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Identification of potential source and sink areas for butterflies on the Iberian Peninsula

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Abstract. 1. The dynamic analysis of geographical distribution is relevant to identify the processes that underlie any changes of geographical ranges. This is an essential element of both biogeography and conservation biology. Fuzzy logic, in particular the fuzzy concept of favourability for species occurrence,

helps to perform a dynamic interpretation of the internal complexity of species ranges.

2. We modelled the distributions of the 222 Iberian butterflies using favourability functions and 92 environmental variables (spatial, climatic, topographic, geological and indicators of human activity). We obtained a significant environmental favourability model for each butterfly.

3. We identified the potential sources and sinks in the distribution area of each butterfly species using their respective favourability and presence–absence maps, considering as sources only those areas with high favourability where the butterfly is present, and sinks only those areas with low favourability where the butterfly is present too.

4. The source areas for the Iberian butterflies are concentrated in the north of the peninsula, mainly in the mountain ranges (Cantabrian Range, Pyrenees and Central Range). Sink areas are more dispersed all around the peninsula. We found a concentration of sink locations in eastern Iberia (Alicante and Murcia provinces) and in the southwestern area (Doñana National Park).

5. This may be helpful when implementing conservation measures, by providing a biogeographical dynamic interpretation of the roles of different parts of the distribution range of the species. Preserving the processes that link sources with sinks is critical for maintaining or improving the sustainability of populations.

Key words. Conservation biogeography, favourability function, fuzzy logic, source-sink dynamic, superfamily Papilionoidea.

Introduction

Insects, even being the group with highest species richness, have largely been neglected in conservation attention. In addition, insects are good indicators of environmental changes and, consequently, should be used more in environmental monitoring programmes (Franzén & Johannesson, 2007; Brereton et al., 2011). The Lepidoptera (butterflies and moths) is one of the hyperdiverse taxa, currently comprising about 160 000 described species [with an estimated number of species of up to half million (Sohn et al., 2015)]. Butterflies, in particular, are often used to illustrate the remarkable change in species distributions that has occurred during the last decades (Maes & van Dyck, 2001; Stefanescu et al., 2009; Mattila et al., 2011). They play an important ecological role in nature. That importance comes from some aspects of their particular biology: they have a predominantly herbivorous diet and limited mobility that makes them vulnerable to predation. In contrast, the adults have the ability to fly, which allows them to disperse, and feed on flower nectar (hence they are plant pollinators). Furthermore, they support a wide range of host-specific insect parasitoids, worthy of conservation in their own right (Van Swaay et al., 2010). All this makes them an important diagnostic group useful as an indicator of ecosystem quality, habitat transformation and, recently, as evidence for the species responses to climate change (Settele et al., 2008; Stefanescu et al., 2011a; Romo et al., 2014b). European butterflies are well known in various aspects of their biology and ecology, from purely taxonomic aspects to the complex environmental relationships that determine their range, ecology or species richness (Habel et al., 2005; Schmitt et al., 2007; Settele et al., 2008; Dincă et al., 2013). The Iberian Peninsula is one of the most species-rich European areas for this insect taxon (Van Swaay et al., 2010). Iberian butterfly distributions are reasonably well known (Romo et al., 2006) even if some areas remain insufficiently sampled (Romo & García-Barros, 2005). Several studies have focused on butterfly ecology in the Iberian Peninsula (Stefanescu et al., 2009) as well as on species richness patterns (Stefanescu et al., 2004; Romo et al., 2007; Stefanescu et al., 2011a) or distribution range modelling for selected species (Romo et al., 2014a,b). To date, no study has attempted to model the geographical range of all the Iberian butterfly species. An essential element of both biogeography and conservation biology is to understand the factors determining the present ranges of organisms and their temporal dynamics (Braby et al., 2014). Therefore, the dynamic analysis of geographical distribution becomes relevant to identify the processes that underlie any changes of geographical ranges. This includes considering the internal complexity of the distribution range, with different areas acting as population sources or sinks (Pulliam, 1988), rather than a homogenous, stable range. Thus, modelling the distribution of species is increasingly being used not only to determine the species ranges but to assess the differential favourability of different parts of the species ranges (Real et al., 2006, 2010; Estrada et al., 2008; Schroeder et al., 2009; Barbosa & Real, 2010, 2012; Romo et al., 2015). New tools make it possible to calculate mathematical expressions that concretely define the parameters and the variables that affect the biogeographical processes in nature. Among these are the favourability functions, which may be obtained from probability through a modification that circumvents the influence

of the prevalence and, so, are independent of the proportion of presences in the dataset (Real et al., 2006; Acevedo & Real, 2012). Both probability and favourability range continuously from 0 to 1, but they differ in a fundamental aspect.

