



Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution

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Abstract

Predictive habitat models rely on the relationship between a response variable (either occurrence or abundance of a species) and a set of environmental predictors. Vegetation is generally preferred as a source of potential predictors because of having a more direct link with reproductive necessities of species than topography and climate. However, vegetation maps are costly to produce and update and most land-use/land-cover maps are usually made with a general purpose, focused on land management, and not thinking on animal distribution. On the contrary, basic topographic and climatic maps are easier to obtain or to derive, are not so sensitive to legend design, and do not need of such frequent updates. In this study, we compare the predictive ability of different sets of environmental predictors when modelling the distribution of breeding birds. Models were generated for 79 bird species in South-western Spain using Generalised Additive Models (GAMs) with binomial errors and logit link. For each species, several models were created that differed in the set of candidate predictors initially tested (either derived from vegetation or from topo-climatic maps) or in the conditional order in which those predictor sets were tested. Within vegetation predictors, a similar strategy was used to ascertain the relative relevance of vegetation landscape (variables describing the surrounding habitat matrix) compared to vegetation cover (variables describing the type of vegetation found on sampling sites).

Vegetation models were significantly more accurate than topo-climatic models, but the difference was due to the higher number of potential predictors in the set of vegetation variables. Vegetation landscape models were significantly more accurate than vegetation cover models, even when controlling for the number of candidate predictors. Models that included both sets of predictors (vegetation and topo-climatic variables) had a slightly superior predictive ability. Our results indicate that, when building predictive models of bird distribution, the best results are obtained using both vegetation and topo-climatic variables as potential predictors. If time or budget constrains compel to concentrate on a single set of predictors, selection should be done on grounds of data availability, because model accuracy is likely to be similar for models derived from vegetation compared to topographic and climatic predictors. In relation to vegetation predictors, vegetation landscape reflects important information not revealed by vegetation cover measures at the sampling site; thus, regional modelling programmes would certainly gain predictive ability by including landscape patterns that are currently disregarded.

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1. Introduction

The study of the relationships between species and their habitats has traditionally been a central issue in ecology and is nowadays of prime importance in conservation and planning (see a review in Morrison

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et al., 1998). Accurate distribution maps of organisms are welcomed in the selection and design of natural parks (Scott et al., 1993), the assessment of human impacts on biodiversity (Lavers and Haines-Young, 1996), or the testing of biogeographical hypotheses (Mourell and Ezcurra, 1996; Leathwick, 1998). However, even a perfect knowledge of the biology of a species cannot guarantee that a static map will reflect dynamic properties of species distribution (Tyre et al., 2001). Moreover, human and logistic limitations make it impractical to survey large areas and, inevitably, our knowledge of the spatial distribution of most species will have many gaps (Osborne and Tigar, 1992). A common solution to this problem is to resort to predictive habitat modelling (reviewed in Guisan and Zimmermann, 2000, and see some recent examples in Osborne et al., 2001; Scott et al., 2002; Seoane et al., 2003) and regard the results as potential habitat, able to be reached and colonised by a species (Tyre et al., 2001).

Predictive habitat models relate the occurrence pattern of a species (either as presence/absence or abundance) with some predictors selected from a set of ecologically plausible candidate variables. A large number of potential predictors are currently easy to obtain thanks to the increasing development of Geographical Information Systems (GIS) techniques (Dettmers and Bart, 1999) and digital cartography (thematic maps and satellite imagery, Guisan and Zimmermann, 2000). Thus, potential predictors, such as topographic and climatic data, on the one hand and vegetation or land-use/land-cover digital maps on the other are widely available potential sources of information for modelling (Goodchild et al., 1996). Raw data must be pre-processed before the analysis, and this can be very time-consuming. For example, maps of predictors must be transformed to the same scale, satellite images have to be georeferenced, and climatic data need to be extrapolated from meteorological stations to the whole study area (Lillesand and Kiefer, 1994; Goodchild et al., 1996). Given time and budget constraints, what kind of candidate predictors should a modeller prioritise?

It may be argued that vegetation affects the distribution of animals proximally, by providing shelter, food and potential nest-sites, while topography and climate affects it indirectly, by modifying the relationships of bird species with vegetation (e.g. differ-

ent habitats may be selected under different climatic conditions; Tellería et al., 2001a,b) or, simply, by modifying the vegetation itself. Therefore, vegetation is expected to be generally a better predictor of animal distribution than topography and climate at local scales (accordingly, most predictive models for bird species prioritise vegetation variables when made at local scales, see: Fielding and Haworth, 1995; Austin et al., 1996). However, high-resolution digital vegetation maps are costly to produce and update (Lillesand and Kiefer, 1994). Moreover, governmental agencies usually build land-cover maps with a general purpose (often focused on land-use) and the information on vegetation cover in natural and semi-natural areas may be not detailed enough to model species distribution (see an example for Southern Spain in Moreira and Fernández-Palacios, 1995). On the contrary, digital elevation models (DEMs) and, to a lesser extent, meteorological data, are more easily available and will be spatially correlated with vegetation in most instances, conveying information redundant with vegetation to some degree (Guisan and Zimmermann, 2000). It is desirable to know whether one source may render predictors that lead to more accurate models (such a case would be if one set of predictors has information that is completely redundant with the other set) or both are necessary to achieve high predictive ability.

