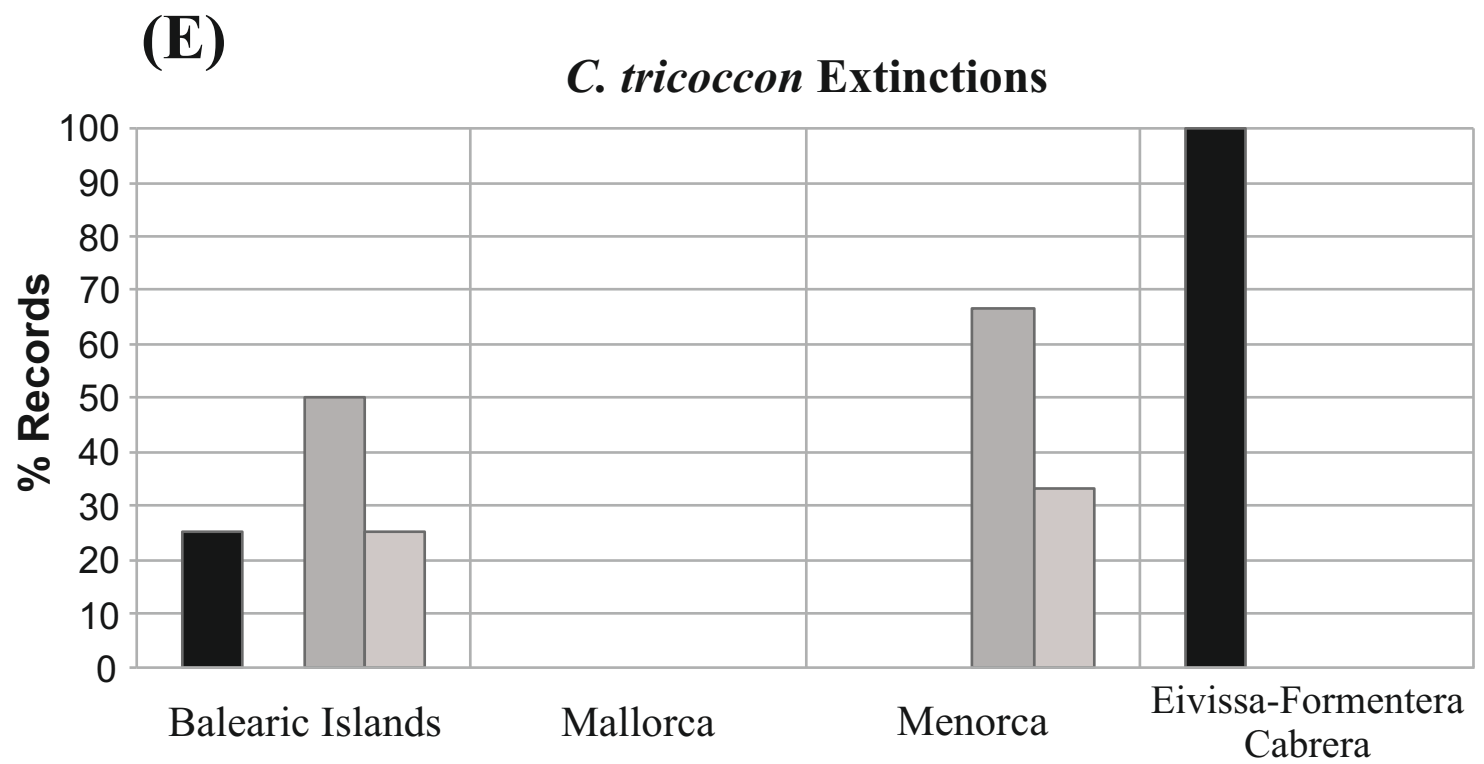
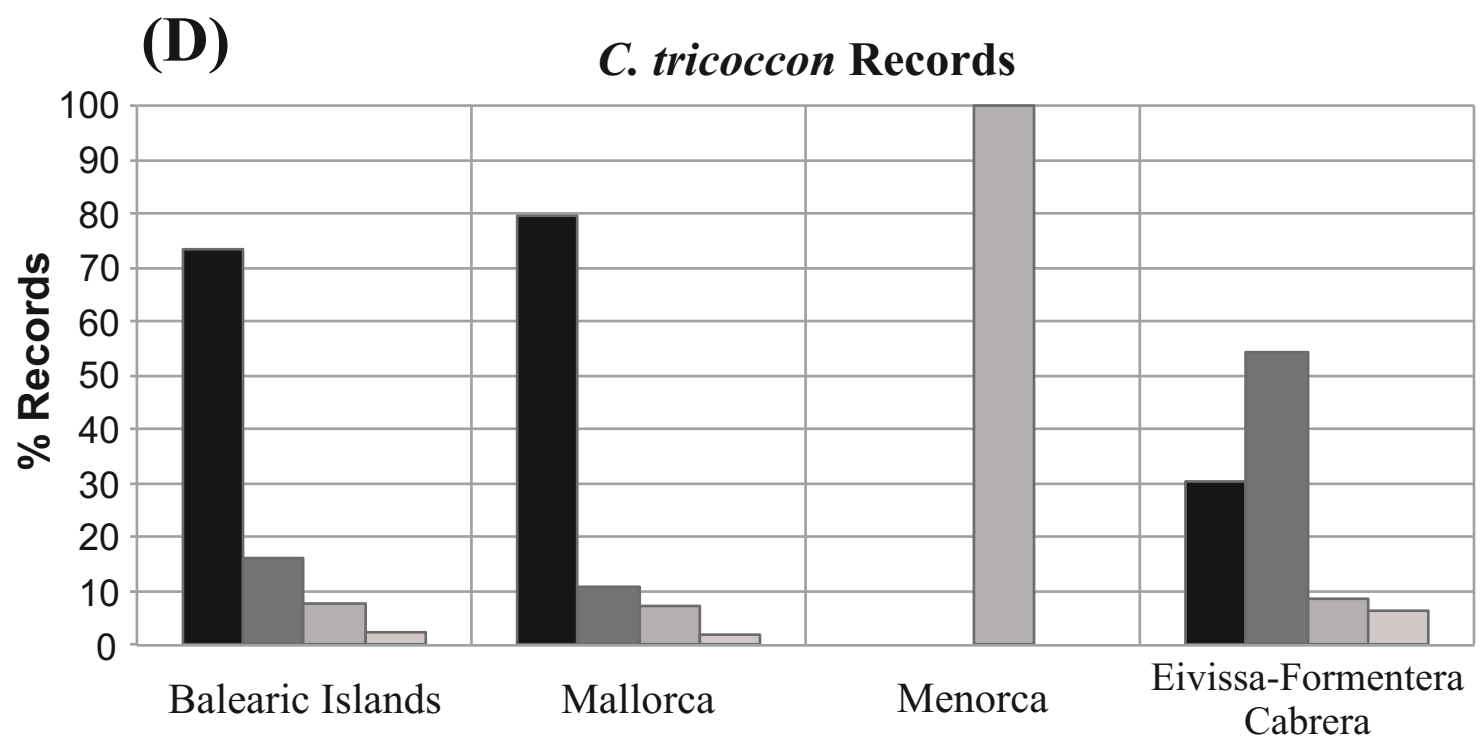
