



Does local habitat fragmentation affect large-scale distributions? The case of a specialist grassland bird

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ABSTRACT

Aim Although the negative effects of habitat fragmentation have been widely documented at the landscape scale, much less is known about its impacts on species distributions at the biogeographical scale. We hypothesize that fragmentation influences the large-scale distribution of area- and edge-sensitive species by limiting their occurrence in regions with fragmented habitats, despite otherwise favourable environmental conditions. We test this hypothesis by assessing the interplay of climate and landscape factors influencing the distribution of the calandra lark, a grassland specialist that is highly sensitive to habitat fragmentation.

Location Iberia Peninsula, Europe.

Methods Ecological niche modelling was used to investigate the relative influence of climate/topography, landscape fragmentation and spatial structure on calandra lark distribution. Modelling assumed explicitly a hierarchically structured effect among explanatory variables, with climate/topography operating at broader spatial scales than landscape variables. An eigenvector-based spatial filtering approach was used to cancel bias introduced by spatial autocorrelation. The information theoretic approach was used in model selection, and variation partitioning was used to isolate the unique and shared effects of sets of explanatory variables.

Results Climate and topography were the most influential variables shaping the distribution of calandra lark, but incorporating landscape metrics contributed significantly to model improvement. The probability of calandra lark occurrence increased with total habitat area and declined with the number of patches and edge density. Variation partitioning showed a strong overlap between variation explained by climate/topography and landscape variables. After accounting for spatial structure in species distribution, the explanatory power of environmental variables remained largely unchanged.

Main conclusions We have shown here that landscape fragmentation can influence species distributions at the biogeographical scale. Incorporating fragmentation metrics into large-scale ecological niche models may contribute for a better understanding of mechanism driving species distributions and for improving predictive modelling of range shifts associated with land use and climate changes.

Keywords

Distribution modelling, ecological niche modelling, edge effects, grassland birds, habitat fragmentation, model selection.

INTRODUCTION

The fragmentation of once continuous habitats is one of the key threats to global biodiversity (Fahrig, 2003; Fischer & Lindenmayer, 2007). Fragmentation reduces the size of local habitat patches and the connectivity among patches, thus increasing edge and isolation effects, which in turn make species more susceptible to extinction due to environmental variability, demographic stochasticity and genetic influences (Fischer & Lindenmayer, 2007). As a consequence, species may be absent from landscapes where remnant patches of suitable habitat have become too small or isolated, despite otherwise favourable environmental conditions. Although these effects have been widely documented at the landscape scale (Debinski & Holt, 2000; Fahrig, 2003; Fischer & Lindenmayer, 2007), particularly for habitat specialists (e.g. Devictor *et al.*, 2008), the extent to which fragmentation effects perceived at the landscape scale influence large-scale distributions remains poorly known (but see Warren *et al.*, 2001; Collier *et al.*, 2012).

Assessing the factors influencing species distributions is generally conducted using models that relate field observations to sets of environmental variables, based on empirically derived response curves (Peterson *et al.*, 2011). In studies modelling species distributions at large scales, it is often assumed that distributions are primarily controlled by climatic factors (e.g. Huntley *et al.*, 2008; Hof *et al.*, 2011), whereas at local scales the assumption is often that biotic interactions and the type, location, size and fragmentation of habitats are the main controls for the distribution of resources and thus of species (e.g. Scott *et al.*, 2002; Pearson & Dawson, 2003). Although the relative contribution of land cover versus climate in large-scale species distribution modelling studies has been occasionally assessed (e.g. Thuiller *et al.*, 2004; Luoto *et al.*, 2007), the relative contribution of structural metrics related to fragmentation has been largely neglected (Opdam & Wascher, 2004). Therefore, the degree to which landscape fragmentation controls for species distributions at large scales is still a matter of debate. For example, Warren *et al.* (2001) suggested that negative effects of habitat fragmentation on butterfly habitat specialists are dominant over the positive effects of (warmer) climate in heavily fragmented landscapes, underlining the importance of discriminating between forces of climate and habitat pattern in distribution modelling. In contrast, Triviño *et al.* (2011) found that landscape configuration variables only rarely improved the fit of ecological niche models for birds at large scales.