Probability of occurrence fits into crisp logic, since the probability that an event occurs does not imply that the event occurs partially, but that the event is more or less likely to occur, depending on the prevalence of the event (common or rare) and on the degree to which the conditions favour the occurrence of the event. The event either happens or not, and the logic is crisp. In our case, a species either occurs or not in a locality, with no situation in between, whatever the probability value. Favourability, however, fits into the framework of fuzzy logic, since favourability for the occurrence of an event is always partial, because the conditions are favourable for the occurrence of the event to a certain degree. The key is not whether the event will occur or not, but to what extent the conditions favour the occurrence of the event, and the logic here is fuzzy. In our case, the degree to which the territories and the conditions in them are favourable for the existence of the species is an important and nuanced characteristic of them. It is possible then to pass from probability to favourability and vice versa, but they represent different logical systems (crisp and fuzzy, respectively). Fuzzy logic is inherent to the fuzzy set theory (Zadeh, 1965) and escapes the discrete true-or-false nature of syllogisms. It emerged as a need to adapt the usual human language to contemporary automation machinery. Its application outside mechanical engineering is scarce and little known, although a fuzzy logic perspective is particularly useful for processing environmental and ecological data (Salski, 2006). The concept of favourability, on the other hand, may be helpful to make the concept of source-sink dynamics operational at biogeographical scales. In the current highly disturbed and fragmented environment due to human activity, wildlife is distributed in a heterogeneous way occurring in diverse habitat patches with differing intensity. In this study, we hypothesize that such zones represent sources or sinks depending on the conditions they offer for the persistence of a particular species (Pulliam, 1988; Boughton, 1999). Pulliam (1988) defined sources as areas with positive population growth and sinks as those with negative population growth. This concept is, thus, based on local birth and death rates which are difficult to assess at local scales and nearly impossible to determine at a biogeographical scale. The assumption that the geographical variation in environmental favourability for butterflies can be related to local birth and death rates makes the source-sink dynamic operational. Environmental favourability might fail to reflect demography, and therefore fail to reflect sources and sinks, but this could be mitigated by restricting the assumption to conditions highly favourable or unfavourable, using them as an operational proxy for sources and sinks. The fundamental feature of source-sink systems is a sustained flow of organisms out of some favourable areas (sources) and into others that are unfavourable (sinks). Sink areas can persist for a long time if they regularly receive immigrants from source areas. This would have important effects on conservation strategies (Dias, 1996; Boughton, 2000; Muñoz et al., 2005; Gervasi et al., 2015). For instance, source areas could be critical to ensure the persistence of threatened or endangered species (Muñoz et al., 2005). Even sink areas can contribute to regional population dynamics by facilitating dispersal between source areas for some species (Bush et al., 2012). In addition, preserving the processes that link sources with sinks is critical for maintaining or improving the sustainability of populations.

The aims of this paper consisted of: (i) modelling the variation in favourability for each Iberian butterfly within their respective range, (ii) identifying the resulting source-sink pattern for each butterfly in the study area, and (iii) summarizing shared source-sink patterns for every family and for all species together. This may be helpful when implementing conservation measures, by providing a dynamic biogeographical interpretation of the roles of different parts of the distribution range of each species.

Material and methods

Study area

The Iberian Peninsula is the westernmost of the Mediterranean peninsulas of Europe. It comprises about 580 000 km² and two main countries: Spain and Portugal. This area includes 6040 cells of 10 9 10 km² in the Universal Transverse Mercator (UTM) grid. The Peninsula is a highly mountainous territory with 600 m of mean elevation, with two plateaus and several mountain systems mainly going from west to east (Fig. 1). There is a clear lithological differentiation between the west (siliceous) and the east (limestone; IGME, 2015) and remarkable climatic variations between the north (without summer drought) and the south (hot and dry summers; AEMET & IMP, 2011).

Distribution data and explanatory variables

The presence/absence of 222 species of butterflies represented in the Iberian Peninsula were extracted from the original data matrix used for the Iberian distribution atlas (García-Barros et al., 2004), updated to 2009 by the authors. Iberian butterflies belong to the superfamily Papilionoidea, including the families Hesperidae, Papilionidae, Pieridae, Nymphalidae and Lycaenidae (Appendix S1). Some authors only include climatic variables when modelling the distribution of species (Beaumont et al., 2005; Parmesan et al., 2015). It is unlikely that a species large-scale distribution will depend only on climate, as other environmental predictors, such as topography, lithology or human activity, are likely also relevant and should be included in the biogeographical modelling of species distributions (Austin & Van Niel, 2011; Márquez et al., 2011). We used 90 explanatory variables: 69 climatic, 6 topographic, 10 geological variables, 4 indicators of human activity and 2 variables related to spatial situation (see details and sources in Table 1). We selected these variables both because of their accessibility at our working scale and for their suspected predictive power in relation to the set of species dealt with. We considered climate and topographic variables because they are the main drivers of butterfly species richness (Stefanescu et al., 2004). Lithological variables are potentially relevant because of their bearing on floral composition, given the herbivore and rather plant-specific nature of butterflies in their larval stage. Human variables were considered important because humans have capacity for modification of the natural environment (Stefanescu et al., 2004; Stefanescu et al., 2011b). In addition, variables describing the spatial structuring of the species allow for the inference of the possible roles of population dynamics, dispersal capacities and historical events on species distributions (Legendre, 1993; Real et al., 2003; Storch et al., 2003; Estrada et al., 2016). The spatial location also affects climatic variables (Márquez et al., 2004), so the true effect of climate must be assessed in the context of the spatial influences both on the species distribution and on climate. Although the number of sites analyzed was large enough to evaluate the effect of these variables, with 6040/90 = 67 sites per tested variable, multiple comparison problems increase with the number of variables analyzed (Harrell et al., 1996), due to the increase of type I error under repeated testing, that is, the familywise error rate (Benjamini & Hochberg, 1995). We dealt with this problem by controlling the false discovery rate (see below).

