

How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models?

Morgane Barbet-Massin, Wilfried Thuiller and Frédéric Jiguet

M. Barbet-Massin (barbet@mnhn.fr) and F. Jiguet, Muséum National d'Histoire Naturelle, UMR 7204 MNHN-CNRS-UPMC, Centre de Recherches sur la Biologie des Populations d'Oiseaux, 55 Rue Buffon, FR-75005 Paris, France. – W. Thuiller, Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Univ. Joseph Fourier, BP 53, FR-38041 Grenoble Cedex 9, France.

Climate suitability models are used to make projections of species' potential future distribution under climate change. When studying the species richness with such modeling methods, the extent of the study range is of particular importance, especially when the full range of occurrence is not considered for some species, often because of geographical or political limits. Here we examine biases induced by the use of range-restricted occurrence data on predicted changes in species richness and predicted extinction rates, at study area margins. We compared projections of future suitable climate space for 179 bird species breeding in Iberia and North Africa (27 of them breeding only in North Africa though potential colonizers in Europe), using occurrence data from the full Western Palaearctic (WP) species range and from the often-considered European-restricted range. Current and future suitable climatic spaces were modeled using an ensemble forecast technique applied to five general circulation models and three climate scenarios, with eight climatic variables and eight modeling techniques. The use of range-restricted compared to the full WP occurrence data of a species led to an underestimate of its suitable climatic space. The projected changes in species richness across the focus area (Iberia) varied considerably according to the occurrence data we used, with higher local extinction rates with European-restricted data (on average 38 vs 12% for WP data). Modeling results for species currently breeding only in North Africa revealed potential colonization of the Iberian Peninsula (from a climatic point of view), which highlights the necessity to consider species outside the focus area if interested in forecasted changes in species richness. Therefore, the modeling of current and future species richness can lead to misleading conclusions when data from a restricted range of occurrence is used. Consequently, climate suitability models should use occurrence data from the complete distribution range of species, or at least within biogeographical areas.

Global climate change is of major scientific and political concerns, especially when considering potential impacts on biodiversity, ecosystem processes and human well-being (Thomas et al. 2004, Patz et al. 2005, Schröter et al. 2005). A central postulate in biogeography is that climate exerts a dominant control over the distribution of species, as shown by evidence from fossil record (Davis and Shaw 2001) and recent observed trends (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). Therefore, climate niche modeling is widely used to estimate the potential impacts of climate change on species distribution ranges (Thuiller 2007). The climate envelope modeling approach has its foundation in the ecological niche theory (Hutchinson 1957). The principle is to predict future suitable climatic space, using future climatic scenarios, assuming that current distributions reflect species' environmental requirements and that these requirements will be maintained. This latter assumption is given credibility by evolutionary conservatism of ecological niches (Peterson et al. 1999). The former assumption has rarely been challenged, though for the theory to hold, variables used

for modeling must reliably capture the bioclimatic limits of the distribution. Related to this concern, the geographic extent of the study has to be considered carefully. When the extent of a study is defined with political limits or simple geographic or biogeographic barriers and where species occurrences are known across these limits, distribution modeling can lead to a truncated climatic niche, unless outside presences occur within the climatic niche defined by the presences under study (Van Horn 2002, Thuiller et al. 2004, Guisan and Thuiller 2005). If such a restricted climatic niche is modeled, further projection of the niche under future climate scenarios can produce misleading future potential predicted distribution, and as a result, predict false local extinctions or extirpations and hence biased predictions of future species richness at range margins. In order to estimate the extent of such a bias, we focused on the Europe-Africa geographical/political interface and the case of bird species richness. Indeed, numerous bird species have mainly European distributions with further populations breeding in North Africa. Predictions of range shifts or extinction risks in Europe

often consider populations restricted within political or geographical limits, as a result of good-quality atlas or census data within Europe only (Huntley et al. 2008). This is probably not a major flaw if modeling current distributions within Europe, but when projecting these distributions under future climates, it could predict false local extinctions in southern Europe as a result of species distributions shifting northwards, and therefore underestimate future species richness at southern European margins.