Clearly, there is a need to assess the extent to which fragmentation metrics may improve the performance of large-scale species distribution models. Grassland birds provide an interesting study model because they are habitat specialists adapted to open landscapes, and they are often sensitive to habitat fragmentation (Goriup, 1988; De Juana, 2005). Specifically, grassland birds are often area sensitive, selecting large and homogeneous patches of open habitat, while being absent or

occurring at low density in patches below a given size (Helzer & Jelinski, 1999; Winter & Faarborg, 1999; Johnson & Igl, 2001; Hamer *et al.*, 2006). Furthermore, grassland birds are often edge sensitive (e.g. Coppedge *et al.*, 2004; Fletcher, 2005), that is, avoid habitat edges and are expected to decline with increasing density of edges in smaller and more convoluted patches (Ewers & Didham, 2007). Studies on the large-scale distribution of grassland birds have shown that species occurrence is strongly influenced by the distribution of herbaceous habitats such as natural grasslands and steppes, pastureland and fallow fields (e.g. Suárez-Seoane *et al.*, 2002; Vallecillo *et al.*, 2009), but the role of habitat fragmentation remains uncertain.

In this study, we used a specialist grassland bird inhabiting open farmland habitats of the Iberian Peninsula, the calandra lark *Melanocorypha calandra*, to analyse the importance of landscape metrics in large-scale species distribution models. This issue is of conservation relevance, because Iberian grasslands are critical for a range of open farmland birds of conservation concern, which are threatened by ongoing processes of agricultural intensification and habitat fragmentation (EEA, 2004; Bota *et al.*, 2005). Although calandra lark remains one of the most abundant species despite some local declines (e.g. Estrada & Nieves, 2004), it provides a particularly interesting case study because previous research showed that it is strongly affected by habitat fragmentation (Reino *et al.*, 2009, 2010; Morgado *et al.*, 2010). Calandra larks tend to be absent from habitat patches < 100 ha (Morgado *et al.*, 2010), and they avoid areas at < 200 m from wooded edges (Reino *et al.*, 2009). It may thus be hypothesized that landscape patterns, such as the availability of open habitat and its fragmentation, can affect the occurrence of calandra lark at biogeographical scales (here the Iberian Peninsula). Here, we test this hypothesis, using an ecological niche modelling approach to assess the relative roles of climate, topography and landscape fragmentation variables on calandra lark distribution (Peterson *et al.*, 2011), assuming a hierarchical organization of environmental effects (Pearson *et al.*, 2004), coupled with a variation partitioning procedure that quantifies the relative contribution of sets of explanatory variables to variation in species distributions (Borcard *et al.*, 1992).

METHODS

Study area and data sources

Our study used presence-absence data for calandra lark in the Iberian Peninsula, including 6111 10 × 10 km UTM squares and a total of 2194 occurrences (121 for Portugal and 2074 for Spain) encompassing 35.9% of the sampled squares in Iberia (Fig. 1). Data were compiled from the breeding bird atlas of both Portugal (Equipa Atlas, 2008) and Spain (Martí & Moral, 2003). Field atlas data were gathered during 1999–2005 for Portugal, and 1998–2002 for Spain. Sampling strategies for the atlases were basically similar, including extensive surveys for each square, but also a stratified sampling considering a set of 2 × 2 km squares.

