Effects of climate change on three species of *Cupido* (Lepidoptera, Lycaenidae) with different biogeographic distribution in Andalusia, southern Spain

R. Obregón, J. Fernández Haeger & D. Jordano

Obregón, R., Fernández Haeger, J. & Jordano, D., 2016. Effects of climate change on three species of *Cupido* (Lepidoptera, Lycaenidae) with different biogeographic distribution in Andalusia, southern Spain. *Animal Biodiversity and Conservation*, 39.1: 115–128.

Abstract

Effects of climate change on three species of Cupido *(Lepidoptera, Lycaenidae) with different biogeographic distribution in Andalusia, southern Spain.*— Knowledge of the spatial distribution of rare or endangered species is of key importance to assess conservation status at different geographic scales and to develop conservation and recovery programs. In this paper we review and update the distribution of three species of Lycaenid butterflies in Andalusia (southern Spain): *Cupido carswelli, C. lorquinii*, *and C. osiris*. *Cupido carswelli* is endemic in south east Spain and is considered a vulnerable species in the Red Book of Invertebrates of Andalusia. *Cupido lorquinii* is an Iberian–Maghrebian endemism, found in the southern half of the Iberian peninsula. *Cupido osiris*, widely distributed in Europe and Central Asia, has its southern limit of distribution in Andalusia. We modeled the potential current distribution of these species in Andalusia, using Maxent. Their potential distribution was mainly conditioned by the presence of their host plants and, to a lesser extent, by climatic variables: rainfall during the warmest and coldest quarters of the year and annual mean temperature. AUC test values, sensitivity, and specificity for the three models were high, confirming the accuracy of the models and their high predictive values. We also modeled the potential future distributions of the three species under the climate change scenario A2a. Our results predict a significant reduction in the potential distribution for *C. lorquinii* —which has a wider distribution in Andalusia than the other two species— and for the more localized species, *C. osiris* and *C. carswelli*. This expected decline in the south of the Iberian peninsula highlights the pressing need to design and implement specific conservation plans for these species.

Key words: Modeling, Global Change, *Cupido*, Lepidoptera, Iberian peninsula

Resumen

Efectos del cambio climático en tres especies del género Cupido *(Lepidoptera, Lycaenidae) con diferente distribución biogeográfica en Andalucía (sur de España).*— El conocimiento de la distribución espacial de especies raras o amenazadas es un elemento clave para evaluar su estado de conservación a diferentes escalas geográficas y para elaborar programas de conservación y recuperación. En este trabajo se revisa y actualiza la distribución en Andalucía (sur de España) de tres especies de licénidos: *Cupido carswelli, C. lorquinii* y *C. osiris*. *C. cars*welli es endémica del SE de España y se considera una especie vulnerable en el Libro Rojo de los invertebrados de Andalucía. *C. lorquinii* es un endemismo iberomagrebí encontrado en la mitad meridional de la península ibérica. Por el contrario, *C. osiris* está ampliamente distribuida por Europa central y Asia, y tiene su límite meridional de distribución en Andalucía. Utilizando Maxent, se han elaborado modelos de la actual distribución potencial de estas especies en Andalucía, que resultó estar condicionada principalmente por la presencia de sus plantas nutricias y, en menor medida, por ciertas variables climáticas: la precipitación durante el trimestre más cálido, la precipitación durante el trimestre más frío y la temperatura media anual. Los valores obtenidos de AUC, sensibilidad y especificidad para los tres modelos fueron altos, lo que confirma la exactitud y el elevado valor predictivo de los modelos. Además, se ha elaborado un modelo de la distribución potencial futura de las tres especies en un contexto de cambio climático A2a. Los resultados obtenidos muestran una reducción significativa de la distribución potencial tanto para *C. lorquinii*, cuya distribución en Andalucía es más amplia que la de las otras dos especies, como para las especies más localizadas, *C. osiris* y *C. carswelli*. Esta disminución prevista en el sur de la península ibérica pone de manifiesto la inminente necesidad de elaborar y poner en práctica planes de conservación específicos para estas especies.

ISSN: 1578–665 X
eISSN: 2014–928 X

Palabras clave: Elaboración de modelos, Cambio global, *Cupido*, Lepidoptera, Península ibérica

Received: 30 IX 15; Conditional acceptance: 11 XII 15; Final acceptance: 23 II 16

Rafael Obregón, Juan Fernández Haeger & Diego Jordano, Dept. of Botany, Ecology and Plant Physiology, Univ. of Córdoba, E–14071, Córdoba, Spain.

Corresponding author: Rafael Obregón. E–mail: rafaobregonr@gmail.com

Introduction

In the current scenario of biodiversity decline conditioned by habitat loss and climate change, the populations of an increasing number of species have shown a marked decline in recent years (Asher et al., 2001; Fox et al., 2011; PECBMS, 2013; Balmer et al., 2013; Inger et al., 2015). There is therefore a pressing need to prioritize conservation to mitigate the anticipated effects of global change (Balmford & Bond, 2005) and to elaborate recovery plans. To do so requires the detailed assessment of the state of populations of many species amongst which the geographical distribution is a key aspect. The limits of the area of occupancy are important quantitative criteria to assess the status of species included in any of the categories of the Red List (IUCN, 2012).

Current knowledge of the distribution of many species remains vague and incomplete, and is usually based on data that have not been collected following standardized sampling procedures. Data is therefore spatially biased to areas that have been prospected more intensively (Soberón et al., 1996; Hortal et al., 2008; Fernández & Nakamura, 2015) according to their accessibility or attractiveness to researchers (Romo et al., 2006). In this sense, as inland Andalusia is one of the least prospected area in Spain it has the lowest number of records of butterflies in the country (Romo & García–Barros, 2005).

Species distribution models (SDMs) are a powerful tool to assess population status because, when properly used (Kramer–Schadt et al., 2013; Merrow et al., 2013), they allow estimation of the main environmental requirements of the species and their geographic projection, from which, maps of the potential or real distribution of the species can be obtained (Guisan et al., 2006; Drake & Bossenbroek, 2009). SDMs have also been used to predict the potential future distribution of species under the influence of climate change (Thuiller, 2003; Parmesan, 2006), thereby helping to detect sensitive areas and to mitigate possible effects (Balmford & Bond, 2005). However, the results of this type of application should be treated with caution (Merrow et al., 2013).

In this paper we analysed the current distribution and potential distributions (southern Spain) of the three species of the genus *Cupido* (Schrank, 1801) in Andalusia (*C. lorquinii*, *C. osiris*, and *C. carswelli*) using Maxent (Phillips et al., 2006; Phillips & Dudik, 2008). Modeling of their potential distributions is particularly useful as it predicts the location of sites that provide the conditions and resources necessary for their presence, and thus indicates priority areas for conservation action.

