Distribution models of the Spanish argus and its food plant, the storksbill, suggest resilience to climate change

A. Zarzo–Arias, H. Romo, J. C. Moreno, M. L. Munguira

Abstract

Distribution models of the Spanish argus and its food plant, the storksbill, suggest resilience to climate change. Climate change is an important risk factor for the survival of butterflies and other species. In this study, we developed predictive models that show the potentially favourable areas for a lepidopteran endemic to the Iberian Peninsula, the Spanish argus (*Aricia morronensis*), and its larval food plants, the storksbill (genus *Erodium*). We used species distribution modelling software (MaxEnt) to perform the models in the present and in the future in two climatic scenarios based on climatic and topographic variables. The results show that climate change will not significantly affect *A. morronensis* distribution, and may even slightly favour its expansion. Some plants may undergo a small reduction in habitat favourability. However, it seems that the interaction between this butterfly and its food plants is unlikely to be significantly affected by climate change.

Key words: Distribution models, Climate change, Interaction, Butterfly, Larval food plants, MaxEnt

Resumen

Los modelos de distribución de la morena española y las plantas nutricias de sus larvas sugieren resistencia frente al cambio climático. El cambio climático representa un importante factor de riesgo para la supervivencia de las mariposas y de otras especies. En este estudio se han elaborado modelos predictivos que muestran las zonas potencialmente favorables para un lepidóptero endémico de la península ibérica, la morena española (*Aricia morronensis*), y las plantas nutricias de sus larvas, los alfilerillos o agujas de pastor (género *Erodium*). Se ha utilizado el programa informático MaxEnt para elaborar modelos de la distribución de las especies en el presente y en el futuro, bajo dos escenarios de condiciones climáticas, basadas en variables climáticas y topográficas. Los resultados muestran que el cambio climático no afectará significativamente a la distribución de *A. morronensis*, sino que incluso podría favorecer levemente su expansión. Algunas de las plantas podrían sufrir una pequeña reducción de la favorabilidad del hábitat. Sin embargo, la interacción entre la mariposa y sus plantas nutricias probablemente no se vea afectada significativamente por el cambio climático.

Palabras clave: Modelos de distribución, Cambio climático, Interacción, Mariposa, Plantas nutricias de las larvas, MaxEnt

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Introduction

The effects of climate change are subject to much attention in conservation studies due to their influence on biodiversity, the changes produced on populations, communities and ecosystem dynamics, and the biotic interactions (Walther, 2010; Dawson et al., 2011; Giannini et al., 2013). One relevant effect is the temporal and spatial mismatch between life cycles and resource availability, particularly threatening for herbivore insects (Cornelissen, 2011; Bellard et al., 2012). These insects also appear to be negatively affected by climate change because of their sensitivity to changes in the environment, particularly temperature (Wilson and Maclean, 2011). Butterflies have proven to be good climate change indicators, and have commonly been used to assess its effects (Roy et al., 2001; Walther et al., 2002; Diamond et al., 2011). Settele et al. (2008) performed climate change models for all European butterflies of the superfamily Papilionoidea to assess the risk it could represent to the European butterfly species. Their results suggest a severe loss of climatically suitable habitat for most species.

In this study we focused on the Spanish argus butterfly, *Aricia morronensis* (Ribbe, 1910) (Lycaenidae, Lepidoptera), an Iberian endemic species that can be found above 1,000 meters in the Peninsula, occupying most of the main mountain systems. Munguira and Martín (1988) stated that this species could have occupied lower altitude habitats, and that the postglacial rising of temperatures may have forced it to move to higher elevations as is currently occurring in several butterfly species in response to climate change (Hill et al., 2002; Konvica et al., 2003; Wilson et al., 2007). Nowadays, as *A. morronensis* only occupies high–altitude habitats, climate change can potentially represent a threat to this species (Dirnböck et al., 2011; Stefanescu et al., 2011; Lambers, 2015). It was listed as endangered by De Viedma and Gómez–Bustillo (1976), but was later considered out of danger by Munguira (1989), although its endemic character and the fact that it is not included in Settele's et al. (2008) atlas still raises interest from the conservation point of view. Furthermore, although most butterfly species are influenced by climate, other factors related to habitat quality and composition can determine their survival (Stefanescu et al., 2004; Brückmann et al., 2010; Krämer et al., 2012). Therefore, it seems of great importance to study how *A. morronensis* is able to cope with potential future shifts under global change in order to take the necessary conservation measures. Besides, recently performed genetic studies show that this species could be split into two different entities according to its distribution (Dincă et al., 2015). With this subdivision, some of the butterfly's populations could be highly restricted and thus endangered.

To increase effectiveness in predicting the evolution of these butterfly populations, in this study we considered the interaction between *A. morronensis* and its food plants, as suggested by Gilman et al. (2010), Romo et al. (2014) or Valiente–Banuet et al. (2015). The butterfly is a stenophagous species, and its larvae only feed on some perennial species of the plant genus *Erodium* L'Her. (storksbills, Geraniaceae). The species can survive feeding on any of the five species mentioned by Munguira and Martín (1988), but only one species is used in each location on which the species was found. Besides, in captivity larvae can survive using common annual *Erodium* species, but these species were never recorded in the field (Munguira, unpublished data). Therefore, its survival also depends on the future distribution of these plants, which may also be influenced by climate change, and on their interaction (Thuiller et al., 2005; Romo et al., 2014). According to systematic reviews conducted by Fiz–Palacios et al. (2010) and Alarcón et al. (2012), *A. morronensis* feeds on the following five *Erodium* species: *E. carvifolium* Boiss. and Reut, *E. cazorlanum* Heywood, *E. daucoides* Boiss, *E. foetidum* (L.) Rothm and *E. glandulosum* Dumort. *E. cazorlanum* is also interesting because it is an endemic plant catalogued as Vulnerable. The butterfly lays its eggs on the plant leaves during the summer flight period. Larvae feed on the leaves of the plant and overwinter at the third or fourth larval instar. Pupation takes place in the late spring and the pupal stage lasts 10 days on average (García–Barros et al., 2013).