Within vegetation variables, the relative effect of site-specific local descriptors or landscape configuration on the distribution of animals is of great interest for conservation management (e.g. Saab, 1999; Dale et al., 2000). If the surrounding matrix of vegetation types and land uses, that is, the landscape (see Table 1), has any relevance in the patterns of occurrence for a particular species, then the design of reserves or corridors for this species should take landscape into account. This is so because apparently suitable areas may be in fact unsuitable, for example, if the areas are too small or too close to a habitat edge. If landscape has a major effect on the distribution of organisms, site-specific measures of land-cover could render poor candidate predictors for models. However, the effects of landscape and its relative importance compared to site-specific features are not yet well understood. Landscape has been found to affect patterns of abundance and distribution seriously in some studies (Bolger et al., 1997; Vander Haegen et al., 2000), but the ubiquity and

Table 1
 Predictive variables tested to model breeding bird species occurrences in two areas of Western Andalusia

Predictive variable type and name	Description
Vegetation predictors	
Vegetation cover	
Agriculture	Proportion of 50 m pixels belonging to agricultural land use categories (non-irrigated cereal crops and olive groves) in circles 150 m in diameter centred in sampling points
Herbaceous	Proportion of 50 m pixels belonging to any herbaceous type category (whether natural or cultivated) in circles 150 m in diameter centred in sampling points
Forest	Proportion of 50 m pixels belonging to any forest type category (including sparse forested areas, such as <i>dehesas</i> but not olive groves) in circles 150 m in diameter centred in sampling points
Shrub	Proportion of 50 m pixels belonging to any shrub type category in circles 150 m in diameter centred in sampling points
Riparian vegetation	Proportion of 50 m pixels belonging to any riparian type category (from scrub to forested masses) in circles 150 m in diameter centred in sampling points
Vegetation landscape	
Distance to agricultural patches	(3 variables) Distance (in m) to the nearest patch with an agricultural land use: (1) patch larger than 2 ha, (2) larger than 10 ha and (3) larger than 100 ha
Distance to herbaceous vegetation patches	(3 variables) Distance (in m) to the nearest patch with herbaceous vegetation: (1) patch larger than 2 ha, (2) larger than 10 ha and (3) larger than 100 ha
Distance to forest patches	(3 variables) Distance (in m) to the nearest forest patch: (1) patch larger than 2 ha, (2) larger than 10 ha and (3) larger than 100 ha
Distance to shrub patches	(3 variables) Distance (in m) to the nearest shrub patch: (1) patch larger than 2 ha, (2) larger than 10 ha and (3) larger than 100 ha
Distance to riparian vegetation patches	(3 variables) Distance (in m) to the nearest riparian vegetation patch: (1) patch larger than 2 ha, (2) larger than 10 ha and (3) larger than 100 ha
Perimeter/area	(4 variables) Perimeter/area ratio of the patch where the sampling point was performed considering any of the above vegetation cover variables (except riparian vegetation)
Topo-climatic variable	
Altitude	Mean altitude in circles 150 m in diameter centred in sampling points
Slope	Mean slope (%) in circles 150 m in diameter centred in sampling points
Precipitation	Mean annual precipitation (mm) (modelled to a pixel size of 1 km ²)
Temperature	Mean annual temperature (°C) (modelled to a pixel size of 1 km ²)
Radiation (insolation)	Mean annual potential solar radiation (kJ/m ²) in circles 150 m in diameter centred in sampling points

relevance of this effect is controversial (MacGarigal and MacComb, 1995), and it is not explicitly considered in some successful regional modelling efforts like the GAP programme in USA (Scott et al., 1993). Once one has a GIS database, measuring landscape or site-specific vegetation predictors requires approximately the same effort (personal observation), so selecting either one or the other (or both) type of variables should be done on the grounds of accuracy of predictions.

In this work, we build predictive models for several species of breeding birds in South-western Spain and address the following questions: (i) What set of

variables has a greater predictive ability: vegetation variables or topo-climatic variables? (ii) Both sets of variables are expected to be correlated, but do they have some degree of independent information? (iii) Is a single set of variables enough to generate reasonably accurate models, or do we need both sets? (iv) Within vegetation variables, does vegetation landscape contribute to a greater predictive accuracy or is site-specific vegetation cover enough? (v) Finally, are the results influenced by methodological issues like the number of potential predictors in the set or the conditional order in which predictors are incorporated to the models?

2. Study area and methods

2.1. Study sites and variables analysed

The study sites are two 70 km × 70 km squares in Western Andalusia, Southern Spain (Fig. 1). Both include low, flat areas, mainly devoted to agriculture, surrounded by mountainous areas with more natural vegetation (altitude ranges from 0 to 1600 m a.s.l.). In both areas land-cover is mainly dominated (~70%) by Mediterranean vegetation (shrubland and evergreen oak *Quercus ilex* ssp. *ballota* L. and cork oak *Quercus suber* L. forests and *dehesas*—areas of pastures sparsely forested devoted to cattle raising), and *Pinus* spp. and *Eucalyptus* spp. plantation. One third of each area is cultivated, mainly with non-irrigated wheat, sunflower crops and olive groves. Villages and urbanised areas are widely interspersed.

We analysed the occurrence of 79 species detected in 1144 unlimited-distance point counts of 15-min duration made between April and June in 1999 and 2000. Bird species (listed in Appendix A) were mostly passerines (80%), and their sizes ranged

from the Firecrest *Regulus ignicapillus* (~5.3 g) to the Short-toed eagle *Circus gallicus* (~1600 g). To reduce the possibility of double counting the same individuals in different sampling points, the minimum distance between points was 300 m, being most of them (~75%) at least 1 km apart.

We considered two sets of candidate predictors, one related to vegetation (named hereafter as *vegetation* predictors) and the other to topography and climate (named *topo-climatic* predictors) (Table 1). The vegetation set consisted of 24 variables, and included two subsets. The first, aimed to describe the site-specific vegetation type, was the *vegetation cover* predictors (five variables), and the second, related to landscape measures at the sampling points and conveying information about the surrounding habitat matrix, was the *vegetation landscape* predictors (19 variables). The topo-climatic predictors included three variables descriptive of topography and two climatic variables. We assumed that the two sets convey partially different (but correlated) information about the environment around the sampling point. We think that vegetation has a proximal effect on patterns of