Distribution modelling

We built an environmental favourability model for each butterfly species applying the following favourability function (Real et al., 2006; Acevedo & Real, 2012): $F = \frac{1}{4} \frac{P_{1-P_{n1}}}{P_{1-P_{n0}}}$; where F is environmental favourability, P is probability of occurrence, which we obtained using logistic regression (see below), and n_1 and n_0 are the number of presences and absences in the dataset, respectively. The favourability function reflects the degree (between 0 and 1) to which the local probability values differ from that expected according to the species prevalence, where $F = 0.5$ corresponds to a local probability value equal to the species prevalence in the Iberian Peninsula. Probability depends both on the response of the species to the predictor variables and on the overall prevalence of the species (Cramer, 1999), whereas favourability values only reflect the response of the species to the predictor variables (Acevedo & Real, 2012; Real et al., 2017). In other words, the probability of a species occurrence in a location is affected both by the overall prevalence of the species and by the degree to which the local conditions favour the occurrence of the species. Favourability is only this second part. A high probability of presence could correspond to low favourability if prevalence is even higher. A location is favourable only if probability at that location is higher than the prevalence of the species. Models were built on the species presence/absence on 10 910 squares of the Iberian Peninsula and based on the predictor variables (Table 1). Many of the variables, especially within the climate subset, were correlated. In our case, collinearity is only a concern in terms of redundancy of variables, because the models were applied to describe the qualities of the observed data and, consequently, the collinearity between variables remained constant (Dormann et al., 2013). To reduce redundancy, we performed a selection of variables in three steps following the recommendation of Hosmer and Lemeshow (2000, pp. 92–97). First, for each species, we performed a univariate analysis of the effect of each variable, controlling the increase in type I error due to the number of variables tested by evaluating the false discovery rate (FDR) (Benjamini & Hochberg, 1995), accepting the variables that were significant in a univariate logistic regression under a FDR of $q < 0.05$. Second, we performed a forward–backward stepwise multiple logistic regression on the variables that were retained in the FDR test, to produce increasingly more complex and informative models, using Akaike information criterion (AIC) to select the model that best balances information and parsimony, avoiding the inclusion of redundant variables (Akaike, 1974). Sometimes some coefficients for retained variables in these models are non-significant according to the z values due to multicollinearity with the other retained variables (e.g. Crawley, 2007, p. 442; Barbosa & Real, 2010, 2012). Consequently, we used in a third step the ModelTrim function of the R package FuzzySim (Barbosa, 2015, 2016) to remove variables automatically until all remaining coefficients for the variables were significant, which yielded the final model. We assessed the classification power of the models by calculating their Correct Classification Rate (CCR), sensitivity, specificity (Fielding & Bell, 1997), under-prediction rate (UPR), over-prediction rate (OPR; Barbosa et al., 2013) and their Cohen's kappa (Cohen, 1960), using the favourability value of $F = 0.5$ as classification threshold. The models' discrimination capacity was evaluated using the area under the curve (AUC) of the receiver operating characteristic (Lobo et al., 2008), which is calculated along every possible favourability threshold. The model calibration was evaluated using the Hosmer & Lemeshow calibration index (HL) using 10 bins of equal probability (Hosmer & Lemeshow, 2000). All analyses were performed in R 2.15.2 (R Core Team 2012) with the packages FuzzySim (Barbosa, 2015, 2016) and ModEvA (Barbosa et al., 2014). Specifically, we used the functions, multGLM, modelTrim and stepByStep of fuzzySim, and multModEv of modEvA. The source–sink dynamics derive from the existence of favourable and unfavourable areas in the butterfly ranges (Pulliam, 1988; Mu~noz et al., 2005). We classified the favourability values (F) in three levels: low ($F \leq 0.2$), medium ($0.2 < F < 0.8$) and high ($F \geq 0.8$). We then identified the sources and sinks in the distribution area of each butterfly species using these favourability classes and the species presences. We considered as sources those areas with high favourability where the butterfly is present and as sinks those areas with low favourability where the butterfly is present too. For each grid cell, we computed its consideration as source or sink for every species. Given that favourability is computed in relation to the species prevalence in the study area, it is a commensurate unit useful to compare and combine models of different species. This cannot be done based on probability values, for example, because these are higher in common than in rare species, so the values for the former would prevail over those for the latter. Therefore, we aggregated the favourability values for every family and for all butterflies together. In this way, we obtained a general pattern of source sink for the Iberian butterflies. The resulting maps were processed using the graphical interface of Quantum GIS 2.8.4 (QGIS Development Team, 2015).

Results

We obtained a significant environmental favourability model for each butterfly species. Every predictor variable was selected for at least one of the favourability models, which confirmed that all the variables actually had predictive power for butterflies, as we had previously hypothesised. There was an average of 21 predictor variables per final model; this involved an average of 20 presences and 488 absences per predictor variable in the models, which is widely considered more than enough to prevent bias in the estimated regression coefficients (Peduzzi et al., 1996). Elevation range (ER), mean annual actual evapotranspiration (AET), days with precipitation >0.1 mm in spring (DP01Spr), longitude (LONG), latitude (LAT) and human population density (HPd) were selected most often (45–75%). Consequently, the factors most represented in the favourability models are topography, climate, space and human activity (Table 2). The relation of ER with the distribution of the species was always positive (100% of cases), indicating that higher values of ER were more favourable for all the species that included this variable in the model. The relations with the distributions were also mostly positive for AET (98% of cases), DP01Spr (98%) and HPd (99%).

Appendix S2 shows the evaluation criteria for the favourability model of each butterfly. All the models had at least acceptable discrimination values; discrimination was considered as acceptable ($0.7 \leq \text{AUC} < 0.8$) for 31 species, as excellent ($0.8 \leq \text{AUC} < 0.9$) for 51 species, and as outstanding ($\text{AUC} \geq 0.9$) for 139 species, according the categories proposed by Hosmer and Lemeshow (2000). Most favourability models (161) were well calibrated according to the Hosmer and Lemeshow goodness-of-fit test, showing few significant differences between the observed and the expected frequencies of the species presences along the probability gradient. The classification power of the models was acceptable too with most of the favourability models with Cohen's kappa higher than 0.2 and CCR higher than 0.7.