Distribution and habitat suitability models are useful tools in fields like ecology and biogeography (Guisan and Zimmermann, 2000; Elith et al., 2011; Titeux et al., 2016). They can provide information about the consequences of climate change on the species distribution (Elith et al., 2010). The effect of climate change has been studied for many butterfly species, showing a significant reduction on their distribution range that would eventually lead to future extinctions in most cases (Settele et al., 2008; Romo et al., 2015). These models can also serve as a basis for spatial planning and they can provide tools for an optimum conservation strategy (Kearney et al., 2010). When building potential distribution models, the main problem is the lack of information, attached to poor coverage of the territories due to insufficient sampling efforts (Ramos et al., 2001). As Romo and García–Barros (2005) concluded, the sampling effort on butterflies in the Iberian Peninsula showed a geographic bias, which supports the usefulness of potential distribution models in order to improve the knowledge about this group. However, the endemic character of the study species has attracted the interest of butterfly experts and our knowledge of the species distribution has increased substantially (around 600 %) in the last 40 years.

From among the software available to perform potential distribution models, we selected MaxEnt (Philips et al., 2006) given that it is based on species presence–only data and has been widely used to successfully predict species distribution (Pliscoff and Fuentes–Castillo, 2011; Syfert et al., 2013). This program is based on maximum entropy to model the potential distribution of a species from their presence distribution points and geographical information (variables) available. These variables impose restrictions on the distribution of the species, so the obtained models will show the suitability of the predicted area for the presence of this species.

The updated known distribution of the butterfly *A. morronensis* and the storksbills that serve as food plants for its larvae were considered in the main objectives of this study, which were: (1) to create potential distribution models for the butterfly and its food plants; (2) to project these into the future using different climate change scenarios; (3) to combine the two models (interaction butterfly–plant) to see how climate change will affect the biotic interaction between these species; and (4) to discuss whether conservation measures are necessary for the butterfly and/or its food plants.

Methods

Study area and species occurrence data

The taxa of the study include an Iberian endemic butterfly (*A. morronensis*) and the five *Erodium* species on which the larvae of the butterfly feed. Although some of these plants species have a wider distribution, the study area of this paper focuses only on their range within the Iberian Peninsula. MGRS (Military Grid Reference System) network with squares of 10 x 10 km was selected as operative geographic units. The occurrence data of the butterfly was taken from García–Barros et al. (2004), and updated to 2016 from different references (Gil–T, 2009; Vicente Arranz and Parra Arjona, 2010; Manceñido González and González Estébanez, 2013; Monasterio León et al., 2014; and unpublished data) resulting in a total of 124 10 x 10 km MGRS squares, which were used to run the models.

Data concerning presence of the food plants was first taken from bibliographic and public electronic sources. Several distribution atlases were revised (Aseginolaza et al., 1984; Villar et al., 1997; Uribe–Etxebarria et al., 2006; Serra Laliga, 2007; Alejandre et al., 2009) and data were incorporated from different websites as SIVIM (http://sivim.info/sivi/), ANTHOS (http://www.anthos.es/), GBIF (http://www.gbif.org/species/), BDBC (http://biodiver.bio.ub.es/biocat/), ORCA (http://biodiver.bio.ub.es/orca/) and the Atlas of Flora of Aragón (http://proyectos.ipe.csic.es/floragon/index.php). All these electronic datasets were checked in November 2014 and all data were georeferred when coordinates were not available. Doubtful occurrences were filtered and deleted following the criteria of Alarcón et al. (2012) and expert opinion, which resulted in a total of 81 presence squares for *E. carvifolium*, 11 for *E. cazorlanum*, 51 for *E. daucoides*, 166 for *E. foetidum* and 132 for *E. glandulosum* to build the models.

Variables

We selected climatic and non–climatic variables (topographic, spatial, human activity and geological related variables) to build the potential distribution models (table 1s of the supplementary material). The bioclimatic variables came from WorldClim database (http://www.worldclim.org/) and were described by Hijmans et al. (2005). The remaining variables came from the GLCF (Global Land Cover Facility) database. All the variables were obtained in a 5 arc–minute resolution, which is the most similar to our species presence data resolution (MGRS 10 x 10 km), and correspond to the mean value of the variable in each cell, except for landcover, which represents the main landcover type in the cell.

To run the models we excluded the variables that were correlated to other variables (Pearson correlation coefficient > 0.7 with SPSS version 15.0 [SPSS, 2006] [Braunisch et al., 2013]), keeping in that case only the most biologically relevant variable for the species. With the final set of uncorrelated variables, we obtained a potential distribution model for the present situation that was then projected to future scenarios, retaining the climatic and non–climatic variables that will not change in the future. All these variables used to build the models are shown in table 1s of the supplementary material.

The models were projected to two future periods: 2041–2060 (2050) and 2061–2080 (2070), using the general circulation model (GCM) CCSM4 (Community Climate System Model from the University Corporation for Atmospheric Research, UCAR). They were performed under two Representative Concentration Pathways (RPCs) scenarios (2.6 and 8.5) that differ in climate change severity. RPC 2.6 assumes that global annual greenhouse gas emissions will peak between 2010 and 2020 and then decline with a global mean temperature rise of 1 ºC. RPC 8.5 infers a continuous increase throughout the 21st century, estimating a rise between 2 ºC and 3.7 ºC until 2100 (Meinshausen et al., 2011; IPCC, 2013).

Modelling potential distribution maps

To build the potential distribution maps, we used the Maxent program, version 3.3.3 k (Phillips et al., 2006). Maxent works better than other techniques with low sample sizes (Hernández et al., 2006; Pearson et al., 2007; Kumar and Stohlgren, 2009) and it can also be used alone to produce accurate models (Fernández et al., 2015; Fourcade et al., 2017; Jacinto–Padilla et al., 2017). We considered the default parameters (10^{-6} convergence limit, 10,000 background points) recommended by Phillips et al. (2006). Fifteen replicates were performed for each model with 5,000 maximum iterations and subsample replicated run type (Young et al., 2011) using the logistic output format that is easier to interpret (Phillips and Dudik, 2008). We used 75 % of the data to build the models, and the remaining 25 % were randomly used to validate their quality, following other authors (Pawar et al., 2007; Davis and Cipollini, 2016). With *E. cazorlanum*, and because its number of presence occurrence data was < 25, we used the Jacknife (leave–one–out) procedure recommended by Pearson et al. (2007). In this case, we built as many models as number of known presences we had (11), and removed in each model, one of the occurrence points each time to perform it.

