

# Declining relict plants: Climate effect or seed dispersal disruption? A landscape-scale approach

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## Abstract

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

## 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* und *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

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(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. tricocon* 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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**Keywords:** Species distribution modelling; Maxent; Mutualisms; Seed dispersal interactions; *Cneorum tricocon*; *Daphne rodriguezii*

## Introduction

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

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

ecosystems offers a perfect scenario to carry out conservation studies, and particularly on seed dispersal interactions (Hansen & Traveset 2012). Island populations are especially vulnerable to introduced species (i.e. predators and competitors) because they have evolved in the absence of interactions with them (Kawakami, Mizusawa, & Higuchi 2009). Actually, invasive species are currently considered the main threat to native biodiversity on many islands (Kueffer et al. 2010).

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

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

Moreover, across the Balearic Islands, the mutualism between the two study plant species and their native seed-disperser is different on each island. While in some islands the mutualism has remained unaltered, in others the native seed-disperser has been replaced for an exotic new one, or even, it has disappeared and the mutualism has been lost (Rodríguez-Pérez & Traveset 2010; Traveset 1995; Traveset & Riera 2005). These three different situations, plus the hypothesis that the effect of microhabitat on plant species was constant across the islands, allowed distinguishing how each seed-disperser affected plant distributions. Additionally, it enabled

us to evaluate how habitat selected by plants, in terms of quality, might be affected by the mutualism disruption.

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

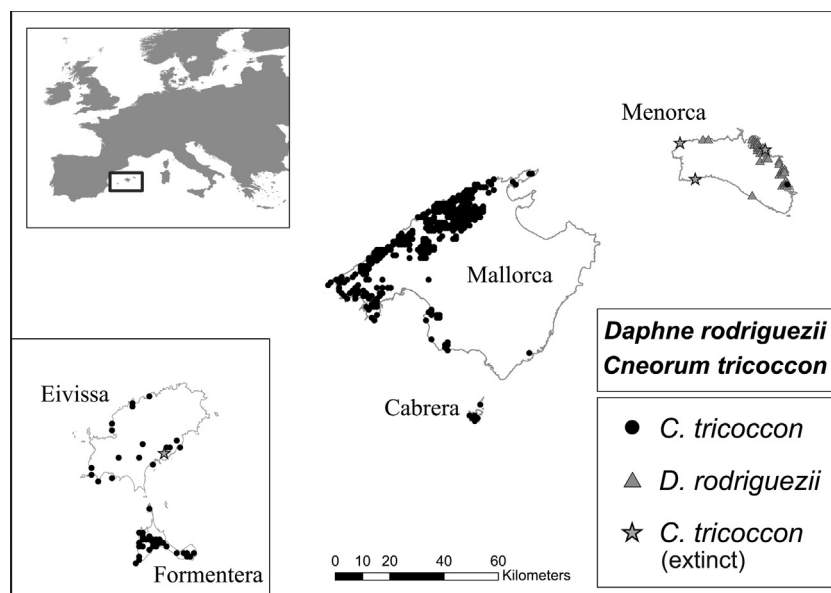
## Material and methods

### Study area

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

### Study plant species and their seed-dispersers

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



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

**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 1994 1993b)

The native dispersers of *C. tricocon* are two endemic lacertid lizards: *Podarcis lilfordi* Günther in the Gymnesic Islands (Mallorca, Menorca, Cabrera and surrounding islets), and *Podarcis pityusensis* Boscá in the Pythiusic Islands (Eivissa, Formentera and surrounding islets). *P. lilfordi* is currently extinct from the two larger islands, Mallorca and Menorca. Introduced mammals, mainly pine martens *Martes martes* L. (Mustelidae), are the current dispersers of the two study plant species in these two islands (Celedon-Neghme, Traveset, & Calvino-Cancela 2013; Riera, Traveset & Garcia 2002; Traveset 1995). In Menorca, however, pine martens have been found to have a less frugivorous behaviour (Clevenger 1993b) and the dispersal of the plant is almost zero (Riera et al. 2002; Traveset 1995). By contrast, *D. rodriguezii* is exclusively dispersed by the endemic *P. lilfordi* (Rodríguez-Pérez et al. 2010; Traveset & Riera 2005). Thus, after the extinction of this lizard on Menorca, the lizard–plant interaction persists only on an islet (Colom) offshore Menorca.