Climate data included three variables (Table 1): total annual precipitation (PREC), annual mean air temperature (TANN) and temperature range (difference between the mean temperature of the warmest and the coldest month; TRANGE), compiled from point data with 10-min resolution (New *et al.*, 2000). One topographical variable expressing the terrain slope (SLOPE) was considered (Table 1), because a strong association of calandra lark to flatness was reported in other studies (Suárez-Seoane *et al.*, 2002). SLOPE was derived from the Digital Terrain Model of the NASA Shuttle Radar Topographic Mission (Jarvis *et al.*, 2008), with approximately 90-m resolution. Climatic and topographical data were resampled at the same grid resolution as the species' occurrence data, by computing the mean value per 10×10 km grid square. Corine Land Cover 2000 (EEA, 2010) was used to build a GIS layer containing polygons representing calandra lark habitats. Suitable habitat (dry steppe grasslands; Suárez *et al.*, 1991) resulted from aggregating two Corine Land Cover classes: non-irrigated arable land (code: 211) and pastures (code: 231). Two alternative map layers of suitable habitat were produced: one layer containing all the Corine Land Cover polygons of suitable habitat, and a second layer obtained by subtracting a 200-m buffer from the edge of the original polygons of suitable habitat. The first layer represents the total habitat potentially available for the species, whereas the second layer represents the effective area of suitable habitat, because the 200-m edge strip is strongly avoided by calandra larks (Reino *et al.*, 2009). For each alternative habitat layer, three landscape metrics were computed per 10×10 km grid square: total area, number of patches and edge density (Table 1). Edge density was computed using the total edge length of all suitable habitat patches at each grid square. There was low pairwise correlation (< 0.70)

Table 1 Summary statistics (mean \pm standard deviation) of predictor variables considered in the analyses of factors affecting the presence or absence of the calandra lark in 10×10 km squares across the Iberian Peninsula

Variables (Abbreviation; Units)	Presence	Absence
Total annual precipitation (PREC; mm)	504.0 \pm 102.4	730.6 \pm 276.3
Mean annual air temperature (TANN; °C)	12.9 \pm 23.4	12.6 \pm 30.3
Annual temperature range (TRAN; °C)	28.6 \pm 26.1	24.9 \pm 40.6
Mean slope (SLOP;%)	3.6 \pm 2.4	8.5 \pm 5.4
Habitat area (AREA; km ²)		
Total	29.9 \pm 25.2	6.9 \pm 11.3
Effective	11.9 \pm 21.6	1.5 \pm 5.4
Number of patches (NUMP; N)		
Total	7.5 \pm 5.8	7.5 \pm 7.1
Effective	6.2 \pm 4.3	5.2 \pm 5.03
Edge density (EDEN; km ha ⁻¹)		
Total	0.59 \pm 0.31	0.25 \pm 0.28
Effective	0.72 \pm 0.34	0.40 \pm 0.37

between the seven variables used in this study, and so collinearity problems in model development and parameter estimation were unlikely. All GIS analyses were performed using Arc GIS 9.2 (ESRI, Redlands, CA, USA).

Statistical analyses

To investigate the relative influence of climate/topography, landscape metrics and spatial structure on calandra lark distribution, we fitted logistic regression models. Modelling assumed explicitly a hierarchically structured effect among explanatory variables (Pearson *et al.*, 2004; Anadón *et al.*, 2007), with climatic/topographic variables operating at broader spatial scales than landscape variables (e.g. Thuiller *et al.*, 2004). Therefore, the effect of landscape variables was treated after accounting for the effect of climatic/topographic variables.

In a first step, we developed models exclusively based on climate and topographical variables, considering all possible combinations of variables. The best approximating model was then selected based on the information theoretic approach (ITA) (Burnham & Anderson, 2002), using the Akaike information criterion (AIC) as a measure of information loss of each candidate model, with the best fitting model having the lowest AIC and consequently the highest Akaike weight (w_i) (Burnham & Anderson, 2002). The relative importance of the selected variables was assessed using the probability of each variable to be included in the best approximating models, estimated by summing the Akaike's weights of all candidate models where the variable was included (Burnham & Anderson, 2002). In a second step, the landscape variables were considered for inclusion in the model, but retaining the climate/topographical variables selected in the best candidate model of the first step. Quadratic terms of the original landscape variables were considered in model development, to account for eventual unimodal relationships. The interaction term between habitat area and edge density was also considered, because low edge densities may occur in landscapes with either very low or very high habitat availability. Model selection was carried out as in step 1.