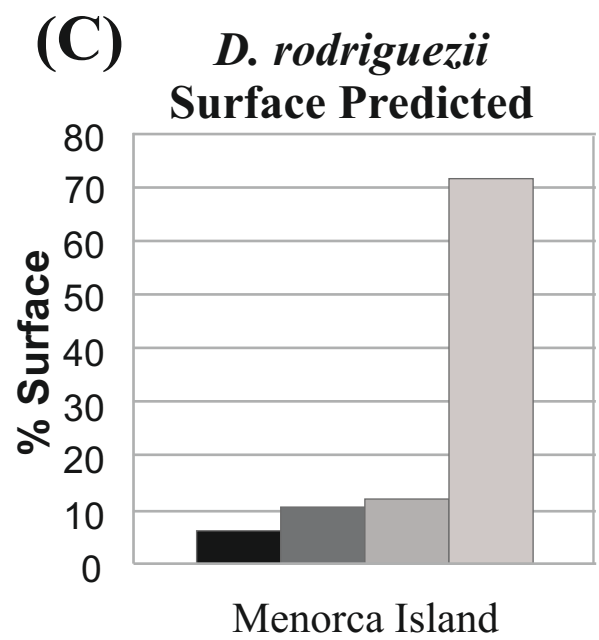
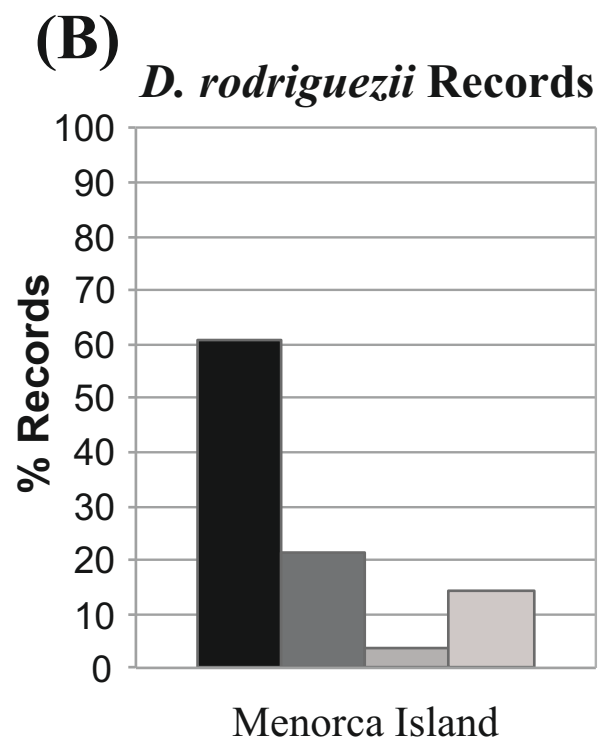
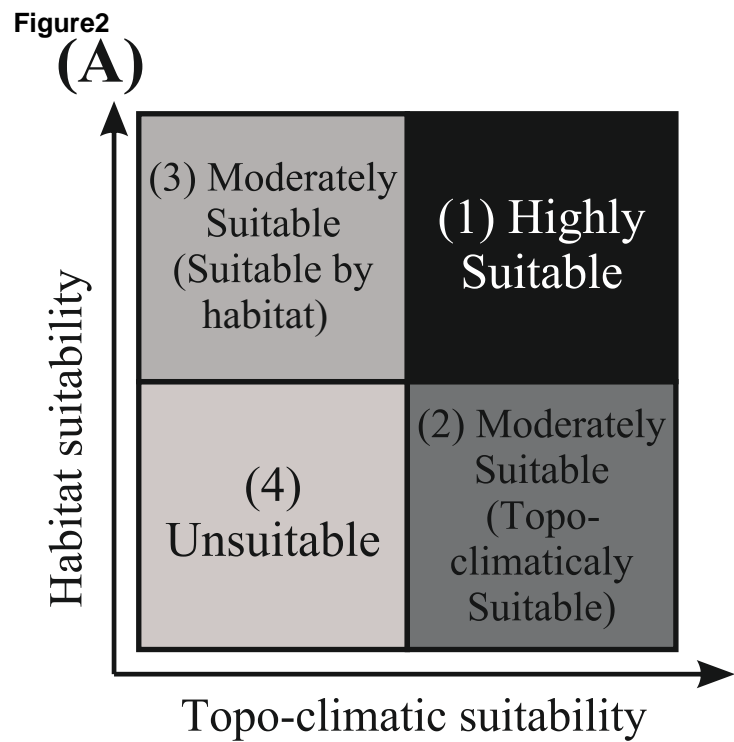


