



Evaluating the reliability of species distribution models with an indirect measure of bird reproductive performance

Olatz Aizpurua, Lisette Cantú-Salazar, Gilles San Martín, Francesc Sardà-Palomera, Gabriel Gargallo, Sergi Herrando, Lluís Brotons and Nicolas Titeux

O. Aizpurua (<http://orcid.org/0000-0001-6579-0064>), L. Cantú-Salazar and N. Titeux (<http://orcid.org/0000-0002-7719-7417>) (nicolas.titeux@ctfc.es), Luxembourg Inst. of Science and Technology (LIST), Environmental Research and Innovation (ERIN), Belvaux, Luxembourg. – G. San Martín, Centre Wallon de Recherche Agronomiques (CWRA), Dépt des Sciences du Vivant, Unité Protection des Plantes et Ecotoxicologie, Glembloix, Belgium. – F. Sardà-Palomera, S. Herrando, L. Brotons, OA and NT, European Bird Census Council (EBCC) and Forest Sciences Centre of Catalonia (CEMFOR-CTFC), InForest Joint Research Unit (CSIC-CTFC-CREAF), Solsona, Spain. SH and LB also at: Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Vallés, Spain. LB also at: Consejo Superior de Investigaciones Científicas (CSIC), Cerdanyola del Vallés, Spain. – G. Gargallo, SH and LB, Catalan Ornithological Inst. (ICO), Natural History Museum of Barcelona, Barcelona, Spain.

Measures of fitness such as reproductive performance are considered reliable indicators of habitat quality for a species. Such measures are, however, only available in a restricted number of sites, which prevents them from being used to quantify habitat quality across landscapes or regions. Alternatively, species presence records can be used along with environmental variables to build models that predict the distribution of species across larger spatial extents. Model predictions are often used for management purposes as they are assumed to describe the quality of the habitats to support a species. Yet, given that species are often present both in optimal and suboptimal areas, the use of data collected during the breeding season to build these models may potentially result in misleading predictions of habitat quality for the reproduction of the species, with potentially significant conservation consequences. In this study we analysed the relationship between fitness parameters informing on habitat quality for reproduction and predictions of species distribution models at multiple spatial scales using two independent sets of data. For 19 passerine bird species, we compared an indirect measure of reproductive performance (ratio of juveniles-to-adults) – obtained from Constant Effort Sites (CES) mist-netting data in Catalonia – with the predictions of models based on bird presence records collected during the Catalan Breeding Bird Atlas (CBBA). A positive relationship between the predictions derived from species distribution models and the reproductive performance of the species was found for almost half of the species at one or more spatial scales. This result suggests that species distribution models may help to predict habitat quality for some species over some extents. However, caution is needed as this is not consistent for all species at all scales. Further work based on species- and scale-specific approaches is now required to understand in which situations species distribution models provide predictions that are in line with reproductive performance.

The greatest threat to wild bird populations is the degradation and loss of habitat (Johnson 2007), i.e. ‘the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism’ (Hall et al. 1997). To assess which habitats are more or less valuable for a particular species, especially for those of conservation concern, it is necessary to use robust measurements of habitat quality, that is, of ‘the ability of a given habitat to provide resources and conditions appropriate for the per capita contribution to population growth’ (Johnson 2007). This implies that estimates of habitat quality require measures of demography. One of the most cited definitions of habitat quality is that of Van Horne (1983), who describes habitat quality in terms of fitness, as ‘the product of density, mean individual survival probability, and mean expectation of future offspring’. Gathering such demographic information to describe habitat quality can be costly and time

consuming, and is usually needed over long periods, thus limiting its availability to a restricted number of sampling sites; therefore, the use of proxies to reflect how habitat quality varies across landscapes and regions is often necessary (Stephens et al. 2015).