A Moran's test was performed to check for spatial autocorrelation in the residuals of the best approximating model including both climate/topographical and landscape variables. In case the test was significant ($P < 0.05$), we used an eigenvector-based spatial filtering approach to cancel the bias introduced by the spatial autocorrelation of the residuals (Diniz-Fillho & Bini, 2005). Only a subset of the computed spatial filters was retained as the set of candidate variables in the subsequent model selection process. First, as the purpose of using spatial filters is to cancel the spatial structure remaining in residuals, we only retained those with enough spatial structure (Moran's I values greater than 0.3). Second, because the residual spatial structure can be assumed to be driven by unmeasured processes that affect a species' distribution (e.g. Dormann *et al.*, 2007; Dray *et al.*, 2012), only

those that contributed to a significant improvement of model fit were retained. In a third step, the spatial filters were selected for inclusion in the final model, after retaining the predictors selected in the first two steps. At this step, all possible combinations of spatial filters were considered for inclusion, but restricting their number to a maximum of four. Finally, the resulting model was again checked for spatial autocorrelation in the residuals using Moran's test.

Model fit was assessed using deviance and AIC values. The relative contribution of landscape variables to explain variation in species occurrence data was assessed using a variation partitioning procedure. The pure and shared contributions of climatic/topographical, landscape and spatial variables were estimated using the approach developed by Borcard *et al.* (1992), which is frequently used with three groups of predictors (e.g. Heikkinen *et al.*, 2004; Reino, 2005). The estimated proportions of explained variation were based on the Nagelkerke R-square (Nagelkerke, 1991).

Finally, classification accuracy of models was based on three commonly used measures (Fielding & Bell, 1997): area under the ROC curve (AUC), sensitivity (percentage of correctly classified presences) and specificity (percentage of correctly classified absences). These measures, and their respective standard deviation values, were estimated from 999 random splits of the original dataset into a calibration subset with 70% of the data and a validation subset with 30% of the data. As the cut-off point for the computation of

sensitivity and specificity we used the probability value that maximized the sum of sensitivity and specificity (Liu *et al.*, 2005), which corresponds to the point in the ROC that is closer to the left upper corner of the ROC plot.

All statistical analyses were performed using functions and routines implemented in R software version 2.12 (R Development Core Team, 2011), except the computation of eigen-vector-based spatial filters that was performed using SAM, version 3.3 (Rangel *et al.*, 2010). Moran's I values and tests were computed with the library *spdep* for R (Bivand, 2011).

RESULTS

In the first step of model development, all four climatic and topographic variables were included in the best candidate model, and all coefficients were significant (*t*-test, $P < 0.001$; Table 2). Probability of calandra lark occurrence declined with increasing mean annual temperature, precipitation and slope, and increased with temperature range (Table 2; Fig. 2). The best climatic/topographic model was very strongly supported ($w_i = 0.999$), and the selection probability of all variables was close to one.

In the second step, habitat area and edge density were included in their quadratic form ($x + x^2$) in the best candidate model (Table 2; Fig. 2). This model suggested that the probability of calandra lark occurrence increased as habitat area increased, but tended to stabilize for higher values of

Table 2 Logistic regression models relating the occurrence of calandra lark in 10×10 km squares across the Iberian Peninsula to climate (Cl), landscape (Ld) and spatial (Sp) sets of variables