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

### Data compilation on plant distribution and environmental conditions

We first obtained presence data of the plant species from BIOATLES (2007), a public database that provides data for most of the Balearic species with up to 1 km resolution. This resolution is considered adequate regarding the requirements

of conservation and management planning (Guralnick & Hill 2009). BIOATLES contained a total of 475 and 32 occurrence records for *C. tricocon* and *D. rodriguezii*, respectively. In addition, we had three *C. tricocon* occurrence records from paleontological deposits in Menorca and another one from Eivissa (Traveset & Riera 2005). These records can be classified as extinctions because the species is no longer present in these locations. Seed-disperser data were too scarce and highly biased to be used for the purpose of this study.

A total of 30 variables were compiled as possible predictors of the distribution of both plant species (see Appendix A: Methods A1 for further details). In order to reduce the excessive number of predictor variables, especially for *D. rodriguezii* with low number of occurrences, and also to avoid multicollinearity in the set of predictor variables, we discarded the less easily interpretable variables, in terms of plant ecology, from those with a Pearson's correlation coefficient higher than 0.7 (Dormann et al. 2013). Thus, we ended up with a total of 11 predictor variables for *C. tricocon* and 10 for *D. rodriguezii* (see Appendix A: Table A1). This number of variables has been shown to perform well with different modelling methods, even with fewer occurrences than those we had (Hernandez, Graham, Master & Albert 2006).

### Modelling process and categories of suitability

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

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

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

### Construction of Single-Models

The SMs were developed with the maximum entropy algorithm of species distribution modelling, MaxEnt (version 3.3.3k; Phillips, Anderson, & Schapire 2006; see Appendix A: Methods A1 for further details on the modelling process). MaxEnt is a widely applied tool for distribution modelling with presence-only data (Elith et al. 2011). It was chosen because it is considered one of the strongest performers in different comparative studies (Elith et al. 2011; Hernandez et al. 2006), and also because it allows using small sets of data (Elith et al. 2011). MaxEnt not only builds the predictive



model based on the environmental variables implemented, but also provides response curves for each variable. The response curves from the *C. tricocon* LAND-model were used to test the hypothesis that the microhabitat affecting plant species was not variable from island to island and, thus, what LAND-models captured was basically an appropriate environment allowing the presence of the seed-disperser.

For *C. tricocon*, we fitted two SMs (i.e. CLIM-model and LAND-model) for all the study area excluding Menorca, because currently there is only one record in this island, and this could have distorted the goodness-of-fit of the models (Elith et al. 2011). Thus, we used Mallorca, Eivissa, Formentera and Cabrera as the areas for randomly locating background points (i.e. 10,000 points) and, then, the two models obtained were projected to Menorca. We randomly selected 70% of the records to train the models and reserved the rest to test them (see Williams et al. 2009 for a similar methodology). We obtained two final models in a logistic output format resulting from the average of 10 replicates (each replicate run with a different random selection of train and test records). As a goodness-of-fit of the models we used the AUC test. It is usually accepted in species distribution modelling that fair models have an  $AUC \geq 0.7$  (Araújo, Pearson, Thuiller, & Erhard 2005, and references therein). Additionally, to determine the accuracy of the model, we also used the prediction success of the test data set (i.e. proportion of presences correctly predicted of the test subsample) after applying the threshold that maximizes the specificity plus the sensitivity (Baldwin 2009). Likewise, we used this threshold to transform the models from logistic format to binary.