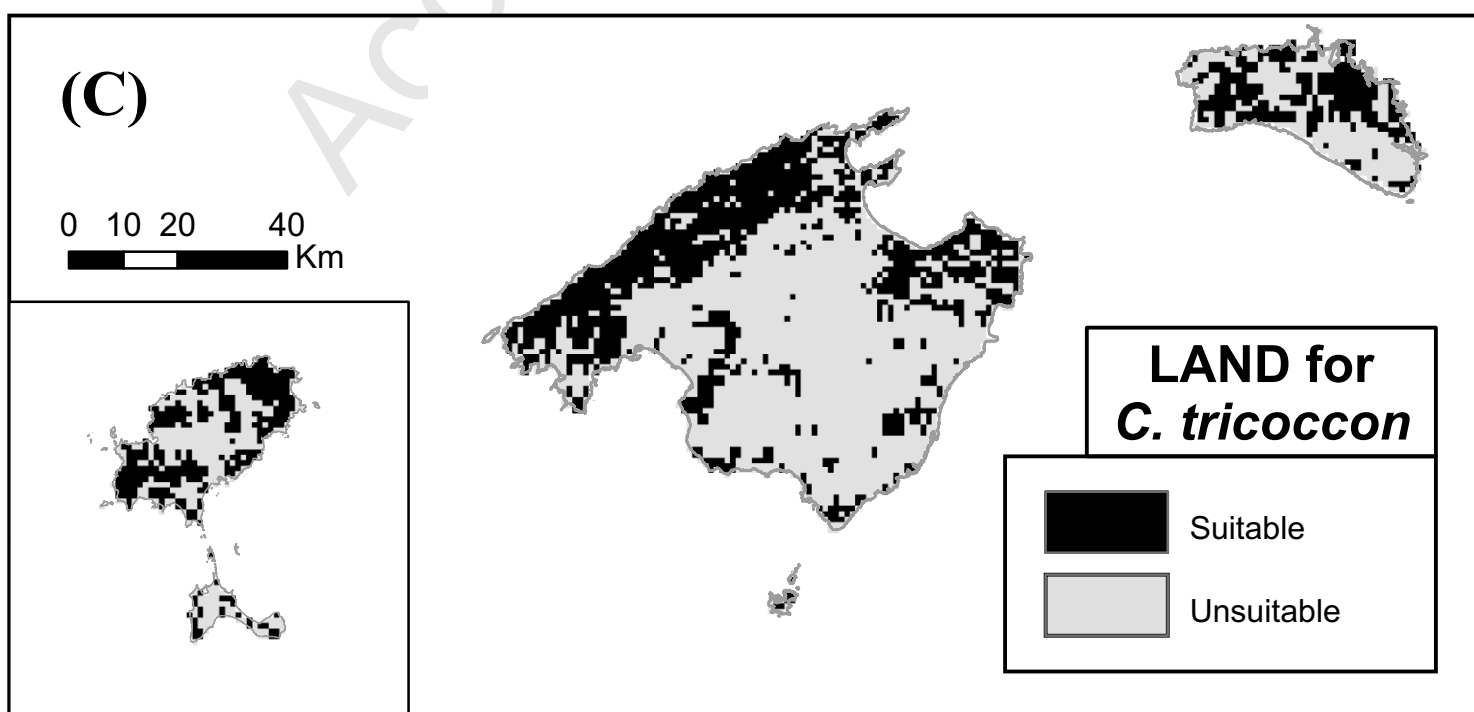
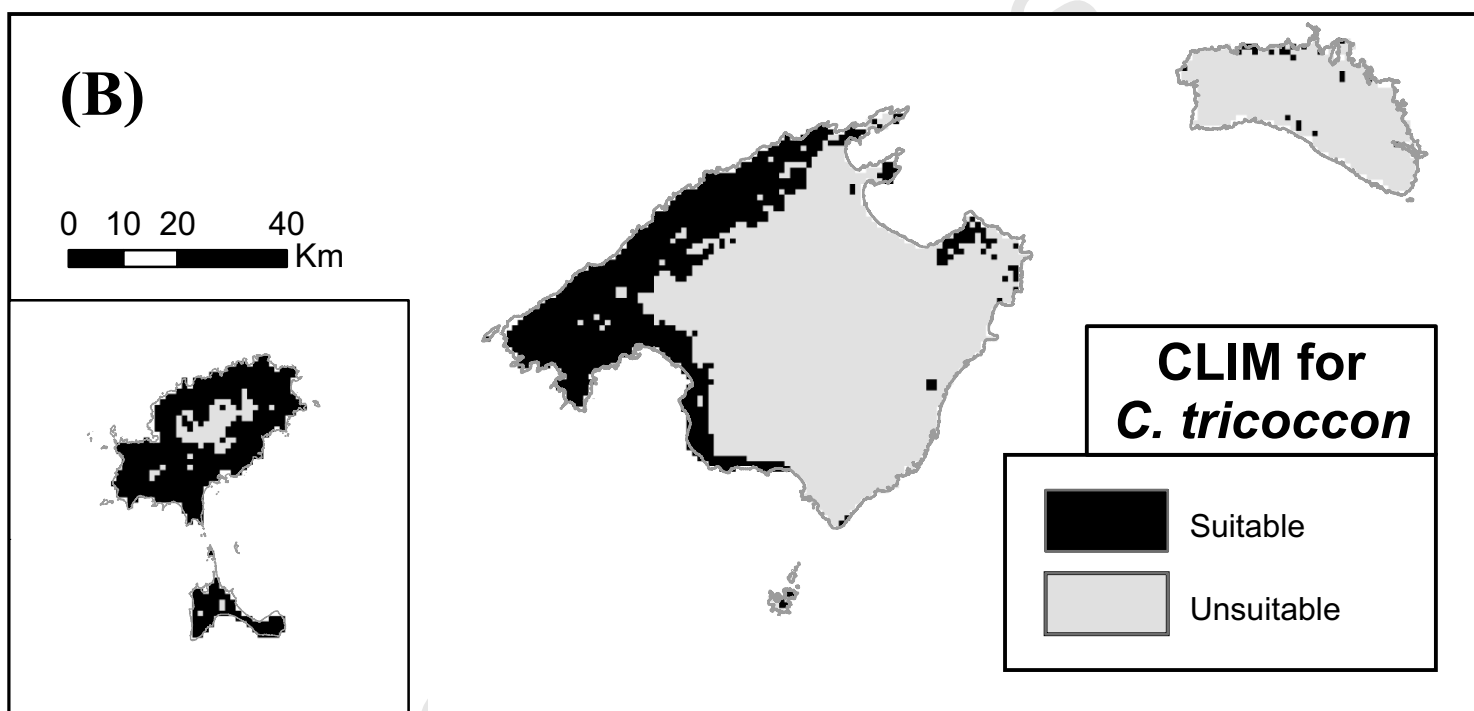