Species distribution models statistically link species presence records with known environmental conditions to predict the likelihood of a species to occur at any site in a given area (Araújo and Guisan 2006, Elith et al. 2010). Model predictions are often based on species presence records available from atlas projects or museum inventories, and then used for management and conservation purposes (Brotons et al. 2004, Guisan et al. 2013) under the assumption that they directly inform on the quality of the habitats for the species. Although the predictions of these models correlate well in general with species abundance (Weber et al. 2016), not much quantitative information is available regarding the

link with population growth. Yet, outcomes of these models are often used as proxies for demographic parameters to differentiate between areas with high individual fitness or positive population growth and areas that are not suitable for viable populations (Pulliam 2000, Guisan and Thuiller 2005, Franklin 2009, VanDerWal et al. 2009, Pellissier et al. 2013). One of the most important assumptions of these models is that the species is present wherever the local environmental conditions are within the species demographic niche (populations at equilibrium, Peterson et al. 2011). However, these models frequently ignore possible deviations from this equilibrium, such as source-sink dynamics (Pulliam 2000, Thuiller et al. 2014) or ecological traps (Robertson and Hutto 2006, Hollander et al. 2011), where individuals occur under certain environmental conditions beyond the boundaries of their demographic niche. Previous studies examined the link between the predictions of species distribution models and a variety of fitness parameters informing on habitat quality (Titeux et al. 2007, Stephens et al. 2015). Although they found a positive correlation between model predictions and abundance for an endangered rodent species, Bean et al. (2014) reported an absence of correlation with two fitness parameters (i.e. survival and body condition). In contrast, Brambilla and Ficetola (2012) showed that their species distribution models predicted accurately the number of fledglings in the red-backed shrike. Pellissier et al. (2013) found a significant relationship between model predictions and nest success but only for one of the three wader species they studied. The contrasting results from studies examining the link with fitness parameters call into question the use of model predictions as proxies for habitat quality. This draws attention to the need for a better understanding of the link between model predictions and habitat quality (Falcucci et al. 2009).

In addition, most species are influenced by ecological processes and interactions acting beyond the local scale, e.g. the habitat patch (Kareiva and Wennergren 1995, Steffan-Dewenter et al. 2002). Hence, fitness parameters such as measures of reproductive performance collected in a specific site may not necessarily reflect only the habitat quality of this site, but may be also influenced by the quality of the neighbouring areas (Chalfoun and Martin 2007). For instance, the proportion of juveniles captured in a site may include those juveniles produced locally and also those produced in suitable nearby areas that had dispersed into the site (Greenwood and Harvey 1982). Hence, it is necessary to understand how the relationship between the predictions of the models based on presence records and the fitness parameters documenting habitat quality varies across multiple spatial scales. It is also worth testing this scale dependency using a sample of species, because factors such as juvenile dispersal are species-specific traits.

In this study we assessed, for 19 passerine bird species in a Mediterranean region, how the predictions derived from species distribution models are related to measures of reproductive performance obtained from data collected in Constant Effort Sites (CES) mist-netting stations. We used the species presence records collected in the frame of a breeding bird atlas project and we built species distribution models using the same procedure as the one applied in this atlas. The predictions of these models have been extensively used to guide

conservation and management strategies aiming to protect or preserve suitable habitats for birds (Brotons et al. 2004, Bosch et al. 2010, Herrando et al. 2010, Sardà-Palomera et al. 2012). The proportion of juveniles captured in each CES across Catalonia was used as a measure of reproductive performance of the bird species. We tested at multiple spatial scales if the reproductive performance measured in the CES matched the predictions derived from the species distribution models.

Methods

Study area

Catalonia is a 32 114 km² region located in the north-east of the Iberian Peninsula. This region is mostly dominated by Mediterranean climate but has a large altitudinal range (from 0 to 3143 m a.s.l.), which creates a highly heterogeneous landscape. Catalonia has a long tradition in ornithology that has allowed the development of the Catalan Breeding (CBBA) and Wintering (CWBA) Bird Atlases and several long-term bird monitoring programmes (Estrada et al. 2004, Brotons et al. 2007, Herrando et al. 2011).

