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The fate of European breeding birds under climate, land-use and dispersal scenarios

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Abstract

Many species have already shifted their distributions in response to recent climate change. Here, we aimed at predicting the future breeding distributions of European birds under climate, land-use, and dispersal scenarios. We predicted current and future distributions of 409 species within an ensemble forecast framework using seven species distribution models (SDMs), five climate scenarios and three emission and land-use scenarios. We then compared results from SDMs using climate-only variables, habitat-only variables or both climate and habitat variables. In order to account for a species' dispersal abilities, we used natal dispersal estimates and developed a probabilistic method that produced a dispersal scenario intermediate between the null and full dispersal scenarios generally considered in such studies. We then compared results from all scenarios in terms of future predicted range changes, range shifts, and variations in species richness. Modeling accuracy was better with climate-only variables than with habitat-only variables, and better with both climate and habitat variables. Habitat models predicted smaller range shifts and smaller variations in range size and species richness than climate models. Using both climate and habitat variables, it was predicted that the range of 71% of the species would decrease by 2050, with a 335 km median shift. Predicted variations in species richness showed large decreases in the southern regions of Europe, as well as increases, mainly in Scandinavia and northern Russia. The partial dispersal scenario was significantly different from the full dispersal scenario for 25% of the species, resulting in the local reduction of the future predicted species richness of up to 10%. We concluded that the breeding range of most European birds will decrease in spite of dispersal abilities close to a full dispersal hypothesis, and that given the contrasted predictions obtained when modeling climate change only and land-use change only, both scenarios must be taken into consideration.

Keywords: climate change, European birds, land-use scenario, natal dispersal, shifts, species distribution models, species richness

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Introduction

Global climate and land-use changes are of major scientific and political concern, especially when considering their potential impacts on future biodiversity, ecosystem processes and human well-being (Thomas *et al.*, 2004; Patz *et al.*, 2005; Schroter *et al.*, 2005; Thuiller *et al.*, 2011). Forecasted changes in climatic conditions imply that the distribution of a species will shift if it is able to spatially track shifting climatic conditions. Although many species have already shifted their distributions polewards and/or upward (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006), most of the species studied seem to have expanded polewards/upward more slowly than if climate was their only constraint (Menendez *et al.*, 2006; Devictor *et al.*, 2008). Species distribution models (SDMs) have been widely used to study central research topics in ecology and evolution (Guisan & Thuiller, 2005). One of their applications has been to predict potential species' range shifts under various climate change scenarios (Thuiller, 2004; Huntley *et al.*, 2006) and to estimate species turnover and local extinction (Thuiller *et al.*, 2005; Jetz *et al.*, 2007). Most recent efforts have focused on different sources of uncertainties such as the choice of the modeling method, the general circulation model, and the gas emission scenario, in order to quantify their relative influence (Buisson *et al.*, 2009; Diniz-Filho *et al.*, 2009). However, one major uncertainty in predicting species' range shifts lies in one biological trait, namely the ability of a species to disperse in order to track the shifting climate. Dispersal has generally been studied using a dynamic metapopulation model for predicting potential climate change impact on two lagomorph species (Anderson *et al.*,

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2009) and a dispersal limitation model for plant species (Midgley *et al*., 2006). However, in most cases, only two extreme (unlimited or not) dispersal scenarios are generally assumed (e.g., Thomas *et al*., 2004). Given the range of species' dispersal strategies worldwide, these two extreme cases remain one of the critical drawbacks of most existing SDMs (Higgins *et al*., 2003; Pearson, 2006; Thuiller *et al*., 2008).