To avoid the effect of spatial autocorrelation between presence points and, thus, to improve the model performance (Vaclavik, Kupfer, & Meentemeyer 2012), we tested the autocorrelation significance of the model residuals (observed occurrence minus probability of occurrence) (Marcer, Pino, Pons, & Brotons 2012, and references therein) by using a Monte-Carlo simulation of Mantel test (ade4 package; Dray & Dufour 2007). As subsampling the original data matrix substantially reduces the inflation effect of spatial autocorrelation (Segurado, Araújo, & Kunin 2006), we randomly subsampled our data up to the distance between points so that the Monte Carlo simulation significantly showed no spatial autocorrelation. Even with this, our models might still be overestimated because of some degree of dependence of the presence records. However, this is the best tool available so far and the more commonly used (Bahn & McGill 2013).

Analogously, we also constructed SMs for *D. rodriguezii*. As we had few presence records for this species, it was not possible to separate data for training and testing the model. Thus, in this case we used a jackknife approach to assess the significance of the model, as described by Pearson, Raxworthy, Nakamura and Peterson (2007) (see Appendix A: Methods A1 for further details on how this methodology was implemented). Hence, we obtained two models in a logistic output format and transformed them to a binary format applying the threshold that maximized both specificity and

sensitivity. As in *C. tricocon* SMs, we checked the model residuals for significant spatial autocorrelation by using a Monte-Carlo simulation of Mantel test.

### Construction of Combined-Models (CM)

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

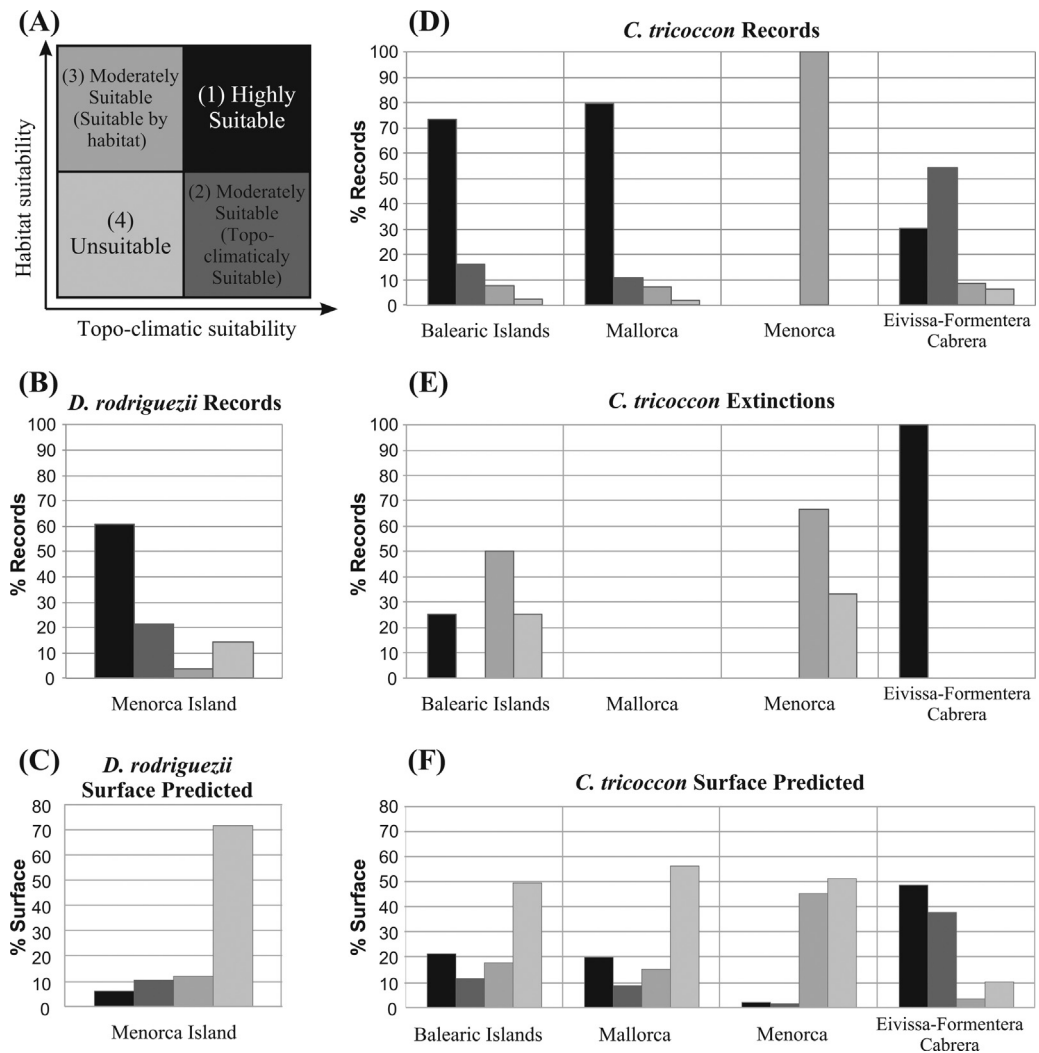
To formally assess the accuracy of the two CM, it would have been ideal to have independent presence data, and also expected dynamics such as recolonization of suitable areas (Mladenoff, Sickley, & Wydeven 1999) or extinctions in unsuitable areas (Naves et al. 2003). However, these data were not available for any of the two plant species; thus, the categorization of the CM may have some degree of arbitrariness (Falcucci, Ciucci, Maiorano, Gentile, & Boitani 2009). Nevertheless, all records, including those four considered extinctions, were used to calculate the relative frequency of presence points in each of the four categories and to fairly validate the two CMs.

