Use of ring recoveries to predict habitat suitability in small passerines

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ABSTRACT

Aim Abundance of small passerines may be distributed over large wintering areas according to geographical patterns that are difficult to detect. This may prevent the identification and conservation of the most suitable sectors, or the detection of local and regional features affecting the species during winter. In this paper, we explore the usefulness of ring recoveries to predict bird distribution in wintering grounds by using Maxent, one of the presence-only techniques available for modelling species distributions. We test whether suitability indices obtained in 2.5×2.5 km UTM squares from ring recoveries were positively correlated with the actual abundance of robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*) inside the squares.

Location Spain.

Methods We used 686 and 1139 localities across the country in which blackcap and robin ring recoveries were recorded by the Spanish Office of Migratory Species to generate the suitability maps. In addition, we sampled bird abundance inside 70 control squares independent of ring recovery localities along a belt crossing mountains, highlands and lowlands of the Iberian Peninsula during January from 2006 to 2011.

Results Suitability indices predicted by Maxent were positively correlated with robin ($r = 0.42$, $n = 70$, $P < 0.001$) and blackcap ($r = 0.52$, $n = 70$, $P < 0.001$) abundances in the 70 control squares along the belt crossing the Iberian Peninsula.

Main conclusions These results suggest that the use of distribution models with ring recoveries may be used to describe the habitat suitability of the winter ranges of small, common passerines. This also means that the huge number of ring recoveries stored in national and transnational data banks could be used to explore the factors shaping bird ranges and to forecast the geographical distribution of suitable wintering areas of migratory birds in large, poorly known regions. This may be useful in biogeography and conservation.

Keywords
Abundance patterns, migratory birds, modelling spatial distribution, occurrence data, ring recoveries.

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INTRODUCTION

There are an increasing number of cartographical approaches designed to forecast species distribution in large areas by combining occurrence data with environmental variables (Elith *et al.*, 2006). These models present the possibility of predicting the distribution of poorly known, rare or threatened species,

the invasion routes of pests and vectors or the effect of some ongoing environmental changes on species ranges (Elith & Leathwick, 2009).

Despite the fact that data recorded in the literature or stored in natural history museums and herbaria have been used to predict species distribution, little attention has been devoted to exploring the usefulness of data provided by bird ringing

schemes. They have been used to explore bird movements between breeding and wintering areas, mortality rates or population trends, but have not been used to predict species distribution by assessing suitability indices across large areas at different times of year (Baillie *et al.*, 2009; Clark *et al.*, 2009). However, ringers have stored several millions of georeferenced data on the presence of birds (Tautin, 2005; Baillie *et al.*, 2007), which are available from national and supranational data banks (e.g. Euring in Europe). Consequently, this information can be useful to forecast bird distribution of poorly known species or in poorly studied regions where direct bird counting is difficult. As ring data are produced continuously, these data may be used to forecast the distribution of bird populations at different times of year. This presents the possibility of comparing the main environmental features affecting the distribution of migratory species in breeding and wintering grounds and how changes in these factors may contribute to controlling the populations along the migratory circuit (Webster *et al.*, 2002). There is growing evidence that habitat quality greatly affects body condition of wintering birds, an effect that may carry over to subsequent stages of the annual cycle (such as migration and breeding; Norris *et al.*, 2004; Studds & Marra, 2005). Obviously, the usefulness of these data to predict bird distributions must be initially tested by comparing predicted vs. true distributions on well-known species and territories (Elith & Leathwick, 2009). It is possible, for instance, that these data are unsuitable for this purpose because of the potential effect of inaccurate spatial location of ring recoveries (many of them reported before the GPS era) or the uneven spatial distribution of people able to report the presence of ringed birds (Busse, 2001).

In this paper, we explore the effectiveness of ring recoveries to predict the spatial distribution of common, widespread small passerines in wintering grounds of Spain, a main wintering area for birds in the Western Palearctic (Tellería *et al.*, 1999). More specifically, we test whether habitat suitability predicted with ring recoveries by using Maxent (Phillips *et al.*, 2006), one of the best models to predict species distribution from occurrence data (Elith *et al.*, 2006, 2010b), fits the actual abundance distribution of robins (*Erithacus rubecula* L.) and blackcaps (*Sylvia atricapilla* L.). We also explore whether the strength of these predictions is similar to that provided by more costly approaches in which field sampling is used to assess, through conventional multivariate statistical approaches, the effect of environmental variables on bird numbers.

METHODS

The species

Breeding blackcaps and robins are common woodland species in Spain, which each winter receive huge numbers of migratory conspecifics from central and northern Europe (Tellería *et al.*, 1999). In this period, all small passerines are constrained by the metabolic cost of thermoregulation (Calder & King, 1974).