Predicted future species richness could also be underestimated at range margins if account is not made for species not currently present in the study area but which could colonize in the future. In the European case, local decreases in species richness in the Iberian Peninsula (Huntley et al. 2006) could be compensated by colonization by North African species (Huntley et al. 2007).

In order to address these issues, we modeled the distribution of some bird species breeding either in the Iberian Peninsula and Morocco (n = 152) or in Morocco only (n = 27). These 179 species were considered throughout their complete Western Palaearctic (WP) distribution range. In order to decrease the impact of models' variability, we used 8 different niche modeling algorithms, five climate models (GCMs) and three climate scenarios to predict the current and future breeding distributions. Robust forecasts were achieved by a consensus approach through ensemble forecasts (Araújo and New 2007, Marmion et al. 2009). To assess the bias in predicted species richness due to the geographical extent to which presence data are considered, we first focused on the 152 species breeding in Iberia and Morocco and compared local extinction rates obtained when considering European-restricted data or the extensive WP distribution. We further studied 27 species currently breeding in Morocco but not in Europe, and potentially able to colonize Europe (i.e. with populations occurring north of the Atlas chain) and predict their potential contribution to future Iberian species richness under future climate scenarios. We then compare predicted species richness across Iberia for the global set of 179 species considering again European-restricted data or the extensive WP distribution.

Materials and methods

Species data

The European-restricted breeding distributions came from the EBCC atlas of European breeding birds (hereafter called European atlas; Hagemeijer and Blair 1997). The presence data, originally at a ca 50 × 50 km resolution, was translated to a $1^{\circ} \times 1^{\circ}$ resolution, because we used the latest IPCC scenarios (2007), only available at a 2.5° resolution. Because the aim of the study is to compare models results at the level of species richness with two different sets of data, and not to focus on models results for specific species, the $1^{\circ} \times 1^{\circ}$ resolution is precise enough for that purpose. The extensive ranges were considered across the whole Western Palaearctic (WP) biogeographical area, by further completing the European atlas data by geo-referencing and digitizing maps from the handbooks of the birds of the each species, we were able to get the coordinates of the points not represented in the European atlas data. A pixel was considered to be a presence point if at least part of its surface overlaid the distribution. This allowed us to account for the distribution of populations breeding in northern Africa (north of the Sahara), the Middle East (from Turkey to Kuwait including Irak), to the Ural mountains (from western Kazakhstan to western Siberia), so that the complete WP range was considered for each species. Because we focused on the southern edge of Europe we considered species known to breed in Spain and/or Portugal and in North Africa, excluding wetland birds, for a total of 152 species (see Supplementary material Appendix S1 and S2 for the names of the considered species). For each one of these species, distribution modeling was carried out with either the Europeanrestricted distributional data – from the European atlas only - or with the full WP range. We also examined 27 bird species breeding in Morocco (and often elsewhere in North Africa, occasionally also in the Middle East; Supplementary material Appendix S2), but not in Iberia, to evaluate their eventual contribution to future Iberian species richness if such species would be predicted to breed in the south of Europe under future climate scenarios. For these species, presence data was only obtained by geo-referencing and digitizing maps from BWPi (2006). We therefore worked on a global set of 179 species.