For each species, we built a present potential distribution model that was projected to the future in two emission scenarios (2.6 and 8.5) for 2041–2060 and 2061–2080 considering all the variables specified in table 1s of the supplementary material. Then, we built

Table 1. Percentage contribution to the distribution models of the main environmental and climatic variables included in the models of the butterfly *A. morronensis* and its larval food plants of the genus *Erodium.* The values of the variables that most contributed to the performance of the model in each species are highlighted in bold: Amr, *A. morronensis*; Ecr, *E. carvifolium*, Ecz, *E. cazorlanum*; Edc, *E. daucoides*; Eft, *E. foetidum*; Egl, *E. glandulosum.*

Tabla 1. Porcentaje de contribución a los modelos de distribución de las variables ambientales y climáticas más importantes incluidas en los modelos de la mariposa A. morronensis *y las plantas nutricias de sus larvas del género* Erodium. *Los valores de las variables que más contribuyeron a la realización del modelo de cada especie se resaltan en negrita. (Para las abreviaturas de las especies, véase arriba).*

Variables	Species					
	Amr	Ecr	Ecz	Edc	Eft	Egl
Elevation	**46.6**	**40.3**	7.1	**28.3**	–	–
Slope	27.4	1.8	21.4	14.2	27.1	10.4
Mean temperature of wettest quarter	6.5	2.6	–	4.5	0.7	6.5
Latitude	1.9	21	15.5	–	**37.9**	–
Precipitation of wettest quarter	–	12.1	–	–	–	–
Annual temperature range	–	–	**28.4**	2.2	–	–
Longitude	–	–	15.8	25.1	20.4	2.7
Calcareous/siliceous	3.8	8.4	–	17.3	0.8	
Precipitation of driest month	–	–	–	–	–	**53.8**
Mean temperature of driest quarter	3.2	7.5	–	6.1	0.6	10.7

a model representing the interaction butterfly–food plants (in present and future scenarios) overlapping the model of the butterfly and the sum of the plant species in each period, by calculating the minimum number of squares that they had in common.

As representation threshold we used the 'equal training sensitivity and specificity logistic threshold', since it is one of the five best–suited thresholds recommended by Liu et al. (2005). However, it presented very low values and did not fit the known distribution of the species. Therefore, to adjust the predictions to the most favourable areas, we chose the mean suitability value predicted by the models for the upper 75 % of all MGRS presence points, revealed to be 0.6. For this purpose, we extracted the suitability values (0–1) of each pixel given by the models with QGIS 2.6.0 (Quantum GIS Development Team, 2015) and made the average of the 75 % of the grids with higher values. This means that values given by the models higher than 0.6 were considered as very favourable areas for the presence of the species, due to the good adequacy of the considered variables.

We measured the change in favourable areas for the species according to the different future scenarios. For this purpose, we compared the percentage of pixels above the threshold mentioned before (0.6) within the different models and scenarios. Finally, favourable areas for the present models of the butterfly and the plants were extracted to study their intersection with the Spanish network of protected areas (http://www.mapama.gob.es/).

Model validation

To evaluate the models, first we used the AUC (Area Under a Receiver Operating Characteristic –ROC– Curve) value, which shows the accuracy of the model (Newbold et al., 2009). AUC values between 0.7 and 1 mean that the model is well fitted and is better than one randomly classified (Pearce and Ferrier, 2000; Philips and Dudík, 2008).

We next used the equal training sensitivity and specificity logistic threshold (Liu et al., 2005) to calculate a classification percentage (obtained as the number of test locations with predicted probabilities above this threshold divided by the total number of test locations), which shows the number of squares that have been well classified (Baldwin and Bender, 2008).

Finally, the statistical significance of the models was calculated using the 11 omission binomial default tests given by MaxEnt (Phillips et al., 2006).

Results

Significant variables

Due to the minimum contribution of some of the non–climatic variables (such as landcover or sun radiation) to the present potential distribution models of all species (table 2s of the supplementary material), we did not include them in the comparison between future and current potential distribution models. This is

because the same variables are needed to compare the different models.

In our models, the variable that most contributed (47 %) to the performance of the models for *A. morronensis* was elevation. This variable was highly correlated to the annual mean temperature (Pearson coefficient –0.87) that was not included in the models. For two of the larval food plant species (*E. carvifolium* and *E. daucoides*), elevation was also the variable with major contribution, but latitude, annual temperature range and precipitation of the driest month were also important to build the models for *E. foetidum, E. cazorlanum* and *E. glandulosum* respectively (table 1). Slope, latitude and longitude were also important for the interaction model that considered the butterfly and its food plants. Table 3s of the supplementary material presents the contribution percentage of all the variables to the projected and not projected to the future models for the butterfly and its larval food plants.

Present potential distribution models

Most of the known occurrence points of the species appeared in suitable areas, in accordance with the prediction of the present distribution models obtained with MaxEnt for the butterfly (fig. 1) and for the plants (fig. 2). For *A. morronensis, E. cazorlanum* and *E. daucoides* more than 50 % of the areas predicted as suitable appear within the limits of the Spanish network of protected areas.

The result of overlapping the present potential distribution model obtained with MaxEnt for the butterfly and the sum of the five plant species showed a lower amount of favourable squares (fig. 3). For this map, only the minimum number of squares that they had in common was represented (see methods).

Future potential distribution models

Future potential distribution models show a slight increase in the number of favourable squares, both for the butterfly and for the joint model for the plant species, especially in the most radical scenario (8.5) in 2070 (fig. 4).