In Andalusia, the three species are distributed as local, isolated, small populations as would be expected given that *C. osiris* and *C. lorquinii* are at the limits of their respective ranges, while *C. carswelli* is an endemic species with highly limited distribution. These factors, combined with their short flight periods and poor ability for dispersal, makes them difficult to locate. Their distributions on a continental scale are very different. *Cupido osiris* has a wide, but fragmented distribution from southern and central Europe to central Asia (López–Vaamonde et al., 1994; García–Barros et al., 2013), with Andalusia being the southern limit of its range on the continent. This southern distribution of taxa of Eurosiberian origin is the result of north–south migrations during glacial–interglacial periods and their postglacial shelter in mountain ranges of the southeastern Iberian peninsula (Martín & Gurrea, 1990; Romo & García–Barros, 2010; Obregón & Gil–T., 2015). In contrast, *C. lorquinii* is an Ibero–Maghrebi endemism common in the Rif Mountains in northern Morocco and Algeria, while in Europe it is distributed only in the southern half of the Iberian peninsula (García–Barros et al., 2013). The third species included in this study, *C. carswelli,* has the narrowest geographic range because it is endemic to the Bético systems of northeastern Andalusia and Murcia. *Cupido carswelli* is considered as a species by some authors (Kudrna, 2002; Gil–T., 1998, 2003, 2006, 2008) but as a subspecies of *C. minimus* by other authors such as García–Barros et al. (2013). In this paper we consider *C. carswelli* as a species, in agreement with Kudrna (2002), Gil–T. (2003, 2006), Cuvelier & Tarrier (2002), Obregón (2011), and studies of DNA barcoding (COI) (Dincă et al., 2015). *Cupido carswelli* is listed as vulnerable in the Andalusian region according to the Red Book of the Invertebrates of Andalusia (Gil–T., 2008). This level of protection is not extended to the national level due to its consideration by some authors (García–Barros et al., 2013) as a subspecies of the widely distributed in Europe *C. minimus*.

Climate change is a matter of record and its effects on the distribution of organisms and particularly butterflies have already been demonstrated (Parmesan & Yohe, 2003; Gutiérrez–Illán et al., 2010). According to the models of the IPCC (2014), rises in temperature will affect the dynamics of rainfall and, as a direct consequence, affect the spatial distribution of ecosystems and their functioning (De Groot et al., 2009).

Climate change will affect all species, but especially those with very limited dispersal ability (Hoyle & James, 2005). The genus *Cupido*, like many other species of Lycaenid, is one such species. Several studies on the effects of global warming on butterflies predict shifts to areas of higher latitude and/or altitude (De Groot et al., 2009; Gutiérrez–Illán et al., 2010). However, the latitudinal displacement of butterflies found at medium and high altitude could be prevented by the presence of barriers —such as vast agricultural areas at low altitude that would be impassable for species of low mobility— and a lack of equivalent displacement of their host plants (Romo et al., 2014). This work aims to provide a predictive view of how the distribution of these three rare Lycaenids in Andalusia could change under a climate change scenario.

Material and methods

Maps of the current distribution in Andalusia

Andalusia (southern Spain) covers an area of 87,000 km^2. It includes the continuous mountain range of Sierra Morena to the north and the discontinuous system formed by the Béticas ranges (Subbética and Penibética mountains) in the south, separated by the extensive fluvial valley of the river Guadalquivir. The transformation of the landscape for agricultural uses over centuries has eliminated many species of fauna that depended on the natural vegetation. In some cases, such species have been reduced to small, fragmented populations within the agricultural matrix or confined to mountainous areas with a very thin soil cover. In addition, certain species of central European distribution maintain local populations in some areas of the Andalusian mountains (the southernmost limit of their distribution) where they find microclimates and conditions appropriate for their persistence, as in the case of *C. osiris*.

Our analysis of the current distribution of these three species is based on chorological information published in the form of articles and short notes in scientific journals (Gil–T., 1998, 2002, 2003, 2006, 2008; Lara Ruiz, 2009; Obregón, 2011) and in atlases (García–Barros et al., 2004; Moreno–Benítez, 2015), on records available in different museums and institutions, on online databases (GBIF, 2013), and on data from specimens in the collections of the authors and Felipe Gil–T.

In addition, given that Andalusia has areas that have been subjected to little or no prospection, between 2004 and 2015 a series of field surveys were carried out to confirm the presence of these three species at previously–surveyed sites and to locate new populations in Andalusia. The presence data collected by these two means, initially with a resolution of 1x1 km, were processed with ArcGIS 10.2 (ESRI, 2010) to map the distribution of the three species in UTM projection with a resolution of 10x10 km, to safeguard, as far as possible, the local populations.

Ecology of the species studied

Cupido lorquinii is a univoltine species (March to June) that can have a partial second generation in some years (Gil–T., 2002). Its presence is strongly conditioned by the presence of its host plant *Anthyllis vulneraria*. *Cupido osiris* is a univoltine Lycaenid (May–June) that has a a close relationship with its host plants of the genus *Onobrychis* (Munguira et al., 1997; Settele et al., 2008). *Cupido carswelli* is a univoltine Lycaenid (April and May) distributed in colonies very localized in habitats preferably located in ravines and forest clearings where *A. vulneraria* grows (Gil–T., 2008; Obregón, 2011).

For all three species of *Cupido*, the diapause may last over 300 days and includes both summer and winter. It is, therefore, the most vulnerable stage because of the risks of dehydration, freezing, and attack by parasitoids, predators, or diseases.

Current potential distribution

To produce the potential distribution models, we used Maxent v. 3.3.3 (Phillips et al., 2006; Elith et al., 2011). In a defined geographic area, Maxent uses data for the presence of the species (the localities where it has been recorded) as the dependent variable and a set of environmental variables: bioclimatic, topographic, and lithological, and also in our case, the probability of the presence of host plants, as predictors (Anderson et al., 2003).

The presence data used in the models are georeferenced in UTM squares of 1 km^2. Table 1 shows the details of the environmental variables used as predictors. Climatic variables (resolution: 1 km^2) extracted from the national data bases of the AEMET (Spanish Meteorological Agency) and topographic altitude variables extracted from a digital model of terrain (250 m resolution) were included in the model.

The species of *Cupido* studied appears to form local colonies associated with stands of their host plants. We therefore considered the presence of these plants should be included as an additional predictor. For this purpose, we modeled the current potential distribution of *Anthyllis vulneraria* and of the genus *Onobrychis* in Andalusia using data collected from the GBIF and our own data recorded in surveys relating to the following taxa: (1) *A. vulneraria*, including the subspecies *reuteri*, *maura*, *gandogeri*, *microcephala*, and *arundana*, but not *pseudoarundana* – a strict acidophile growing on shale soils in Sierra Nevada (Granada); (2) in the case of the genus *Onobrychis*, the distribution in Andalusia was modeled for the following species: *O. caput–galli*, *O. argentea*, *O. humilis*, *O. saxatilis*, *O. spartaea*, *O. stenorhiza*, and *O. viciifolia* together.

The variables used for the modeling of host plants were annual average temperature, annual precipitation, and pH in the first 30 centimeters of soil (Harmonized World Soil Database; FAO, 2009). The soil pH on a 5x5 km scale was extrapolated to a cell size of 1 km^2 using ArcGis.

The resulting predicted distributions were subsequently used as independent variables (table 1) in the models of the current potential distribution of the three species of butterfly.

For the modeling, Maxent used a number of presences for 'training' and others for the test. For *C. carswelli*: six for training and one for the test; *C. lorquinii* (65 and 8); *C. osiris* (8 and 1); the host plants *Onobrychis* (195 and 22) and *A. vulneraria* (661 and 74).

To avoid problems of co–linearity, non–parametric correlation analysis (Spearman *r*) was used to detect and eliminate environmental variables that were highly correlated with each other ($r \geq 0.80$) and therefore redundant (Elith et al., 2006, 2011; Merrow et al., 2013). Also discounted were variables whose contribution to the model was negligible. Thus, the number of predictor variables included in the models was reduced, thereby avoiding 'overfitting' (Kramer–Schadt et al., 2013; Fernández et al., 2015). The models were replicated 10 times for each species.

To assess the predictive ability of the model, we used the AUC (area under the receiver–operator curve) and the sensitivity (proportion of presences predicted correctly) and specificity (proportion of absences predicted correctly) (Pearce & Ferrier, 2000; Romo et al., 2013; Merrow et al., 2013; Obregón et al., 2014, in press; Fernández et al., 2015). An AUC value greater than 0.8 is considered to indicate a model with sufficient accuracy and reliability (Newbold et al., 2009).