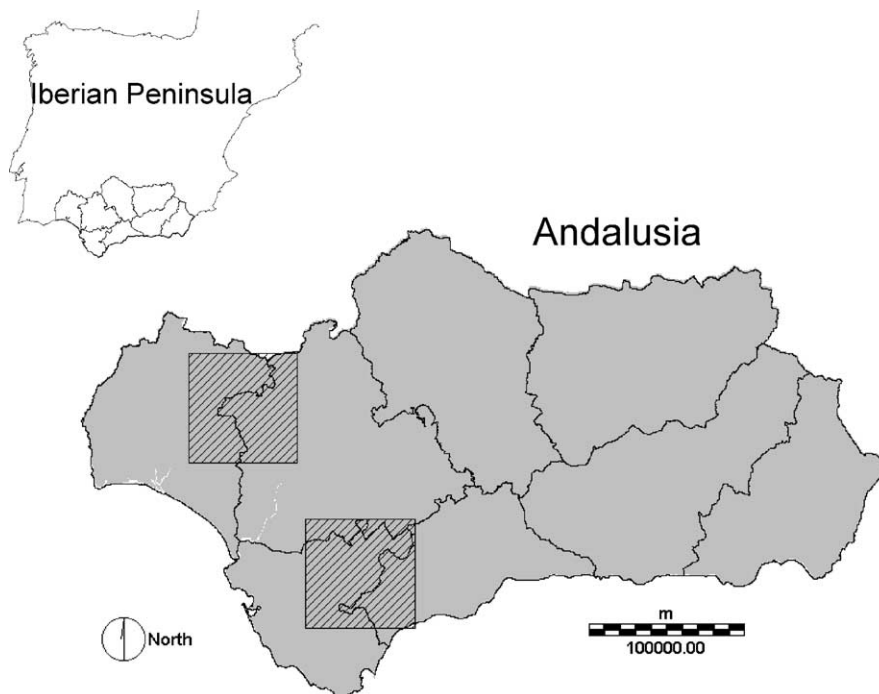


Fig. 1. Location of study sites. The two sampled 70 km × 70 km squares are shown by hatching.

breeding bird occurrence at the scale of our study (vegetation structure is one of the main factors influencing habitat selection in birds, Cody, 1981), while topography and climate may affect them indirectly. Combination of topography and climate may reflect changes of vegetation cover at a finer grain than that of our land-cover map reflects. Because topography and climate may provide information about microclimatic conditions, we decided to join these two types of variables into a single set (topo-climatic).

Vegetation landscape predictors measured both the relationship between area and perimeter of the patches belonging to different vegetation cover categories and the distance to the nearest vegetation patch of a given size. We account for size of patches because it affects occupancy patterns in a species-specific way (for an analysis in our geographical area, see Tellería and Santos, 1997; Santos and Tellería, 1998). Vegetation predictors (vegetation landscape and vegetation cover variables), except those related to riparian forests (see below), were extracted from the 1995 land-use/land-cover digital map of Andalusia (Sinamba) provided by the Environmental Department of the Junta de Andalucía (Moreira and Fernández-Palacios, 1995). Original data in vector format were rasterized to 50 m pixel size. Topographic variables were obtained from a DEM of Andalusia (50 m pixel size). Mean precipitation and temperature data were obtained from the Instituto Nacional de Meteorología (National Meteorological Institute) and interpolated by regression models and kriging to a pixel size of 1 km² (Bustamante, in press; unpublished data). Finally, a map of mean annual potential solar radiation was estimated from the DEM (according to the model developed by Ninyerola et al., 2000). The land-use/land-cover map of Andalusia (Moreira and Fernández-Palacios, 1995) was not precise enough for riparian vegetation. This type of vegetation occupies mostly narrow and fragmented patches in the study area, and thus small vegetated watercourses are likely to be disregarded and lumped with neighbouring land-use/land-cover classes (land-use and land-cover patches smaller than 25 ha tend to be grouped in the vegetation map, Moreira and Fernández-Palacios, 1995). Therefore, we made a map of riparian vegetation from an interpretation of two spring scenes of the sensor LISS III (Linear Imaging Self Scanning sensor) on board of the Indian Remote Satellite (IRS),

aided by an overlay of the drainage network extracted from the DEM. All predictors, except distances, were averaged for circles 150 m in diameter centred on the sampling points. Admittedly, the resolution at which we defined local predictors ideally should be species-specific, but we have no reliable clues to select the optimal resolutions (indeed, such clues do not exist for most species); so, we choose to average in circles 150 m in diameter to achieve a high resolution that is above expected georeferencing errors (Global Positioning System receptors accuracy were subjected to 100 m degradation during the first half of the study). Extraction of predictors from the GIS was undertaken using IDRISI 32 (Eastman, 1999), IDRISI for Windows (Eastman, 1997) and MiraMon (Pons, 2000).

2.2. Statistical analysis

We performed Generalised Additive Models (GAMs, Hastie and Tibshirani, 1990) of presence/absence of each bird species using binomial errors and logit link. GAMs are semi-parametric extensions of GLMs whose basic formula is:

$$\text{Logit}(p) = a_0 + f_1x_1 + f_2x_2 + \dots + f_kx_k$$

where p represents presence or absence, and the f_1 to f_k are smooth functions of the k predictor variables (see Guisan et al., 2002 for a brief introduction). Predictors for each model were selected from each set of potential candidates (Table 1) by a forward-backward stepwise procedure (with the step.gam function of S-PLUS 2000 software, MathSoft, 1999) that used an approximation of Akaike's Information Criterion (AIC, Sakamoto et al., 1986) as the criterion to enter or to remove variables in the model. Predictors were allowed to enter the models as linear terms or as smoothing splines with two or three degrees of freedom (to achieve respectively a lower or higher degree of smoothing). Computational constraints prevented us from building the models with a fully automatic scheme. Therefore, the semi-automatic procedure we finally implemented first tested each predictor as a smoothing spline with three degrees of freedom, and then, in a second step, tried to simplify the model by testing the variables entered previously as smoothing splines with two degrees of freedom and, finally, as linear terms. Automatic and semi-automatic methods