Climate is often assumed to be one of the main drivers of bird distributions at large spatial scales (Pigot *et al*., 2010; Jimenez-Valverde *et al*., 2011), and SDMs that use climate-only variables have a better predictive accuracy than SDMs that use habitat-only variables at a large spatial scale (Thuiller *et al*., 2004; Luoto *et al*., 2007). However, including habitat variables can significantly improve the explanatory power of bioclimatic models if they are poorly or not explained by climate (Thuiller *et al*., 2004). Both climate and habitat variables are therefore shaping current bird distributions, while the dominance of one factor type over the other depends on the spatial resolution considered. Most studies that use SDMs to predict future distributions generally consider only climate variables (but see Bomhard *et al*., 2005), while habitat changes are expected to have the largest effects for terrestrial ecosystems (Sala *et al*., 2000), especially for birds (Lee & Jetz, 2011). Even though the addition of habitat variables to purely climate-based SDMs does not greatly improve their predictive accuracy, it could significantly change their projection under future scenarios. In addition to considering climate and land-use variables and their change scenarios to improve the modeling of both current and future distributions, comparing predicted future distributions obtained with either climate variables only or habitat variables only would make it possible to investigate the consistency of predicted changes between both scenarios.

Here, we aim at addressing these two main issues (species dispersal and land-use change) by predicting the future distributions of 409 European bird species for 2050, using range data from the entire western Palaearctic zone to account for the full realized niche of each species within a large biogeographical area (Barbet-Massin *et al*., 2010). We used climate scenarios and land-cover scenarios to predict and compare their potential impacts on bird breeding distributions. Current and future distributions were modeled with both climate and habitat variables to improve the accuracy of the modeling and to predict a more realistic response to global changes. Birds, as flying vertebrates, are generally considered to be good dispersers. Hence, a null dispersal assumption is clearly inappropriate for these species, while a full dispersal assumption can lead to the prediction of future suitable areas very far from their current range and possibly out of reach according to the true dispersal ability of the species. Our goal was therefore to obtain and to use more realistic estimates of the ability of bird species to disperse, and to develop a new approach that takes the dispersal ability of species into consideration in future predictions. To account for the ability of species to disperse, we used estimates of mean natal dispersal (and the associated standard deviation, Paradis *et al*., 1998) and mean generation times. Since we also predicted future breeding distributions under the full dispersal assumption, we further compare both scenarios and therefore estimate the effect of accounting for bird dispersal when predicting potential effects of global changes. Finally, predicted trends in species richness are illustrated to identify the potential footprint of ongoing climate and land-use changes on terrestrial birds that breed in Europe.

Methods

Species and environmental data

The presence-absence data were obtained by geo-referencing and digitizing breeding distribution maps of 409 species from the handbooks of the birds of the Western Palaearctic (BWPi 2006) at a 0.5° resolution. We did not consider seabirds in our analysis as climate and habitat variables may not be the most relevant drivers of the restricted terrestrial distribution of their breeding sites. Besides, our spatial analysis focused on predicted changes in Europe, so we considered only species which current breeding range is at least partly included in Europe. Nevertheless, for all these species, we considered their whole Western Palaearctic range (including North Africa and the Middle East) in order to model the full extent of their niche (Barbet-Massin *et al*., 2010). We used the following eight climatic variables from the Climate Research Unit (CRU) (Mitchell & Jones, 2005): (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. These variables consisted of mean values over the 1961–1990 period at a 0.5° resolution. Temperature and precipitation are expected to impose direct or indirect constraints on bird distributions (Root, 1988; Araújo *et al*., 2009).

Habitat variables consisted of the proportion of the grid cell covered by (1) broadleaved deciduous trees, (2) needle-leaved trees, (3) mixed leaf-type trees, (4) shrubs, (5) herbaceous or cultivated pasture, (6) cultivated and managed areas, (7) mosaic cropland/natural vegetation, (8) bare areas, and (9) artificial surfaces and associated areas. These variables were derived from the 19 land cover types (by grouping some of them together) available in the IMAGE 2.4 model (MNP, 2006) that was developed at a 0.5° resolution for all decades since