Appendix S3 shows the favourability map (a) and the source-sink map (b) for every butterfly species. These maps show an inner complexity of the species distribution range that was not appreciated on the presence–absence map. For example, for *Iphiclides podalirius*, one of the largest European butterflies which is widespread across the Iberian Peninsula (Fig. 2a, b), we found two main source areas separated by a sink area (Fig. 2c). Figure 3 shows the cumulated sources and sinks for all the Iberian butterflies. The source areas for the Iberian butterflies are concentrated in the north of the peninsula, mainly in the mountain ranges (Cantabrian Range, Pyrenees and Central Range). Sink areas

are more dispersed all around the peninsula, although a certain concentration of sink locations can be seen in eastern Iberia (Alicante and Murcia provinces) and in the southwestern part of the Peninsula (Doñana National Park). The source-sink dynamics for the butterfly families (Hesperiidae, Papilionidae, Pieridae, Nymphalidae and Lycaenidae) (Fig. 4) were similar to the overall pattern described above, which makes this pattern highly consistent.

Discussion

The present study reveals the internal complexity of the butterfly distribution ranges based on the relationship between the environmental variables and the intensity of occurrence of the species (Real et al., 2017). This relationship is described in terms of environmental favourability for species occurrence, which we hypothesized to be related to the species demography. Birth and mortality rates are not available for butterflies in any locality, and even less so at broader scales. Muñoz et al. (2015) demonstrated that environmental favourability is related to species density. At a local scale, species density is not always related to local population growth, which is why the concept of population sinks includes localities with high density (because of high immigration) but negative population growth. Consequently, local animal density may belie habitat quality (Van Horne, 1983). Over multiple occupied localities, high habitat quality characteristics must appear frequently, as they favour occupation, and are likely to appear in a favourability function, whereas sinks typically lack shared habitat characteristics and, thus, are unlikely to significantly affect a favourability function. Therefore, at the broad scale used here (over 6040 cells of 100 km² each), favourability for occurrence is likely related to the factors affecting the species demography. In other words, although population growth represents the criterion for assessing habitat quality (Kreuzer & Huntly, 2003), at the scale of variation (the Iberian Peninsula) and resolution (100 km²) encompassed by our study, highly favourable and unfavourable areas constitute a reasonable proxy for unavailable data about the geographical variation in species demography. Topography and climate were the most important factors determining these complexity patterns for most species. Perhaps, this is why these were also the factors that Stefanescu et al. (2004) found to be the main determinants of butterfly species richness in the north-east of the Iberian Peninsula. The positive relationship of elevation range with most butterfly distributions indicates that mountainous areas currently play an important role for most species. This agrees with the general pattern found by Van Swaay et al. (2010) in southern Europe. It is difficult to tell whether this trend is due to a preference for mountains or if it is a surrogate of the negative effects of human settlements and roads (but see below), which are more prevalent in lowlands, on butterflies. In any case, mountains are currently associated to most areas that function as source for butterfly populations in the Iberian Peninsula (Figs 3 and 4). Regarding climate, the generally positive effects of days with precipitation ≥ 0.1 mm in spring and mean annual actual evapotranspiration indicate greater favourability for butterflies in areas with many days of light spring precipitation and simultaneous availability of water and energy. Days with maximum temperature ≥ 25 °C in spring also has a relevant representation in the models, being significant for about 40% of species. The relationship, however, is negative in 95.40% of these models, indicating an unfavourable effect of high spring temperatures. This may explain the high species richness in the highest latitudes of Spain or the low species richness in areas where summer drought is dominant (Martín & Gurrea, 1990; Stefanescu et al., 2004).

The effect of human activity on the overall source-sink pattern is complex. Variables such as Human population density (HPd), Distance to the nearest highway (Dhi) or Distance to towns with more than 500 000 inhabitants (U500) were present in many models (HPd: 107; Dhi: 87; U500: 82). The relationships were negative in 94.25% of the cases for Dhi, as well as in 94% for U500, whereas they were positive in practically all cases with HPd (99%). In other words, areas closer to highways and big towns and with higher human population density tended to favour the presence of many species. This seems to indicate that disturbance and habitat degradation produced by human activity do not have a detrimental effect on butterflies, in general, at the resolution scale used in this work. Probably the only effect of human activity at this scale was constraining the distribution of many species to mountains, which in most models was already accounted for by elevation range. The exact nature of this complex interrelation of human activity, mountains and butterfly distributions needs to be solved on a species-specific basis, which is outside of the scope of the present paper. Our hypothesis was that human-induced disturbance should mostly lead to a decline in favourability, except perhaps for some species that could be linked to crops or ornamental botany (such as *Pieris brassicae*, *P. rapae*, *P. napi*, *Cacyreus marshalli* or *Danaus plexippus*). Human activity and population density have been found to be positively related with species richness in other groups such as birds (Luck et al., 2010) and with biodiversity in general (e.g. Luck, 2007). In the Iberian Peninsula, this pattern could reflect the relatively coarse scale of our approach, as well as the tendency of human presence to be scarcer in areas of low butterfly favourability outside the mountains, particularly in the two Iberian plateaus divided by the Central Range (Fig. 1). There could be also a positive effect of human population density and activity on recording density (Pautasso, 2007), as well as a positive discrimination of recorders for species-rich areas (Romo et al., 2006).