## Results

### Single-Models for *C. tricocon*

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

*Cneorum*-CLIM showed 90.5% and 89% prediction success for test and training records, respectively, and the AUC test indicated fair performance ( $AUC_{\text{test}} = 0.788 \pm 0.026$ ). Residuals of the model showed no significant spatial autocorrelation (Mantel correlation test:  $-0.037$ ;  $p$ -value = 0.743). In



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

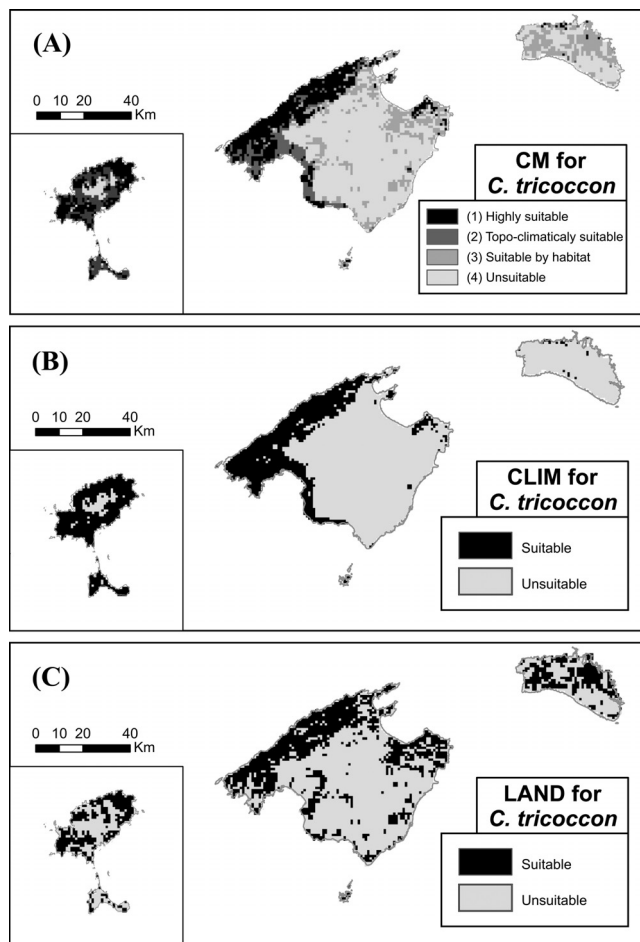
the suitability representation of the binary model (Fig. 3B), a clear pattern was detected in Eivissa and Formentera, where the best conditions were given in the whole coastal area, and also in Mallorca, where the main best zone coincided with the Tramuntana Mountains and with the Western Coast. On the other hand, in Menorca, where the presence of *C. tricocon* is almost zero, only 3.48% of pixels were predicted as suitable (Fig. 2F), all scattered throughout the island.