We overlapped these maps (butterfly and plants), using the same procedure used for the present potential distribution model (fig. 5), to obtain the future representation of the interaction between the butterfly and its food plants in 2070, which better shows the real probable scenario for *A. morronensis*.

We calculated the percentage of favourable habitat loss for each species above the 75 % upper threshold selected to represent a major probability of occurrence (0.6) as the difference between potential present and future distribution models for the butterfly, for each plant and for their interaction (table 2). Negative values imply loss of favourable areas for the species. The species predicted to lose favourable habitat in most scenarios and periods are *E. carvifolium, E. foetidum* and *E. glandulosum*, with *E. foetidum* having the greatest losses (between 19 and 20 % of its favourable habitat), while for the other species and for their interaction with the butterfly, suitable areas slightly improve.
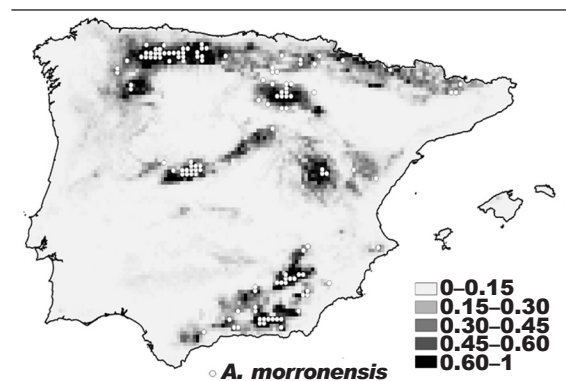

Fig 1. Occurrence data and present potential distribution model of *A. morronensis*. Known records and present potential distribution model obtained with MaxEnt for *A. morronensis* are shown. White dots represent its currently known distribution and darker colours show most favourable areas for the species.

Fig. 1. Datos de distribución y modelo de distribución potencial en el presente de A. morronensis. *Se muestran las presencias conocidas y el modelo de distribución potencial en el presente obtenido con MaxEnt para* A. morronensis. *Los puntos blancos representan la distribución actual conocida y los colores más oscuros muestran las zonas más favorables para la especie.*

Model validation

All AUC values were above 0.9 (table 3), showing that the developed models are suitable and have a high discriminatory power. More than 78 % of the squares presented logistical probability values with greater probability than that required for each model (classification percentage in table 3), supporting their reliability and showing that at least 78 % of the grids were correctly classified as favourable areas for the species. The 11 binomial default tests worked out with MaxEnt had values of statistical significance smaller than 0.01 for all species except *E. cazorlanum* (table 3), showing that the prediction can be considered reliable for most species.

Discussion

As ectothermic animals, butterflies appear to be highly influenced by climate, mainly temperature (Steigenga and Fischer, 2009). Supporting this idea, our study shows that elevation, which is highly correlated to temperature (Pearson coefficient of –0.87), is the variable that mainly contributes to the potential distribution models of *A. morronensis* (46.6% contribution). Thus, climate change that will produce global increases in temperature could potentially be a threat to this spe-
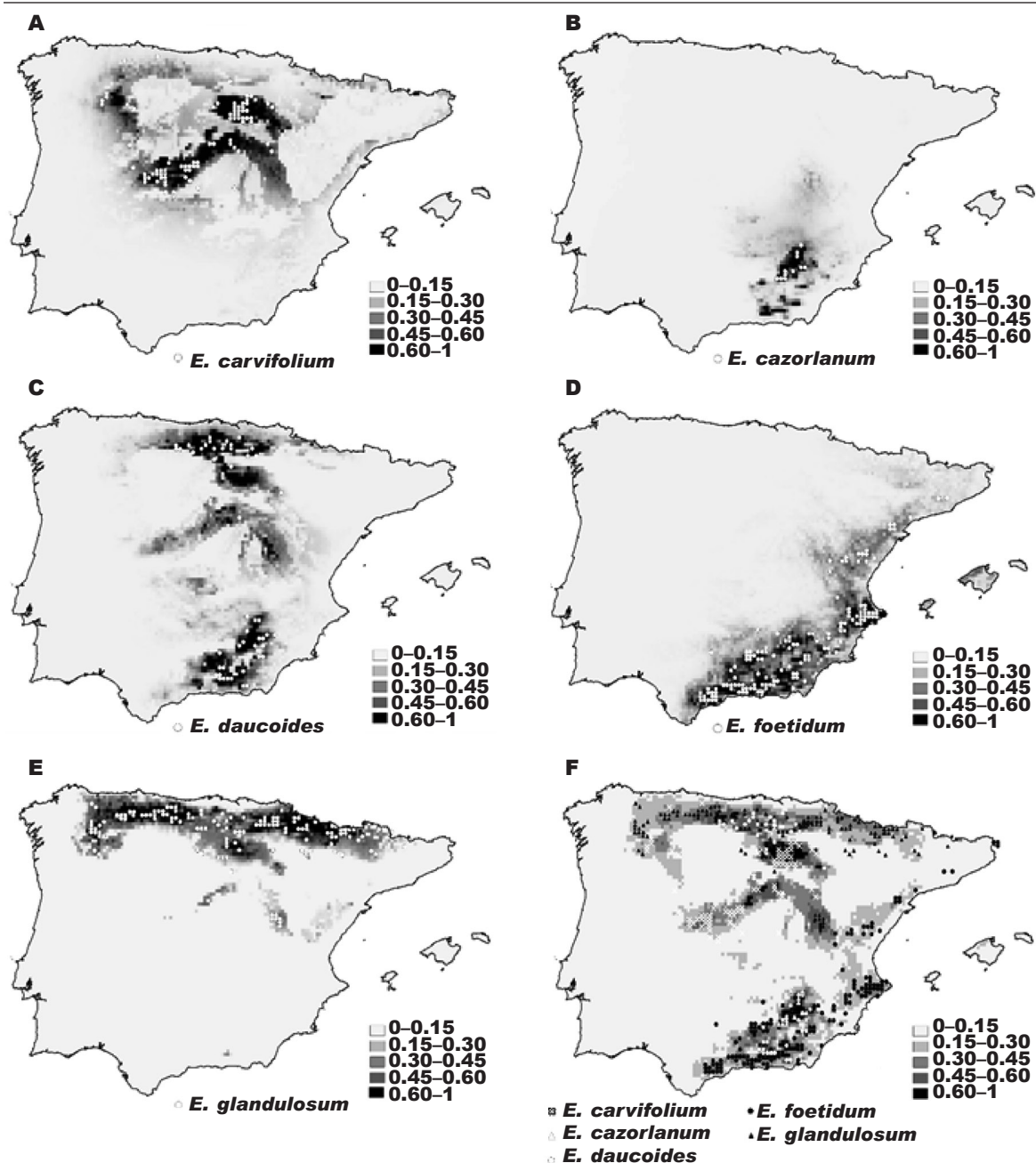
Fig. 2. Occurrence data and present potential distribution models of all *Erodium* species. Known records and present distribution models obtained with MaxEnt for each *Erodium* species that are used by *A. morronensis* larval stage are shown: A, *E. carvifolium*; B, *E. cazorlanum*; C, *E. daucoides*; D, *E. foetidum*; E, *E. glandulosum*. White dots represent the currently known distribution of each species. The last figure (F) represents the sum of all *Erodium* present potential distribution models, with symbols for the known distribution of each species. Darker colours show more favourable areas for the species.