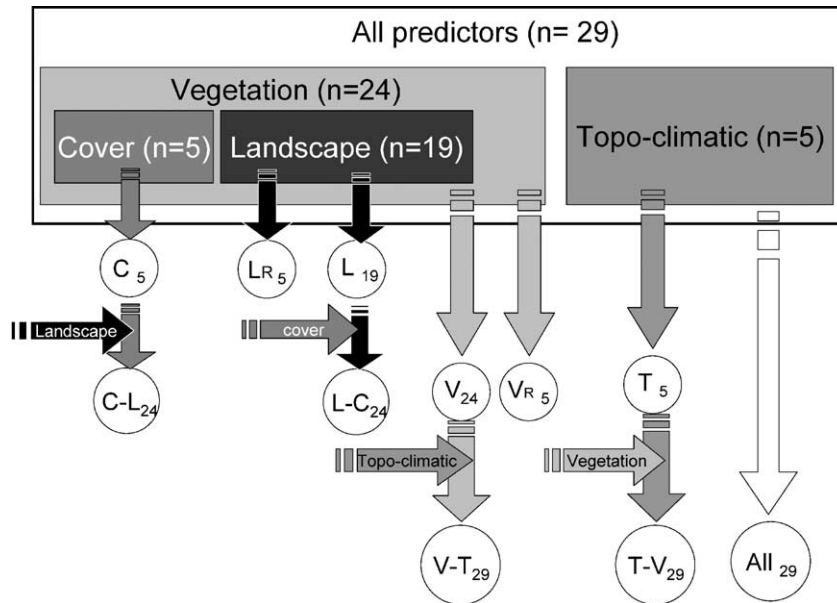


Fig. 2. Relation between the different bird distribution model types in this study (circles) and the different sets of predictors (rectangles) used. All the predictors are divided in vegetation (V) and topo-climatic (T) sets. The vegetation set is further subdivided in vegetation cover (C) and vegetation landscape (L) subsets. The order of the letters (V-T vs. T-V and L-C vs. C-L) indicates the order in which potential predictors are tested. The subindexes indicate the total number of candidate predictors considered in each single bird species models. V_R and L_R indicate models with a reduced subset of five candidate predictors (vegetation and vegetation landscape, respectively), selected at random.

of variable selection such the one outlined above have been criticised (Burnham and Anderson, 2002) because they can create spurious relationships (Flack and Chang, 1987; MacNally, 2000) or render biologically implausible models (James and McCulloch, 1990). However, they frequently are used in ecological analyses (Scott et al., 2002) because they facilitate a rapid generation of models; moreover, automated models compare well with models that include expert opinion (Pearce et al., 2001b; Seoane et al., submitted), so we think our procedure is justified (at least as a heuristic comparison).

We built several models for each bird species that differed in the set of predictors allowed to enter or in the order in which they were tested (Fig. 2), with the aim of answering several questions.

First, in order to compare the predictive ability of vegetation versus topo-climatic predictors, we modelled species occurrence using only vegetation predictors (V models), and then we tested if these models could be improved by the inclusion of topo-climatic predictors (keeping the vegetation predictors that had

entered previously; V-T models). Analogously, we built models using only topo-climatic predictors (T models), and then tested if vegetation could improve these models (T-V models). We also tried a complete model in which predictors of both sets were tested simultaneously and entered the model according to their AIC value.

Second, to explore the relative relevance of the different vegetation subsets, we built species predictive models with only those vegetation predictors reflecting vegetation cover at the sampling point (C models) and with only those vegetation variables reflecting vegetation landscape (L models). Then, we tested if models with vegetation landscape predictors could be improved with the inclusion of vegetation cover predictors (L versus L-C) and if models with vegetation cover predictors could be improved with the inclusion of vegetation landscape predictors (C versus C-L).

The set of potential vegetation predictors is considerably larger than the set of potential topo-climatic predictors (24 versus 5 predictors, Table 1), and thus the vegetation models could be better, on average,

because they consider as potential candidates a wider set of measures of environmental conditions (Elith, 2000). To evaluate the predictive ability of the vegetation set independently of the initial number of candidate predictors tested in the model, we randomly subdivided the vegetation set in five subsets of five predictors (to be able to generate five groups of five predictors from 24 variables, one vegetation variable selected at random was present in two groups). Then, we built for each bird species five vegetation models (V_{R1} to V_{R5}), one with each of those reduced sets of five potential predictors (the same number as in topo-climatic models). The set of vegetation landscape variables is also larger than the set of vegetation cover variables (19 versus 5). To compare the predictive ability of vegetation landscape with vegetation cover independently of the greater number of candidate predictors in the first set we subdivided at random the vegetation landscape set into four subsets of five variables (L_{R1} to L_{R4}). To be able to do this with 19 predictors one selected at random appeared in two groups.

To assess the accuracy of each model, we estimated the area under the curve (AUC) of Relative Operating Characteristic (ROC) plots (Swets, 1988; Murtaugh, 1996) with AccuROC 2.4 for Windows (Vida, 1993). The ROC curve is built by plotting the sensitivity of a model (or true-positive rate) on the ordinate against 1-specificity (or false-positive rate) on the abscissa. This was made for every possible threshold value that can be chosen to convert the predicted probability of occurrence (a continuous value given by the models in the interval 0–1) to predicted presence or absence (a dichotomous variable). The AUC summarises ROC plots with a measure of overall accuracy independent of a threshold (Fielding and Bell, 1997). AUC ranges between 0.5 (chance performance) and 1 (perfect discrimination), and can be interpreted as the probability of a model to render a higher predicted value of presence for a species in a site where the species exists than for a site where the species is not present (Zweig and Campbell, 1993; Cumming, 2000). AUC for models V_{R1} to V_{R5} and L_{R1} to L_{R4} were averaged to obtain a single estimate for each bird species (V_R and L_R , respectively). Differences among model types were tested with a repeated measures factorial ANOVA with an error term due to species to control for the between-species variation, of no interest in this study (Pearce and Ferrier, 2000). Models were

not validated with external data, because the number of recorded presences was limited for several species (that had a low frequency of occurrence but were kept in order to sample over a wide range of frequencies), nor through randomisation, because the building procedure could not be made fully automatic. Therefore, all the reported AUC will be somewhat inflated but they will adequately serve—as it is our main concern in this work—to make relative comparisons among models built with each set of predictors. Data sets and code are available upon request.