Because low temperatures increase starvation risk, birds avoid cold areas or look for more productive habitats to compensate the costs of thermoregulation with food (Root, 1988; Meehan *et al.*, 2004). In addition, while autumn–winter rainfall in warm Mediterranean lowlands affects winter primary productivity and fruit production (Ogaya & Peñuelas, 2007), high rainfall in cold areas (e.g. mountains and highlands in Spain) will produce frequent or persistent snow cover that will prevent the use of the ground as a feeding substrate and will result in the abandonment of these areas by many species (e.g. robins; Santos *et al.*, 2010). All things being equal (e.g. similar temperature and rainfall), sites with plenty of food will usually have many birds (Newton, 2004). Blackcaps and robins wintering in Spain feed on invertebrates and fruits (Tellería *et al.*, 1999). Invertebrates are evenly distributed across space, but fruits tend to be patchily distributed with some places having plenty of fruit 1 year and none the next (Levey & Stiles, 1992). For this reason, blackcaps and robins adjust their numbers to the spatio-temporal patterning of fruit food despite inter-specific differences in the use of space (vagrant blackcaps vs. territorial robins; Cramp, 1988, 1992). Taking into account the winter ecology of the two study species, we may conclude that their distributions will be strongly related to vegetation cover (both species inhabit woodland and scrubland areas), food availability and climatic variables related to thermoregulation and the effect of snow cover (Tellería *et al.*, 2008; Santos *et al.*, 2010).

Ring recovery distribution modelling

We used ring recoveries provided by the Spanish Office of Migratory Species, which included the data recorded by the Spanish ringing scheme in December, January and February from 1919 to the end of 2009. These data were collected in 686 and 1139 localities where blackcaps and robins, respectively, were recorded at least once. The area extends over 497,000 km^2 of contrasting environmental conditions ranging from cold highlands to warm coastal sectors typical of European Mediterranean countries (Fig. 1). From the 19 Worldclim variables (http://www.worldclim.org/), we initially selected those variables likely to have the greatest influence on the thermal biology and winter distribution of the two study passerines (see above): Minimum Temperature of Coldest Month (bio06), Mean Temperature of Wettest Quarter (bio08), Mean Temperature of Coldest Quarter (bio11), Precipitation of Wettest Quarter (bio16) and Precipitation of Coldest Quarter (bio19). We also generated a layer of short-wave winter radiation derived from a digital elevation model of 1 km pixel size in ArcGIS 10.0 as another potentially influential climatic variable related to thermoregulation in birds (Carrascal & Díaz, 2006). Additionally, we used the CORINE 2006 land cover (version 12/2009: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-2009/) for information about the habitats and their potential relationships with vegetation structure and food availability (Seoane *et al.*, 2004) and the 'Human footprint' data set (Sanderson *et al.*,
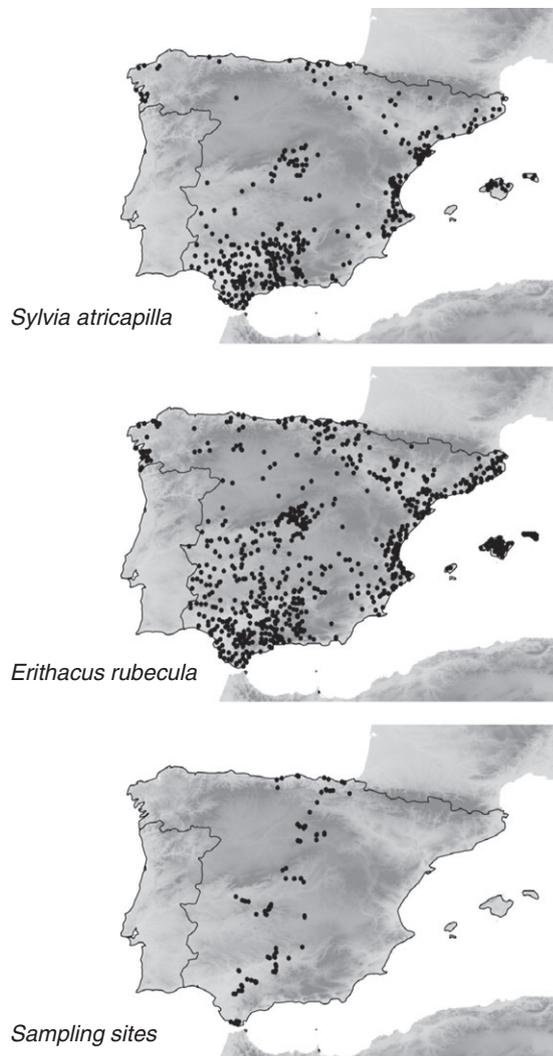
Figure 1 Distribution of the ring recovery for blackcaps and robins, and location of sites where bird abundance was sampled by line transects. Increasing grey tones show increasing altitudes, with darkest areas representing altitudes over 1000 m above sea level.