Variables	Cl	Total habitat		Effective habitat	
		Cl + Ld	Cl + Ld + Sp	Cl + Ld	Cl + Ld + Sp
Intercept	1.146	−0.046	1.583	0.115	1.571
PREC	−0.003***	−0.004***	−0.005***	−0.004***	−0.005***
SLOP	−0.363***	−0.224***	−0.235***	−0.220***	−0.231***
TANN	−0.020***	−0.009***	−0.018***	−0.009***	−0.018***
TRAN	0.017***	0.011***	0.011***	0.010***	0.011***
AREA	—	0.567***	0.608***	0.247***	0.245***
AREA ²	—	−0.024*	−0.028**	—	—
EDEN	—	0.905	0.917	3.417***	3.524***
EDEN ²	—	−0.915***	−0.989***	−2.031***	−2.107***
NUMP ²	—	—	—	−0.002**	−0.002*
SF16	—	—	19.716***	—	20.162***
SF18	—	—	−30.669***	—	−29.674***
SF22	—	—	13.276***	—	13.676***
SF25	—	—	20.480***	—	20.055***
Deviance	5091.7	4598.7	4376.1	4596.0	4376.3
AIC	5101.7	4616.7	4402.1	4614.0	4402.8
w_i	0.999	0.329	0.998	0.707	0.999

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Landscape variables were based on either the total or the effective habitat (see text for details). In each case, the regression coefficients of the best approximating model are provided, together with the corresponding deviance, AIC and Akaike weights. Abbreviations as in Table 1.

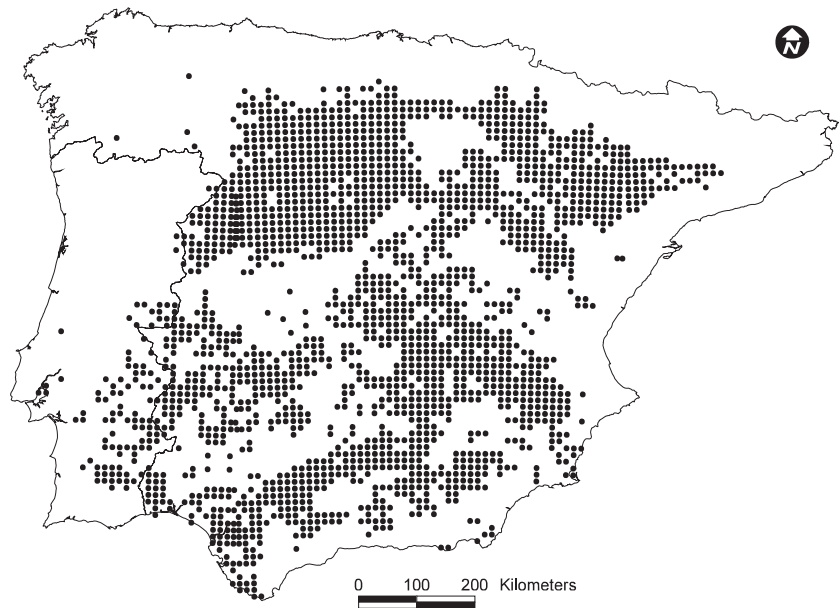


Figure 1 Distribution map of the calandra lark (*Melanocorypha calandra*) in the Iberian Peninsula using 10 × 10 km UTM grid. Redrawn from Martí & Moral (2003) and Equipa Atlas (2008).

habitat area (Fig. 2). Seemingly, the effect of edge density was small in landscapes with low density of edges, while the probability of occurrence declined rapidly with edge density in landscapes with high density of edges (Fig. 2). Although this model had a low Akaike weight (0.33; Table 2), it highlighted relationships that were also shown by the two alternative models that were at < 2 AIC units from the best model. Both the second ($w_i = 0.26$) and the third ($w_i = 0.16$) most supported models included the positive effect of habitat area and the negative effect of edge density; though, in the third best model, only the quadratic term of edge density was included. The second best model also included the positive effect of the number of habitat patches, but the overall selection probability of this variable (0.28) was much lower than that of either habitat area (0.97) or edge density (0.99), and its effect was inconsistent across alternative models (i.e. showing either positive or negative effects). The interaction term between area and edge density had a very low selection probability (0.07).

