



Living on the edge in species distribution models: The unexpected presence of three species of butterflies in a protected area in southern Spain



Pilar Fernández*, Diego Jordano, Juan Fernández Haeger

Department of Botany, Ecology and Plant Physiology, Universidad de Córdoba, Campus de Rabanales, Edificio C-4, 14071 Córdoba, Spain

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ABSTRACT

MaxEnt (Maximum Entropy) modelling method is probably the most popular technique to model species distributions based only on the presence records across broad spatial scales. Although it is widely used, there is much controversy about the transferability of models between different geographical areas. Transferability might be more questionable when it comes to predict the distribution of peripheral populations at the margin of the species geographical range, where they may be affected by and adapted to environmental conditions different from those of core populations. To explore transferability of MaxEnt models among sectors of the geographic range, we selected three butterfly species with wide distributions and peripheral populations at their southernmost margin in the Iberian Peninsula, namely *Plebejus argus*, *Cyaniris semiargus* and *Pyronia tithonus*.

Using data from the Atlas of the butterflies of the Iberian Peninsula and Balearic Islands as well as both climate and land use data, we modelled their potential distribution ranges in Spain. In addition, we also independently modelled their distributions separately in three concentric sectors of their range. We then investigated the transferability of the models between sectors and the effect of varying the regularization parameter.

Our results show that when developing species distribution models the quality of occurrence data should be carefully checked, paying special attention to both their number and spatial distribution and avoiding possible significant biases.

The transferability of the models tends to decrease when data from increasingly distant sectors are used as test data. More precisely, and independently of the regularization parameter value, models built using occurrence data either from the core or the intermediate sectors failed to adequately predict the distribution of the three butterfly species in the peripheral sector, especially in Doñana National Park.

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1. Introduction

Species distribution models (SDMs) are specific tools developed for predicting the habitat and potential distribution of plant and animal species given a set of occurrence data, albeit incomplete, and environmental data. SDMs have acquired increasing importance in biodiversity conservation (Fielding and Bell, 1997; Araújo and Luoto, 2007; Mateo et al., 2011), and to exploring the potential effects of global climate change on biodiversity loss and on shifts in species distributions (Pearson and Dawson, 2003; Elith et al., 2010; Romo et al., 2013).

A variety of modelling techniques ranging from classic logistic regression models coupled with GIS, generalized additive models (GAM), GARP (a genetic algorithm approach) and others, are available (Virkkala et al., 2005; Wisz et al., 2008; Titeux et al., 2009). Some authors focus on modelling the environmental conditions that meet a species' ecological requirements and predict the relative suitability of habitat, aiming to produce the so called environmental niche models (ENMs) (Warren and Seifert, 2011). In practice, when modelling across large geographic areas there is usually a lack of data concerning important niche dimensions linked to biotic factors, while detailed data of climatic variables, altitude, slope, or aspect are more easily available.

In any case, the model results are often flawed by problems like small sample sizes, biased data or unrepresentative samples (Dennis and Thomas, 2000; Stockwell and Peterson, 2002; Romo et al., 2006; Pearson et al., 2007; Papeş and Gaubert, 2007).

* Corresponding author. Tel.: +34 957218596.
E-mail address: bv2ferop@uco.es (P. Fernández).

Additional problems are lack of real absences, or the choice of variables to be included (Araújo and Luoto, 2007; Titeux et al., 2009). Moreover, the ecological characteristics of the target species may have potential effects on the model output (Osborne and Suárez-Seoane, 2002; McPherson et al., 2004).

MaxEnt is a maximum entropy modelling method that performs extremely well in predicting occurrences, especially when sample size is small (Phillips et al., 2006; Pearson et al., 2007; Wisz et al., 2008).

On the other hand, transferability or the ability of a model calibrated in one context to make useful predictions in a different context, has also been the centre of several papers and the focus of discussion (Lobo et al., 2007; Peterson et al., 2007; Phillips, 2008). However, the environmental envelope of a given species may drastically change across its geographic range from the core area to the edges due to spatial heterogeneity. Under these circumstances, a model cannot always include the full spectrum of conditions of the target species if its range is not well sampled. In cases where the sampling distribution is expected to be strongly biased, its negative effect on the model's accuracy can be minimized in MaxEnt by targeting background locations from heavily sampled areas to provide unbiased results (Phillips et al., 2009).

The spatial patterns shown by many species across their ranges can also compromise the predictive ability of MaxEnt models. Near the core of the distribution area local populations tend to be bigger in size, more abundant and experience a more suitable environment than the more fragmented, peripheral populations occupying less favourable habitats near the edge of their geographic distribution, (Brown, 1984; Lawton, 1993) (but see Sagarin et al., 2006; Munwes et al., 2010). Moreover, contrary to initial expectations peripheral populations have been shown to be adapted to the edge of their range (Zakharov and Hellmann, 2008), can persist as well as core populations (Channell and Lomolino, 2000), and may have different genetic traits and more genetic diversity than core populations (Munwes et al., 2010). For these reasons, differences in population numbers, extent and size from core to peripheral areas can lead to misinterpretation of the predicted habitat through SDMs. However, this problem has received little attention.