Table 1. Environmental and ecological variables analyzed, references and units.

Tabla 1. Variables ambientales y ecológicas analizadas, referencias y unidades.

	Abbreviation	Source/Reference	Units
Environmental variables			
Mean temperature in warmest quarter	TWQ	AEMET	ºC
Precipitation in warmest quarter	PWQ	AEMET	mm
Precipitation in coldest quarter	PCQ	AEMET	mm
Altitude	ALT	Digital Elevation Model (DEM)	m
Ecological variable			
Occurrence probability of *A. vulneraria*	AVU	GBIF + unpublished own data	0–1
Occurrence probability of *Onobrychis*	ONO	GBIF + unpublished own data	0–1

Distribution in a climate change scenario

To investigate the possible effects of climate change on the distribution of the three species of *Cupido*, and given the high dependence of the three species of butterflies on their host plants, we constructed two separate models of the distribution of the host plants. We used the variables annual average temperature and annual precipitation, employing the values expected in a hypothetical scenario of climate change for Andalusia, as predicted by the IPCC (IPCC, 2014; scenario A2a), with a spatial resolution of 1 km^2. The IPCC (2014) estimates an increase in temperature of 0.2°C for each period of 10 years, with a maximum increase of 1.5–4.5ºC by the end of the 21st century.

The continuous logistical outputs of the Maxent models were converted into binary outputs according to the ETSS (Equal Training Sensitivity and Specificity) threshold, to represent the loss of potential habitat with respect to the model of current distribution. In the bitmap, the 1 km^2 squares with a probability below the ETSS threshold will have a value of 0 while those equal to or above the threshold will have a value of 1. Each model has a different ETSS threshold value.

Results

Map of the current distribution in Andalusia

The data published on the distribution of these three species of butterflies showed their presence in a total of 78 UTM squares of 100 km^2 (*C. lorquinii* = 65, *C. osiris* = 5, *C. carswelli* = 6). The data from new locations collected during 10 years of fieldwork provided a total of 33 new squares (*C. lorquinii* = 30, *C. osiris* = 2, *C. carswelli* = 1) in which their presence was recorded, representing an increase of 42.3%. Figure 1 shows the locations where the presence of each of the species was confirmed.

In the distribution of the known locations of *C. osiris* according to precipitation and annual average temperature, two locations were clear 'outliers' (red circles); these corresponded to the sites in the province of Cadiz cited by Ocete et al. (1985a, 1985b), which we consider erroneous identifications. In terms of potential niche, the optimum annual average temperature and annual precipitation for *C. osiris* and *C. carswelli* were very similar, with *C. lorquinii* being the most eurioic of the three species (fig. 2).

Because of the high specificity of the three species in terms of their use of host plants, we also updated the distribution in Andalusia of *A. vulneraria* (all subspecies together) and seven species of the genus *Onobrychis* (*O. caput–galli*, *O. argentea*, *O. humilis*, *O. saxatilis*, *O. stenorhiza*, and *O. viciifolia*). Figure 3 shows the known distribution maps of the species of the genus *Onobrychis* and of *A. vulneraria*, as well as the distribution of the host plants in Andalusia according to the model.

Models of the current potential distribution and under a future scenario of climate change

The logistical analysis with Maxent showed the contribution of the variables and the results of the AUC, sensitivity, and specificity tests to evaluate the models of the current potential distribution and future potential distribution (table 2). As can be seen, the three species are closely dependent on the distribution of their host plants, and on the precipitation of the coldest or warmest quarters of the year. Figure 1 shows the logistical outputs of the maps of the current potential distribution of the species.

Figure 4 shows the response curves of the two variables with the greatest weight in the respective models of the current distribution (excluding host plant variables), in relation to the probability of occurrence of the species. The most stenoic species were *C. osiris* and *C. carswelli*, which showed similar responses to

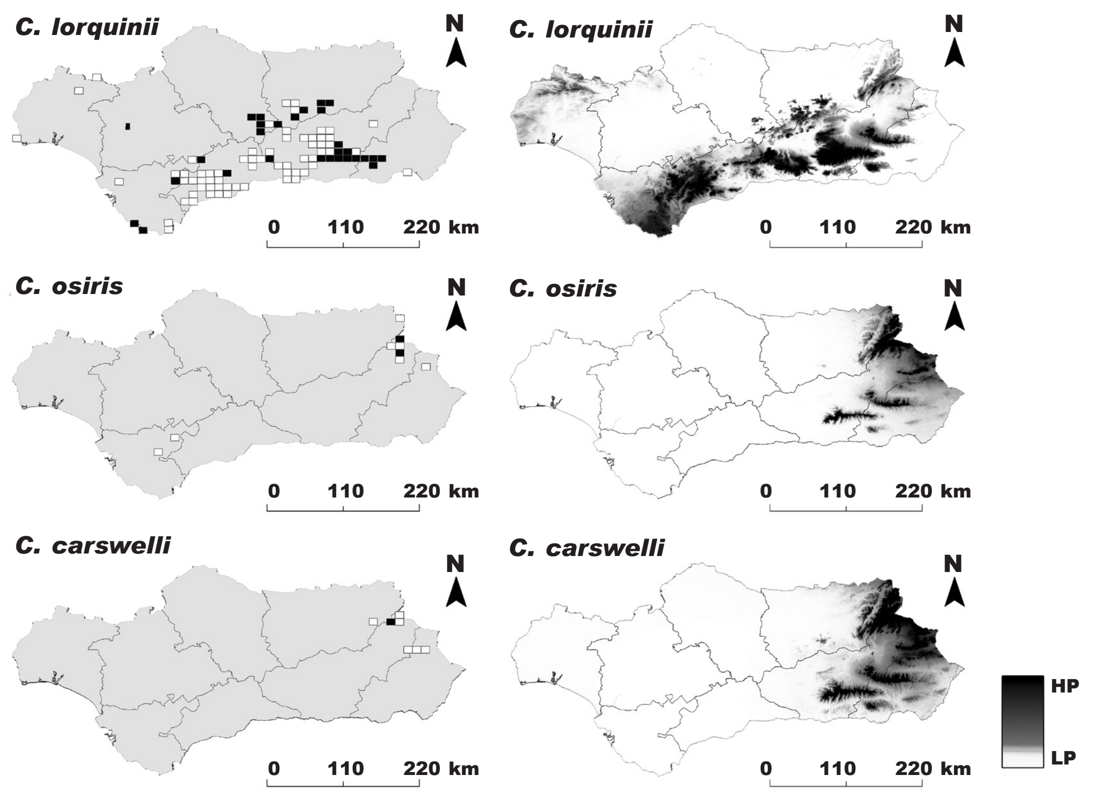

Fig. 1. Distribution map and current distribution model of species of the genus *Cupido* in Andalusia (southern Spain). Distribution maps: new UTM squares are in black and squares obtained from the bibliography are in white (UTM 10 km). Distribution model: in grey: low probability (LP) to high probability (HP) of occurrence (resolution of the squares: 1 km^2).

Fig. 1. Mapa de distribución y actual modelo de distribución de las especies del género Cupido *en Andalucía (sur de España). Mapas de distribución: en negro se muestran las nuevas cuadrículas UTM y en blanco, las bibliográficas (UTM 10 km). Modelo de distribución: es escala de grises: de menor probabilidad (LP) a mayor probabilidad (HP) de presencia (resolución de cuadrícula: 1 km^2).*

the variables PWQ and PCQ. The probability of presence increased with the precipitation accumulated in the warmest quarter and with decreasing precipitation in the coldest quarter —that, being mid–mountain areas, is usually in the form of snow. For *C. lorquinii*, an Ibero–North African species with greater environmental tolerance and more habitats in Andalusia, the probability of its presence rose with increasing ALT. In contrast, with decreasing TWQ, the probability of occurrence of *C. lorquinii* decreased significantly.