The application of source-sink theory to these favourability patterns has the potential to make source-sink theory operational at a biogeographical scale, so enhancing our understanding of the inner complexity of species distributions. According to the source-sink dynamic theory, the populations of the sink areas are regularly supported by immigration from the populations of the nearby source areas (Pulliam, 1988; Boughton, 1999). Consequently, an environmental deterioration in source areas of these species could cause local extinctions in the sink areas, leading to conservation problems for the species. Therefore, source areas should be key areas for monitoring and conservation plans. Thus, this kind of biogeographical analysis is a practical tool for guiding the application of effective conservation efforts for each species (Donker & Krebs, 2012). On the other hand, Loreau et al. (2013) underlined the importance of considering source-sink dynamics jointly for multiple species in conservation planning for preserving ecosystem services. We considered this approach for all the butterfly species in the study area, showing a general pattern of sources related with mountainous areas in the Iberian Peninsula and sinks more scattered throughout the territory (Figs 3 and 4). Favourability is also a key concept in this regard. Acevedo and Real (2012) highlighted that suitability outputs of modelling techniques such as ENFA Hirzel et al., 2002) or MaxEnt (Phillips et al., 2006) produce idiosyncratic values that rank local sites according to their capacity to hold the species, but are not commensurate and, thus, not comparable for different species, territories or, in general, different datasets. Thresholds for establishing suitable and unsuitable areas with these techniques should be set on a species-specific way, for example, and even so, there would be no guarantee that the thresholds are equivalent. Mountain systems are currently quite important for Iberian butterflies, as they concentrate most of the sources (Figs 3 and 4). Some Iberian mountain ranges (Central Pyrenees, Cantabrian Range, Central Range, Baetic Range) include the highest butterfly species richness in the study area. Threatened butterfly species are concentrated too in mountain areas (Romo et al., 2007). Bumblebees also tend to be more diverse in Iberian mountain ranges (Penado et al., 2016). This pattern is not common for other groups, especially for vertebrates, which are mainly found in other areas of the Iberian Peninsula (López-López et al., 2011; Martins et al., 2014).

and of Europe (Assunc_~ao-Albuquerque et al., 2012), nor for other Iberian invertebrates such as aquatic beetles (Guareschi et al., 2015). In addition, analysing the potential distributions of butterfly species listed in the Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora), Romo et al. (2014b) found that the predicted ranges for all these species were concentrated on the Pyrenees, the Cantabrian Range and the Iberian System. This only differs from our results in that we found the Central Range to be a more significant source than the southern part of the Iberian System. Regarding sinks, they show the importance of Alicante and Murcia provinces, which operate as concentrated sink areas in the eastern part of the study area, and the Do~nana National Park, which concentrates sink areas in the southwestern part (Figs 3 and 4). Our results regarding the concentration of sinks in eastern Iberian Peninsula are in agreement with Romo et al. (2014a), who also considered eastern Iberia as precarious for butterflies. Most of the sink cells are dispersed all around the Iberian Peninsula. In our study, the presence of a species on each grid unit was combined with its level of favourability (high, low) to identify them as source or sink areas. Therefore, it can be considered a good complement to the Atlas of Iberian butterflies (García-Barros et al., 2004) that will serve to better target future efforts to search new territories and has the potential to influence conservation programmes (Boughton, 2000). This has direct consequences in the territorial planning of biodiversity conservation: for any species efforts should concentrate in preserving the present conditions in source areas (where conservation is theoretically guaranteed), as well as to improve the conditions in the sinks areas (where local circumstances appear not to guarantee the persistence of the species). Butterfly conservation strategies on source areas should focus on preservation preferentially, because they are already favourable. In a source area, the intrinsic environmental characteristics allow for the presence of a species and its maintenance over time. In a sink area, the conservation focus should be not for preservation but for restoration, for improving those unfavourable areas, which could reduce their mortality rate (Vandermeer et al., 2010; Heinrichs et al., 2015). A conservation focus should be applied as well for facilitating dispersal from source to sink areas (Pulliam, 1988; Furrer & Pasinelli, 2016), as sources mostly maintain sink areas, which would disappear without immigration (Thomas et al., 1996; Boughton, 1999; Timus et al. 2016). Distribution maps tend to conceal these patterns. The possibility of arriving at a sink from a source territory can generate a pattern of continuous presence in the sink that is dependent on both the frequency of arrival of new individuals and the permanence in the sink of those that already occupy it. The overlap between these two processes can mask the effect of the environmental factors, giving the appearance to the naked eye of population stability. However, our approach allowed for the extraction from the distribution atlas a pattern that was, in fact, part of the dark biodiversity (Mokany & Paini, 2011; P~cartel et al., 2011; Real et al., 2017) of the region. P~cartel et al. (2011) called dark diversity the set of species that are absent from a community but have potential for inhabiting according to the ecological conditions. Mokany and Paini (2011) suggested that the dark diversity of a locality could be calculated from the ratio of the summed probabilities of species not present there, and the summed probabilities of all species present in the wider region. Real et al. (2017) proposed that all species, whether or not they have been observed, can be understood in terms of the favourability (rather than probability) for being found in each location, and that local favourability for each species is their contribution to the 'potential biodiversity' of the location. The difference between the contribution of each species to the potential biodiversity of a location (the local favourability value) and their contribution to the observed biodiversity (presence = 1 or absence = 0) gives the contribution of each species to the dark biodiversity of the location. We applied here this concept to the observed presences, by considering the favourability for the species being present in addition to the fact that it was observed there, thus bringing to light a complex pattern of possible sources and sinks. This confirmed that the favourability for the species presence reflects its distribution better than the record of previously observed presence and absence (Real et al., 2017). In sum, this biogeographical analysis revealed much more than what could be appreciated merely from direct observation of the available presence-absence maps. This application of source-sink theory to the favourability patterns should be done, at this level of knowledge, with care, because the connection between environmental favourability and population growth is reasonable but hypothetical and lacks a direct confirmation in the field. The actual identification of source and sink areas will always require field work. Our results show this approach is useful to generate hypotheses about sources and sinks operationally at biogeographical scales, with the potential to be key tools for broad scale biodiversity conservation initiatives and plans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/ icad.12297: Appendix S1. List of Iberian butterflies used in this study. Appendix S2. Model assessment based on classification, discrimination and goodness of fit. Criteria of classification: correct classification rate (CCR), sensitivity (Sensit.), specificity (Specif.), under-prediction rate (UPR), overprediction rate (OPR) and their Cohen's kappa, using the favourability value of $F = 0.5$ as classification threshold. Discrimination capacity: area under the curve (AUC) of the receiver operating characteristic. Goodness of fit: Hosmer & Lemeshow calibration index (HL). Appendix S3. Favourability map (a) and source-sink map (b) of each butterfly species. A, Fam. Hesperiidae-Papilionidae; B, Pieridae; C, Fam. Nymphalidae; D, Fam. Lycaenidae.