2002) to assess the spatial relationship of ring recoveries with human presence and accessibility (Busse, 2001). These layers were intersected with the recoveries layer to perform a basic exploratory data analysis, after which some outliers were excluded from the data set. To avoid multicollinearity, we ran a correlation analysis and eliminated one of the variables in each pair with a Pearson correlation value > 0.8. The final data set included as variables Minimum Temperature of Coldest Month (TEMP herein), Precipitation of Coldest Quarter (PRECIP), Winter Solar Radiation (SUNRAD), CORINE and Human Footprint (HUMAN).

We used Maxent, a machine-learning technique based on the principle of maximum entropy (Phillips *et al.*, 2006; Phillips & Dudík, 2008). It seeks a marginal suitability function for each variable that matches the empirical data, is maximally uninformative (close to the uniform distribution) elsewhere and has a mean equal to that of the empirical data (Warren &

Seifert, 2011). The latter property can have the undesired result of overfitting the data used to train the model, so Maxent has a regularization parameter that can tune the model to avoid such overfitting. In this study, the default settings of Maxent 3.3.3a (http://www.cs.princeton.edu/~schapire/maxent) were used (regularization multiplier β = 1; autofeatures; number of background points = 10,000; convergence threshold = 0.00001). Background points were randomly selected from the whole of the Spain. Background points must be selected from areas representing the full environmental range of the species, particularly, from areas pertaining to the same biophysical type (Phillips, 2008; Phillips *et al.*, 2009; Elith *et al.*, 2010a; Webber *et al.*, 2011). Both robins and blackcaps are widespread in Spain, and their presences were intersected with a layer representing Köppen (1936) bioclimatic system (Kriticos *et al.*, 2011; Webber *et al.*, 2011), which resulted in all bioclimatic classes present in Spain being selected for background extraction.

We ran 10 replicates, in each of which we trained the model with 70% of the presences and did the Maxent intrinsic test validation with the remaining 30% using the subsample option, which removes that random test percentage without replacement for evaluation. The final model was, for both species, the average of their replicates. The aim of this study is precisely to test whether the habitat suitability predicted with ring recoveries fits the actual abundance of birds, and thus, we did not perform any further analysis of model performance such as extrinsic AUC or binomial tests.

Abundance distribution modelling

We sampled bird abundance in 70 localities covered by woodlands, scrublands, tree plantations and wooded farmlands along a belt crossing mountains, highlands and lowlands of the Iberian Peninsula during January from 2006 to 2011 (Fig. 1). We did not include croplands, orchards, grasslands or other habitats intensively managed by humans or unsuitable to these woodland species. In each locality, we sampled two to six 500 m line transects. The abundance of species was recorded inside a band of 25 + 25 m (Bibby *et al.*, 1992). The structure of vegetation was measured by means of two 25 m radius circles separated by 200 m intervals along each transect in which we estimated shrub cover (the percentage of vegetation between 0.5 and 2 m in height; Larsen & Bock, 1986). We also counted the number of fruiting shrubs available to birds (e.g. *Ilex aquifolium* L., *Pistacia lentiscus* L., *Myrtus communins* L., *Olea europea sylvestris* (Mill.), etc.) along each transect in a belt of 5 + 5 m in 62 of these localities. We averaged the scores of bird abundance, shrub cover and fruit availability to obtain mean scores per locality. In addition, we extracted the climate data from each locality used to run Maxent that were also included as predictor variables. We also removed from analyses one coastal locality in which these climatic variables were not provided by Worldclim. In this way, we had a full set of environmental variables to model the distribution of wintering blackcaps and robins at 61 localities. The final set of