Presence records

Bird presence records during the breeding period were sourced from the CBBA. Bird data collection is described in details in Estrada et al. (2004) and an English version of the methodology chapter can be freely downloaded from the website of the Catalan Ornithological Inst. (<www.ornitologia.org/ca/quefem/monitoratge/atles/atles_nidificants/atles_nidificants_metodologia.pdf>). During 1999–2002, volunteers and professionals surveyed the 10-km resolution squares ($n = 385$) according to a grid system covering the whole of Catalonia. They recorded the presence, the breeding evidence and estimated the abundance of each species. In addition, a sample of 5–10 1-km resolution squares was selected within each 10-km resolution square, where observers recorded the presence of each species during two 1-h timed surveys in early and late spring. These 1-km resolution squares were spatially distributed to cover the different habitat types following a stratified random sampling procedure. In our analyses, we only used information on bird presence from the 1-km resolution squares enclosed in 10-km resolution squares where breeding evidence was reported. The number of 1-km resolution squares with bird presence used to build the species distribution models for each species is reported in Table 1.

Predictor variables

We decided to follow the same methodology to build the species distribution models as the one implemented in CBBA and CWBA, because the maps produced by these models in these atlases are broadly used in Catalonia by the administrations in charge of biodiversity conservation or land use planning. In addition, they are assumed to directly inform on the quality of the breeding or wintering habitats for the bird species and used as such in many scientific

Table 1. Detailed information for each bird species used in this study: number of presence records at 1-km resolution used in the modelling procedure, average modelling performance (AUC) \pm standard deviation (SD) over the 10 evaluation datasets, number of Constant Effort Sites (CES) used in this study, total number of juveniles captured and total number of individuals captured during the study period in the CES.

| Species | Acronym | Number of presence records | Model performance (AUC \pm SD) | Number of CES | Number of juveniles | Number of total captures |
|----------------------------------|---------|----------------------------|----------------------------------|---------------|---------------------|--------------------------|
| <i>Acrocephalus arundinaceus</i> | acraru | 132 | 0.90 \pm 0.03 | 10 | 81 | 416 |
| <i>Acrocephalus scirpaceus</i> | acrsci | 102 | 0.93 \pm 0.01 | 24 | 542 | 2514 |
| <i>Aegithalos caudatus</i> | aegcau | 1274 | 0.73 \pm 0.01 | 43 | 594 | 996 |
| <i>Carduelis carduelis</i> | carcar | 1812 | 0.65 \pm 0.01 | 32 | 130 | 559 |
| <i>Certhia brachydactyla</i> | cerbra | 1451 | 0.69 \pm 0.01 | 44 | 245 | 561 |
| <i>Cettia cetti</i> | cetcet | 751 | 0.81 \pm 0.01 | 29 | 859 | 1490 |
| <i>Chloris chloris</i> | chlchl | 1637 | 0.67 \pm 0.01 | 35 | 190 | 739 |
| <i>Cyanistes caeruleus</i> | cyacae | 1590 | 0.70 \pm 0.01 | 43 | 461 | 957 |
| <i>Eriothacus rubecula</i> | erirub | 1733 | 0.71 \pm 0.01 | 42 | 1388 | 2445 |
| <i>Hippolais polyglotta</i> | hippol | 842 | 0.74 \pm 0.01 | 44 | 178 | 1492 |
| <i>Luscinia megarhynchos</i> | lusmeg | 2038 | 0.67 \pm 0.01 | 49 | 664 | 2694 |
| <i>Parus major</i> | parmaj | 2435 | 0.64 \pm 0.01 | 50 | 1280 | 2046 |
| <i>Passer domesticus</i> | pasdom | 1994 | 0.68 \pm 0.01 | 36 | 443 | 2156 |
| <i>Serinus serinus</i> | serser | 2334 | 0.64 \pm 0.01 | 44 | 376 | 970 |
| <i>Sylvia atricapilla</i> | sylatr | 1701 | 0.68 \pm 0.01 | 46 | 1197 | 2720 |
| <i>Sylvia cantillans</i> | sylcan | 893 | 0.75 \pm 0.01 | 32 | 315 | 669 |
| <i>Sylvia melanocephala</i> | sylala | 1512 | 0.72 \pm 0.01 | 39 | 1574 | 2599 |
| <i>Troglodytes troglodytes</i> | trotro | 1565 | 0.70 \pm 0.01 | 36 | 240 | 524 |
| <i>Turdus merula</i> | turner | 2613 | 0.61 \pm 0.01 | 50 | 1615 | 3721 |