When the effective habitat was used in modelling instead of the total habitat, the best candidate model included the effective habitat area, the number of patches and edge density (Table 2). This model suggested that the probability of calandra lark occurrence increases with the amount of effective habitat and declines with edge density and the number of habitat patches (Table 2). The shape of the response curve to edge density was similar to that obtained for the previous model, with a rapid decrease of occurrence probability in landscapes with higher density of edges. Although the best approximating model had a relatively low Akaike weight ($w_i = 0.71$; Table 2), the alternative models were much less supported ($w_i < 0.15$). In contrast to the models based on total habitat, the selection probability of the number of patches (0.74) was closer to that of habitat area (0.97) and edge density (0.99), and its negative effect was largely

consistent across models. The interaction term between area and edge density had a very low selection probability (0.02).

The last step in model development involved the fitting of spatial filters, thereby controlling for spatial structure in the environmental model (Table 2). The models developed for both the total and the effective habitat were much similar, including the same set of four spatial filters, and showing nearly equal deviances, AICs and Akaike weights. In both cases, the models were strongly supported ($w_i > 0.99$), and all coefficients of the climate/topographical and landscape components remained significant (Table 2).

For models based on either the total or the effective habitat, the percentage of explained variation was close to 60% (Fig. 3). In both cases, the magnitude of the pure effects of climate/topography was about three times larger than that of landscape variables (Fig. 3). However, the largest contribution to explained variation (about 50%) was that of the shared effects of climate/topography and landscape (Fig. 3), pointing out a large correlation between sets of factors operating at different hierarchical scales. Both the pure and the shared effects of spatial variables showed a very low contribution to explained variation in the distribution of the calandra lark (all < 3%).

Classification accuracy was high for models based on either the total or the effective habitat (Table 3). In both cases, the AUC estimate was > 0.90, which is considered an excellent agreement according to Swets' (1988) rule of thumb. The percentage of correctly classified presences (sensitivity) was > 85% for both models, whereas the percentage of correctly classified absences (specificity) was always > 80.0%.

DISCUSSION

At the landscape scale, previous studies reported that calandra lark is a farmland species with a strong affinity for large

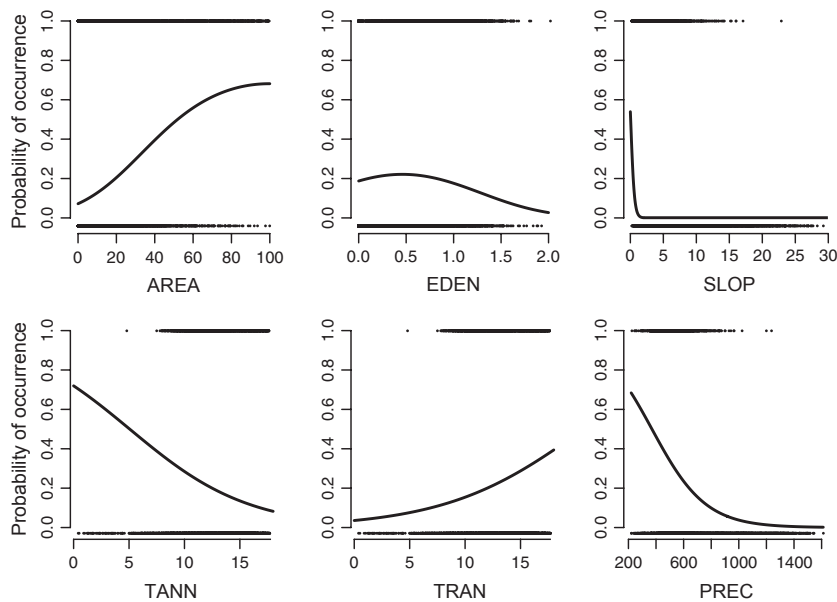


Figure 2 Modelled relationships between environmental variables and the probability of occurrence of calandra lark in 10×10 km squares across the Iberian Peninsula. Response curves were obtained from the best approximating model containing climatic/topographic, landscape and spatial variables, with landscape variables based on total habitat (Table 2). For each variable, the response curve was obtained by setting all other variables to their mean values. Abbreviations as in Table 1.