3. Results

It was possible to build predictive models better than a null model for every species and set of predictors (except for Southern Grey Shrike *Lanius meridionalis* and the topo-climatic set). Mean AUC (\pm S.E., Table 2) ranged from 0.69 ± 0.099 for models with vegetation cover predictors only (C) to 0.85 ± 0.100 for models with topo-climatic and vegetation predictors (included in this order, T-V). More than half of

Table 2
Bird prediction accuracy: mean AUC (\pm S.E.) values for the models generated with the different sets of predictors

Model	AUC \pm S.E.	% AUC > 0.7
T	0.75 ± 0.113	70
V	0.81 ± 0.104	94
T-V	0.85 ± 0.100	99
V-T	0.84 ± 0.104	96
All	0.84 ± 0.102	99
V_R	0.75 ± 0.081	67
C	0.69 ± 0.099	38
L	0.80 ± 0.084	91
L-C	0.81 ± 0.082	96
C-L	0.81 ± 0.104	94
L_R	0.78 ± 0.083	67

Models considered the following variables: (1) T, topo-climate; V, vegetation; T-V, topo-climate followed by vegetation; V-T, vegetation followed by topo-climate; All, predictors of both sets tested simultaneously; V_R , a reduced set of five randomly selected vegetation variables (AUC is the average of five V_{R1} to V_{R5} models). (2) C, vegetation cover; L, vegetation landscape; L-C, vegetation landscape followed by vegetation cover; C-L, vegetation cover followed by vegetation landscape; L_R , a reduced set of five randomly selected vegetation landscape predictors (AUC is the average of four L_{R1} to L_{R4} models). Also given is the percentage of models with AUC > 0.7 (a subjective threshold to consider models accurate enough to be of any use).

the species models within each model type reached at least a moderate accuracy (we considered a subjective threshold of $AUC > 0.7$ for the models to be considered potentially useful), except for C models (Table 2 and Appendix A).

Vegetation models (V) were significantly more accurate than topo-climatic models (T) showing on average a 6% increase in AUC (mean \pm S.E., $V = 0.81 \pm 0.104$, $T = 0.75 \pm 0.113$; $F_{1,312} = 94.4$, $P < 0.0001$, Table 3). Topo-climatic models were improved by the inclusion of vegetation predictors (there was a significant increase in AUC: T versus T-V, $F_{1,312} = 250.84$, $P < 0.0001$, Table 3), and vegetation models were improved by the inclusion of topo-climatic predictors (V versus V-T, $F_{1,312} = 16.22$, $P < 0.0001$, Table 3). The improvement in accuracy was relatively important (10%) when vegetation variables were allowed to enter the topo-climatic model, but was relatively minor (3%) when topo-climatic variables entered the vegetation model ($T-V = 0.85 \pm 0.100$, $V-T = 0.84 \pm 0.104$). However, the mean AUC of vegetation models built with a reduced set of potential predictors (V_R) did not differ from mean AUC of topo-climatic models ($V_R = 0.75 \pm 0.081$; T versus V_R , $F_{1,312} = 0.040$, $P = 0.84$, Table 3), indicating that the greater predictive ability of vegetation versus topography and climate was in part due to a larger initial set of potential predictors.

Table 3
Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of using vegetation or topo-climatic predictors

Variable	d.f.	SS	MS	F	P
Error: species					
Residuals	78	3.324	0.043	–	–
Error: within					
Vegetation vs. topo-climatic variables	4	0.760	0.190	90.384	<0.0001
T vs. V	1	0.199	0.199	94.438	<0.0001
T vs. T-V	1	0.527	0.527	250.835	<0.0001
V vs. V-T	1	0.034	0.034	16.221	<0.0001
T vs. V_R	1	0.000	0.000	0.040	0.84
Residuals	312	0.656	0.002		

Planned comparisons test if vegetation differs from topo-climatic variables in predictive accuracy (T vs. V), if vegetation improves topo-climatic models (T vs. T-V), if topo-climatic variables improve vegetation models (V vs. V-T), and if mean predictive accuracy of vegetation variables differs from that of topo-climatic variables (T vs. V_R). Names of models as in Table 2.

Table 4
Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of using vegetation cover or vegetation landscape predictors

Variable	d.f.	SS	MS	F	P
Error: species					
Residuals	78	2.628	0.037	–	–
Error: within					
Vegetation cover vs. vegetation landscape	4	0.888	0.222	119.330	<0.0001
L vs. C	1	0.275	0.275	148.070	<0.0001
C vs. C-L	1	0.408	0.408	239.398	<0.0001
L vs. L-C	1	0.008	0.008	4.418	0.036
L_R vs. C	1	0.196	0.196	105.436	<0.0001
Residuals	312	0.580	0.002		

Planned comparisons test if vegetation landscape models differ in accuracy from vegetation cover models (L vs. C), if vegetation landscape variables improve vegetation cover models (C vs. C-L), if vegetation cover variables improve vegetation landscape models (L vs. L-C) and if mean predictive accuracy of a vegetation landscape variable differs from mean predictive accuracy of a vegetation cover variable (C vs. L_R). Names of models as in Table 2.

Models built using only vegetation landscape predictors (L) were significantly more accurate than models built using only vegetation cover predictors (C), showing on average an 11% difference in AUC (mean \pm S.E., $L = 0.80 \pm 0.084$, $C = 0.69 \pm 0.099$; $F_{1,312} = 148.1$, $P < 0.0001$, Table 4). The inclusion of vegetation landscape predictors improved greatly (12% on average) and significantly the vegetation cover model for each species (C versus C-L, $F_{1,312} = 239.4$, $P < 0.0001$, Table 4), but the inclusion of vegetation cover predictors improved only slightly the vegetation landscape model (1% on the average) and this difference was only slightly significant ($L = 0.80 \pm 0.084$, $L-C = 0.81 \pm 0.082$; L versus L-C, $F_{1,312} = 4.4$, $P = 0.04$, Table 4). Mean AUC of vegetation landscape models built with a reduced random set of potential predictors (L_R) was significantly higher (L_R versus C, $F_{1,312} = 105.4$, $P < 0.0001$, Table 4) than that of vegetation cover models (a 9% of average difference), indicating a greater intrinsic predictive potential of vegetation landscape variables.