Fig. 2. Datos de distribución y modelos de distribución potencial en el presente de todas las especies de Erodium. *Se muestran las presencias conocidas y los modelos de distribución potencial en el presente obtenidos con MaxEnt para cada especie de* Erodium *utilizada por* A. morronensis *en su estado larvario: A,* E. carvifolium; *B,* E. cazorlanum; *C,* E. daucoides; *D,* E. foetidum; *E,* E. glandulosum. *Los puntos blancos representan la distribución actual de cada especie. La última figura (F) representa la suma de todos los modelos de distribución potencial en el presente de las diferentes especies de* Erodium, *con símbolos diferentes para la distribución conocida de cada especie. Los colores más oscuros muestran zonas más favorables para la especie.*

cies. Another factor that could aggravate this situation is the fact that this species lives in high–altitude habitats, one of the most vulnerable areas to climate change (Wilson et al., 2007; Engler et al., 2011). In our models, we also considered the interaction of the butterfly with its *Erodium* larval food plants, in order to improve the quality of the prediction (Kissling et al., 2012; Wisz et al., 2013). We did not consider the mutualistic relationship with ants (Romo et al., 2015) because in this case, ant attendance is facultative and, as far as we know, the presence of ants does not represent a limiting factor for the survival of the butterfly (García–Barros et al., 2013).

The habitat of *Erodium* plants is also generally restricted to mountains, but they have a wider range than the butterfly. The environmental variables that most influenced the potential distribution models of plant species were elevation (highly correlated to temperature) and precipitation. A reasonable hypothesis would therefore be that their distribution could also be affected by climate change (Grabherr et al., 1994; Dullinger et al., 2012; Gottfried et al., 2012). On the other hand, non–climatic variables such as landcover and radiation contribute little to the models. The reason for this could be that the species are mainly present in open areas (rocks, screes, grasslands) that would have similar values for the mentioned variables.

Regarding the results of the present potential distribution models, and given the actual distribution of the butterfly, some known occurrence points appear in unfavourable areas. Most of these points are close to favourable patches and are likely to be the result of an expansion of nearby populations (Munguira and Martin, 1988). They are also located in areas where
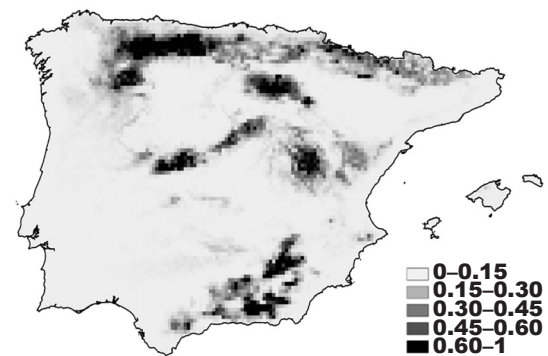

Fig. 3. Present potential distribution model of the interaction between *A. morronensis* and the *Erodium* species. Overlap of the present potential distribution models for *A. morronensis* and the five *Erodium* species considered in the study worked out as the minimum number of squares that all the species have in common. Darker colours show more favourable areas for the butterfly.

Fig. 3. Modelo de distribución potencial en el presente de la interacción entre A. morronensis *y las especies de* Erodium. *Superposición de los modelos de distribución potencial en el presente de* A. morronensis *y las cinco especies de* Erodium *analizadas en el estudio, calculado como el número mínimo de cuadrículas que todas las especies tienen en común. Los colores más oscuros muestran zonas más favorables para la mariposa.*
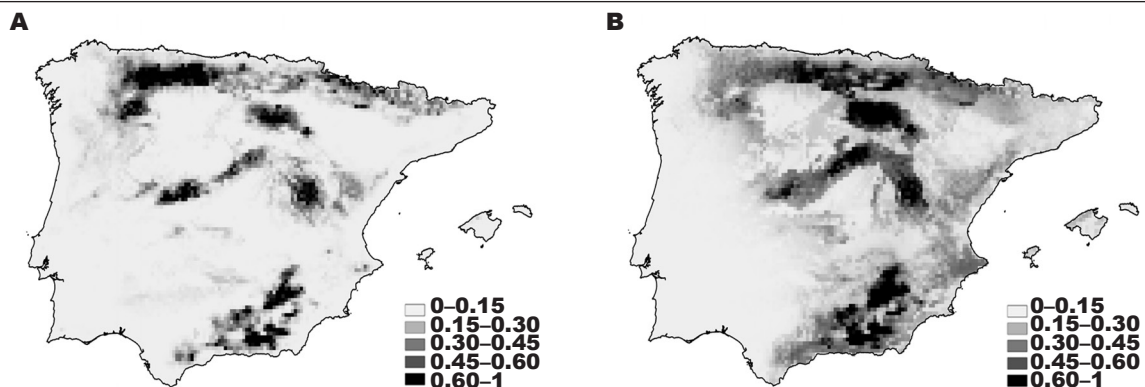

Fig. 4. Future potential distribution models for *A. morronensis* and the set of all *Erodium* species. Future potential distribution models for *A. morronensis* (A) and *Erodium* plants (B) projected to 2070 using the most radical climate change scenario (RPC 8.5) in order to show the most pessimistic prediction for the species in the future. Darker colours show more favourable areas for the species in both maps.