1960. To be consistent with climatic variables, we used the average of variables from 1960 to 1990.

We calculated the climate variable predictions (for 2050) for five general circulation models (GCM; BCM2, ECHAM5, HADCM3, MIROHIC3_2-HI, and MK3) and three different emission scenarios (SRES: A1B, B1, and A2, when available). Monthly mean predictions were only available at coarse scales (IPCC 2007), so we downscaled the anomalies (differences between predicted future values and actual values) to the 0.5° resolution using a bilinear interpolation. We then added the downscaled anomalies to current monthly mean data and calculated the future predictions of all climate variables used in this study. Future land cover projections (for 2050) were obtained from the three SRES scenarios, A1B, A2, and B1, of the IMAGE 2.4 model (MNP, 2006). The IMAGE 2.4 model is an Earth system model that includes the major feedback mechanisms in the biophysical system. It assumes population and the macro-economy as key drivers to establish physical indicator for both the energy/industry system and the agriculture/land-use system for assessment of changes in land cover (MNP, 2006).

Niche modeling

To model species distributions, we used seven different modeling techniques implemented within the BIOMOD package (Thuiller *et al.*, 2009) in R (R Development Core Team 2010): three regression methods (GLM, GAM, and MARS), a recursive partitioning method (CTA), and three machine-learning methods (ANN, GBM, and RF). In order to evaluate the predictive performance of the SDMs for each species, we used a random subset of 70% of the data to calibrate the model, and then used the remaining 30% for evaluation, using a threshold-independent method, the area under the relative operating characteristic curve (AUC) (Fielding & Bell, 1997). The data splitting approach was replicated five times and was the basis for calculating the mean AUC of the cross-validation. The final calibration of each model used for making projections used 100% of the available data.

For each species, we computed three different sets of SDMs with different sets of variables: climate variables, habitat variables or climate and habitat variables. For the SDMs obtained with both climate and habitat variables, we did not use all 17 variables (eight climate variables and nine habitat variables) described above so that differences between model accuracy could not be interpreted as the result of modeling with different numbers of variables (eight variables used to obtain climatic SDMs and nine to obtain habitat SDMs). For each species, a first distribution was obtained using all 17 variables and the relative contribution of each variable was estimated. The importance of the variable for each modeling technique and each species was calculated as one minus the correlation between the standard prediction and the prediction where the considered variable was randomized. For each species, we then calculated the mean importance of each variable (across modeling techniques) and used the nine variables that contributed the most to the species distributions to obtain the climate and habitat SDMs. The variables used for the climate and habitat SDMs therefore depended on the species.

Ensemble forecast

For each set of variables, we used an ensemble forecast technique to account for variability among distribution modeling techniques, climate models, and climate/land-use scenarios, in order to obtain the central tendency (Thuiller *et al.*, 2005; Araújo & New, 2007). For each species, we obtained seven modeled current distributions for all three sets of variables (climate, habitat, and both climate and habitat), 91 (7 SDMs × 13 (GCM × SRES)) future distributions modeled from climate variables, 21 (7 SDMs × 3 SRES) future distributions modeled from habitat variables, and 91 (7 SDMs × 13 (GCM × SRES)) future distributions modeled from both climate and habitat variables. Current and future consensus distributions were obtained by calculating the weighted mean distributions across SDMs: the seven models were ranked according to their predictive performance, and a decay of 1.6 gave the relative importance of the weight, producing respective weights of 0.38, 0.24, 0.15, 0.09, 0.06, 0.04, and 0.02 (Coetzee *et al.*, 2009; Marmion *et al.*, 2009). The consensus between different GCM and SRES scenarios was obtained by calculating the mean of the model consensus across GCM and SRES. In order to transform the probabilistic consensus distribution to a presence/absence distribution, we preserved the suitability values for pixels above the sensitivity–specificity sum maximization threshold, and set the suitability for pixels under the threshold to zero (Liu *et al.*, 2005; Jimenez-Valverde & Lobo, 2007). The four evaluation criteria, AUC, sensitivity, specificity, and true skill statistic (TSS; Allouche *et al.*, 2006) were calculated for the three current distributions obtained for each species.