The conditional order in which each general set of predictors (vegetation or topo-climatic predictors)

Table 5
Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of the order of inclusion of topo-climatic or vegetation predictors

Variable	d.f.	SS	MS	F	P
Error: species					
Residuals	78	2.410	0.031	–	–
Error: within					
Order of inclusion of predictors	2	0.0023	0.0011	5.191	0.007
T-V vs. All	1	0.0023	0.0023	10.312	0.002
V-T vs. All	1	0.0000	0.0000	0.070	0.791
Residuals	156	0.0343	0.0002		

Planned comparisons test if including topo-climatic predictors first renders models that differ in accuracy from those in which all predictors are tested simultaneously (T-V vs. All), and if including vegetation predictors first renders models that differ in accuracy from those in which all predictors are tested simultaneously (V-T vs. All). Names of models as in Table 2.

was included did not affect the prediction ability of the resulting models, though there was a slight significant improvement (1%) when topo-climatic predictors were included first (T-V versus all predictors, $F_{1,156} = 10.3$, $P = 0.002$; V-T versus all predictors, $F_{1,156} = 0.07$, $P = 0.791$, Table 5).

4. Discussion

Our analysis shows correlational relationships between breeding bird distribution and some coarse predictors easily derived from common cartographic data. By providing breeding substrates and foraging habitats, vegetation is likely to have an effect on breeding bird distribution at a fine scale, closer to causality than topography and climate. Therefore, vegetation variables may be more promising to build accurate predictive models at the scale of this present study. Accordingly, our vegetation models (V) have a greater predictive ability than topo-climatic models (T) and the models with both sets of predictors (T-V, V-T, and all predictors) greatly improved topo-climatic models, but were only slightly superior to vegetation models. However, this relative greater predictive ability of vegetation seems to be due to the larger number of potential initial candidate predictors in the set tested to enter the models, because there were no differences

between vegetation and topo-climatic models when controlling for the number of the potential predictors in the initial set. A larger set of potential predictors may contain more information about the environment and is likely to include more variables that correlate with the presence/absence of a species. This is possibly the reason why the vegetation models here developed were more accurate than topo-climatic models. Vegetation, climate and topography are expected to be correlated (Woodward, 1987; Brown, 1995); for example, in our study area the more xeric, low-altitude and flat zones are mainly covered by cereal crops. However, our results suggest that both sets of potential predictors have some degree of independent information about the environment, because models with both sets of predictors reached the highest predictive abilities and, in particular, the inclusion of vegetation variables notably improved the predictive ability of topo-climatic models. This pattern is in agreement with a previous study by Beard et al. (1999), who found similar results in a coarser scale study that considered other climatic and vegetation cover variables (not considering vegetation landscape predictors) and analysed with a different modelling approach data from the Breeding Bird Survey of Idaho (area of study $\sim 200,000 \text{ km}^2$). This agreement in the results of two disparate analyses further supports our conclusion that topo-climatic and vegetation data are equally suitable for bird distribution modelling. Models considering both sets of predictors (vegetation plus topo-climatic variables) somewhat improve the predictive ability and, what is more important, generate reasonably accurate predictions ($\text{AUC} > 0.7$) for almost every breeding bird species (>95%) considered in this study.

Within vegetation variables, vegetation landscape had a greater predictive ability than vegetation cover. This is so even when controlling for the number of the potential predictors in the initial set, which means that, on the average, a single vegetation landscape predictor is more useful for modelling than a single vegetation cover predictor. Vegetation landscape characteristics and vegetation cover categories are well known to be spatially correlated (MacGarigal and MacComb, 1995), but in our study these two sets of potential predictors are not totally redundant, since the inclusion of vegetation landscape predictors greatly improved vegetation cover models. Therefore, our results suggest

that vegetation landscape indeed may have a profound effect on breeding bird distribution, which could be of particular concern in heterogeneous areas. A caveat to make is that we did not thoroughly explore individual models; so, there may be some species for which vegetation cover predictors are as good as (or even better than) vegetation landscape, since species differ in their sensitivity to landscape features (Knick and Rotenberry, 1995; Bolger et al., 1997; Santos and Tellería, 1998).

The relative importance of landscape configuration and site-specific vegetation variables in bird species distribution is open to discussion. Some studies have found a relevant and direct influence of simple landscape patterns (e.g. distance to borders) on bird species distribution (Bolger et al., 1997; Sánchez-Zapata and Calvo, 1999), while others have found more moderate and complex effects (MacGarigal and MacComb, 1995). Landscape may be relevant in explaining bird distribution, as our results suggest, for two reasons. First, according to a hierarchical view of habitat selection (Johnson, 1980), landscape patterns provide environmental clues that are used for birds to select their home range, so that potentially resourceful areas within the range of a species may remain unoccupied or sub-occupied if they lack those clues (Rolstad et al., 2000). Second, the adequacy of apparently homogeneous habitats for a particular species may not be spatially constant if, for example, habitat quality changes with the distance to the edge between suitable and unsuitable habitats (Bolger et al., 1997). Indeed, there is some evidence of negative effects of landscape quality on birds' physiology (e.g. feathers grew more slowly on individuals in smaller forest fragments, Stratford and Stouffer, 2001).

If the relevance of landscape on animal distribution is prevalent among different communities and taxa, then the regional programmes that (courageously) aim to model distributions at a high spatial resolution, such as the GAP in USA (Scott et al., 1993), LANDSPOT

in Switzerland (Guisan et al., 2000), or the NFBS in Australia (see Pearce and Ferrier, 2001; Pearce et al., 2001a) should consider landscape among their candidate predictor variables (or, at least, in what concerns bird distribution). To our knowledge, only the latter explicitly includes predictors related to landscape configuration (e.g. the probability of certain vegetation types in a surrounding area), and their models have proven useful and accurate for many taxa (Pearce and Ferrier, 2001).

To conclude, our results have two implications in the modelling of bird–habitat relationships. First, the selection among sources of potential explanatory variables (if any) should be done on the grounds of data availability, since model accuracy is likely to be similar for models derived from general land-cover and land-use vegetation maps, and for models derived from topographic and climatic information. However, we would recommend using the two sources of information. Second, models that do not take into account landscape parameters are probably missing a relevant source of variables affecting bird distribution.