A comparative analysis of the model predictions of the current potential distribution and future potential distribution highlights significant differences, regarding the increase or decrease in potential habitat in the future climate change scenario (fig. 5). Resultant maps show a decrease in potential habitat in a global change scenario for the three *Cupido* species (black). This loss is remarkable in the most restricted distribution in Andalusia: *C. osiris* and *C. carswelli*.

Table 3 shows the number of 1 km^2 squares considered by the model as optimal habitat ($p \geq$ ETSS threshold) under current conditions and those predicted for the future climate change scenario according to the IPCC (2014), thus providing an estimate of the hypothetical loss of habitat that the latter would cause.

Discussion

Assessment of the status of populations of animals and plants is essential to prioritize the conservation of species and the habitats on which they depend, and is therefore crucial in the current biodiversity crisis. To carry out such assessment, key elements are a sufficiently detailed knowledge of their geographical distribution and, if necessary, the prediction of changes that may occur over time (Bartel & Sexton, 2009). Unfortunately, despite the efforts being made, substantial knowledge gaps in this field are impractical to solve by conducting systematic inventories due to constraints concerning time and resources (financial, human, logistic). For these reasons, species distribution

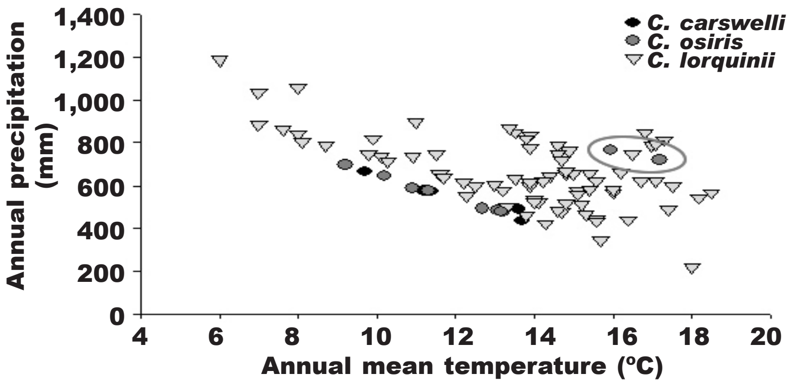

Fig. 2. Average annual temperature and rainfall recorded in the localities where *Cupido* species are present in Andalusia. *C. lorquinii* has a higher tolerance to both parameters than the other two species. The sites marked with a red circle (*C. osiris*) correspond to citations in the province of Cadiz that we consider erroneous (spatial resolution: 1 km^2).

Fig. 2. Temperatura media anual y precipitación anual registradas en las localidades en las que las especies del género Cupido *están presentes en Andalucía.* C. lorquinii *tiene una mayor tolerancia a ambos parámetros que las otras dos especies. Las localidades marcadas con un círculo rojo (*C. osiris*) corresponden a citas bibliográficas de la provincia de Cádiz que consideramos erróneas (resolución espacial: 1 km^2).*

models are becoming more and more useful (Heikkinen et al., 2007a; Gutiérrez–Illán et al., 2010).

As a result of our intensive field work over 10 consecutive years (2004–2014) and using unpublished data provided by other Andalusian entomologists we have significantly increased the number of known locations of the genus *Cupido* in Andalusia. Specifically, the number of 10 km^2 UTM squares occupied has been augmented by 30 for *C. lorquinii* (46%), by two for *C. osiris* (40%), and by one for *C. carswelli* (17%). When combined, this represents an increase of 42% in the number of grids occupied by these species.

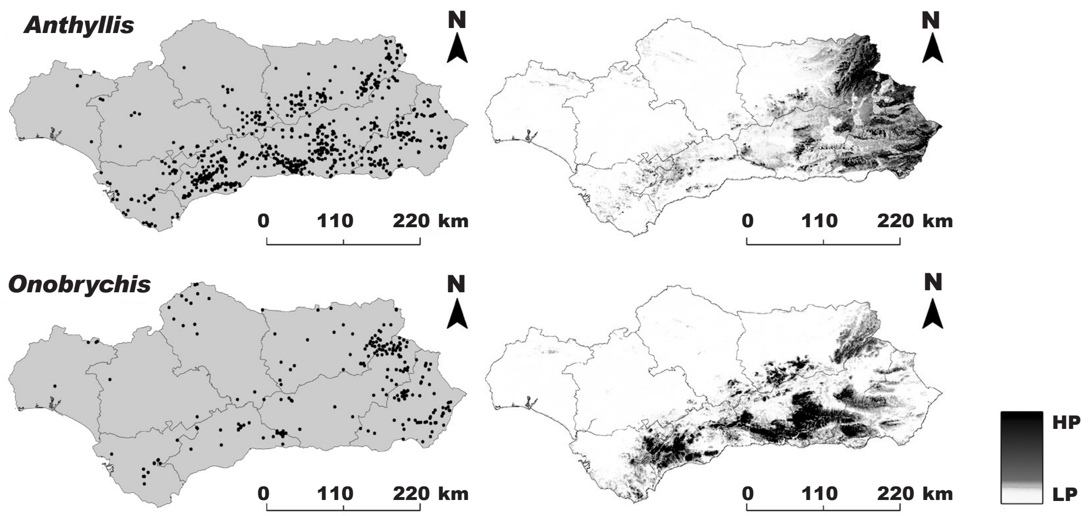

Fig. 3. Distribution map and current distribution model of *Anthyllis vulneraria* and species of the genus *Onobrychis*.

Fig. 3. Mapa de distribución y actual modelo de distribución de Anthyllis vulneraria *y las especies del género* Onobrychis.

Table 2. Predictive variable contributions (%) analyzed in the current and future distribution models, AUC, Sensitivity and Specificity tests, and equal training sensitivity and specificity (ETSS) threshold: Clr. *C. lorquinii;* Ccr. *C. carswelli;* Cos. *C. osiris*.

Tabla 2. Contribución (%) de las variables predictoras analizadas en los modelos de distribución actual y futuro, AUC, pruebas de sensibilidad y especificidad y umbral de igualdad de sensibilidad y especificidad en la calibración (ETSS en su sigla en inglés). (Para las otras abreviaturas, véase arriba.)

	Current model			Future model		
Environmental variable	Clr	Ccr	Cos	Clr	Ccr	Cos
Mean temperature in warmest quarter	2.9	10.0	2.1	82.1	0.6	0
Precipitation in warmest quarter	2.1	21.2	4.4	1.5	53.2	74.8
Precipitation in coldest quarter	2.1	10.2	2.3	16.5	46.2	25.2
Altitude	4.8	0	0	–	–	–
Occurrence probability of *A. vulneraria*	–	–	91.2	–	–	–
Occurrence probability of *Onobrychis*	88.1	58.6	–	–	–	–
ETSS threshold	0.351	0.484	0.357	0.509	0.614	0.459
AUC–scores	0.888	0.976	0.908	0.798	0.917	0.980
Sensitivity test	0.911	0.832	0.939	0.921	0.896	0.871
Specificity test	0.038	0.109	0.201	0.021	0.111	0.098

The three species of *Cupido* are distributed non–uniformly over Andalusia, as shown on the updated distribution maps, with a preference for mountainous areas of the Béticas ranges (the Subbéticos and Penibéticos Systems). The current distribution of the three species and their host plants in Andalusia is conditioned by previous sheltering from glaciers and the glacial–interglacial climatic variation. It is also largely a reflection of the landscape fragmentation that has occurred for centuries due to intensification of agriculture.