studies (Brotons et al. 2004, Bosch et al. 2010, Herrando et al. 2010, Sardà-Palomera et al. 2012).

We used the same set of environmental variables as the ones that were used to build the models in the CWBA. These variables ($n = 55$) were selected to incorporate the factors known a priori to determine the current distribution of birds at different spatial scales (Vaughan and Ormerod 2003). Our objective was to reproduce the atlas modelling approach and to generate predictive models that represented the distribution of the species as accurately as possible. As we did not project the outcomes of such models to other areas or time periods, we considered that potential overfitting due to the high number of variables was not a too serious issue for our study aims. Environmental variables were calculated within each 1-km resolution square to reflect: 1) habitat and land-use: variables describing the different types of land use and land cover. 2) Climate: variables describing temperature and precipitation regimes over the course of the year. 3) Relief: variables describing altitude and slope. 4) Human influence: variables describing the potential impacts of human infrastructures (e.g. urban areas, roads). 5) Others: variables used to account for spatial patterns not directly explained by other environmental variables (e.g. mean latitudinal and longitudinal coordinates for each square, mean distance to the sea).

Detailed information about each predictor variable used in the CWBA, their sources and how they were generated can be found in Herrando et al. (2011). An English version of the methodology of the CWBA can be freely downloaded from the website of the Catalan Ornithological Inst. (<www.ornitologia.org/ca/quefem/monitoratge/atles/atles_hivern/atleshivern_metodologia.pdf>).

Species distribution modelling

We applied the presence-only maximum entropy framework Maxent 3.3.1 (Phillips et al. 2006) because it is moderately

sensitive to sample size and outperforms other methods when sample size is small (Hernandez et al. 2006, Wisz et al. 2008, Bean et al. 2011). Models were computed at a spatial resolution of 1 km using the Maxent default parameters, but limiting the response to environmental variables to linear and quadratic functions. For each species, the set of 1-km resolution squares with presence records was randomly split into a calibration dataset (70% of the presence records) and an evaluation dataset (remaining 30% of the records). This procedure was repeated 10 times using a subsampling approach. The predictive performance of the models was evaluated using the evaluation datasets and the area under the curve (AUC) of the receiver operating characteristics (ROC) curve. As bird presence records were collected during the breeding period, we used the average model outcomes across the 10 replicates to predict breeding habitat quality for each of the bird species in the 1-km resolution squares. The values of the model outcomes ranged from 0 to 1 and reflected an increasing habitat quality.

Bird mist-netting and fitness parameter

Bird mist-netting using a constant effort methodology and standard field procedures (Robinson et al. 2009) started in the early 1990s in Catalonia within the frame of the SYLVIA project and includes now over 60 Constant Effort Sites (CES) (Grup Català d'Anellament 2002). These CES are distributed all across Catalonia and are often located within protected areas, but they represent the whole diversity of habitat types in the region. SYLVIA focuses on the study of demographic parameters through captures of birds carried out from 1 May to 6 August. This allows covering the whole breeding season for all bird species across the whole climatic gradient in Catalonia, including the breeding period of late migrants (e.g. *Acrocephalus arundinaceus*, *Acrocephalus scirpaceus* or *Hippolais polyglotta*) and the second or replacement clutch of resident species (e.g. *Carduelis carduelis*, *Chloris chloris* or

Passer domesticus). To match the time frame of the CBBA data used to build the models, we used the demographic data collected in CES active between 1996 and 2005.