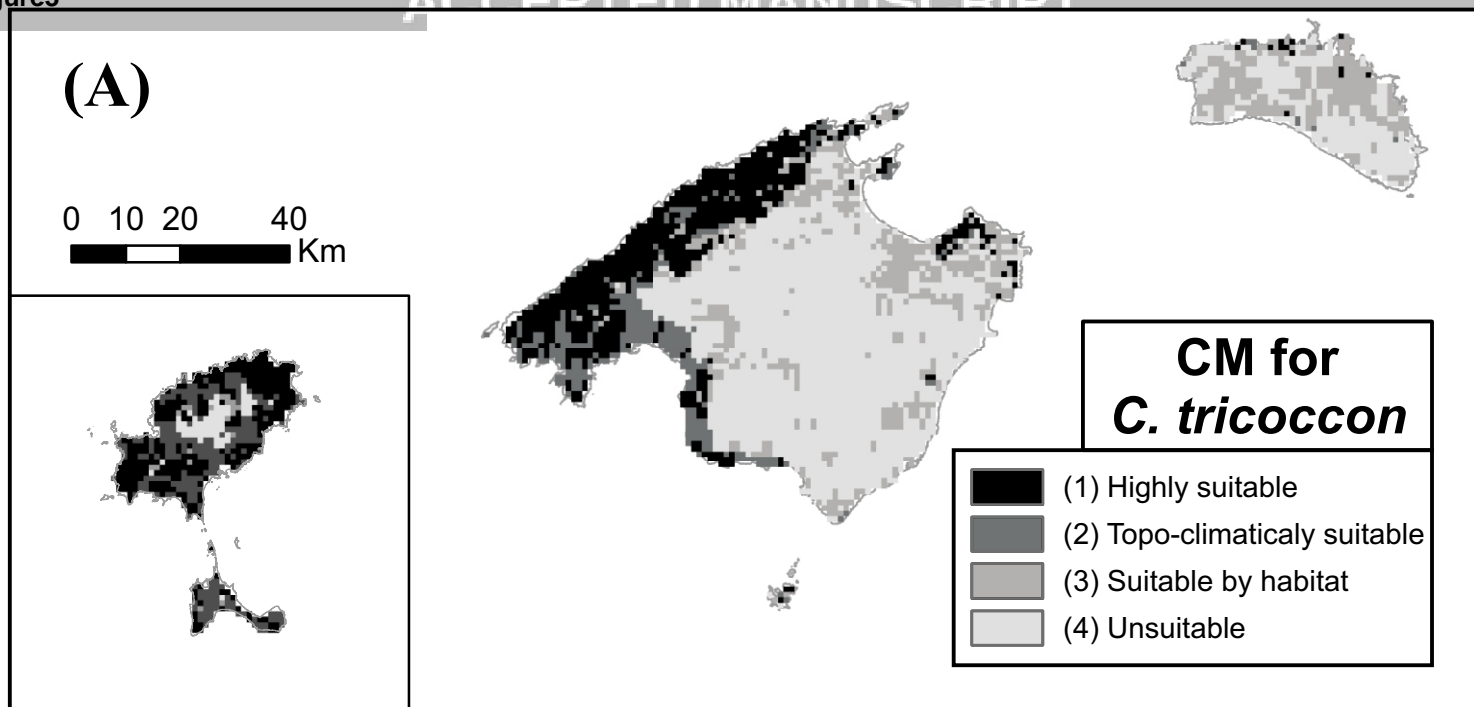
Formentera