Today, the distribution of these Lycaenid species is restricted to mountainous areas with steep slopes, where farming is not viable. The dominance of calcareous soils in these mountains determines the probability of the presence of the host plants on which these species depend. In addition, significant differences in rainfall and temperature between the mountainous areas occupied by butterflies and the coastal areas, river valleys, and plains make these areas optimal locations for these Lycaenids. Based on these findings and on prior knowledge of the ecological requirements of these butterflies, we developed predictive models of their distribution and analyzed the contributions to the models of the variables used as predictors.

The ecological niche and distribution models are the initial step in the ecological study of a species (Khanum et al., 2013). They constitute an efficient tool that is widely used to gain insight into the set of conditions most suitable for the presence of the species tested, and hence indicate the locations where the probability of occurrence of the species is highest (Guisan & Zimmermann, 2000; Khanum et al., 2013). These models are valuable for planning and implementing conservation action and management. However, they often include only bio–climatic and, in some cases, topographical variables (Guisan et al., 1999; Gutiérrez–Illán et al., 2010), although anthropic factors —such as the types and intensity of land use (livestock, agriculture, urban development, reforestation, fire,...)— can significantly affect the distribution of species (Obregón et al., 2014; Bubová et al., 2015). These variables are difficult to quantify, so the models generated are credible only for those habitats where there is no significant, negative human disturbance. In our case, the robustness of the models was increased by the incorporation, as a predictor, of the distribution of host plants —a key component of the habitat of these butterflies which, in turn, responds to the effects of the anthropic factors mentioned above. Nevertheless, distribution models tend to overestimate the potential distribution areas, not taking into account other essential ecological interactions, including mutualism, competition, parasitism, etc. (Heikkinen et al., 2007b). In myrmecophilous lycaenid species, the presence of mutualistic ants is also of great importance, especially in obligate interactions (Filz & Schmitt, 2015).

In our models, the most important variables that had most weight were the presence of host plants, together with altitude and climatic variables: seasonal rainfall and temperature during the summer. The presence of their host plants, which show optimum growth in soils of pH 6.5–7.8, also conditions the occurrence of *Cupido* species. This ecological variable makes a strong contribution to the models: up to 91.2% for

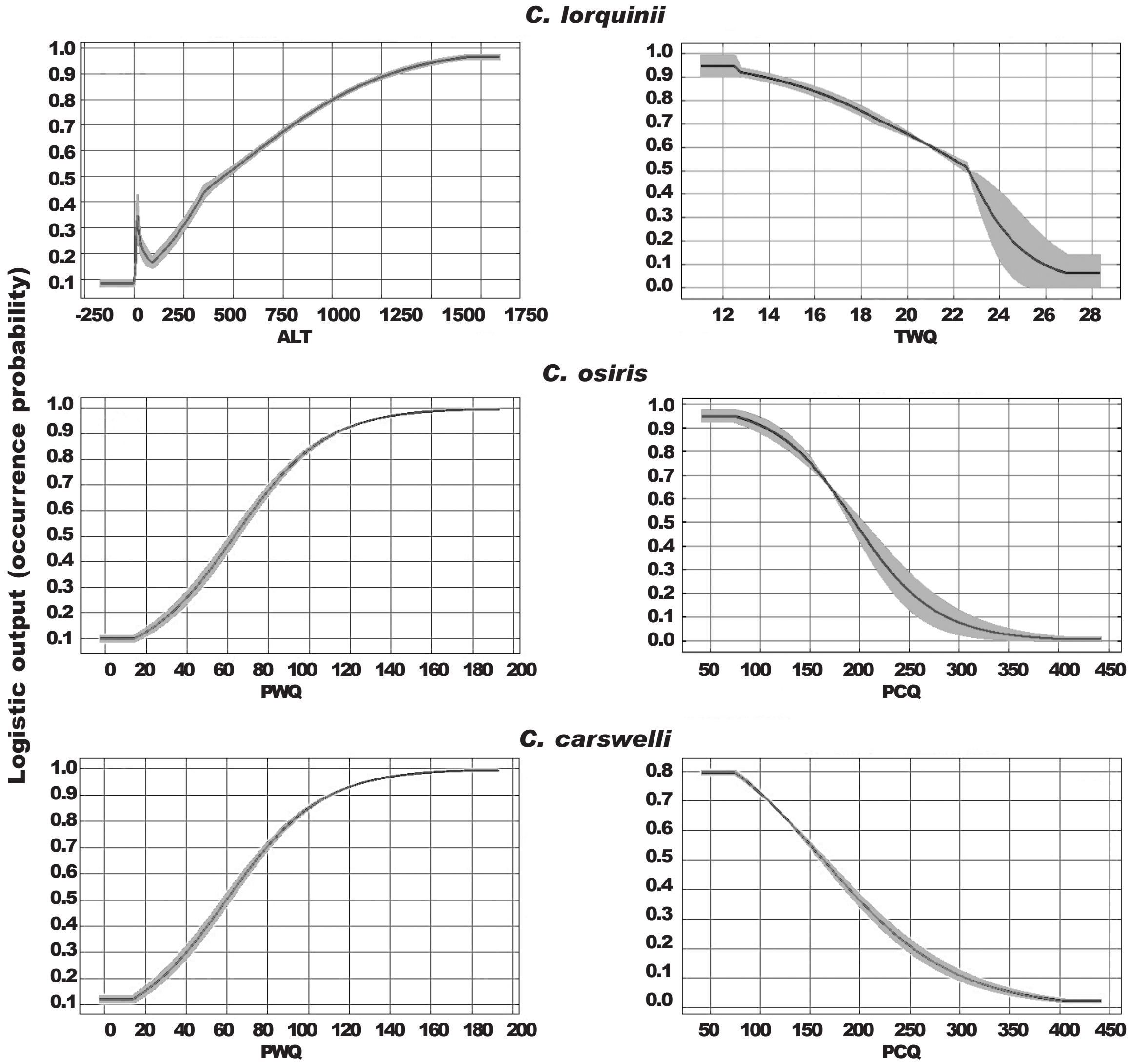

Fig. 4. Response curves (current model) showing the relationships between the probability of the presence of a species and the two top predictors (excluding the host–plant variable), for *C. lorquinii, C. osiris* and *C. carswelli*. Values shown are the averages of 10 replicate runs; grey margins show the standard deviation (SD) for 10 replicates: ALT. Altitude; TWQ. Temperature of the warmest quarter; PWQ. Precipitation of the warmest quarter; PCQ. Precipitation of the coldest quarter.

Fig. 4. Curvas de respuesta (modelo actual) que muestran la relación entre la probabilidad de presencia de una especie y las dos variables predictoras que más contribuyen al modelo (con exclusión de la variable de planta nutricia) de C. lorquinii, C. osiris *y* C. carswelli*. Los valores mostrados representan la media de las 10 réplicas del modelo; los márgenes en gris reflejan la desviación estándar (DE) de las 10 réplicas: Alt. Altitud; TWQ. Temperatura del trimestre más cálido; PWQ. Precipitación del trimestre más cálido; PCQ. Precipitación del trimestre más frío.*

C. osiris. For *C. carswelli,* the contribution of this variable is lower (58.6%), while climatic variables, such as precipitation in summer, are more important. Regarding the remaining variables, the precipitation during the summer or winter, when the preimaginal phases of *Cupido* are in diapause, may modify the survival of caterpillars. Altitude, as a variable, made no contribution to the models for the more stenoic species of *Cupido* (*C. osiris* and *C. carswelli*), while it was the variable with the second–greatest weight in the *C. lorquinii* model —a result of the broad altitudinal range of the localities where the presence of this species has been confirmed (7–1,885 m; mean = 923.8; SD = 486.9).