Western Palearctic (BWPi 2006). After geo-referencing the

handbook map and overlaying the European atlas data for

Climate data

Future climatic projections were derived from five general circulation models (BCM2, ECHAM5, HADCM3, MIROHIC3 2-HI, and MK3), which are mathematical models representing physical processes in the atmosphere, ocean, cryosphere and land surface, and are the most advanced tools currently available for simulating the response of the global climate system to increasing greenhouse gas concentrations. For each of these climate models, we used climate parameters derived from two or three recent IPCC SRES scenarios (A1B and B1 for all circulation models, and A2 for ECHAM5 and HADCM3) reflecting the potential impacts of different assumptions with respect to demographic, socio-economic and technological development on the release of greenhouse gases. For each climate model × climate scenario, we used the latest predictions from the IPCC fourth assessment report (AR4, IPCC 2007), consisting of the monthly mean temperatures and precipitations over the intervals 1961-1990 and 2080-2099. We interpolated (bilinear interpolation) these values for a $1^{\circ} \times 1^{\circ}$ latitude \times longitude grid over the WP (for a total of 3211 pixels). We built up the following eight variables to be used in niche modeling: 1) annual mean temperature, 2) mean temperature of the warmest month, 3) mean temperature of the coldest month, 4) temperature seasonality, 5) annual precipitation, 6) precipitation of the wettest month, 7) precipitation of the driest month and 8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. Temperature and precipitation are expected to impose direct or indirect

constraints on bird distributions (Root 1988, Araújo et al. 2009).

Representation of the data in climatic space

A first visual way to see if the use of the WP data instead of the European-restricted data leads to an extension of the species climatic niche is to geographically plot the data in climatic space. In order to obtain a 2D visualization for each species, a principal component analysis (PCA) was run to represent the positions of occurrence in climatic space for both datasets of occurrence (the full WP data, including the European atlas data, or the restricted range with only the European atlas data). As a way of summarizing the distribution of the points, a 1.5 inertia ellipse was drawn (Broennimann et al. 2007). We present results for two species. The plot of the presence data could also be realized within the global climate space of all available pixels in the study area (Supplementary material Fig. S3).

Climate-suitability modeling

We realized the projections for eight different niche-based modeling techniques, performed with the BIOMOD computational framework (Thuiller et al. 2009 for further details on modeling techniques): 1) generalized linear model (GLM), a regression method with polynomial terms for which a stepwise procedure is used to select the most significant variables, 2) generalized additive model (GAM), another regression method with four degrees of freedom and a stepwise procedure to select the most parsimonious model, 3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance, 4) artificial neural networks (ANN), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results, 5) mixture discriminant analysis (MDA), a classification method based on mixture models, 6) multivariate adaptive regression splines (MARS), a regression method, 7) generalized boosting model (GBM), a machine learning method which combines a boosting algorithm and a regression tree algorithm to construct an "ensemble" of trees, and 8) Random Forest (RF), a machine learning method which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest.

In order to evaluate the predictive performance of a species distribution model, for each species, we used a random subset of 70% of the data to calibrate the model, then used the remaining 30% for evaluation, using a threshold independent method, the area under the relative operating characteristic curve (AUC) (Fielding and Bell 1997). The data splitting approach was then replicated five times from which we calculated the mean AUC of the cross-validation. The final calibration of every model for making predictions uses 100% of available data. All models used in this study need information about presences and absences to be able to determine suitable conditions for a given species. However, our dataset contains only presence

data, so a random set of pseudo-absences was selected, so that the total number of presences and pseudo-absences is constant and equals 2000 (60% of the 3211 available pixels). The pseudo-absences were selected randomly from all the points of the study area not taken as presences. We did not fix the number of pseudo-absences because the presence points (European atlas data and completed atlas maps) should be a good display of the species ranges. Indeed, a species with a small distribution, so a small number of presence locations is more likely to be absent from a large area in the WP. We preferred to select a random sample of the non-presence pixels and to consider them as pseudo-absences, instead of using all non-presence points as absences, because sampling effort varies across the atlas range and species distributions are not well known in some remote areas of the WP (e.g. in Polar Ural, western Kazakhstan). We could also have used another method to select the pseudo-absences, accounting for a potential bias of the presence data (Phillips et al. 2009). Selecting pseudoabsences with the same bias as occurrence data could have been used with the restricted data, but without any presence points from North Africa and Middle East, no pseudoabsences from that area could have been drawn, making it impossible to project any distribution over the whole study area.