The *Cneorum*-LAND model showed worse but still acceptable levels of performance ( $AUC_{test} = 0.708 \pm 0.036$ ; 81.5% and 82.3% prediction success for test and training data, respectively) and no significant residual spatial autocorrelation (Mantel correlation test: 0.021;  $p = 0.339$ ). Its binary representation (Fig. 3C) did not show so clear patterns of suitable areas, except that cultivated areas are the most unsuitable for *C. tricocon* (see response curves and jackknife test provided by MaxEnt in Appendix A: Figs. A1 and A2).

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

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

Comparing the predictions of the *Cneorum*-CM with the full set of observed presences (Fig. 2D), we found that most of them were located in Highly Suitable (73.6%) and Moderately Suitable (23.8%) sites. Only 2.6% of presence records



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

were predicted as Unsuitable sites. Furthermore, there was a larger proportion of observed records in Topoclimatically Suitable sites than in the Suitable by Habitat category (16.2% vs. 7.6%, respectively). Additionally, three of the four extinction records were located in suboptimal predictions (Fig. 2E).

When considering the results separately by islands or group of islands, depending on the identity and behaviour of the *C. tricoccon* seed-disperser (Fig. 2D), we found diverse results. On the one hand, the highest proportion of *C. tricoccon* records (79.7%) in Mallorca, where dispersers are pine martens, was predicted as Highly Suitable sites by the model. Presences predicted as Topoclimatically Suitable and Suitable by Habitat were 11% and 7.2%, respectively. Tolerance to unsuitable topoclimatic conditions (presences predicted as Suitable by Habitat plus Unsuitable) was 9.3% whereas tolerance to unsuitable habitat conditions (presences predicted as Topoclimatically Suitable plus Unsuitable) was 13.1%. On the other hand, on the islands where lizards are the main dispersers, the trend was not so clear: the largest proportion

was for Moderately Suitable predictions (54.3% for Topoclimatically Suitable sites and 8.7% for Suitable by Habitat), whereas Highly Suitable sites obtained 30.4% of presence records. Tolerance to unsuitable topoclimatic conditions was 15.3% whereas tolerance to unsuitable habitat conditions was 60.9%. Finally, in Menorca, where dispersal of *C. tricoccon* seeds is almost zero, the only presence record for this species was predicted for a Suitable by Habitat site.