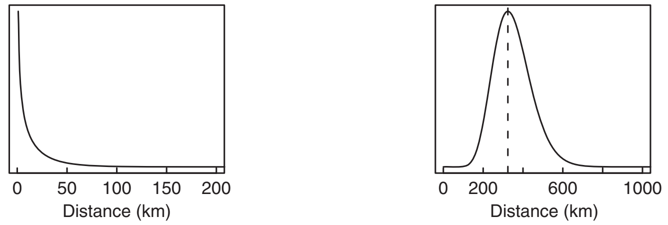
Accounting for dispersal ability in predicted future distributions

To account for the ability of a species to disperse and to therefore reduce the predicted future potential distributions to those areas already occupied or within realistic colonization distances, we used published measurements of natal dispersal for 75 species based on ringing data (Paradis *et al.*, 1998). All species showed the same distribution pattern of natal dispersal with the proportion of recoveries declining with the distance from the ringing site. Species varied in terms of two parameters – the spatial extent of the distribution and the importance of the tail relative to the peak. The means and standard deviations estimated in Paradis *et al.* (1998) provide good estimates of these two parameters. To account for the difference between the mean and the standard deviation of natal dispersal for a species, we used a gamma distribution to model the dispersal distribution instead of a negative exponential distribution for which the mean and standard deviation are equal (see Fig. 1 for an illustration of the methods using the Dartford Warbler *Sylvia undata*). For each species, the parameters of the gamma distribution were calculated from the mean and standard deviation of the natal dispersal of that species, available from Paradis *et al.* (1998), with $k = (\text{mean}/\text{SD})^2$ and $\theta = \text{mean}/k$ (Fig. 1a). The overall natal dispersal of a species for the 50-year time period considered in our study was then calculated as the product of the natal dispersal and the mean number x of generations for a 50-year period. Information on generation time was extracted from BirdLife International (BirdLife International 2004). The overall natal dispersal distribution of a species for the 50-year period is therefore the sum of x gamma distributions. Given the properties of the gamma distribution, this overall distribution corresponds to a gamma distribution with parameters xk and θ, which is an asymmetric unimodal curve (Fig. 1b). Instead of choosing a dispersal threshold beyond which the species is not able to disperse, we chose to combine this approach with a probabilistic method. We considered that all pixels located at less than the maximum value of the overall gamma distribution from the closest current occurrence pixel could be colonized. We assumed that these pixels had the same future suitability as those calculated from the ensemble forecast. Conversely, we assumed that the suitability of all pixels located beyond this maximum could not reflect the future presence probability of the species because of the low probability species to colonize.

Given that we considered all pixels located at less than the distribution maximum to have the same future suitability, we rescaled this distribution so that its maximum would be associated with a colonization probability of one (Fig. 1c). We then reduced the future suitability of pixels located beyond the maximum, depending on their distance from the closest current occurrence pixel: the future suitability of a pixel located beyond the maximum was multiplied by the rescaled probability associated with its distance from the closest current pixel (ranging from 0 to 1) (Fig. 1d–f). Mean and standard deviations of natal dispersal were available for 75 species only, so we further completed the missing information for all other species by assuming that means and standard deviations of phylogenetically closely related species would provide reasonable estimates of actual values. Values of natal dispersal found in the literature or extrapolated from available estimates are given in Appendix S1.

(a) Probability distribution of natal dispersal distance for one generation

(b) Probability distribution of total natal dispersal distance for 50 years



(c) Probability applied to the future suitability of a pixel

(d) Current distribution

(e) Future distribution (total dispersal)

(f) Future distribution (accounting for dispersal)

Fig. 1 Different stages of the method considered to account for dispersal (example of *Sylvia undata*). (a) Gamma distribution used for modeling natal dispersal distribution (mean = 14 km; SD = 19 km). (b) Gamma distribution used for modeling the total dispersal (over 50 years) distribution (mean generation time = 2 years). (c) Probability applied to a future species distribution models suitability according to its distance from the closest current occurrence pixel. (d) Modeled current breeding range. (e) Future predicted range (full dispersal hypothesis). (f) Future predicted range (accounting for dispersal).