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Table 1. Environmental variables considered. In all cases, variables are the average value for each UTM 10 x10 cells.

<i>Code</i>	<i>Frequency</i>			<i>Code</i>	<i>Frequency</i>		
Spatial	+	-	Total	Climatic	+	-	Total
LONG	94	11	105	DP30Win	26	37	63
LAT	87	16	103	DTN0	18	10	28
Climatic	+	-	Total	DTN0Spr	7	47	54
PAnn	16	15	31	DTN0Sum	26	11	37
PSpr	73	6	79	DTN0Aut	64	6	70
PSum	17	23	40	DTn0Win	15	14	29
PAut	33	9	42	DTN20	7	54	61
PWin	4	49	53	DTN20 Aut	47	19	66
TAnn	22	4	26	DTx25	16	24	40
TSpr	7	27	34	DTx25Spr	4	83	87
TSum	40	2	42	DTX25Sum	73	1	74
TAut	9	28	37	DTx25Aut	9	33	42
TWin	9	11	20	SID	26	13	39
TJan	27	9	36	SIDSpr	24	15	39
TJul	8	34	42	SIDSum	41	25	66
TnAnn	11	12	23	SIDAut	51	26	77
TnSpr	19	13	32	SIDWin	24	23	47
TnSum	35	7	42	SIS	20	20	40
TnAut	9	30	39	SISSpr	28	46	74
TnWin	7	19	26	SISSum	42	38	80
TnJan	19	12	31	SISAut	13	60	73
TnJul	9	43	52	SISWin	22	31	53
TxAnn	10	20	30	PET	24	54	78
TxSpr	13	38	51	AET	127	2	129
TxSum	16	19	35	Topographic	+	-	Total
TxAut	22	13	35	E	42	13	55
TxWin	16	36	52	ER	165	0	165
TxJan	20	24	44	SE	34	1	35
TxJul	8	27	35	WE	1	8	9
DP01	10	40	50	Slop	35	15	50
DP01Spr	102	4	106	CTI	10	44	54
DP01Sum	4	49	53	Lithological	+	-	Total
DP01Aut	5	38	43	Clay	29	0	29
DP01Win	37	8	45	PClay	8	10	18
DP10	3	23	26	Sil	56	1	57
DP10Spr	7	56	63	PSil	7	29	36
DP10Sum	9	50	59	Calc	64	3	67
DP10Aut	20	21	41	PCalc	21	9	30
DP10Win	43	5	48	Grav	20	3	23

DP1	11	17	28	PGrav	15	6	21
DP1Spr	11	14	25	Gyp	8	11	19
DP1Sum	49	16	65	PGyp	13	3	16
DP1Aut	17	33	50	Human activity	+	-	Total
DP1Win	4	46	50	Dhi	5	82	87
DP30	22	21	43	HPd	106	1	107
DP30Spr	34	10	44	U100	30	41	71
DP30Sum	31	8	39	U500	10	72	82
DP30Aut	37	5	42				

¹⁾ IGN (1999); ²⁾ AEMET 2011; ³⁾ US Geological Survey (1996); ⁴⁾ <http://hydrosheds.cr.usgs.gov>; ⁵⁾ IGME (2015); ⁶⁾ DERA 2013; ⁷⁾ ORNL (2001). Jarvis, Reuter, Nelson & Guevara, 2008

Table 2. Contribution frequency (Total) of predictor variables in the 222 butterfly favourability models, with the number of positive (+) and negative (-) relationships with environmental favourability (full name of the variables in Table 1).

<i>Code</i>	<i>Frequency</i>			<i>Code</i>	<i>Frequency</i>		
Spatial	+	-	Total	Climatic	+	-	Total
LONG	94	11	105	DP30Win	26	37	63
LAT	87	16	103	DTN0	18	10	28
Climatic	+	-	Total	DTN0Spr	7	47	54
PAnn	16	15	31	DTN0Sum	26	11	37
PSpr	73	6	79	DTN0Aut	64	6	70
PSum	17	23	40	DTn0Win	15	14	29
PAut	33	9	42	DTN20	7	54	61
PWin	4	49	53	DTN20 Aut	47	19	66
TAnn	22	4	26	DTx25	16	24	40
TSpr	7	27	34	DTx25Spr	4	83	87
TSum	40	2	42	DTX25Sum	73	1	74
TAut	9	28	37	DTx25Aut	9	33	42
TWin	9	11	20	SID	26	13	39
TJan	27	9	36	SIDSpr	24	15	39
TJul	8	34	42	SIDSum	41	25	66
TnAnn	11	12	23	SIDAut	51	26	77
TnSpr	19	13	32	SIDWin	24	23	47
TnSum	35	7	42	SIS	20	20	40
TnAut	9	30	39	SISSpr	28	46	74
TnWin	7	19	26	SISSum	42	38	80
TnJan	19	12	31	SISAut	13	60	73
TnJul	9	43	52	SISWin	22	31	53
TxAnn	10	20	30	PET	24	54	78
TxSpr	13	38	51	AET	127	2	129
TxSum	16	19	35	Topographic	+	-	Total
TxAut	22	13	35	E	42	13	55
TxWin	16	36	52	ER	165	0	165
TxJan	20	24	44	SE	34	1	35
TxJul	8	27	35	WE	1	8	9
DP01	10	40	50	Slop	35	15	50
DP01Spr	102	4	106	CTI	10	44	54
DP01Sum	4	49	53	Lithological	+	-	Total
DP01Aut	5	38	43	Clay	29	0	29
DP01Win	37	8	45	PClay	8	10	18
DP10	3	23	26	Sil	56	1	57
DP10Spr	7	56	63	PSil	7	29	36