To reflect breeding habitat quality for each species around the CES, we calculated for each year separately the number of juveniles over the total number of individuals captured (probability of capturing juveniles) (Peach et al. 1996), which is frequently used as a relative measure of reproductive performance in birds (DeSante et al. 1995, Grup Català d'Anellament 2002). This parameter was calculated for those species most commonly captured in the CES in Catalonia ($n = 19$, Table 1) for which the amount of data was sufficiently large to allow a robust analysis, i.e. with over 400 captures during the study period. The number of CES used in subsequent analyses varied among the different species ($n = 10\text{--}50$) because they were not all captured in each CES.

Habitat quality indices at multiple spatial scales

Based on the predictions of the species distribution models, we estimated the habitat quality for the 19 bird species at multiple scales to inform on the quality of the neighbouring areas around each CES. To do so, we drew buffers around the CES using five different radii (1, 2, 4, 8 and 16 km) and we calculated the area-weighted mean habitat quality (AWM-HQ) predicted by the models within these buffers (Fig. 1). We acknowledge that there is an overlap between the buffers of neighbouring CES for the largest spatial scales and that the data are not fully independent from each other.

Statistical analyses

For each species and at each spatial scale, we used generalised linear mixed models (GLMMs) to test for a relationship between the measures of reproductive performance (i.e. the probability of capturing juveniles) and the breeding habitat quality estimated from the models, using a binomial error distribution and a logit link function model to avoid overdispersion. CES identities were included as random effects in all models to control for between-year variations of reproductive performance within the locations. As a high density of individuals may negatively affect reproductive performance through competition (Sardà-Palomera et al. 2011), we included the log-transformed total number of captured adults as a covariate. As some CES are close to each other in some parts of Catalonia, we performed an analysis of spline correlograms of the model residuals using the 'nfc' package in R, and we did not detect any spatial autocorrelation (Bjornstad 2016).

Results

Four of the studied species (*Acrocephalus scirpaceus*, *Chloris chloris*, *Sylvia melanocephala* and *Turdus merula*) showed a significant positive relationship between the probability of capturing a juvenile and the habitat quality derived from the species distribution models across all spatial scales (Fig. 2 and Supplementary material Appendix 1 Fig. A1). *Carduelis carduelis* was the single species with a significant