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

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

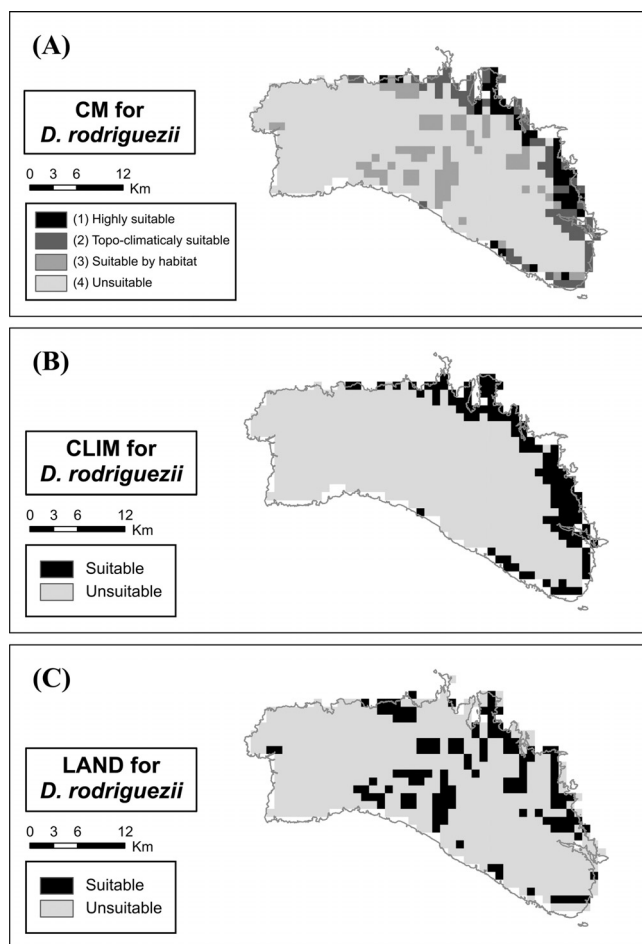
### Combined-model for *D. rodriguezii*

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

Most presence records of this species were predicted as Highly Suitable by the model (60.7%; Fig. 2B). Comparing records predicted as Moderately Suitable, the proportion of sites predicted as Topoclimatically Suitable was higher than those predicted as Suitable by Habitat (21.4% vs. 3.6%), whereas 14.3% were predicted as Unsuitable. Finally, tolerance to unsuitable topoclimatic conditions was 17.9% whereas tolerance to unsuitable habitat conditions was 35.7%.

### Discussion

The introduction of invasive mammals in some of the Balearic Islands, together with the behaviour of such newcomer species, caused different degrees of mutualism disruption: (1) extinction of the native seed-disperser



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

without replacement on Menorca; (2) replacement of the seed-disperser on Mallorca; and (3) survival of the native seed-disperser on Eivissa, Formentera and Cabrera. On the other hand, the habitat suitability of our combined distribution models (CM) implied favourable topoclimatic conditions for the plants (captured by CLIM-models), but also an appropriate environment providing favourable microhabitat conditions and/or the presence of seed-disperser (captured by LAND-models). However, the response curves of the LAND-models showed that the microhabitat (i.e. the environment given by the surrounding land cover) affected the plants uniformly on the islands. Thus, what mainly captured the LAND-models was the seed-disperser effect on plant distributions. These findings allowed us to discern between the different degrees of influence exerted by both topoclimatic conditions and the dispersal pattern on the plant species distributions. Nevertheless, it must be noted that some degree of bias might be introduced into the models by potentially dissimilar factors on each island (e.g. secondary seed-dispersers

or micro-scale effects). In this sense, the European genet (*Genetta genetta*), ants and gulls have been suggested as possible or occasional dispersers of *C. tricocon* seeds (Traveset et al. 2012, and references therein). It has also been reported that *D. rodriguezii*'s seedling survival is related to the presence of nurse-plant species (Rodríguez-Pérez & Traveset 2012, and references therein). The local distribution of *D. rodriguezii* and how it is influenced by the interaction with its seed disperser had previously been studied, using a similar “two-dimensional” approach, by Rodríguez-Pérez, Wiegand, et al. (2012) on an islet offshore Menorca. These authors found that both lizard activity and local habitat features determine the spatial distribution of the plant.

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

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

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

Novel mutualistic relationships with introduced species can compensate for the loss of native mutualist extinctions, but not without long-term consequences (Traveset & Richardson 2014; Kiers et al. 2010). *C. tricocon* is an example of that. It has compensated the loss of its only former seed-disperser with the appearance of a new one, which is, paradoxically, partly responsible for its extinction (as pine martens prey upon lizards). The long-term consequence of such change has been the new distribution of the plant species and its increasing dependence on the optimal conditions to live.



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

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

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

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

## Conclusions

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

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

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.08.003>.

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