Ensemble forecast

The ensemble forecast technique aims to take into account the variability among species distribution models, climate models and climate scenarios, in order to get the central tendency (Araújo and New 2007, Thuiller 2007). For each species, we obtained 40 (8 models \times 5 GCM) modeled current distributions and 96 (8 models \times 12 (GCM \times SRES)) modeled future distributions. The current and future consensus distributions were obtained by selecting the outputs of the four modeling techniques with the best AUC scores, and by further calculating the unweighted mean distributions (Coetzee et al. 2009, Marmion et al. 2009) for the corresponding 20 (4 models \times 5 GCM) present or 48 (4 models ×12 GCM × SRES) future distributions. AUC has been recently criticized (Lobo et al. 2008) because of its dependence on parameters such as the prevalence, the number of pseudo-absences and the spatial extent to which models are carried out, but in this study, it is only used to make a ranking across models for each species, so the prevalence and the number of pseudoabsences are constant, as is the geographical extent. In order to transform the results of species distribution modeling from climatic suitability to presence/absence distribution, we used the "sensitivity-specificity equality approach" threshold (Liu et al. 2005). In order to assess the accuracy of the distribution obtained for each species, we calculated sensitivities and specificities with regard to the restricted or extensive data for the model obtained with restricted data and sensitivities and specificities with regard to the extensive data for the model obtained with extensive data. Local species richness was defined as the sum of species predicted as present within a given grid cell (possible range 0-179). Richness of bird guilds (granivorous, insectivorous, carnivorous and omnivorous) was also

calculated in order to see if the results for the total richness would be different from the richness of bird guilds.

Results

Model accuracy

The accuracy was very good for all the species, with the data used (Supplementary material Appendix S1 and S2): with restricted data the sensitivity ranged from 0.971 to 1 (mean = 0.995 ± 0.05) and the specificity ranged from 0.847 to 1 (mean = 0.929 ± 0.037); with extensive data the sensitivity ranged from 0.983 to 1 (mean = 0.996 ± 0.004) and the specificity ranged from 0.728 to 0.999 (mean = 0.906 ± 0.051). For the distributions obtained from restricted data, the sensitivity calculated from the extensive data ranged from 0.015 to 0.993 (mean = 0.681 ± 0.175) and the specificity calculated from the extensive data ranged from 0.854 to 1 (mean = 0.955 ± 0.028), meaning that for most species, the models computed from restricted data failed to efficiently predict the extensive distribution.

Climatic space variations

Presence data added in this study to the EBCC dataset are not redundant in terms of the information they provide in defining the climatic niche of the species. Indeed, results from PCAs (Fig. 1, Supplementary material Fig. S3 and S4) show that most of them are outside the climatic niche observed using the European-restricted data and therefore when included lead to an extension of the climatic niche. For every species, the majority of the points that were added to get the extensive WP range of the species were on one side of the European atlas inertia ellipse. Therefore, the difference between the two inertia ellipses is more striking when the number of presence points added for the extensive WP range is high compared to the initial number of presence points. This supports the use of extended datasets because the use of European-restricted data would lead to a truncated realized niche and thus truncated response curves. The further color differentiation between presences added from North Africa (blue points) and presence added from Middle East and eastern WP (green points) shows that each of these two parts offers additional information on the climatic niche.

Current species richness

As a summary of the distributions of the 152 species, Fig. 2 shows the data used in both approaches (European-restricted or WP data), as well as maps of the modeled current species richness, as obtained from the ensemble forecast. A first comparison reveals a high congruence between data locations and climate suitability models, though with a slight tendency for over-prediction, which may be due to the fact that we predict here the potential climatic niche of a species and that other factors such as habitat or competition may explain a species being absent from a part of this niche. The modeled current species richness over Europe is similar when



Figure 1. Occurrence data in the climatic space (the two significant axes of the PCA) for (a) Sylvia hortensis and (b) Galerida cristata. The part of the variance explained by each axis is specified. Red points stand for the European-restricted data, whereas blue and green points represent the data points added to get the full WP range (blue points standing for North African pixels and green points standing for pixels from Middle East to Siberia). The 1.5 inertia ellipses for European-restricted data (EBCC, red) and extensive data (WP, blue) illustrate the climatic niche extension (the red ellipse stands for only the red points (European atlas data) and the blue ellipse stands for all the points (full WP data). The projection of the climatic variables in the climatic space defined by the two significant axes of the PCA is added to each graph. Climatic variables are: Tavg = annual mean temperature, Twm = mean temperature of the warmest month, Tcm = mean temperature of the coldest month, Tsd = temperature seasonality, Pavg = annual precipitation, Pwm=precipitation of the wettest month, Pdm = precipitation of the driest month and Psd = precipitation seasonality.