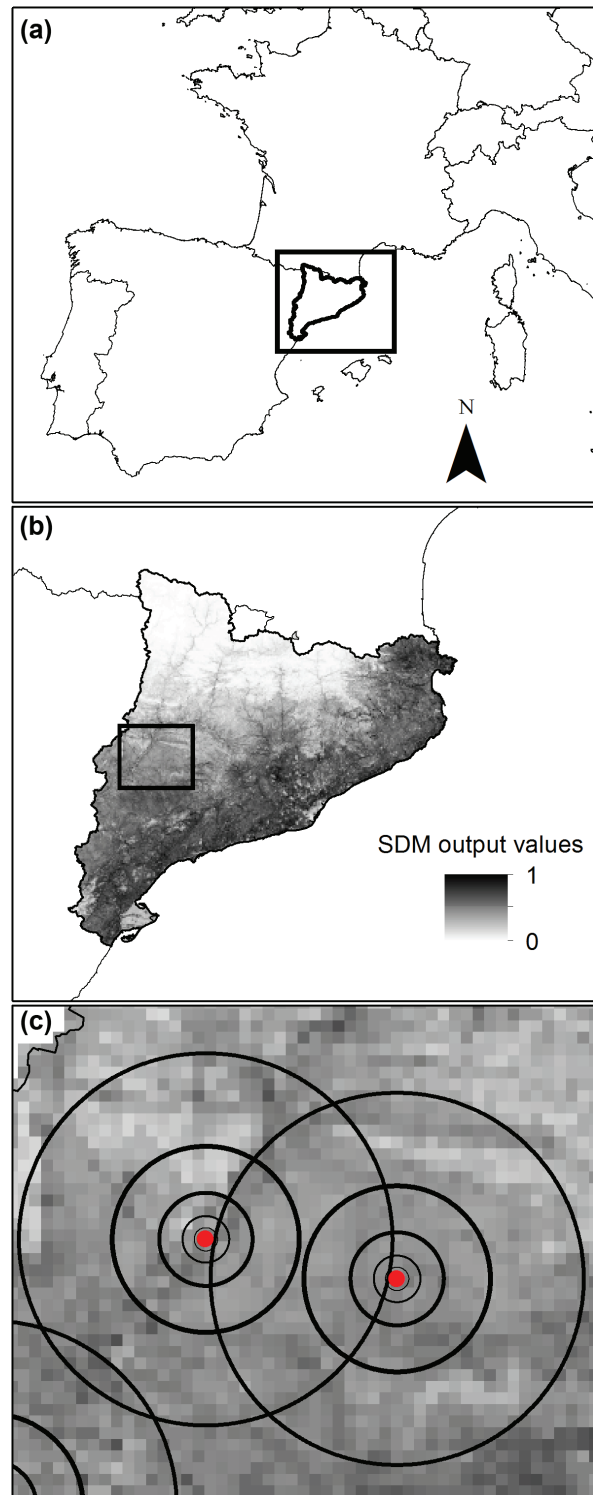


Figure 1. (a) Location of Catalonia in southern-Europe. (b) Predictions of the species distribution model for *Sylvia melanocephala* (example species). (c) Subset of the study area with Constant Effort Sites (CES) marked with red dots and the buffers in black at 1, 2, 4, 8 and 16 km of distance around the CES.

positive relationship between the probability of capturing a juvenile and the habitat quality only at the smallest spatial scales. In contrast, for *Erithacus rubecula*, *Parus major* and *Sylvia atricapilla*, this relationship was significantly positive