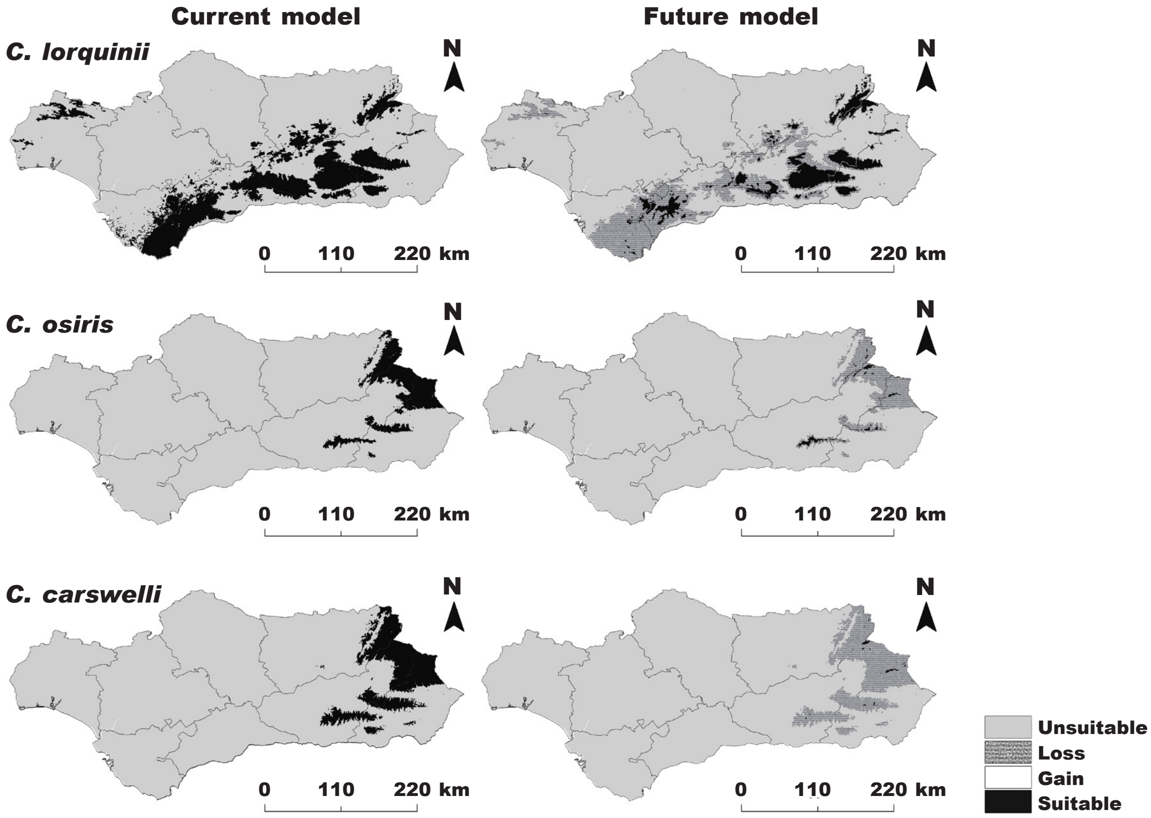

Fig. 5. Modeled current (suitable and unsuitable) and future (suitable, lost, gained and unsuitable) distribution for *Cupido* species. Current predictions are shown as a binarian map (grey ≥ equal training sensitivity and specificity threshold). Future predictions are based on an A2a emission scenario for 2050.

Fig. 5. Modelo de la distribución actual (óptimo y subóptimo) y futura (óptimo, pérdida de hábitat, ganancia de hábitat y subóptimo) de las especies del género Cupido*. Las predicciones actuales se muestran en un mapa binario (color gris ≥ umbral de igualdad de sensibilidad y especificidad en la calibración). Las predicciones futuras se basan en un escenario de cambio climático A2a para 2050.*

Using Maxent, we also modeled, the potential future distribution of the three species under the climate change scenario A2a (IPCC, 2014). In the model for *C. lorquinii*, the mean temperature of the warmest quarter was the variable with most weight. However, *C. carswelli* and *C. osiris* responded in a similar way to seasonal rainfall. In a climate scenario where the temperature increase at the end of the present century would range between 1.5 and 4.5°C (IPCC, 2014) and where the dynamics of rainfall would be affected, the models show a potential loss of habitat of up to 88.1% for *C. osiris*. In this future scenario, the areas with environmental features similar to those of the areas that the species inhabit currently would probably be found at higher altitudes, as has been observed with other species of similar mountain ranges (Gutiérrez–Illán et al., 2010), and at more northern latitudes.

In the case of *C. osiris*, habitat loss in Andalusia is easily interpretable because this species is widespread in Central Europe and because Andalusia represents the southernmost limit of its distribution (García–Barros et al., 2013). Within the northern Iberian peninsula, this species is mainly concentrated in mountainous areas with more xerophilous conditions in the northern third (the Cantabrian and Iberian mountains and the Pre–Pyrenees). That is why *C. osiris* populations in Andalusia are confined to mountain ranges with wet microclimates and mean summer maximum temperatures below 28°C, such as the La Sagra, Cazorla, Segura, and Orce Guillimona ranges. If we extended the predictive model to the whole of the Iberian peninsula, the trend of the loss of habitat with optimal conditions would be even more marked (our own data). In the *Climatic Risk Atlas of European Butterflies* (Settele et al., 2008), the predictions at the European level for *C. osiris* are for a loss of up to 95% of its potential habitat, which is why it has been included in the category HHHR (extremely high risk climate change). The *C. carswelli* model shows that its current endemic distribution, restricted to the NE

Table 3. UTM squares (1 km^2) with a probability of occurrence higher than the equal training sensitivity and specificity (ETSS) threshold, with respect to the total number of squares in Andalusia in the current and future models.

Tabla 3. Cuadrículas UTM (1 km^2) con probabilidad de presencia superior al umbral de igualdad de sensibilidad y especificidad en la calibración (ETSS en su sigla en inglés), respecto al total de cuadrículas de Andalucía para los modelos actual y futuro.

	UTM squares (1 km^2)		
	C. lorquinii	*C. osiris*	*C. carswelli*
Probability > ETSS (future model)	10,902 (11.8%)	498 (0.5%)	649 (0.7%)
Probability > ETSS (current model)	28,338 (30.7%)	3,953 (4.2%)	4,696 (5.0%)
Percentage of change (end of the XXI century)	–61.6%	–88.1%	–86.0%
∑ (total squares)	92,174	92,174	92,174

of Andalusia and Murcia, is a result of the probable extinction of the taxon in nearby mountains, although it is still possible to find it in similar enclaves near to the known populations. However, its restricted distribution and the barcoding data (Dincă et al., 2015) suggest a recent speciation process, starting from *C. lorquinii*. At present, no sympatric populations of *C. lorquinii* and *C. carswelli* have been detected, the Euclidean distance between their closest populations being 53 km. Alternatively, the intermediate morphology of their imagos and preimaginal stages suggests a hybrid between *C. mininus* and *C. lorquinii* as the possible origin of *C. carswelli*.

This prediction, of a drastic reduction in terms of potential habitat, is of particular concern for *C. carswelli* because it is the most vulnerable of these three species since it is endemic to the southeast of the Iberian peninsula.

In contrast, *C. lorquinii* is an Ibero–Maghreb species with a high environmental and ecological tolerance (Gil–T., 2002). This breadth of environmental niche is reflected in the results of the future model for Andalusia, its habitat loss (61.6%) being significantly lower than those of the other two species of *Cupido*. In addition, the decline in butterfly species may be related strongly to the loss of potential habitat for their host plants, on which they depend closely.