Daphne rodriguezii
Cneorum tricocon

- *C. tricocon*
- ▲ *D. rodriguezii*
- ☆ *C. tricocon*
(extinct)







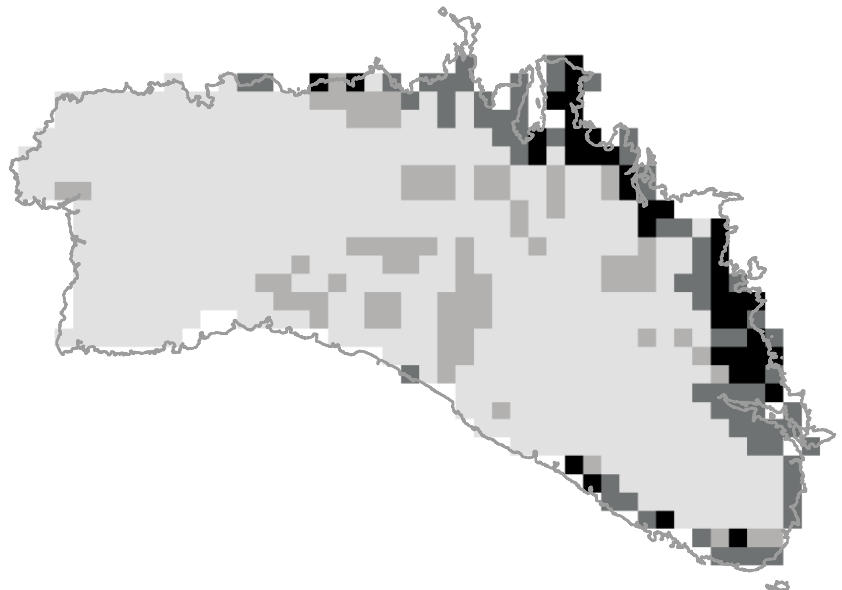




(A)



**CM for
*D. rodriguezii***0 3 6 12
Km

-  (1) Highly suitable
-  (2) Topo-climatically suitable
-  (3) Suitable by habitat
-  (4) Unsuitable



(B)