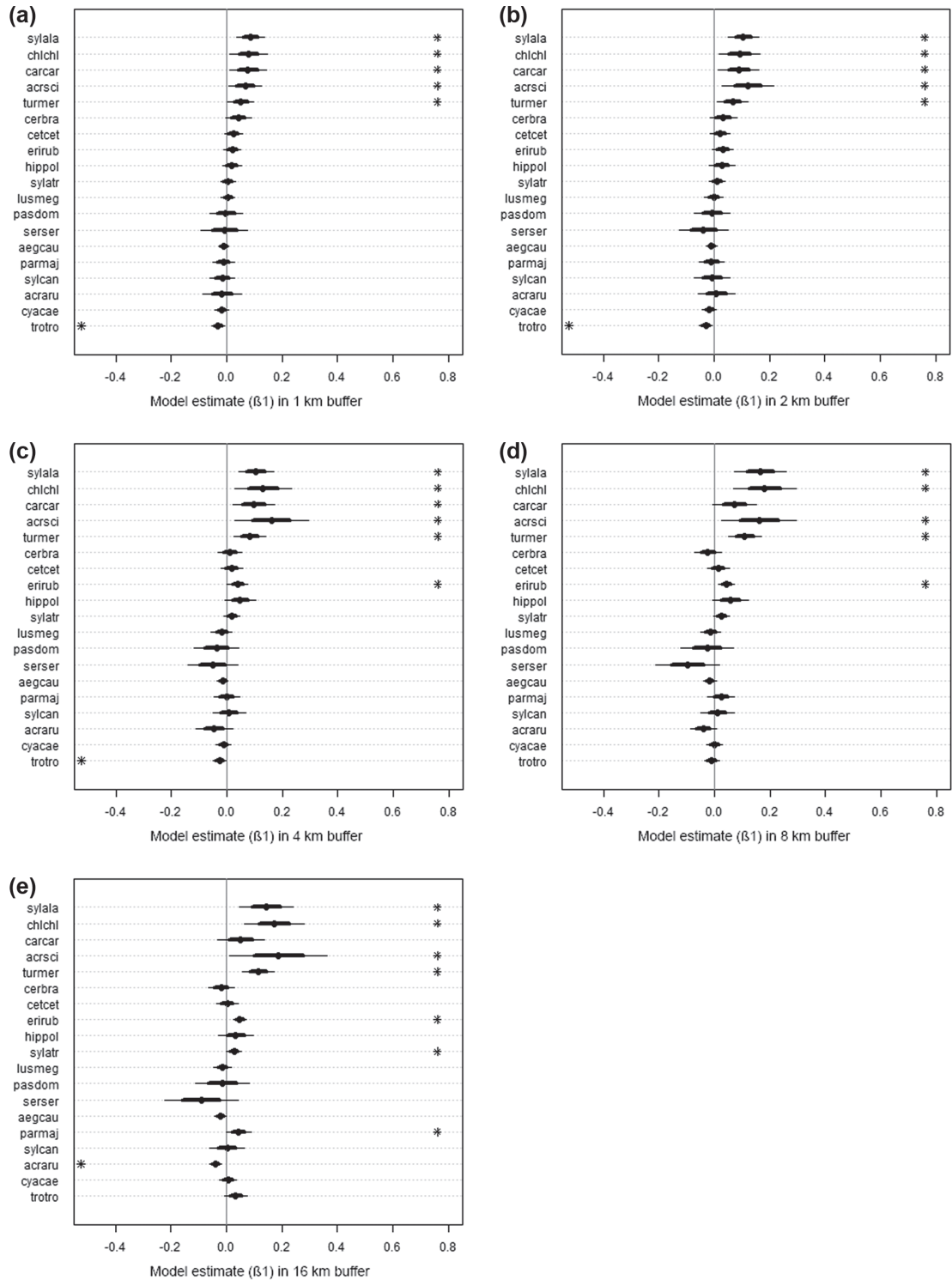


Figure 2. Slope estimate (β_1) for the relationship between reproductive performance (i.e. probability of capturing a juvenile) and habitat quality estimated from the species distribution models around the Constant Effort Sites at multiple spatial scales: (a) 1 km, (b) 2 km, (c) 4 km, (d) 8 km and (e) 16 km buffers. The different bird species are ordered in the same way in the different panels (see Table 1 for acronyms). Points indicate the slope estimate, bold line indicates the standard error and thinner line indicates the 95% confidence intervals. Asterisks indicate a significantly positive or negative relationship ($p \leq 0.05$).

only at the larger spatial scales. Nine of the studied bird species (*Aegithalos caudatus*, *Certhia brachydactyla*, *Cettia cetti*, *Cyanistes caeruleus*, *Hippolais polyglotta*, *Luscinia megarhynchos*, *Passer domesticus*, *Serinus serinus* and *Sylvia cantillans*) showed no significant relationship between the probability

of capturing a juvenile and the predictions of the models at any of the spatial scales. For only two species (*Acrocephalus arundinaceus* and *Troglodytes troglodytes*) we found a significantly negative relationship between the probability of capturing a juvenile and the habitat quality estimated from

the models, but only at the largest spatial scale for the former species and at the smallest spatial scales for the latter.

Discussion

We examined, for a sample of common passerine species over a large spatial extent, the relationship between the predictions obtained from species distribution models (which are typically considered as proxies for habitat quality) using atlas data and the production of juveniles estimated from mist-netting CES. For 21% of the species, we found a positive relationship between the predictions of the models and the estimated reproductive performance across all spatial scales. For almost half of the species, we found a positive relationship at least at one of the different spatial scales. On the other hand, there was no significant relationship between the modelling outcomes and the reproductive performance for the other half of species.