Fig. 4. Modelos de distribución potencial en el futuro de A. morronensis *y el conjunto de las especies de* Erodium. *Modelos de distribución potencial de* A. morronensis *(A) plantas del género* Erodium *(B) extrapolados a 2070 utilizando las condiciones climáticas más drásticas (RCP 8.5) a fin de mostrar la predicción más pesimista para estas especies en el futuro. Los colores más oscuros muestran zonas más favorables para las especies en ambos mapas.*

☐ 0–0.15
◻ 0.15–0.30
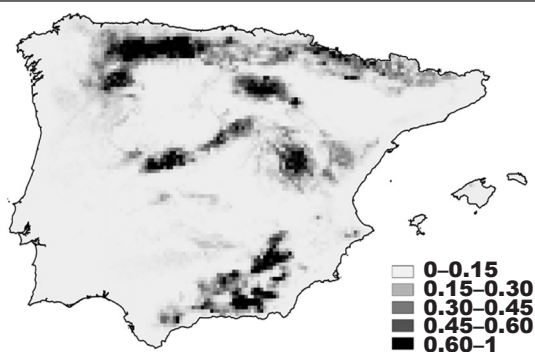▨ 0.30–0.45
▦ 0.45–0.60
■ 0.60–1

Fig. 5. Future potential distribution model of the interaction between *A. morronensis* and the *Erodium* species. Overlap of the 2070 RPC 8.5 models for *A. morronensis* and the five *Erodium* species considered in the study worked out as the minimum number of squares the two groups have in common. Darker colours show the more favourable areas for the butterfly. This map shows the most pessimistic prediction for the butterfly in the future.

Fig. 5. Modelo de distribución potencial en el futuro de la interacción entre A. morronensis *y las especies del género* Erodium. *Superposición de los modelos previstos para 2070 con las condiciones de RCP 8.5 de* A. morronensis *y las cinco especies de* Erodium *analizadas en el estudio, calculado como el número mínimo de cuadrículas que los dos grupos tienen en común. Los colores más oscuros muestran zonas más favorables para la mariposa. Este mapa muestra la predicción más pesimista para la mariposa en el futuro.*

their larval food plants are present. The Pyrenean mountain range is not particularly favourable in our models (only four squares exceed the threshold of 0.6), although there are citations for six distribution points in the area. This could be a result of historical events related to the species distribution, such as local extinctions or previous incomplete colonizations. Also, on the eastern part of the Central Mountain System, a favourable area for the butterfly is predicted; however, it may be unoccupied due to the absence of adequate larval food plants in this region.

Our models only consider the presence of the species in relatively large areas (10 x 10 km²). They did not considerprobable shifts of distribution ranges to higher altitudes (Walther et al., 2002; Parmesan, 2006; Wilson et al., 2007). Therefore, this effect of climate change may have been overlooked in our study. For more comprehensive knowledge on the impact of climate on this species, it would be imperative to improve the sampling effort to detect probable altitudinal shifts on this and other butterfly species. To improve the models performance it would also be necessary to update the available distribution data,

since most of the occurrence data were collected for the 2004 atlas (García–Barros et al., 2004). However, most locations recently visited by the authors are still occupied and show large numbers of the butterfly.

As for the potential distribution model of the plants, the occurrence data on areas predicted as unfavourable in our models could also be explained as an expansion from favourable patches, as they are close to the boundaries of these suitable areas. Besides, it should be taken into account that the map (fig. 2) is a result of the sum of the present potential distribution models of all plant species; the most favourable areas are thus those that include more than one species. The eastern coast areas of the Iberian Peninsula do not seem to have suitable conditions for the studied *Erodium* species, probably as a consequence of the high temperatures during the summer and the limited extension of mountains in these areas.

Studying ecological interactions between species in terms of conservation is becoming an important field of study. Global change is shifting the cycles of the species, decoupling their interactions, that usually disappear before species extinctions themselves (Peñuelas et al., 2002; Valiente–Banuet et al., 2015). Almost all the favourable areas for the butterfly in our predicted models match favourable areas for the plants. Thus, when the overlap of models of the butterfly and the plants was considered, the favourable areas for the butterfly did not change significantly, with the only exception being a slight loss of favourability on the west side of the Cantabrian Mountains and Central Mountain System. Comparing the present and the future overlap of the potential distribution models, the prediction shows no loss of habitat favourability for the interaction between the butterfly and its larval food plants. This observation makes our study particularly interesting, because in our present and future potential distribution models the interaction does not seem to be significantly affected by shifts under climate change.

Moreover, it is relevant to take into account Dincă et al's subdivision of *A. morronensis* populations into two genetic entities, 2015. This subdivision matches the northern and central populations in one of the entities and the southern populations in the other. We did not model these two entities separately because they probably represent different species; a more detailed molecular study based on other non–mitochondrial markers would be needed. But comparing the model predictions with the known distribution of the species, we consider our results show that neither genetic entity would experience loss of habitat adequacy: the northern populations present an increase in the future, while the southern populations remain stable. Figure 1 shows the differences between the known distribution and the present models, where some of the isolated points of the known distribution of the butterfly appear in unfavourable areas as mentioned before.

While the models show that the potential distribution of the butterfly may be optimistic for the future shifts predicted under climate change, the case of some of the plants included in this study may require

Table 2. Evolution of habitat favourability for all the species in the projected future models. Percentage of the loss (negative values) or increase (positive values) in habitat favourability on the obtained future projections for each scenario (RPC 2.6 and 8.5, see methods) regarding the present potential distribution models of *A. morronensis* and its larval food plants of the genus *Erodium*. The values come from the subtraction of the percentage of favourable areas given by the future potential distribution models minus the percentage of these areas in the present distribution models.