independent variables included the vegetation cover (VEG), fruit abundance (FRUIT), rainfall (PRECIP), Minimum Temperature of Coldest Month (TEMP), Winter Solar Radiation (SUNRAD) and Human Footprint (HUMAN). Altitude was not used in this analysis because it was strongly correlated with temperature ($r = 0.86$, $P < 0.001$, $n = 69$). Because vegetation cover might have nonlinear effects on bird abundance (e.g. if birds reach their highest abundance at intermediate values of vegetation cover), we estimated both linear (VEG) and quadratic (VEG^2) effects of this variable when building our models. Finally, we controlled for the spatial autocorrelation with a third-degree Legendre's polynomial (Borcard *et al.*, 1992). Accordingly, we included in the model standardized latitudinal (LAT, LAT^2, LAT^3) and longitudinal scores (LONG, $LONG^2$, $LONG^3$) of the study localities. We used forward and backward stepwise multiple regression models to compute the variance explained by the variables selected in the best model. The analyses were carried out using the General Regression Module of Statistica 7.0 (StatSoft Inc, Tulsa, OK, USA) after exploring the most suitable transformation of variables to improve normality (arcsine square root transformation for vegetation cover and logarithm transformation for the rest; e.g. McDonald, 2009).

RESULTS

Ring recovery distribution modelling

The most important variable for both species was TEMP, and the jackknife tests showed that eliminating it from the analyses dramatically lowered the predictive power of the models (Table 1). Vegetation type (CORINE) and Human Footprint (HUMAN) followed it in importance, although their removal

Table 1 Estimates of relative contributions of the environmental variables.

Variable	*Erithacus rubecula*		*Sylvia atricapilla*	
	Per cent contribution	Permutation importance	Per cent contribution	Permutation importance
TEMP	57 (+)	66.4	64.8 (+)	72.4
PRECIP	3.2 (=)	7.5	3.5 (=)	4.4
SUNRAD	2.2 (=)	4.8	1.2 (=)	3.3
HUMAN	25.1 (+)	9.9	12.1 (=)	4.7
CORINE	12.5	11.4	18.4	15.2
AUC ± SD	0.765 ± 0.013		0.811 ± 0.012	

Per cent contribution indicates the change in regularized gain by adding the corresponding variable. Permutation importance represents, for each environmental variable in turn, the resulting drop in training AUC when the values of that variable on training presence and background data are randomly permuted, normalized to show percentages. Values are averages over replicate runs. The large decrease observed in TEMP (Minimum Temperature of Coldest Month) indicates that the models of both species depend heavily on this variable. Symbols in parentheses show the trend of the response curves for the quantitative variables (+, increase; −, decrease; =, no change).

did not have as dramatic an effect in the models' performance. The remaining two climatic variables (PRECIP and SUNRAD) were only marginally important. Testing AUC was 0.77 for robins and 0.81 for blackcaps (Table 1). The geographical distribution of the Maxent-predicted suitability for the two species in 2.5×2.5 km UTM squares across Spain was relatively similar, with lowest, coastal areas and the south-western corner of the country as the most appropriate wintering grounds (Fig. 2). However, robins showed a broader distribution than blackcaps, whose suitable squares were concentrated in some sectors of the south-western and the Mediterranean coast.

Abundance distribution modelling

The two species showed similar mean densities at the scale of the Iberian Peninsula. However, blackcaps (mean ± SE: 7.14 ± 2.21 birds/10 ha, min–max: 0–180, $n = 70$) depicted sharper inter-site variations in abundance than robins (mean ± SE: 6.90 ± 0.95 birds/10 ha, min–max: 0–32, $n = 70$). This reflected the crowding of blackcaps in some localities with an abundance of fruit and the more even distribution of robins. Forward and backward selection gave the same results in both species. After controlling for the effect of spatial distribution, the best subset of variables explaining robin abundance was composed of TEMP, FRUIT and VEG, while blackcap abundance was strongly correlated with FRUIT and PRECIP (Table 2). These models explained a high percentage of the abundance distribution in both species (69% in robins and 87% in blackcaps; Table 2).

Comparison between Maxent-predicted suitability and actual bird abundance

The predicted suitability values provided by Maxent were positively correlated with the abundance of blackcaps and robins in transects located inside UTM squares (Fig. 3). Maxent scores explained 17% of the variance of winter abundance of robins and 27% of the variance of blackcap abundance. We also explored whether the mean densities (± SE) detected in the UTM squares under and over the median of the occurrence scores for robins (40.0) and blackcaps (28.5) differed significantly. Results (mean ± SE) supported strong differences between 'suitable' and 'unsuitable' squares in blackcaps (under: 0.14 ± 2.86, $n = 36$; over: 14.55 ± 2.94, $n = 34$; ANOVA, $F_{1,68} = 23.26$, $P < 0.001$) and robins (under: 5.19 ± 1.25, $n = 39$, over: 9.05 ± 1.40, $n = 31$; $F_{1,68} = 6.80$, $P = 0.011$).