Table 3 Classification accuracy of the best approximating models including climate, landscape and spatial sets of variables

Classification accuracy	Total habitat	Effective habitat
AUC	0.912 ± 0.005	0.911 ± 0.006
Sensitivity	85.3 ± 2.6	86.0 ± 2.0
Specificity	81.4 ± 2.8	80.7 ± 2.0

Landscape variables were based on either the total or the effective habitat (see text for details). AUC = Area under the receiver operating characteristic (ROC) curve.

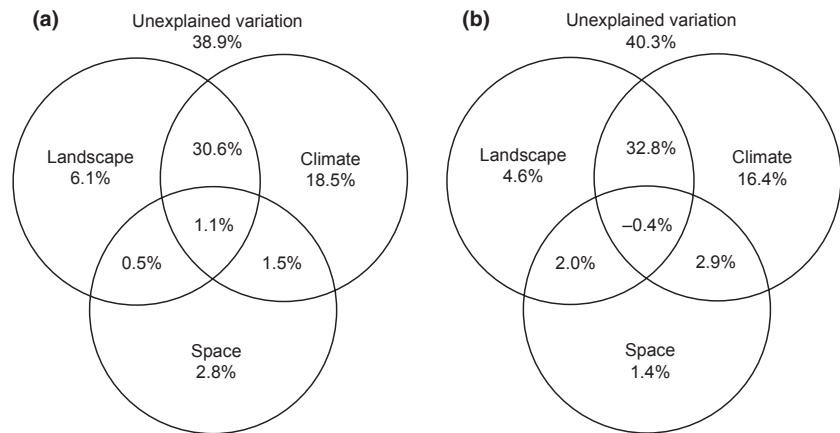
patches of open grassland and a strong avoidance of habitat edges (Reino *et al.*, 2009, 2010; Morgado *et al.*, 2010), and so we hypothesized that local habitat fragmentation should influence its distribution patterns across the Iberian Peninsula. As predicted, we found that the negative effects of edge density and patch number added significant discrimination ability to large-scale distribution models based solely on climate and topographic variables; though, the influence of fragmentation metrics was relatively minor. However, variation partitioning revealed that a very large proportion of the variation explained by climate/topography overlapped with that explained by landscape variables, probably reflecting the strong influence of climate and topography on the spatial distribution of agricultural land uses.

The dominant effect of climate on calandra lark distribution, associated with a significant but much smaller contribution of landscape variables, is consistent with one of the most fundamental assumptions of ecological niche models (Araújo & Peterson, 2012). Moreover, it is in line with the results of most studies analysing large-scale species distributions in response to these predictors (Thuiller *et al.*, 2004; Luoto *et al.*, 2007; Triviño *et al.*, 2011). For example, Thuiller *et al.* (2004) showed that climate was the major driver

of plant and vertebrate distributions across Europe, although land cover variables could help improve models, especially when land cover variables were weakly associated with climate. Luoto *et al.* (2007) also reported a dominant climate effect on bioclimatic models for birds in Finland, although with a significant contribution of land cover on model performance, especially in analyses at finer spatial resolutions (10 km, as in the current study). In a recent study, Triviño *et al.* (2011) reported a dominant contribution of climate in relation to vegetation and land cover variables when modelling distributions of 168 bird species in Iberian Peninsula.