Tabla 2. Evolución de la favorabilidad del hábitat para todas las especies en los modelos extrapolados al futuro. Porcentaje de pérdida (valores negativos) o ganancia (valores positivos) de favorabilidad del hábitat con respecto a la previsiones futuras para cada escenario (RCP 2.6 y 8.5, véanse los métodos) en relación con los modelos de la distribución en el presente de A. morronensis *y las plantas nutricias de sus larvas del género* Erodium*. Los valores se obtienen restando el porcentaje de zonas favorables obtenido en los modelos de la distribución en el presente al porcentaje de estas zonas obtenido por los modelos de la distribución potencial en el futuro.*

| | Models | | | |
| | 2050 | | 2070 | |
Species	2.6	8.5	2.6	8.5
A. morronensis	5.74	9.09	5.26	2.87
E. carvifolium	−5.53	−1.98	−1.19	−3.95
E. cazorlanum	0.00	0.00	0.00	0.00
E. daucoides	−2.59	7.33	6.03	3.45
E. foetidum	−20.58	−20.99	−19.34	−19.75
E. glandulosum	−1.78	−5.33	−2.67	−4.00
Interaction	6.28	8.7	5.8	1.93

Table 3. Validation of models: AUC values (area under the ROC curve), equal training sensitivity and specificity logistic threshold (EtSl), classification percentage (Cp) and significance (*p*–test) for the 11 binomial tests obtained by default with MaxEnt for *A. morronensis* and its larval food plant models (*: for *E. cazorlanum* 60 % of the tests had p < 0.05 while for the remaining tests p was < 0.01).

Table 3. Validación de los modelos. Valores AUC (área debajo de la curva ROC), umbral logístico de la prueba de igualdad de la sensibilidad y especificidad, porcentaje de clasificación y significación de las 11 pruebas binomiales dadas por defecto por MaxEnt para los modelos de A. morronensis *y las plantas nutricias de sus larvas (*: para* E. cazorlanum *el 60 % de las pruebas mostró una significación de p < 0,05 y el resto, de p < 0,01).*

Species	AUC	EtSl	Cp	*p*–test
A. morronensis	0.922	0.234	80.3	< 0.01
E. carvifolium	0.936	0.258	85.7	< 0.01
E. cazorlanum	0.991	0.307	81.8	< 0.05*
E. daucoides	0.95	0.315	83.6	< 0.01
E. foetidum	0.943	0.264	78.4	< 0.01
E. glandulosum	0.931	0.284	78.8	< 0.01

special attention. *E. foetidum* only occurs in the Iberian Peninsula and southern France and, although it is listed as Near Threatened (NT) by the IUCN, according to our predictions it will have its favourable area reduced to around 20 % (table 2). Furthermore, only around 40 % of the favourable areas displayed for this plant in the present potential distribution model occur inside the network of protected areas. This could have been a problem for the butterfly, but as it feeds on any of the studied *Erodium* species and since *E. foetidum* shares its habitat with two more *Erodium* species, our models show no negative effect on habitat suitability for the butterfly. The remaining plant species considered are predicted by our models

to stay more or less stable in their actual range in future projections, with small losses of favourable areas (*E. carvifolium* and *E. glandulosum*), or small increases (*E. daucoides*). *E. cazorlanum,* an Iberian endemic species listed as Vulnerable by the IUCN, is the species of our study with the most restricted distribution range. Nevertheless, the models do not show relevant changes for its populations and over 80 % of the potential present favourable areas appear in protected areas. We have to consider that these species with geographically restricted areas do not usually reflect all the environmental or topographic information where the species really occurs and the results can be biased somehow (Titeux et al., 2017). But even in the hypothetical case that there was a local extinction of the *E. cazorlanum* species, the larvae of the butterfly would be able to feed on other *Erodium* species in that area, such as *E. daucoides* or *E. foetidum.* In fact, recent observations (Munguira, unpublished data) show that the butterfly can use *E. foetidum* in the Sierra de Cazorla (SE Spain). However, it is true that the model obtained for *E. cazorlanum* should be interpreted not as potential areas where it could expand its actual range limit but as regions that have similar environmental conditions to those where the species was recorded (Pearson et al., 2007).

Our results confirm the favourable status of the butterfly from a conservation point of view. Munguira (1989) stated that the species was not a priority for conservation since it was present in a large number of locations (which increased from 14 to 56 in 1975–1988 as a result of better sampling), showed strong populations and had some of its best populations inside protected areas. The present situation, with 50 % of the populations within protected areas, is even better than in 1989, and moreover, the models show stable predictions for the future. Persistence of populations will be easier for those populations living on scree slopes or rocks (most of the populations from Pyrenees, Cantabrian Mountains, Iberian Mountain System and southern sierras) where no specific management is required. Grassland populations (Galicia, Ávila, Soria and some in Burgos) need livestock grazing to keep habitat quality, so traditional land uses should be favoured in these areas. In Abejar (Soria) management already taking place to preserve the Dusky Large Blue *Phengaris nausithous* (Bergsträsser, 1779) populations (Vicente et al., 2013) would favour the survival of *A. morronensis* populations in the same grasslands.

To sum up, the threat of climate change to *A. morronensis* could be minimal while current predictions through climatic models show considerable reductions of distribution ranges for most butterfly species (Beaumont and Hughes, 2002; Settele et al., 2008). Focusing on the Iberian Peninsula, it seems mountain butterflies will also lose habitat favourability in the future, especially when the interaction between the butterfly and the larval food plants is considered (e.g. *Phengaris nausithous*, Romo et al., 2014, 2015). Besides, more than 50 % of the areas considered favourable in the present potential It seems conservation of the butterfly and most of its food plants is probably not jeopardised for the time being. However, it would be interesting to focus new research on how the butterfly would counteract future challenges in climate change, and whether interaction with its larval food plants will remain stable –as predicted by our models– or increase or decline.