Axis 2

33.8%

Tcm

Galerida cristata



Figure 2. Current species richness per grid cell for the 152 bird species under study obtained with geographically European-restricted data (top) or the full WP range (bottom). Left are presented the original data as obtained from the breeding bird atlas (top) or the extensive WP ranges (down), right are reported the maps of modeled current species richness as obtained by ensemble forecast.

modeled with restricted data, or full WP data, but restricted data failed to predict North African, Middle Eastern and Russian parts of the species distributions (see Fig. 3 for an example). The species ranges predicted with the full WP data were significantly higher than when predicted with restricted data, for the current ranges (t = 22.1, DF = 152, p < 0.001, paired t-test by species) and the future ones (t = 22.8, DF = 152, p < 0.001, paired t-test by species).



Figure 3. Current (top) and future (bottom) distributions predicted from restricted (left) or extensive (right) data for *Cercotrichas galactotes*.

Local extinction rates - focus on Iberia

Figure 4, centered on Iberia, presents the proportion of species predicted to become locally extinct from each pixel by 2100. In the first case (European-restricted input data), huge species losses are predicted to occur in the southern half of the Iberian Peninsula: extinction rates over 90% are predicted in 14 $1^{\circ} \times 1^{\circ}$ pixels where 119 to 142 species are currently breeding. Nevertheless, when using extensive WP data, we predicted only a restricted area of high extinction rates, though reaching at the most 50%. Over Iberia, the mean extinction rate is predicted to be 38% (\pm 41%) with the European restricted input data, compared to only 12% (\pm 17%) with the full WP data (t = -7.28, DF = 64, p < 0.001, paired t-test by grid point over Iberia). The spatial trends in local extinction rates for the various bird guilds (granivorous, insectivorous, carnivorous, omnivorous) were almost similar to those obtained for the total richness (Supplementary material Fig. S5).

Potential African colonizers

The modeling of current and future suitable climatic spaces for the 27 species breeding in northern Africa (Fig. 5) shows that the bioclimatic niche of some of these species could appear in southern Iberia, especially along its Mediterranean coast, so that 18 species could breed in southern Europe if first able to colonize there (Supplementary material Fig. S6 for examples). We can also note that nine of them are predicted to be currently able to breed in southernmost Spain.



Figure 4. Local species extinction rates as predicted by 2100 using the ensemble forecast, representing the proportion of species predicted as currently present but predicted to become extinct within a grid cell, when using geographically European-restricted data (top) or extensive WP data (bottom).



Figure 5. Current (top) and future (bottom, by 2100) predicted bird species richness, within the potential pool of the 27 species which breeding distribution is currently restricted to North Africa.

Trends in Iberian species richness

The graphs presented in Fig. 6 compare species richness in each pixel across the Iberian Peninsula as obtained with European restricted data or with extensive WP data, for the current predictions (top) or the future projections (bottom) (Supplementary material Fig. S7 for maps of the variation in the predicted species richness for all 179 species). Regarding the current distributions, the species richness modeled with restricted data is lower than when obtained with extensive data. When species whose ranges are currently restricted to North Africa are taken into account, the species richness in Iberia is higher for a few grid cells, where climate is suitable for some of these species. The mean species richness per grid cell over Iberia estimated from restricted data is 139 species (range 119-144), compared to 143 (133-150) and 143 (133-156) from extensive data, respectively without or with the 27 species breeding only in North Africa. Indeed, accounting for extensive presence data created visible but no large differences in current predicted local species richness across the Iberian Peninsula. This pattern changes dramatically when considering local species richness predicted for 2100 under climatic scenarios. Predicted future species richness per grid cell was largely lower when using geographically restricted data compared to extensive WP data. When geographically restricted data predicted the persistence of <20 species per cell, using the extensive WP ranges led to an heterogeneous richness across points (from 30 to 150 species), with still most grid cells predicted to hold more than 100 species. The average species richness per grid cell across Iberia, as projected for 2100, is 87 species (range 0-148) from restricted data, compared to 128 (37-148) and