DISCUSSION

Results in this paper support the view that the occurrence of robins and blackcaps provided by ring recoveries modelled with Maxent gives a credible prediction of their actual abundance distribution (Fig. 3). This ability to predict bird abundance may be related to the large number of localities used to run the models, a main determinant of the success of
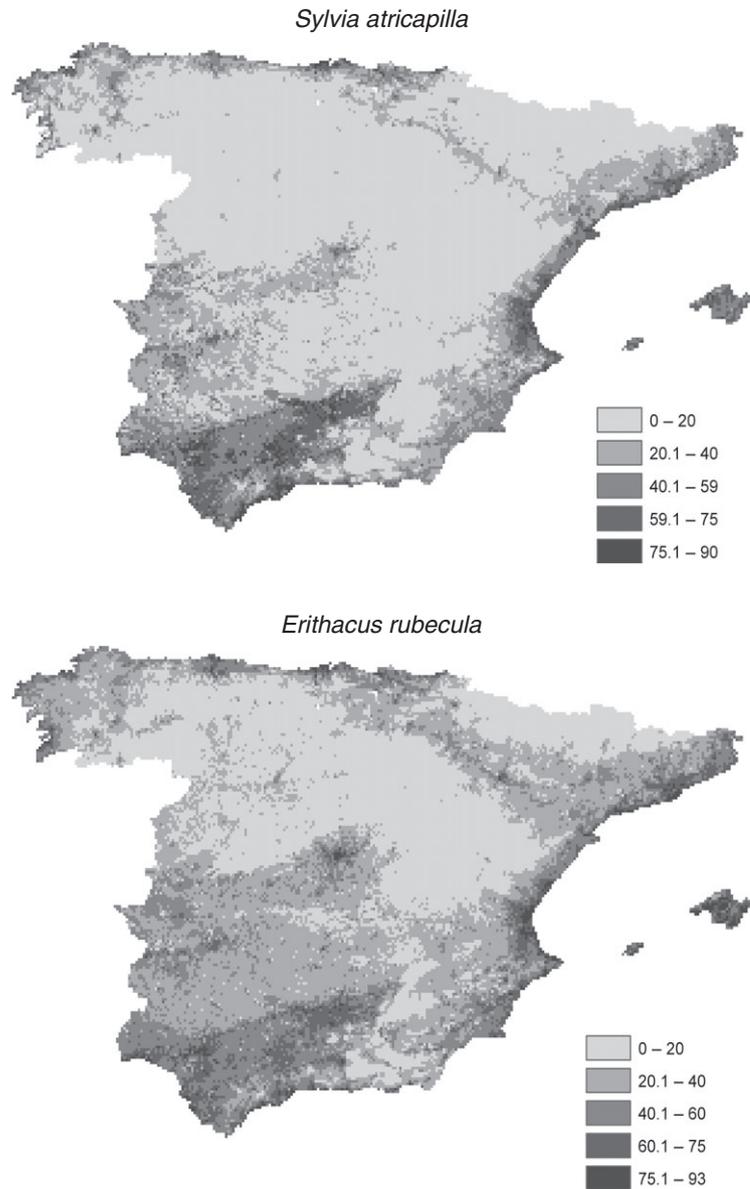
Sylvia atricapilla

	0 – 20
	20.1 – 40
	40.1 – 59
	59.1 – 75
	75.1 – 90

Erithacus rubecula

	0 – 20
	20.1 – 40
	40.1 – 60
	60.1 – 75
	75.1 – 93

Figure 2 Habitat suitability map for blackcaps and robins across the study area predicted from ring recoveries.

these approaches (Stockwell & Peterson, 2002; McPherson *et al.*, 2004). However, it may also be related to the strong specificity of environmental requirements of these species that, particularly in the case of the blackcap (Fig. 2), are constrained to well-defined environmental sectors of the Spanish lowlands (Stockwell & Peterson, 2002; Segurado & Araújo, 2004). However, suitability indices resulting from Maxent predictions only accounted for around 25–30% of the variance in bird abundance explained by the alternative models supported by field data (17% vs. 69% in robins and 27% vs. 87% in blackcaps; Table 2). These relative difficulties in predicting robin and blackcap abundances from the ring recovery databanks can occur for a number of reasons.

First, it is important to realize that Maxent modelled the probability of occurrence of ring recoveries and not the actual distribution of birds. This is a common problem for methods based on the availability of data collected by humans, always biased towards the most accessible or populated areas where species presence is more easily detectable. In fact, the intensity of human activity (HUMAN) was positively related to the distribution model produced by robin ring recoveries (Table 1). This suggests a potential effect of this artefact on the spatial distribution of occurrence probabilities. Nevertheless, it is important to remember that many small passerines are attracted to warm urban areas and gardens in winter where it is easier to feed (Jokimäki *et al.*, 2002). The described patterns can also be affected by some biases related to the difficulties in determining a precise location of the reported rings. In fact, many ring recoveries have been typically noted as detected in villages close to the true recovery point in the countryside. This fact resulting from the difficulties in locating the recovery sites before the use of GPS devices may produce some inaccuracies of predictions based on species distribution models.