Currently, the possibility that these three species could expand their distribution is very limited due to the ongoing loss of natural habitats with optimal conditions. Fragmentation and management in the Andalusian mountain ranges and their surroundings inhibit the establishment of new populations, as for species of the genus *Pseudophilotes* (Obregón et al., 2014). This can be extrapolated to the sparse populations of *C. lorquinii*, which are isolated in mountains in the north of Huelva province, where the intense agrosilvopastoral management could accelerate their decline.

The maps and distribution models generated in this study should be used in the development of management and conservation plans for both the species concerned and their habitat; otherwise, their numbers could decrease and even disappear. This is the case for the Betic endemism *C. carswelli* and the relict populations of *C. osiris* from glacial refuges, for which stochastic phenomena, such as fires or changing land use in their ranges, could have irreversible consequences. According to the results generated by the future distribution models, we consider it necessary to extend the regional protection of *C. carswelli* to the European level. In the case of *C. osiris*, its scarce populations in Andalusia and their high vulnerability require a plan of conservation and protection at the regional level to safeguard the last relict populations in southern Europe.

Acknowledgments

The authors thank Felipe Gil–T. (Granada) for generously providing occurrence data, Javier López–Tirado (Univ. Huelva), Salvador Arenas (Univ. Córdoba) and Pilar Fernández (Univ. Córdoba) for their valuable comments on an earlier version of the manuscript, and Roger Vila and Vlad Dincă (Instituto de Biología Evolutiva; CSIC–Universitat Pompeu–Fabra, Barcelona) for their helpful comments concerning DNA bar–coding. We also wish to express our gratitude to the Editor and two anonymous reviewers for their valuable comments and suggestions to improve this paper.

References

Anderson, R. P., Lew, D., & Peterson, A. T., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162(3): 211–232.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoat, G. & Jeffcoat, S., 2001. *The Millennium Atlas of*

Butterflies in Britain & Ireland. Oxford University Press, Oxford.
Balmer, D. E., Gillings, S., Caffrey , B. J., Swann, R. L. & Fuller, R. J. (Eds.), 2013. *Bird Atlas 2007–11: The Breeding and Wintering Birds of Britain and Ireland*. BTO Books, Thetford, UK.
Balmford, A. & Bond, W. 2005. Trends in the state of nature and implications for human well–being. *Ecology Letters,* 8: 1218–1234.
Bartel, R. A. & Sexton, J. O., 2009. Monitoring habitat dynamics for rare and endangered species using satellite images and niche–based models. *Ecography,* 32: 888–896.
Bubová, T., Vrabec, V., Kulma, M. & Nowicki, P., 2015. Land Management impacts on European butterflies of conservation concern: a review. *Journal of Insect Conservation,* 19: 805–821.
Cuvelier, S. & Tarrier, M., 2002. *Cupido carswelli* Stempffer,1927, toujours présent dans la Sierra de Espuña (Murcia) (Lepidoptera, Lycaenidae). *Linneana Belgica*, 18(8): 391–395.
De Groot, M., Rebeusek, F., Grobelnik, V., Govedic, M, Salamun, A. & Verovnik, R., 2009. Distribution modelling as an approach to the conservation of a threatened alpine endemic butterfly (Lepidoptera: Satyridae). *European Journal of Entomology*, 106: 77–84.
Dincă, V., Montagud, S., Talavera, G., Hernández–Roldán, J., Munguira, M. L., García–Barros, E., Hebert P. D. N. & Vila, R., 2015. DNA barcode reference library for Iberian butterflies enables a continental–scale preview of potential cryptic diversity. *Scientific Reports*, 5: 12395.
Drake, J. M. & Bossenbroek, J. M., 2009. Profiling ecosystem vulnerability to invasion by zebra mussels with support vector machines. *Theoretical Ecology,* 2: 189–198.
Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC. M., Townsend Peterson, A., Phillips, S. J., Richardson, K., Scachetti–Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S. & Zimmermann, N. E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2): 129–151.
Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. & Yates, C. J., 2011. A statistical explanation of Maxent for ecologists. *Diversity and Distributions*, 17: 43–57.
ESRI, 2010. ArcGis10.2. Environmental System Research Institute Inc., Redlands, CA.
Fernández, D. & Nakamura, M., 2015. Estimation of spatial sampling effort based on presence–only data and accessibility. *Ecological Modelling,* 299: 147–155.
Fernández, P., Jordano D. & Fernández Haeger, J., 2015. Living on the edge in species distribution models: the unexpected presence of three species of butterflies in a protected area in southern Spain. *Ecological Modelling,* 312: 335–346.
Filz, K. J. & Schmitt, T., 2015. Niche overlap and host specificity in parasitic *Maculinea* butterflies (Lepidoptera: Lycaenidae) as a measure for potential extinction risks under climate change. *Org. Divers. Evol.*, 15: 555–565.
Fox, R., Brereton, T. M., Asher, J., Botham, M. S., Middlebrook, I., Roy, D. B. & Warren, M. S., 2011. *The State of the UK's Butterflies 2011*. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.
García–Barros, E., Munguira, M. L., Martín Cano, J., Romo–Benito, H., García–Pereira, P. & Maravalhas, E. S., 2004. Atlas de las mariposas diurnas de la Península Ibérica e Islas Baleares. *Monografía Sociedad Entomológica Aragonesa*, 11: 228.
García–Barros, E., Munguira, M. L., Stefanescu, C. & Vives Moreno, A., 2013. Lepidoptera Papilionoidea. In: *Fauna Ibérica*, vol. 37, (M. A. Ramos et al., Eds.) Museo Nacional de Ciencias Naturales–CSIC, Madrid.
GBIF, 2013. *The Global Biodiversity Information Facility*: GBIF Backbone Taxonomy. http://www.gbif.org/species
Gil–T., F., 1998. *Cupido carswelli* y *Cupido osiris*: Primeras citas para la provincia de Almería (Lepid.: Lycaenidae). *Boletín de la Sociedad Entomológica Aragonesa*, 22: 25–26.
– 2002. *Cupido lorquinii* (Herrich–Schäffer, 1847): datos inéditos sobre la biología de sus estadios preimaginales (Lepidoptera, Lycaenidae). Boletín de la Sociedad Entomológica Aragonesa, 31: 37–42.
– 2003. *Cupido carswelli*: descripción de sus estadios preimaginales, biología y distribución. La morfología de la crisálida, ¿clave para su rango específico? (Lepidoptera, Lycaenidae). *Boletín de la Sociedad Entomológica Aragonesa*, 32: 45–50.
– 2006. *Cupido carswelli* (Stempffer, 1927): Morphology of its chrysalis and genitalia compared with those of *Cupido* (Fuessly, 1775) and *Cupido lorquinii* (Herrich–Schäffer, 1847) (Lepidoptera, Lycaenidae). *Atalanta*, 37 (1/2): 150–160, 280–281.
– 2008. *Cupido carswelli* (Stempffer, 1927). In: *Libro Rojo de los Invertebrados de Andalucía*: 308–319 (J. M. Barea-Azcón, E. Ballesteros-Duperón & D. Moreno, Coords.). Ed. Consejería Medio Ambiente, Junta Andalucía, Sevilla.
Guisan, A., Weiss, S. & Weiss, A., 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology*, 143(1): 107–122.
Guisan, A. & Zimmermann, N. E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*, 135: 147–186.
Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A. & Zimmermann, N. E., 2006. Using niche–based models in improve the sampling of rare species. *Conservation Biology,* 20: 501–511.
Gutiérrez–Illán, J., Gutiérrez, D. & Wilson, R. J., 2010. Fine–scale determinants of butterfly species richness and composition in a mountain region. *Journal of biogeography*, 37: 1706–1720.
Heikkinen, R. K., Luoto, M., Kuussaari, M. & Toivonen,