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Supplementary material

Table 1s. Variables considered in the study. The highly correlated variables were removed and those finally used to perform the models are marked with an asterisk (*). Among the non–climatic variables we distinguish only those used for present potential distribution models, and those used in present and future potential distribution models.

Tabla 1s. Variables consideradas en el estudio. Las variables utilizadas para la realización de los diferentes modelos después de eliminar las que estaban muy correlacionadas están marcadas con un asterisco (*). Entre las variables no climáticas se distinguen las que solo se han utilizado para realizar los modelos de distribución potencial en el presente y las utilizadas en los modelos de distribución potencial en el presente y su previsión para el futuro.

Bioclimatic variables	Non–climatic variables
Annual mean temperature	Used for present models
Mean diurnal range (mean of monthly (max temp – min temp))*	Human footprint*
Isothermality*	Human population*
Temperature seasonality (SD x 100)*	Landcover*
Maximum temperature of warmest month	Herbaceous landcover*
Minimum temperature of coldest month	Tree landcover*
Annual temperature range	Sun radiation*
Mean temperature of wettest quarter*	Used for present and future models
Mean temperature of driest quarter*	Calcareous/siliceous (soil type)*
Mean temperature of warmest quarter*	Mean elevation*
Mean temperature of coldest quarter	Latitude*
Annual precipitation*	Longitude*
Precipitation of wettest month*	Position*
Precipitation of driest month*	Slope*
Precipitation seasonality (coefficient of variation)	
Precipitation of wettest quarter*	
Precipitation of driest quarter*	
Precipitation of warmest quarter	
Precipitation of coldest quarter*	

Table 2s. Percentage contribution of the non–climatic variables to the present potential distribution models for the butterflyç *Aricia morronensis* and its larval food plants (genus *Erodium*). The variables shown are those that would not be able to project to the future: Amr, *A. morronensis*; Ecr, *E. carvifolium*, Ecz, *E. cazorlanum*; Edc, *E. daucoides*; Eft, *E. foetidum*; Egl, *E. glandulosum.*

Tabla 2s. Porcentaje de contribución de las variables no climáticas a los modelos de distribución potencial en el presente de la mariposa Aricia morronensis *y las plantas nutricias de sus larvas (género* Erodium*). Las variables que se presentan son las que no se pudieron prever en el futuro. (Para las abreviaturas, véase arriba).*

Variables	Species					
	Amr	Ecr	Ecz	Edc	Eft	Egl
Sun radiation	2.1	–	0.4	0.1	0.9	–
Human footprint	1.2	1	0	0.1	–	0.6
Human population	0.1	–	–	–	–	1.5
Landcover	–	–	2.5	–	1.2	1.1
Herbaceous landcover	0.7	0	–	0.3	–	2.2
Tree landcover	1	4.8	–	–	4.3	1.1

Table 3s. Contribution percentage of the different variables to the models projected (P) and non–projected (N–P) to the future for *A. morronensis* and its larval food plants of the genus *Erodium*: wq, weltest quarter; dq, driest quarter; cq, coldest quarter; wm, welttest month; dm, driest month.

Tabla 3s. Porcentaje de contribución de las diferentes variables a los modelos extrapolados y no extrapolados al futuro para A. morronensis *y las plantas nutricias de sus larvas del género* Erodium.

Variable	%N–P	%P
A. morronensis		
Elevation	46.1	46.6
Slope	24.3	27.4
Mean temperature of wq	6.6	6.5
Mean diurnal range	4.5	4.2
Annual precipitation	4.1	4.7
Calcareous/siliceous	3.1	3.8
Mean temperature of dq	2.8	3.2
Sun radiation	2.1	–
Latitude	2	1.9
Position	1.4	1.6
Human footprint	1.2	–
Tree landcover	1	–
Herbaceous landcover	0.7	–
Human population	0.1	–
E. carvifolium		
Elevation	40.3	39.7
Latitude	21	23.7
Precipitation of wq	12.1	12.7
Calcareous/siliceous	8.4	10.1
Mean temperature of dq	7.5	8.2
Tree landcover	4.8	–
Mean temperature of wq	2.6	2.3
Slope	1.8	2.9
Human footprint	1	–
Temperature seasonality	0.3	0.4
Isothermality	0.1	0.1
Herbaceous landcover	0	–
E. cazorlanum		
Temperature annual range	28.4	28.7
Slope	21.4	21.7
Longitude	15.8	17.2
Latitude	15.5	16.7
Precipitation of cq	8.9	7.7
Elevation	7.1	8
Landcover	2.5	–
Sun radiation	0.4	–
Human footprint	0	–
Mean temperature of wq	0	0

Variable	%N–P	%P
E. daucoides		
Elevation	28.3	29.9
Longitude	25.1	25.5
Calcareous/siliceous	17.3	16.3
Slope	14.2	15
Mean temperature of dq	6.1	6.1
Mean temperature of wq	4.5	3.7
Temperature annual range	2.2	1.9
Precipitation of wm	1.5	1.3
Herbaceous landcover	0.3	–
Position	0.3	0.3
Human footprint	0.1	–
Sun radiation	0.1	–
E. foetidum		
Latitude	37.9	41.3
Slope	27.1	26.5
Longitude	20.4	22.8
Herbaceous landcover	4.3	–
Mean diurnal range	2.5	3
Annual precipitation	2.1	2
Landcover	1.2	–
Sun radiation	0.9	–
Precipitation of dq	0.8	1.1
Position	0.8	0.7
Calcareous/siliceous	0.8	1.3
Mean temperature of wq	0.7	0.8
Mean temperature of dq	0.6	0.6
E. glandulosum		
Precipitation of dm	53.8	57.8
Mean temperature of dq	10.7	9.3
Slope	10.4	11.6
Mean temperature of wq	6.5	8.1
Mean diurnal range	6.2	7.1
Annual precipitation	2.9	3.5
Longitude	2.7	2.2
Herbaceous landcover	2.2	–
Human population	1.5	–
Landcover	1.1	–
Tree landcover	1.1	–
Human footprint	0.6	–
Position	0.3	0.3