This could be the case of *Plebejus argus*, *Cyaniris semiargus* (Lycaenidae) and *Pyronia tithonus* (Satyridae), three butterfly species widely distributed across the European continent. Within the Iberian Peninsula they have their core areas in northern Spain, where they occur in almost every 10 × 10 km UTM square (Universal Transverse Mercator conformal projection), showing a rather continuous distribution. However, as we move to the drier and warmer southern margin of their range, their distributions gradually become more fragmented with increasingly isolated local populations.

Unexpectedly, these three species occur in the Doñana national park (southern Spain) almost at sea level at the southern margin of their continental range, despite the high values of solar irradiance and temperatures and the scarce annual rainfall (Fernandez Haeger et al., 1976). The nearest populations at similar latitude occur in the mountains at much higher elevations.

The maximum predictive accuracy of models may not be independent of range size (Stockwell and Peterson, 2002), and therefore widespread species like these could be modelled less accurately. In these cases, it has been suggested that model accuracy can be improved by splitting species distributions into sub-units or sectors that may have different ecological characteristics (Osborne and Suárez-Seoane, 2002; Thuiller et al., 2004).

The main objective of this work is to model the current potential distribution of the butterflies *P. argus*, *C. semiargus* (Lycaenidae) and *P. tithonus* (Satyridae) in Spain. More specifically we divided the range of each species into three different concentric sectors namely

core, intermediate and peripheral, starting at the core area for each species in Spain. We then produced a set of models using occurrence data from the whole extent of peninsular Spain (global model at national scale) and a separate model for each sector independently, and tested the transferability of the global model to each sector and vice versa. This approach is aimed to test the performance of modelling on core versus marginal populations. We hypothesize that model transferability among sectors will be low, decreasing as the distance between sectors increases. Secondly, we compare alternative models to test the effects of controlling bias and overfitting and evaluate variable contribution.

2. Methods

2.1. Data extraction and sectorization

Presence data of the three species were obtained from the *Atlas of the butterflies of the Iberian Peninsula and Balearic Islands* (García-Barros et al., 2004). This is the most comprehensive review up to date of butterfly distributions in Spain. Although it compiles a large dataset from museums, collections and published records spanning from the 19th century to the present, most of the data belong to the period 1975 onwards. The spatial reference is the 10 × 10 km grid of the Universal Transverse Mercator conformal projection (UTM). The available occurrence data for the three butterfly species totals 1080 UTM squares for *P. tithonus*, 670 for *P. argus* and 399 for *C. semiargus*.

Using ArcGis 10.1 (ESRI, 1998) we mapped the occurrence records for each species in UTM grid (Fig. 1). ArcGis tools allowed us to find for each species the centroid or geometric centre of the occupied squares, as well as to compute the distances from these squares to the centroid and the standard deviation. For each species we divided the geographical extent into a core, a medium and a marginal or peripheral sector (Fig. 1). These three sectors are concentric relative to the centroid of the distribution, with radiuses equal, respectively, to one, two and three times the standard deviation of the mean distance from the centroid to the occupied UTM grid squares (Osborne and Suárez-Seoane, 2002). The underlying assumption for this decision is that environmental conditions change with the distance from the distribution core. The frequency of occurrence data by species and sector (core, intermediate and marginal) were as follows: *P. tithonus* 678, 375 and 27 UTM squares, respectively; *P. argus* 447, 202 and 21 UTM squares, respectively, and *C. semiargus* 285, 99 and 15 UTM squares, respectively.

2.2. Assessing bias

The available occurrence data (museum collections, atlases, etc.) often exhibit strong spatial bias in survey effort (Dennis and Thomas, 2000; Romo et al., 2006; Phillips et al., 2009; Lehtikoinen, 2013). This bias can severely impact model quality and results (Elith et al., 2010; Kramer-Schadt et al., 2013). To control for sampling bias effects in our models we built ordinary MaxEnt models with default settings (MaxEnt 3.3.3.k version) as controls and also modified models including two types of bias files, each of which constitutes a background sample with the same biased error as the occurrence records (Phillips et al., 2009).

The first bias file (hereafter the target group bias, Fig. 2) was generated by pooling the occurrence data of the three butterfly species and assigning a value of 1 to every UTM square with at least a positive record of any of the three butterfly species, and -999 to squares without any single occurrence record. This approach is based on the idea that a specialist visiting a given locality or UTM square would register all the butterfly species he/she might encounter, so the absence of one species where others were present could be

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