T., 2007a. Modelling the spatial distribution of a threatened butterfly: impacts of scale and statistical technique. *Landscape and Urban Planning*, 79: 347–357.
Heikkinen, R. K., Luoto, M., Pearson, R. G. & Körber, J–H., 2007b. Biotic interactions improve prediction of boreal bird distributions at macro–scales. *Global Ecol. Biogeogr.,* 16: 754–763.
Hoyle, M. & James, M., 2005. Global warming, human population pressure and availability of the world's smallest butterfly. *Conservation Biology*, 19: 1113–1124.
Hortal, J., Jiménez–Valverde, A., Gómez, J. F., Lobo, J. M. & Balsega, A., 2008. Historical bias in biodiversity inventories affects the observed realized niche of the species. *Oikos*, 117: 847–858.
Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P. & Gaston. K. J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters* 18 (1), 28–36.
IPCC, 2014. *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R. K. Pachauri and L.A. Meyer, Eds.)]. IPCC, Geneva, Switzerland.
IUCN, 2012. *Red List Categories and Criteria,* Version 3.1, Second edition. (Gland, Switzerland and Cambridge, UK.
Khanum, R., Mumtaz, A. S. & Kumar, S., 2013. Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modeling. *Acta Oecologica*, 49: 23–31.
Kramer–Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder. B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A. K., Augeri, D. M., Cheyne, S. M., Hearn, A. J., Ross, J., Macdonald, D. W., Mathai, J., Eaton, J., Marshall, A. J., Semiadi, G., Rustam, R., Bernard, H., Alfred, R., Samejima, H., Duckworth, J. W., Breitenmoser–Wuersten, Ch., Belant, J. L., Hofer, H. & Wilting, A., 2013. The importante of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, 19(11): 1366–1379.
Kudrna, O., 2002. The distribution atlas of European butterflies. *Oedippus*, 20: 1–342.
Lara Ruiz, J., 2009. Contribución al conocimiento de las mariposas diurnas de las Sierras de Cazorla y Segura (Jaén) (Lepidoptera: Rhopalocera). *Boletín de la Sociedad Andaluza de Entomología*, 16: 33–41.
López–Vaamonde, C., Pino, J. J. & Martínez, A., 1994. Presencia de *Cupido osiris* (Meigen, 1829) en Galicia (Lepidoptera: Lycaenidae). *Boletín de la Asociación española de Entomología*, 18: 3–4.
Martín, J. & Gurrea, P., 1990. The peninsular effect in Iberian butterflies (Lepidoptera: Papilionoidea and Hesperioidea). *Journal of Biogeography*, 17: 85–96.
Merow, C., Smith, M. J. & Silander, J. A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography,* 36: 1058–1069.
Munguira, M. L., García–Barros, E. & Martín, J., 1997. Plantas nutricias de los licénidos y satirinos españoles (Lepidoptera: Lycaenidae y Nymphalidae). *Boletín de la Asociación española de Entomología*, 21(1–2): 29–53.
Newbold, T., Reader, T., Zalat, S., El–Gabbas, A. & Gilbert, F., 2009. Effect of characteristics of butterfly species on the accuracy of distribution models in an arid environment. *Biodiversity and Conservation*, 18: 3629–3641.
Obregón, R., 2011. Nueva localidad y confirmación de *Cupido carswelli* (Stempffer, 1927), endemismo ibérico, en la provincia de Jaén (NE. Andalucía) (Lepidoptera, Lycaenidae). *Boletín Sociedad Andaluza Entomología*, 17: 7–11.
Obregón, R., Arenas–Castro, S., Gil–T., F., Jordano, D. & Fernández–Haeger, J., 2014. Biología, ecología y modelo de distribución de las especies del género *Pseudophilotes* Beuret, 1958 en Andalucía (Sur de España) (Lepidoptera: Lycaenidae). *SHILAP Revista de Lepidopterología*, 42(168): 501–515.
Obregón, R., Fernández Haeger, J., López Tirado, J., Moreno Benítez, J. M. & Jordano, D. (in press). Updating distribution of *Borbo borbonica* (Boisduval, 1833) in southern Iberian Peninsula (Lepidoptera, Hesperiidae). Potential and future distribution models. *North Western Journal of Zoology.*
Obregón, R. & Gil–T., F., 2015. Correcciones y aportaciones corológicas para seis lepidópteros eurosiberianos de restringida distribución en Andalucía (S. España), en el límite meridional europeo (Lepidoptera, Nymphalidae). *Revista de la Sociedad Gaditana de Historia Natural*, 9: 21–26.
Ocete, E., Izquierdo, M. & Molina, J. M., 1985a. Citas nuevas de interés para las provincias de Sevilla y Cádiz, *SHILAP Revista de Lepidopterología*, 13(49): 45–50.
– 1985b. Rectificaciones sobre las citas de Cádiz. *SHILAP Revista de Lepidopterología*, 13(52): 274.
Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change*. Annual Review of Ecology, Evolution and Systematics*, 37: 637–669.
Parmesan, C. & Yohe, G., 2003. A globally coherent finger–print of climate change impacts across natural systems. *Nature*, 421: 37–42.
Pearce, J. & Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, 133: 225–245.
(PECBMS) BirdLife International, 2013. *Europe–wide monitoring schemes highlight declines in widespread farmland birds*. Presented as part of the BirdLife State of the world's birds website. Available from: http://www.birdlife.org/datazone/sowb/casestudy/62.
Phillips, S. J., Anderson, R. P. & Schapired, R. E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190: 231–259.
Phillips, S. J. & Dudik, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31: 161–175.
Romo, H. & García–Barros, E., 2005. Distribución

e intensidad de los estudios faunísticos sobre mariposas diurnas de la Península Ibérica e islas Baleares (Lepidoptera, Papilionoidea y Hesperioidea). *Graellsia*, 61(1): 37–50.

– 2010. Biogeographic regions of the Iberian Peninsula: butterflies as biogeographical indicators. *Journal of Zoology*, 282(3): 180–190.

Romo, H., García–Barros, E. & Lobo, J. M., 2006. Identifying recorder–induced geographic bias in an Iberian butterfliy database. *Ecography*, 29: 873–885.

Romo, H., García–Barros, E., Márquez, L., Moreno, J. C. & Real, R., 2014. Effects of climate change on the distribution of ecologically interacting species: butterflies and their main food plants in Spain. *Ecography*, 37: 1063–107.

Romo, H., Sanabria, P. & García–Barros, E., 2013. Predicción de los impactos de cambio climático en la distribución sobre las especies de Lepidoptera. El caso del género Boloria Moore, 1900 en la Península Ibérica (Lepidoptera: Nymphalidae). *SHILAP Revista de lepidopterología*, 41(162): 267–286.

Settele, J., Kudrna, O., Harpke, A., Kühn, I., van Swaay, C., Verovnik, R., Warren, M. S., Wiemers, M., Hanspach, J., Hickler, T., Kühn, E., van Halder, I., Kars Veling, K., Vliegenthart, A., Irma Wynhoff, I. & Schweiger, O., 2008. *Climatic risk atlas of European butterflies.* Pensoft, Moscow.

Soberón, J., Llorente, J. & Benítez, H., 1996. An international view of national biological surveys. *Annals of the Missouri Botanical Garden*, 83: 562–573.

Thuiller, W., 2003. Biomod – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9: 1353–1362.