Table 2 Results of stepwise multiple regression models of variation in abundance of robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*) wintering in the study localities

	E. rubecula				*S. atricapilla*			
	B	Beta	t	P	B	Beta	t	P
Intercept	0.107	–	0.875	0.385	−0.801	–	−1.994	0.005
VEG	−0.478	−0.249	−2.954	0.005	–	–	–	–
FRUIT	0.340	0.345	2.210	0.031	0.794	0.663	8.930	< 0.001
TEMP	0.905	0.548	5.472	< 0.001	–	–	–	–
PRECIP	–	–	–	–	0.364	0.111	2.072	0.043
LAT	0.742	1.559	4.034	< 0.001	–	–	–	–
LAT^2	−0.906	−1.889	−4.295	< 0.001	–	–	–	–
$LONG^2$	−0.129	−0.267	−2.423	0.019	–	–	–	–
$LONG^3$	0.136	0.281	2.058	0.045	−0.169	0.041	−4.171	< 0.001
Model	$F_{7,53} = 16.492$				$F_{3,57} = 124.841$			
	$P < 0.001$				$P < 0.001$			
	$R^2 = 0.685$				$R^2 = 0.868$			

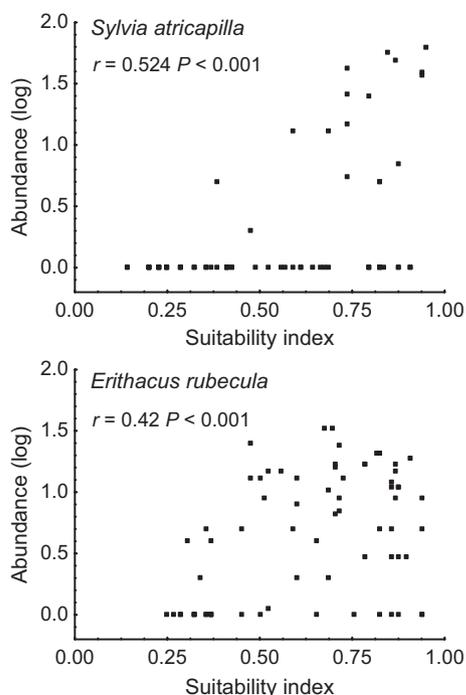Note that only those variables included in the models have been presented.

Figure 3 Relationships between the suitability indices produced by ring recoveries in 2.5 × 2.5 km UTM squares and the abundance of the two study species.

Second, some variables used to model the distribution patterns of ring recoveries are surrogates of the true environmental features affecting bird distribution. In some cases, they were insufficient to predict the distribution patterns of some key, particular features strongly affecting the species distribution. For instance, it is difficult to accept that the cover of habitats provided by CORINE will yield a reliable index of fruit availability despite the fact that they include Mediterranean woodlands and scrublands rich in fruiting plants during winter. Without a proper measure of this key feature affecting the winter distribution of frugivorous birds (Tellería *et al.*, 2008), it is difficult to model the distribution of robins and, particularly, blackcaps in wintering grounds of Spain. This supports the view that other environmental predictors may reflect important information on bird distribution not revealed by vegetation cover, such that regional modelling programmes would certainly gain predictive ability by including features related to food availability or landscape structure (Seoane *et al.*, 2004).

Third, we have used ring recoveries to produce an index of suitability (as determined by the probability of occurrence) on 625-ha (2.5 × 2.5 km) UTM squares. However, we assessed bird abundance on two to six transects of 2.5 ha traced on suitable shrubby and wooded habitats inside each control square. This means that we tested the model on areas covering 0.8–2.4% of the full surface of the square. Thus, the potential of Maxent to predict abundances inside UTM squares will strongly depend on the ability of each sampled site to represent the mean environmental conditions of the whole UTM square. More explicitly, while the occurrence probabilities are related to the mean regional suitability for the species in the UTM square (a feature related to the cover of different habitats inside the square and their relative suitability for the species), line transects provided an evaluation of the ecological density of the sampled habitats alone (see Dunning *et al.*, 1992; Gregory & Blackburn, 1995 for differences between regional and ecological densities).