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Appendix A

List of bird species considered in this study and the AUCs for their different predictive distribution models (names of models as in Table 2).

Species name	T	V	T-V	V-T	All	V _R	C	L	L-C	C-L	L _R
<i>Circaetus gallicus</i>	0.64	0.88	0.88	0.89	0.88	0.74	0.62	0.81	0.81	0.88	0.74
<i>Circus pygargus</i>	0.94	0.97	0.97	0.98	0.97	0.91	0.87	0.95	0.95	0.97	0.91
<i>Hieraaetus pennatus</i>	0.80	0.83	0.94	0.90	0.91	0.75	0.72	0.76	0.78	0.83	0.71
<i>Falco tinnunculus</i>	0.59	0.84	0.88	0.84	0.85	0.70	0.77	0.80	0.83	0.84	0.68
<i>Alectoris rufa</i>	0.73	0.79	0.81	0.81	0.81	0.73	0.71	0.76	0.79	0.79	0.74
<i>Coturnix coturnix</i>	0.75	0.81	0.83	0.82	0.83	0.75	0.68	0.79	0.80	0.81	0.77
<i>Burhinus oediconemus</i>	0.88	0.95	0.98	0.96	0.96	0.89	0.76	0.96	0.96	0.95	0.92
<i>Columba palumbus</i>	0.66	0.70	0.73	0.75	0.74	0.70	0.62	0.67	0.67	0.70	0.67
<i>Streptopelia turtur</i>	0.70	0.73	0.80	0.77	0.77	0.65	0.54	0.73	0.74	0.73	0.66
<i>Cuculus canorus</i>	0.62	0.72	0.74	0.73	0.73	0.63	0.59	0.70	0.72	0.72	0.64
<i>Athene noctua</i>	0.77	0.82	0.86	0.85	0.85	0.76	0.69	0.81	0.82	0.82	0.75
<i>Merops apiaster</i>	0.70	0.71	0.78	0.76	0.77	0.64	0.57	0.71	0.71	0.71	0.66
<i>Upupa epops</i>	0.74	0.74	0.82	0.79	0.80	0.67	0.58	0.73	0.73	0.74	0.69
<i>Jynx torquilla</i>	0.79	0.80	0.85	0.84	0.81	0.69	0.66	0.76	0.78	0.80	0.72
<i>Picus viridis</i>	0.71	0.76	0.79	0.82	0.80	0.69	0.98	0.76	0.76	0.76	0.70
<i>Dendrocopos major</i>	0.76	0.82	0.84	0.83	0.84	0.79	0.68	0.83	0.85	0.82	0.79
<i>Melanocorypha calandra</i>	0.93	0.96	0.96	0.97	0.96	0.94	0.96	0.96	0.96	0.96	0.94
<i>Calandrella brachydactyla</i>	0.91	0.96	0.98	0.97	0.97	0.93	0.87	0.96	0.96	0.96	0.93
<i>Galerida cristata</i>	0.85	0.88	0.91	0.91	0.92	0.87	0.81	0.89	0.89	0.88	0.88
<i>Galerida theklae</i>	0.69	0.74	0.79	0.78	0.79	0.66	0.64	0.75	0.75	0.74	0.68
<i>Lullula arborea</i>	0.75	0.82	0.86	0.85	0.86	0.76	0.68	0.81	0.83	0.82	0.77
<i>Ptyonoprogne rupestris</i>	0.79	0.84	0.89	0.88	0.93	0.74	0.73	0.83	0.88	0.84	0.74
<i>Hirundo rustica</i>	0.69	0.78	0.79	0.76	0.76	0.71	0.70	0.73	0.76	0.78	0.72
<i>Hirundo daurica</i>	0.71	0.73	0.80	0.78	0.77	0.63	0.56	0.72	0.72	0.73	0.68
<i>Delichon urbica</i>	0.68	0.79	0.84	0.84	0.81	0.66	0.66	0.76	0.77	0.79	0.70
<i>Motacilla flava</i>	0.92	0.97	0.96	0.96	0.97	0.92	0.92	0.95	0.96	0.97	0.93
<i>Motacilla cinerea</i>	0.93	0.93	0.99	0.97	0.98	0.84	0.62	0.88	0.93	0.93	0.84
<i>Troglodytes troglodytes</i>	0.79	0.79	0.82	0.85	0.85	0.71	0.70	0.75	0.77	0.79	0.73
<i>Cercotrichas galactotes</i>	0.36	0.47	0.44	0.47	0.45	0.87	0.76	0.96	0.96	0.47	0.89
<i>Erithacus rubecula</i>	0.85	0.91	0.92	0.93	0.92	0.85	0.77	0.90	0.90	0.91	0.87
<i>Luscinia megarynchos</i>	0.73	0.82	0.81	0.81	0.81	0.70	0.64	0.72	0.76	0.82	0.70
<i>Phoenicurus ochruros</i>	0.93	0.96	0.95	0.98	0.96	0.86	0.79	0.94	0.96	0.96	0.88
<i>Phoenicurus phoenicurus</i>	0.83	0.86	0.91	0.91	0.88	0.77	0.64	0.81	0.86	0.86	0.80
<i>Saxicola torquata</i>	0.60	0.80	0.81	0.81	0.81	0.70	0.73	0.76	0.81	0.80	0.69
<i>Oenanthe leucura</i>	0.90	0.97	0.98	0.99	0.98	0.84	0.80	0.96	0.96	0.97	0.87
<i>Oenanthe hispanica</i>	0.68	0.73	0.80	0.78	0.74	0.67	0.59	0.73	0.73	0.73	0.68
<i>Monticola solitarius</i>	0.86	0.90	0.92	0.93	0.93	0.79	0.81	0.87	0.90	0.90	0.81
<i>Turdus merula</i>	0.75	0.81	0.85	0.83	0.83	0.79	0.75	0.80	0.81	0.81	0.79
<i>Turdus viscivorus</i>	0.79	0.76	0.86	0.86	0.83	0.71	0.63	0.71	0.72	0.76	0.70
<i>Cettia cetti</i>	0.58	0.85	0.90	0.86	0.87	0.75	0.81	0.72	0.85	0.85	0.75