DP10Sum	9	50	59	Calc	64	3	67
DP10Aut	20	21	41	PCalc	21	9	30
DP10Win	43	5	48	Grav	20	3	23
DP1	11	17	28	PGrav	15	6	21
DP1Spr	11	14	25	Gyp	8	11	19
DP1Sum	49	16	65	PGyp	13	3	16
DP1Aut	17	33	50	Human activity	+	-	Total
DP1Win	4	46	50	Dhi	5	82	87
DP30	22	21	43	HPd	106	1	107
DP30Spr	34	10	44	U100	30	41	71
DP30Sum	31	8	39	U500	10	72	82
DP30Aut	37	5	42				

Figures

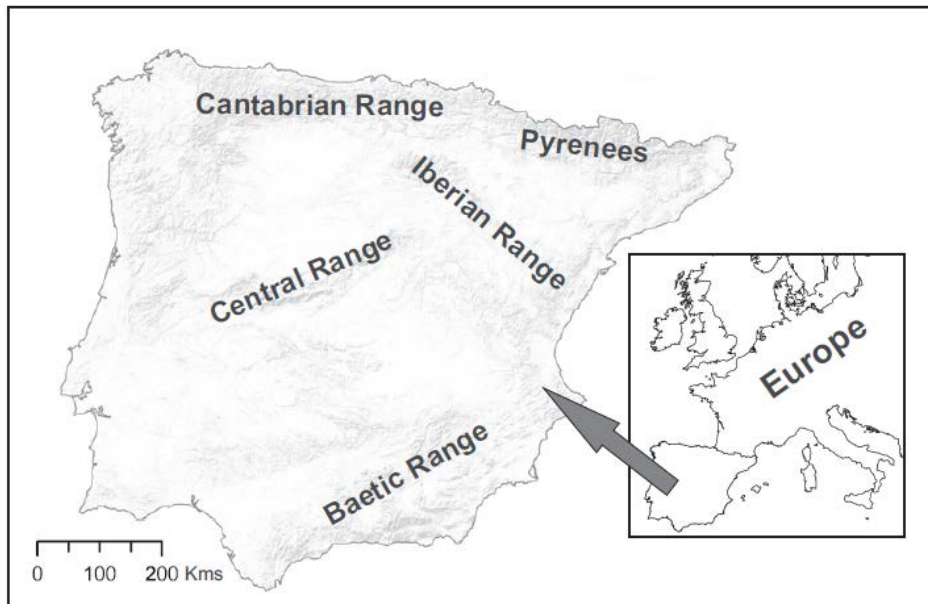


Fig. 1. Main mountain ranges in the Iberian Peninsula.

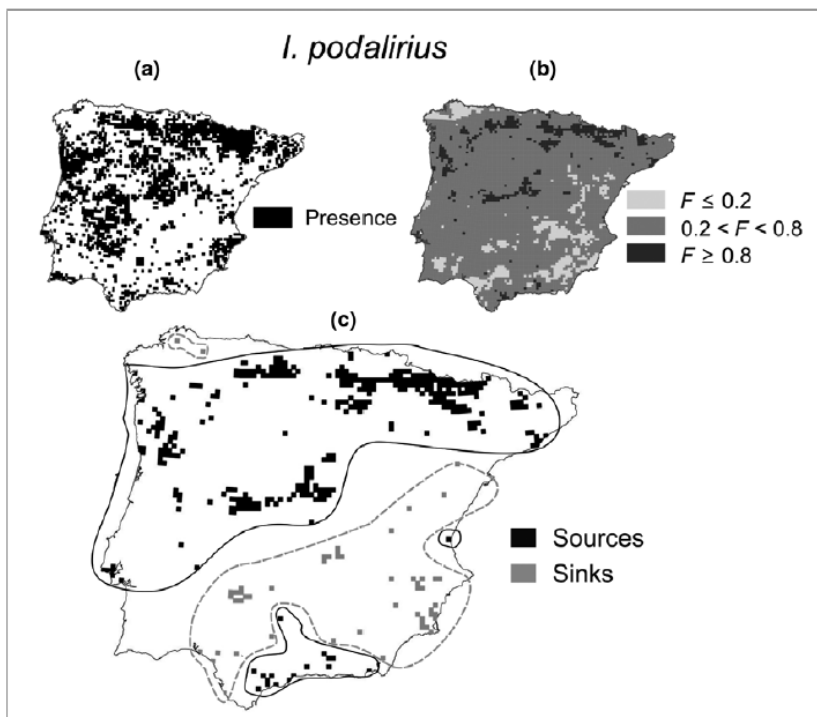


Fig. 2. a) Distribution map, b) Favourability map and c) Source and sink areas map for *I. podalirius*. Source: a grid where the butterfly is present and with very high environmental favourability for it ($F \geq 0.8$). Sink: a grid where the butterfly is present and with very low environmental favourability for it ($F \leq 0.2$).