Finally, the accuracy of species distribution models tends to be inversely related to the mobility and/or to the between-year constancy in the abundance of species (Carrascal *et al.*, 2006; Pöyry *et al.*, 2008). Both problems apply to the studied passerines, which move each winter in search of fruit or change abundance according to the annual breeding success of the European populations wintering in Spain (Tellería *et al.*, 2008). Thus, while the Maxent model predicts mean

conditions (according to mean scores in climate variables, land covers, etc.), abundance recorded in line transects reflects only the actual availability of fruits and the presence of birds on a given day and time during the study winter. Both fruit and bird abundance may change abruptly among sites and winters (Tellería *et al.*, 2008). It is possible that, given the role of fruit resources in the distribution of both species, the lack of fruits in the sampling year of a given site will be responsible for the lack of birds in some squares suggested as highly suitable by the Maxent model (Fig. 3). Consequently, a study designed to assess the inter-annual mean scores of bird and fruit abundance at each study site will considerably improve the predictive ability of the occurrence probability provided by Maxent for each UTM square. This interpretation is supported by strong differences in mean bird densities of suitable and unsuitable UTM squares, which suggests that regional patterns of suitability constructed by Maxent on ring data at the scale of Spain (Fig. 2) may be a good surrogate for the actual distribution of bird numbers in forests and scrublands.

Prospects

This paper supports the potential usefulness of species distribution models resulting from ring recoveries to describe habitat suitability and abundance patterns of two common passerines. The methodological problems discussed above are common to the application of models based on the use of occurrence data (bibliographic records, museums and herbaria databanks) and will be progressively resolved with ongoing investigation on these topics (Elith & Leathwick, 2009). However, despite these shortcomings, it is important to realize that there is a large amount of information recorded by many thousands of ringers over the last century (e.g. European ringers have ringed 115 million birds and have gathered around two million recoveries in Eurasia and the whole of Africa; similar figures may be offered by North American ornithology, with 63 million ringed birds and 3.5 million recoveries; Tautin, 2005; Baillie *et al.*, 2007) and that such information must be viewed as a new opportunity to improve our knowledge of the distribution and migratory connectivity of bird populations (Webster *et al.*, 2002). This is true particularly in poorly studied regions where the construction of winter distribution atlases is very difficult but the number of ring recoveries is increasing (e.g. sub-Saharan Africa; Walther & Rahbek, 2002), and where this information may contribute to expanding our knowledge on the locations of the best wintering areas for small migratory land birds (Walther *et al.*, 2007; Wisz *et al.*, 2007), poorly known compared to migratory water birds tracked by transnational monitoring schemes (e.g. African European Waterbird Agreement) or by some specific research programmes (Jiguet *et al.*, 2011). In addition, given that ringing activity has produced huge amounts of data over recent decades, this information may be used to track historical changes in the distribution of bird species consistent with habitat alteration processes, climatic change and other ongoing environmental trends (Maclean *et al.*, 2008).

REFERENCES

Baillie, S., Bairlein, F., Clark, J., du Feu, C., Fiedler, W., Fransson, T., Hegelbach, J., Juillard, R., Karcza, Z., Keller, L.F., Kestenholz, M., Schaub, M. & Spina, F. (2007) *Bird ringing for science and conservation.* EURING, Samen.

Baillie, S., Robinson, R., Clark, J.A. & Redfern, C.P. (2009) From individuals to flyways: the future of marking birds for conservation. *Ringing & Migration*, **24**, 155–161.

Bibby, C., Burgess, N.D. & Hill, D.A. (1992) *Bird census techniques.* Academic Press, London.

Borcard, G., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Busse, P. (2001) European passerine migration system – what is known and what is lacking. *Ring*, **23**, 3–36.

Calder, W.A. & King, J.R. (1974) Thermal and caloric relations of birds. *Avian biology Vol. 4* (ed. by D.S. Farner and J.R. King), pp. 259–413, Academic Press, New York, NY.

Carrascal, L.M. & Díaz, L. (2006) Winter bird distribution in abiotic and habitat structural gradients: a case study with mediterranean montane oakwoods. *Ecoscience*, **13**, 100–110.

Carrascal, L.M., Seoane, J., Palomino, D., Alonso, C.L. & Lobo, J.M. (2006) Species-specific features affect the ability of census-derived models to map winter avian distribution. *Ecological Research*, **21**, 681–691.

Clark, J.A., Thorup, K. & Stroud, D.A. (2009) Quantifying the movement patterns of birds from ring recoveries. *Ringing & Migration*, **24**, 180–188.

Cramp S. (ed.) (1988) *The birds of the western Palearctic. Vol. 5. Tyrant flycatchers to thrushes.* Oxford University Press, Oxford.