Appendix A. (Continued)

Species name	T	V	T-V	V-T	All	V _R	C	L	L-C	C-L	L _R
<i>Cisticola juncidis</i>	0.87	0.92	0.94	0.94	0.94	0.90	0.87	0.92	0.92	0.92	0.89
<i>Hippolais pallida</i>	0.71	0.96	0.99	0.99	0.97	0.85	0.81	0.89	0.88	0.96	0.85
<i>Hippolais polyglotta</i>	0.65	0.75	0.78	0.78	0.78	0.69	0.60	0.76	0.76	0.75	0.69
<i>Sylvia undata</i>	0.66	0.72	0.76	0.73	0.73	0.57	0.69	0.72	0.72	0.72	0.70
<i>Sylvia conspicillata</i>	0.71	0.90	0.95	0.92	0.95	0.85	0.79	0.92	0.94	0.90	0.87
<i>Sylvia cantillans</i>	0.75	0.88	0.88	0.89	0.87	0.78	0.64	0.86	0.87	0.88	0.79
<i>Sylvia melanocephala</i>	0.73	0.71	0.79	0.78	0.79	0.69	0.67	0.71	0.73	0.71	0.69
<i>Sylvia hortensis</i>	0.63	0.75	0.78	0.76	0.77	0.64	0.61	0.75	0.75	0.75	0.68
<i>Sylvia atricapilla</i>	0.82	0.82	0.88	0.87	0.88	0.74	0.67	0.81	0.82	0.82	0.78
<i>Phylloscopus bonelli</i>	0.84	0.86	0.87	0.89	0.86	0.78	0.69	0.84	0.84	0.86	0.80
<i>Phylloscopus brehmii</i>	0.83	0.86	0.86	0.92	0.89	0.77	0.69	0.86	0.86	0.86	0.80
<i>Regulus ignicapillus</i>	0.86	0.89	0.92	0.92	0.90	0.79	0.74	0.88	0.88	0.89	0.82
<i>Muscicapa striata</i>	0.79	0.79	0.88	0.87	0.88	0.79	0.72	0.70	0.70	0.79	0.77
<i>Aegithalos caudatus</i>	0.73	0.82	0.85	0.87	0.85	0.72	0.71	0.79	0.81	0.82	0.73
<i>Parus cristatus</i>	0.72	0.86	0.87	0.87	0.87	0.81	0.77	0.85	0.87	0.86	0.82
<i>Parus caeruleus</i>	0.75	0.76	0.81	0.80	0.79	0.75	0.70	0.76	0.76	0.76	0.75
<i>Parus major</i>	0.68	0.72	0.74	0.73	0.73	0.69	0.68	0.71	0.72	0.72	0.69
<i>Sitta europaea</i>	0.79	0.83	0.86	0.86	0.86	0.79	0.74	0.81	0.82	0.83	0.79
<i>Certhia brachydactyla</i>	0.27	0.28	0.24	0.26	0.23	0.76	0.27	0.78	0.80	0.28	0.77
<i>Oriolus oriolus</i>	0.68	0.68	0.74	0.72	0.74	0.65	0.57	0.68	0.71	0.68	0.64
<i>Lanius meridionalis</i>	0.50	0.86	0.83	0.83	0.80	0.71	0.68	0.80	0.79	0.86	0.70
<i>Lanius senator</i>	0.68	0.76	0.78	0.77	0.78	0.68	0.65	0.76	0.77	0.76	0.70
<i>Garrulus glandarius</i>	0.72	0.80	0.81	0.83	0.81	0.76	0.65	0.79	0.79	0.80	0.77
<i>Cyanopica cyana</i>	0.85	0.85	0.91	0.91	0.91	0.74	0.62	0.85	0.85	0.85	0.79
<i>Pyrhcorax pyrrhcorax</i>	0.95	0.95	0.97	0.97	0.94	0.79	0.71	0.94	0.95	0.95	0.87
<i>Corvus monedula</i>	0.77	0.91	0.94	0.91	0.92	0.82	0.68	0.91	0.91	0.91	0.84
<i>Corvus corax</i>	0.73	0.75	0.80	0.80	0.79	0.65	0.67	0.71	0.75	0.75	0.61
<i>Sturnus unicolor</i>	0.73	0.71	0.79	0.80	0.79	0.63	0.59	0.69	0.70	0.71	0.63
<i>Passer domesticus</i>	0.68	0.75	0.78	0.74	0.78	0.70	0.68	0.72	0.75	0.75	0.70
<i>Petronia petronia</i>	0.81	0.79	0.86	0.87	0.87	0.75	0.69	0.80	0.80	0.79	0.75
<i>Fringilla coelebs</i>	0.77	0.87	0.90	0.88	0.88	0.85	0.81	0.86	0.87	0.87	0.85
<i>Serinus serinus</i>	0.65	0.71	0.74	0.72	0.73	0.63	0.64	0.68	0.70	0.71	0.64
<i>Carduelis chloris</i>	0.59	0.66	0.75	0.66	0.74	0.67	0.53	0.70	0.71	0.66	0.68
<i>Carduelis carduelis</i>	0.57	0.66	0.74	0.67	0.72	0.67	0.62	0.71	0.72	0.66	0.67
<i>Carduelis cannabina</i>	0.62	0.73	0.76	0.74	0.74	0.69	0.67	0.72	0.73	0.73	0.70
<i>Coccothraustes coccothraustes</i>	0.70	0.85	0.81	0.89	0.83	0.72	0.66	0.73	0.81	0.85	0.75
<i>Emberiza cirrus</i>	0.79	0.74	0.84	0.81	0.84	0.68	0.60	0.75	0.75	0.74	0.69
<i>Emberiza cia</i>	0.75	0.74	0.83	0.79	0.81	0.73	0.65	0.76	0.78	0.74	0.73
<i>Miliaria calandra</i>	0.71	0.78	0.82	0.80	0.81	0.73	0.67	0.76	0.78	0.78	0.74

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