Our study was carried out at multiple spatial scales because the reproductive performance of a species at a site does not necessarily reflect only the local quality of the habitat, but also that of the neighbouring areas (Chalfoun and Martin 2007). Results showed that the relationship between the predictions of the models and the habitat quality estimated from the reproductive performance measure may considerably vary across spatial scales. *Erithacus rubecula*, *Sylvia atricapilla* and *Parus major* showed a significantly positive relationship only when the more distant areas around the mist-netting site were included in the analysis. The juveniles of these species most probably disperse more across the landscape than those of other species and their numbers may not necessarily reflect the quality of the local habitat conditions for breeding. It is known that passerine juveniles disperse from their natal home range after birth and that dispersal behaviour might vary across species depending on the landscape composition and the learning strategies (Skórka et al. 2016). A quantitative analysis of the link between this scale dependency observed in our results and traits such as juvenile dispersal (DeSante et al. 1995) would provide insights into the mechanisms behind the observed pattern. However, such an analysis was beyond the scope of our study because those species-specific traits are very difficult to measure and depend on external factors such as weather conditions or geographic location. Thus, this level of detailed information is only available over small spatial extents and for a limited set of species that may not be representative of the bird species assemblages. As recently recommended by Pellissier et al. (2013), we opted for carrying out an analysis using as many species as possible over a large spatial extent to test the generality of the relationship between the predictions of species distribution models and fitness parameters informing on habitat quality. Our results suggest that species distribution models may help to predict habitat quality for some species over some extents, but also show that the generality of this relationship is not straightforward, as there is strong variability among species and across spatial scales.

Further work is now warranted to further examine the link between species life histories and the ability of these models provide predictions that are in line with reproductive performance across varying spatial scales. Although we

selected here the probability of capturing juveniles as a frequently used measure of reproductive performance (DeSante et al. 1995), it is also needed to test alternative measures to represent fitness more completely. It is worth mentioning that we also tested the relationship between the probability of capturing a female with brood patch and the habitat quality values obtained from the species distribution models (Supplementary material Appendix 2 Fig. A2). The results using this alternative reproductive performance measure showed a similar pattern to that obtained when using the probability of capturing juveniles.

In addition to the life history traits of the species, the relationship between the predictions of the models and habitat quality estimated from reproductive performance measures collected in the field may also be influenced by the modelling procedure itself. Even though the variables selected for the models were ecologically relevant predictors of bird distributions, they were not tailored to species-specific environmental requirements and were probably more relevant for some species than for others. The link between the observed distribution of the species and the quality of the habitat may also vary among species (Pulliam 2000). The predictions of the species distribution models such as those used in our study, however, inform on the potential of a species to be present in different locations from the statistical associations between the species presence records and the environmental conditions. Hence, these models might not necessarily capture information on the behavioural mechanisms that can lead animals to select poor or to avoid the most suitable habitats (Johnson 2007, Hollander et al. 2011, Robertson et al. 2013) and the demographic consequences (e.g. reproduction performance) of such maladaptive selection (Kristan 2003, Lamb et al. 2016). Research efforts are underway to evaluate the extent to which these processes affect a large number of species (Hale and Swearer 2016, Robertson and Chalfoun 2016, Hollander et al. 2017).

In line with previous studies on this issue (Pellissier et al. 2013, Bean et al. 2014, Thuiller et al. 2014), we conclude that the predictions of species distribution models may prove useful but should be interpreted with extreme caution, especially when they are used to guide conservation or management actions that are expected to induce changes in habitat quality for the species. Depending on the type of data used to build the models and the link between the spatial distribution and the habitat requirements of the species (Pulliam 2000, Peterson et al. 2011), it might be risky to use the predictions of the models as direct proxies for habitat quality in the lack of careful species- and scale-specific assessments in the area of interest.

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Supplementary material (Appendix JAV-01218 at <www.avianbiology.org/appendix/jav-01218>). Appendix 1–2.