Cramp S. (ed.) (1992) *The birds of the western Palearctic. Vol. 6. Warblers.* Oxford University Press, Oxford.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Elith, J., Kearney, M. & Phillips, S. (2010a) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2010b) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Gregory, R.D. & Blackburn, T.M. (1995) Abundance and body size in British birds: reconciling regional and ecological densities. *Oikos*, **72**, 151–154.

Jiguet, F., Massemin, S. & Chevallier, D. (2011) Predictive distribution models applied to satellite tracks: modelling the western African winter range of European migrant Black Storks *Ciconia nigra*. *Journal of Ornithology*, **152**, 111–118.

Jokimäki, J., Clergeau, P. & Kaisanlahti-Jokimäki, M.L. (2002) Winter bird communities in urban habitats: a comparative study between central and northern Europe. *Journal of Biogeography*, **29**, 69–79.

Köppen, W. (1936) *Das geographische system der Klimate*. Gebrüder Borntraeger, Berlin.

Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J. & Scott, J.K. (2011) CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, **3**, 54–63.

Larsen, D.L. & Bock, C.E. (1986) Determining avian habitat preference by bird-centered vegetation sampling. *Wildlife 2000: modelling habitat relationships of terrestrial vertebrates* (ed. by J. Verner, M.L. Morrison and C.J. Ralph), pp. 37–43, University of Wisconsin Press, Madison, WI.

Levey, D.J. & Stiles, F.G. (1992) Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *The American Naturalist*, **140**, 447–476.

Maclean, I.M.D., Austin, G.E., Rehfisch, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceuninck, B., Günther, K., Laursen, K., van Roomen, M. & Wahl, J. (2008) Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology*, **14**, 2489–2500.

McDonald, J.H. (2009) *Handbook of biological statistics*, 2nd edn. Sparky House Publishing, Baltimore, MD.

McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, **41**, 811–823.

Meehan, T.D., Jetz, W. & Brown, J.H. (2004) Energetic determinants of abundance in winter landbird communities. *Ecology Letters*, **7**, 532–537.

Newton, I. (2004) Population limitation in migrants. *Ibis*, **146**, 197–226.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 59–64.

Ogaya, R. & Peñuelas, J. (2007) Species-specific drought effects on flower and fruit production in a Mediterranean holm oak forest. *Forestry*, **80**, 351–357.

Phillips, S.J. (2008) Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson *et al.* (2007). *Ecography*, **31**, 272–278.

Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only species distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.

Pöyry, J., Luoto, M., Heikkinen, R.K. & Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, **17**, 403–414.

Root, T. (1988) Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330–339.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.

Santos, T., Galarza, A., Ramírez, A., Pérez-Tris, J., Carbonell, R. & Tellería, J.L. (2010) Vegetational versus topographical effects on forest bird communities: a test in the Cantabrian Mixed Forest Ecoregion (Spain). *Ardeola*, **57**, 431–436.

Segurado, P. & Araújo, M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555–1568.

Seoane, J., Bustamante, J. & Díaz-Delgado, R. (2004) Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. *Ecological Modelling*, **171**, 209–222.

Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.

Studds, C.E. & Marra, P.P. (2005) Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology*, **86**, 2380–2385.

Tautin, J. (2005) One hundred years of bird banding in north America. *USDA Forest Service Gen. Tech. Rep. PSW-GTR*, **191**, 815–816.

Tellería, J.L., Asensio, B. & Díaz, M. (1999) *Aves Ibéricas. Vol. 2. Passeriformes*. J.M. Reyero Ediciones, Madrid.

Tellería, J.L., Ramírez, A. & Pérez-Tris, J. (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography*, **31**, 381–388.

Walther, B.A. & Rahbek, C. (2002) Where do Palearctic migratory birds overwinter in Africa? *Dansk Ornitologisk Forenings Tidsskrift*, **96**, 4–8.

Walther, B.A., Schäffer, N., Van Niekerk, A., Thuiller, B., Rahbek, C. & Chown, S.L. (2007) Modelling the winter

distribution of a rare and endangered migrant, the Aquatic Warbler *Acrocephalus paludicola*. *Ibis*, **149**, 701–714.

Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.

Webber, B.L., Yates, C.J., Maitre, D.C.L., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Roux, J.J.L. & Midgley, G.F. (2011) Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions*, **17**, 978–1000.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, **17**, 76–83.

Wisz, M.S., Walther, B.A. & Rahbek, C. (2007) Using potential distributions to explore determinants of Western Palaearctic migratory songbird species richness in sub-Saharan Africa. *Journal of Biogeography*, **34**, 828–841.

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