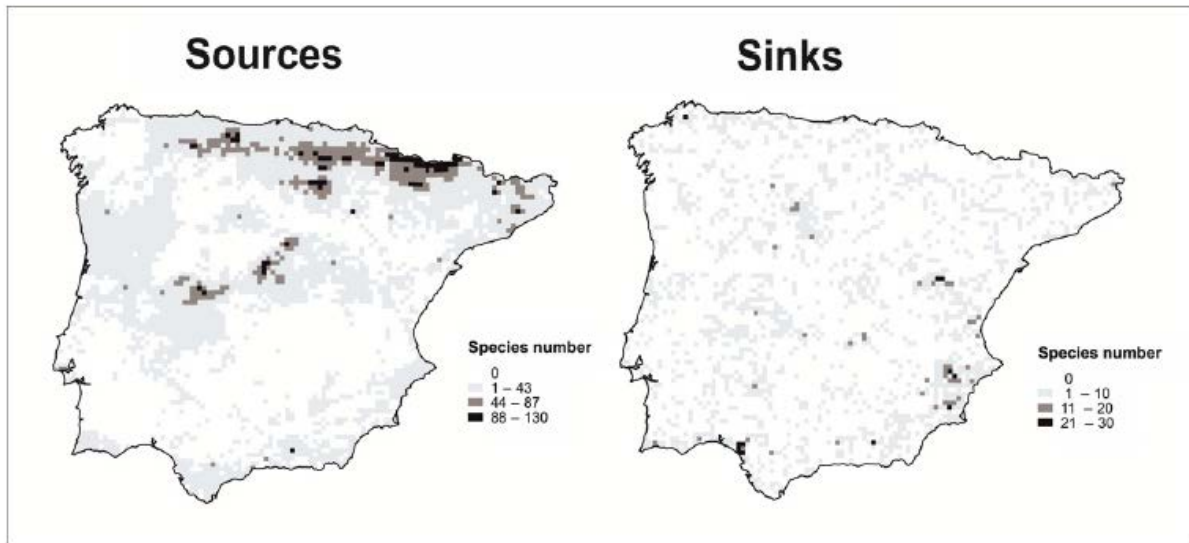


Fig. 3. Source and sink areas for all the butterflies. Source: a grid where the butterfly is present and with very high environmental favourability for it ($F \geq 0.8$). Sink: a grid where the butterfly is present and with very low environmental favourability for it ($F \leq 0.2$). The darker colour symbolizes that the grid acts as source or sink, respectively, for a greater numbers of species.

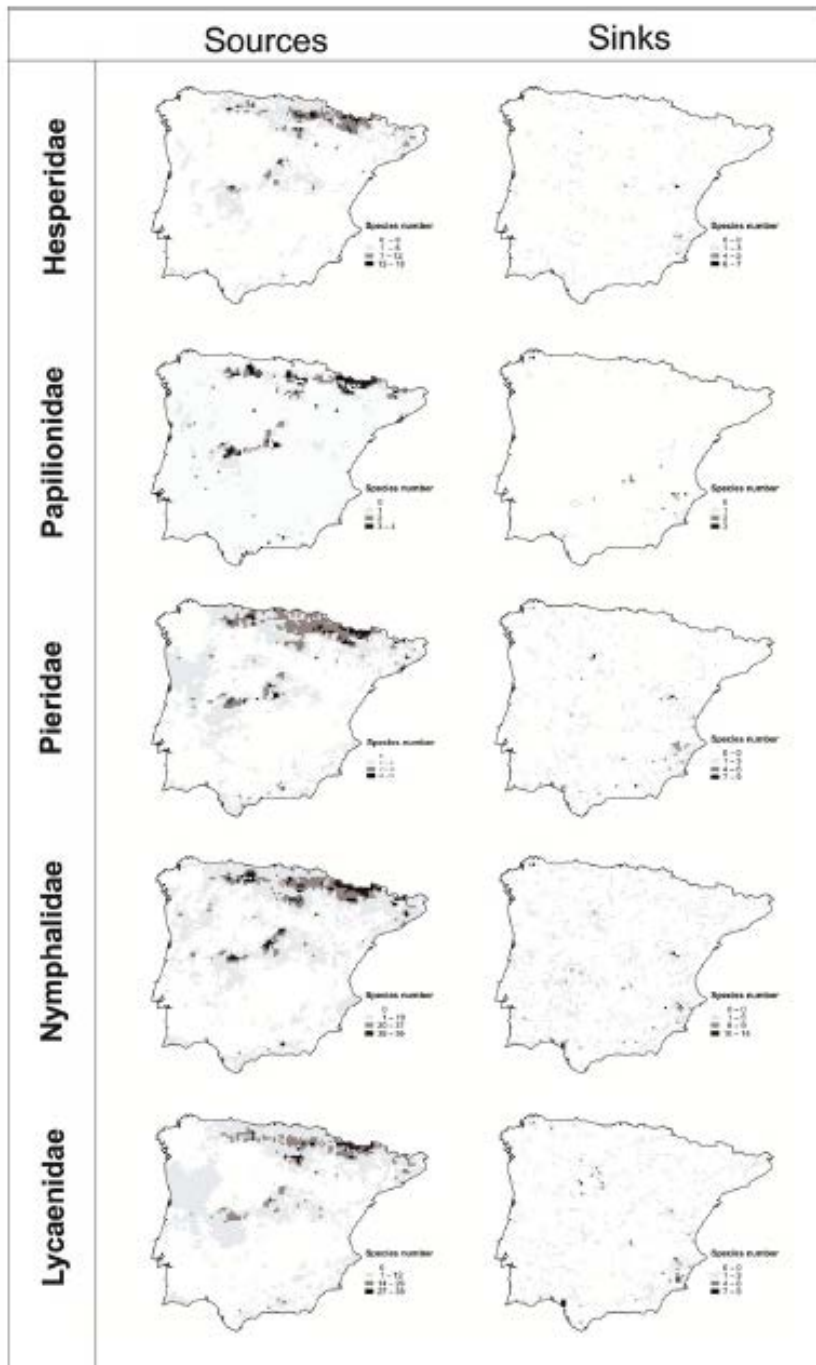


Fig. 4. Source and sink areas for each butterfly family (Hesperidae, Papilionidae, Pieridae, Nymphalidae and Lycaenidae). Source: a grid where the butterfly is present and with very high environmental favourability for it ($F \geq 0.8$). Sink: a grid unit where the butterfly is present and with very low environmental favourability for it ($F \leq 0.2$). The darker colour symbolizes that the grid acts as source or sink, respectively, for a greater numbers of species.