Despite a dominant effect of climate, there was evidence that habitat fragmentation also affected calandra lark distributions across Iberia. Such evidence was supported by hierarchical modelling showing that landscape variables still contributed significantly to the discrimination ability of the species distribution model, after accounting for the effect of climate variables. Furthermore, variation partitioning showed that the shared effects of climate/topography and landscape variables had a much stronger contribution to explained variation in the models than the sum of the unique effects of either climate/topography or landscape variables. One possible reason for this result is that climate/topography effects on the calandra lark were largely indirect, resulting from their influence on the spatial distribution and configuration of the open farmland systems to which the calandra lark is strongly associated (Reino *et al.*, 2009; Morgado *et al.*, 2010). This is in line with previous studies on the factors influencing calandra lark distribution in Spain showing that models with good predictive power could be developed from variables reflecting vegetation cover, without considering climate variables (Suárez-Seoane *et al.*, 2002; Osborne *et al.*, 2007). It is worth noting, however, that some of the previous models showed non-stationarity (i.e. variation in modelled

Figure 3 Variation partitioning Venn diagrams representing the pure and shared contributions of climatic/topographic, landscape and spatial sets of variables to the explained variation in the distribution of calandra lark in the Iberian Peninsula. Landscape variables were computed considering either the total (a) or the effective habitat (b).



relationships over space; Osborne *et al.*, 2007), which could be due to spatial variation in species responses to habitat quantity conditional on landscape fragmentation.

Both variables that were used as indicators of habitat fragmentation showed significant effects on calandra lark distribution, indicating that the likelihood of species occurrence declined with increasing number of habitat patches and edge density. This suggests that the preference for large open patches and the avoidance of habitat edges observed in landscape-scale studies (Reino *et al.*, 2009; Morgado *et al.*, 2010) may upscale to influence species distributions in the Iberian Peninsula. Despite this result, the landscape metrics that explicitly took into account the effective habitat, based on local-scale measurements of edge effect on species density (Reino *et al.*, 2009), did not contribute significantly for the improvement of the model. This was evident both in terms of model fit and model predictive power. Probably, this was a consequence of edge effects operating at the scale of hundreds of metres (< 200 m) being lost due to the coarse resolutions of the Corine Land Cover map (minimum mapping unit = 25 ha) and of the occurrence data (10 × 10 km grid) used in this study. Therefore, although edge density was found to influence calandra lark distribution, the additional refinement of incorporating edge avoidance processes to estimate the effective area of usable habitat appeared unwarranted.

The effects of fragmentation on large-scale distribution of the calandra lark were probably limited by the current patterns of habitat availability, as the species still has very large areas of continuous open habitat across the Iberian Peninsula (Suárez-Seoane *et al.*, 2002). Under these circumstances, it is likely that fragmentation was mostly influential outside the core areas of species distribution, where calandra larks often occur as small and isolated populations (Fig. 1). This is where the species may be most affected by patch area and edge effects (Reino *et al.*, 2009; Morgado *et al.*, 2010), which can thus contribute to shaping large-scale distributions. In contrast, where the habitat is largely continuous, it is unlikely that these effects are influential, and so the species may be mostly

influenced by climate drivers. Fragmentation effects should probably be stronger for other steppe birds with a sparser and more fragmented distribution, such as for instance the Dupont's lark, *Chersophilus duponti* (Méndez *et al.*, 2011). Further insights on the role of landscape fragmentation on large-scale distributions could probably be gained by examining several species with different fragmentation patterns at the range-wide scale.

Taken together, results of our study suggest that fragmentation processes occurring at the landscape scale may affect large-scale species distributions; though, these effects may be partly confounded by correlations between factors operating at different hierarchical levels. Nevertheless, the results support the view that more attention should be given to the incorporation of fragmentation metrics on the development of large-scale species distribution models, particularly for species such as the calandra lark, where research at the landscape scale revealed a strong influence of habitat fragmentation. More generally, our results underline the value of using information on local habitat affinities to generate hypothesis on the processes influencing large-scale species distributions, thereby tailoring the variables used in model building to the known ecological characteristics of each species. Explicitly considering this type of links between local processes and large-scale patterns is recognized as one of the key avenues of research for understanding species distributions, enabling better predictions of future patterns under climate and land use change conditions (Beck *et al.*, 2012).

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