Figure 6. Predicted species richness per grid cell across the Iberian Peninsula, as obtained from restricted data plotted against as obtained from complete Western Palaearctic data – for outputs concerning the 152 species breeding in Iberia (o) only or with the 27 species currently breeding in northern Africa (\times) for a total of 179 species. Results are presented for the current predictions (a) or the future projections (b). Each dot or cross represents one Iberian grid cell.

131 (37–152) from extensive data, respectively within the pool of 152 or 179 species. The average difference in future projected species richness per grid cell in Iberia, when comparing predictions obtained with WP distribution of all 179 species and those obtained with the European-restricted atlas distribution of 152 species, is 45 (range -2 to 138).

Discussion

The range edges of the modeled suitable climatic spaces are significantly different when geographically restricted or extensive presence data are used. The minimum latitude of the species distributions is on average 5.6° (ca 500 km) more southerly when the full WP distributional data are used. This illustrates the already recognized underestimation of the extent of the climatic niche of a species when using geographically restricted data. This can be critical when suitable climatic space are projected under future climate scenarios because the truncated niche can be responsible for an overprediction of local extinctions at southern distribution edges (Bakkenes et al. 2002, Huntley et al. 2006). The same can occur even if the complete distribution range is considered for modeling, but when range limits are not determined by climatic factors but by orographic barriers (even separating vicariant species), like the Strait of Gibraltar for short-distance dispersive (e.g. non-flying or habitat-restricted) or nondispersive animals (Araújo et al. 2006). The use of restricted data therefore limits the possibilities of using models to project or to infer future potential distribution and extinction risk, as noticed by Thuiller et al. (2004). Indeed, if the limits of the modeled niche are not climatic, the species might well be able to survive under climatic conditions not yet captured by the model. One could argue that the use of geographically-restricted presence data, i.e. here north of the Strait of Gibraltar, is an acceptable solution when predicting future ranges under climatic scenarios, as most species could be unable to disperse there from Africa to Europe because of a strong geographic barrier, even if global models would predict a northward shift of suitable climatic ranges, although birds are good dispersers. However, accounting for all populations within the species range or within an extended biogeographic area allows one to consider the full extent of the species potential climatic adaptations, and so doing, the potential climatic adaptability of European populations. Even if arctic populations from a widely distributed species could not adapt to Mediterranean climatic conditions, it is not unlikely that Iberian populations from a species present in North Africa today can adapt to a warmer climate in the future (similar to some current North African climates). Besides, large populations with extensive breeding distributions may sustain greater genetic variability (Møller et al. 2008), thus providing a higher adaptation ability. Such a pitfall in climate suitability modeling can be easily overcome by considering all available data for species whose ranges edges are imposed by climate. More generally, studies aimed at modeling species distributions with climatic suitability models should consider global ranges, or at least ranges across large biogeographic units (such as the Palaearctic), otherwise they can lead to unfounded conclusions (Beale et al. 2008, and response in Araújo et al. 2009) and associated results from future projections are to be considered cautiously. A previous map of local predicted extinction rates for European bird species under climatic scenarios has been provided by Huntley et al. (2007), reporting rates that differed from those we present here, though this is logical as the modeling techniques applied here are different, we only use a subset of the 431 species considered in the latter study and the future species distributions were predicted with IPCC scenarios released in 2007, which predict a much stronger effect of the global warming than the ones released in 2001 and used by Huntley et al. (2007).