**CLIM for
*D. rodriguezii***0 3 6 12
Km

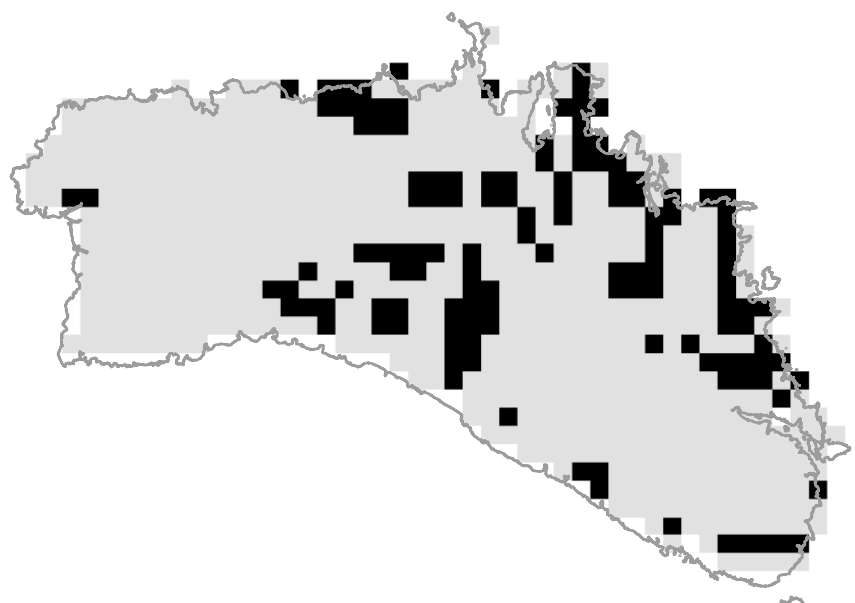
-  Suitable
-  Unsuitable



(C)

**LAND for
*D. rodriguezii***0 3 6 12
Km

-  Suitable
-  Unsuitable



Zusammenfassung

Der Verlust von Biodiversität und auch der Rückgang der Diversität von ökologischen Interaktionen können die Fähigkeit von Ökosystemen, die Auswirkungen des globalen Wandels zu verkraften, verringern. Wir untersuchten, ob die Verbreitung und das Überleben von zwei im Rückgang befindlichen Pflanzenarten, *Daphne rodriguezii* and *Cneorum tricoccon*, durch die Unterbrechung des Mutualismus mit ihren einzigen Samenausbreitern, durch klimatische und/oder Habitatbedingungen beeinflusst wurden. Wegen fehlender demographischer Daten wählten wir einen indirekten Ansatz. Wir benutzten Daten zum Vorkommen und Fehlen als abhängige Variablen und wählten zwei Sätze von Steuervariablen (Habitat- und topoklimatische Bedingungen), von denen wir annahmen, dass sie entscheidend für die demographischen Prozesse sind. Mit diesen beiden Datensätzen passten wir Artenverteilungsmodelle in MaxEnt an. Diese Modelle wurden später benutzt, um "Kombinierte Artenverteilungsmodelle zu konstruieren. Für beide Pflanzenarten erlaubten diese Modelle, die Bedeutung von klimatischen und nicht-klimatischen Faktoren (z.B. Mutualismusunterbrechung) zu ermitteln. Unsere Ergebnisse zeigten, dass sowohl Klima- als auch Habitatbedingungen die gegenwärtige Verbreitung der beiden Arten auf der Landschaftsebene bestimmten. Die Mutualismusunterbrechung zwischen *C. tricoccon* und seinem nativen Samenausbreiter beeinflusste die Verbreitung der Pflanze, wobei sie hin zu Gebieten ausgedehnt wurde, in denen ein neuer invasiver Samenausbreiter vorkam. Dieser modifizierte die Habitatwahl durch die Pflanzen, indem ihr Vorkommen in suboptimalen Gebieten reduziert wurde, worauf ihr Überleben gründen könnte. Unsere Ergebnisse belegen die Notwendigkeit eines besseren Verständnisses der Rolle von Mutualismen in natürlichen Gemeinschaften, um die passenden Schutzmaßnahmen für bedrohte Pflanzenpopulationen unternehmen zu können. Auf die entscheidenden Faktoren einzuwirken, die die Pflanze-Ausbreiter-Beziehung unterbrechen (z.B. durch Kontrolle invasiver Arten), könnte

dazu beitragen, die Effekte des globalen Wandels auf zurückgehende Reliktpflanzen abzumildern.

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