For some African bird species, with current breeding range not reaching Europe, the geographical realization of their bioclimatic niche is predicted to shift northward and to include some parts of the Iberian Peninsula. Indeed, accounting for species not currently present in Europe but

breeding within the associated global biogeographic area (here the Western Palaearctic) is necessary if focusing on trends in species richness (Huntley et al. 2007). This step obviously assumes that initially out of range species are able to colonize the focused area. In the case of birds here, the colonization of Iberia is possible e.g. through the Strait of Gibraltar, as birds are prone to disperse, with natal dispersal up to a few kilometers even in the small passerines (Jiguet et al. 2007). Indeed, 14 of the 27 African species studied here have already been observed in Europe (either on migration or during post-breeding dispersal), so are able to disperse to southern Spain and eventually breed there. Indeed, the little swift Apus affinis is known to have bred on regular occasion in southern Spain in recent years (Purroy 1997), while four pairs of cream-coloured courser Cursorius cursor bred successfully in southern Spain in spring 2001 (Gutiérrez 2001). The house bunting Emberiza sahari has expanded from the Atlas northwards in Morocco since the 1960s, and has recently reached Tangier so now faces European coasts (Amezian et al. 2006). A last species cited here as an example is the trumpeter finch Bucanetes githagineus, originating from North Africa and now established along the Mediterranean coast of Spain (first breeding recorded in 1971, García 1972, Carrillo et al. 2007). It is therefore not senseless to assume that North African bird species whose climatic niche is predicted to occur in Spain under future climate scenarios will be able to colonize that area as did the trumpeter finch and to contribute to the local future species richness. A decrease in bird species richness due to climate change is therefore more likely to occur just north of the Sahara, because current climatic conditions south of the Sahara are not predicted to occur in the future north of the Sahara (Barbet-Massin et al. 2009). Nevertheless, the study of the potential impacts of climate change over the distribution of initially outof-range species will only make sense for species with physiological and morphological abilities to disperse across eventual geographic barriers within time periods similar to those of the climatic scenarios. This is probably not the case for reptiles and amphibians (Araújo et al. 2006).

The recognition that African species could contribute to future European species richness is therefore important to consider, resulting in more realistic projections and allow one to identify more precisely areas which are projected to experience decreases in local species richness. In the case of Iberia, the south-west coast along the Atlantic Ocean is projected to face the highest bird local extinctions, while the south-east Mediterranean coast is projected to benefit from potential African colonizers. Besides, even if little change is predicted regarding the number of species, if colonizations compensate for local extinctions, changes in community composition could have important ecological consequences if associated with changes in functional traits of species. The question of spatial resolution that should be used in niche modeling studies has been raised (Pearson and Dawson 2003, Guisan and Thuiller 2005), with the use of different scales leading to different environmental variables being the most important factors affecting the distributions. Beyond this topic, the geographic extent of the study area should

also be considered carefully, so that climatic suitability models capture correctly the full climatic potential of species, or inferences on future range location, size and extinction risk might be seriously flawed.

Acknowledgements – We thank the EBCC for the access to the atlas data. WT received support from the FP6 EU funded Ecochange (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe, No. 066866 GOCE) project. We also thank Stuart Newson (BTO) for his careful reading and improvements of the manuscript.

References

- Amezian, M. et al. 2006. Is house bunting about to colonize Europe? – Birding World 19: 263.
- Araújo, M. B. and New, M. 2007. Ensemble forecasting of species distributions. – Trends Ecol. Evol. 22: 42–47.
- Araújo, M. B. et al. 2006. Climate warming and the decline of amphibians and reptiles in Europe. – J. Biogeogr. 33: 1712– 1728.
- Araújo, M. B. et al. 2009. Reopening the climate envelope reveals macroscale associations with climate in European birds. – Proc. Nat. Acad. Sci. USA 106: E45–E46.
- Bakkenes, M. et al. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biol. 8: 390–407.
- Barbet-Massin, M. et al. 2009. Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. – Biol. Lett. 5: 248–251.
- Beale, C. M. et al. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. – Proc. Nat. Acad. Sci. USA 105: 14908–14912.
- Broennimann, O. et al. 2007. Evidence of climatic shift during biological invasion. Ecol. Lett. 10: 701–709.
- BWPi 2006. Birds of the Western Palearctic interactive. BirdGuides, UK.
- Carrillo, C. M. et al. 2007. Northward expansion of a desert bird: effects of climate change? Ibis 149: 166–169.
- Coetzee, B. W. T. et al. 2009. Ensemble models predict important bird areas in southern Africa to become less effective for conserving endemic birds under climate change. – Global Ecol. Biogeogr. 18: 701–710.
- Davis, M. B. and Shaw, R. G. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292: 673–679.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. – Environ. Conserv. 24: 38–49.
- García, L. 1972. Primera nidificación verificada de *Rhodopechys* githaginea en el sureste de Europa. Ardeola 16: 215–222.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8: 993–1009.
- Gutiérrez, R. 2001. The first breeding record of cream-coloured courser in Europe. Birding World 14: 323–324.
- Hagemeijer, E. J. M. and Blair, M. J. 1997. The EBCC Atlas of European breeding birds: their distribution and abundance. – T. and A. D. Poyser.
- Huntley, B. et al. 2006. Potential impacts of climatic change upon geographical distributions of birds. Ibis 148: 8–28.

- Huntley, B. et al. 2007. A climatic atlas of European breeding birds. Lynx Edicions.
- Huntley, B. et al. 2008. Potential impacts of climatic change on European breeding birds. – PLoS One 3: e1439, doi:10.1371/ journal.pone.0001439.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415–457.
- Intergovernmental Panel on Climate Change (IPCC) 2007. Climate change 2007: impacts, adaptation, and vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the IPCC. – Cambridge Univ. Press.
- Jiguet, F. et al. 2007. Climate envelope, life history traits and the resilience of birds facing global change. – Global Change Biol. 13: 1672–1684.
- Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. – Ecography 28: 385–393.
- Lobo, J. M. et al. 2008. AUC: misleading measure of the performance of predictive distribution models. – Global Ecol. Biogeogr. 17: 145–151.
- Marmion, M. et al. 2009. Evaluation of consensus methods in predictive species distribution modelling. – Divers. Distrib. 15: 59–69.
- Møller, A. P. et al. 2008. Genetic similarity, breeding distribution range and sexual selection. J. Evol. Biol. 21: 213–225.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.
- Patz, J. A. et al. 2005. Impact of regional climate change on human health. Nature 438: 310–317.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate

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envelope models useful? – Global Ecol. Biogeogr. 12: 361–371.

- Peterson, A. T. et al. 1999. Conservatism of ecological niches in evolutionary time. Science 285: 1265–1267.
- Phillips, S. J. et al. 2009. Sample selection bias and presence–only distribution models: implications for background and pseudoabsence data. – Ecol. Appl. 19: 181–197.

Purroy, F. J. 1997. Atlas de las Aves de España. - Lynx Edicions.

- Root, T. 1988. Environmental-factors associated with avian distributional boundaries. J. Biogeogr. 15: 489–505.
- Root, T. L. et al. 2003. Fingerprints of global warming on wild animals and plants. – Nature 421: 57–60.
- Schröter, D. et al. 2005. Ecosystem service supply and vulnerability to global change in Europe. – Science 310: 1333–1337.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. - Nature 427: 145–148.
- Thuiller, W. 2007. Biodiversity, climate change and the ecologist. – Nature 448: 550–552.
- Thuiller, W. et al. 2004. Effects of restricting environmental range of data to project current and future species distributions. – Ecography 27: 437–448.
- Thuiller, W. et al. 2009. BIOMOD a platform for ensemble forecasting of species distributions. Ecography 32: 369–373.
- Van Horn, B. 2002. Approaches to habitat modelling: the tensions between pattern and process and between specificity and generality. – In: Scott, J. M. et al. (eds), Predicting species occurrences: issues of accuracy and scale. Island Press, pp. 63–72.
- Walther, G. R. et al. 2002. Ecological responses to recent climate change. – Nature 416: 389–395.