Predicted shifts and variations of species distribution

Species range size was calculated for each species' consensus distribution by summing the suitability values of the filtered distribution (the distribution obtained from the ensemble forecast after applying the sensitivity–specificity sum maximization threshold with or without the further dispersal threshold) and weighting each pixel by its area (thus accounting for latitudinal variations). The latitude and longitude of the range centroids were also estimated from the filtered distributions, using suitability as weight. For each species, the distance between present and future range centroids was calculated as a measurement of range shift. We further calculated the ratio between future and current range sizes as a measurement of the potential impact on range size.

Predicting changes in species richness

To map the spatial distribution of species richness for European breeding birds, we summed all suitability values of species considered as present for each grid cell for current distributions and future distributions. The predicted variation in species richness was deduced from both species richness distributions (current and future).

Results

Model accuracy

The predictive accuracies of models were very good for all three sets of environmental variables (Table 1). Modeling accuracy was better with climate-only variables than with habitat-only variables (paired *t*-test for the TSS: $t = 18.3$, df = 408, $P < 0.001$), and better with both climate and habitat variables (paired *t*-test with TSS from climate models: $t = 5.4$, df = 408, $P < 0.001$).

Accounting for dispersal

Predicted future distributions were not affected by dispersal in the same way for all species. For 75% of the 409 studied species, the decrease in predicted future distribution due to dispersal ability was less than 5%. Twelve percent and 5% of the species had their predicted future distribution reduced by more than 10% and 20%, respectively, due to their specific dispersal ability. This resulted in reductions of the predicted species range shifts and species range changes (Table 2; Fig. 2) and, locally, in the reduction of the future predicted species richness of up to 10–15 species, representing a 10% decrease at the local level (Fig. 3).

Predicted shifts and variations of species distributions

Using both climate and habitat variables, it was predicted that the range of 71% of the species would decrease by 2050, and 35% and 10% would undergo a decrease of at least 25% and 50% respectively (Fig. 2). Conversely, the range of only 7% of the species was predicted to increase of at least 25%. We obtained the same pattern with climate variables only, whereas habitat models predicted smaller variations in range size with a lower number of species whose range was predicted to decrease in size by 2050 (only 58%). Although these overall results were quite consistent according to the set of variables used for SDMs, results from climate models and habitat models were often contrasted at the species level (Appendix S2). When considering species with predicted increasing or decreasing range sizes over 5%, more species revealed opposite predicted changes with climate and with habitat variables (110 compared to only 92 species with consistent range direction changes).

Predicted species distribution shifts by 2050 substantially differed between the three types of variables used in the models (Table 2, Fig. 4; Appendix S3). Shifts were larger when using climate variables only (a median shift of 378 km), intermediate when using both climate and habitat variables (median shift of 335 km) and lower when using only habitat variables (a median shift of 97 km). For the first two, it was predicted that most species would experience a shift with a northern and eastern component (95% and 78%, respectively) (Appendix S3). Conversely, with habitat variables, it was predicted that more species would experience a shift with a southern and western component (63% and 56%, respectively). Predicted range shifts were spatially structured (Fig. 4). When species distributions were modeled with climate variables only or with both climate and habitat variables, western species were

Table 1 Accuracy results (mean ± SD) of the 409 bird species according to the variables used

	Climate variable	Habitat variables	Climate and habitat variables
AUC	0.998 ± 0.001	0.992 ± 0.011	0.999 ± 0.001
TSS	0.963 ± 0.021	0.927 ± 0.048	0.965 ± 0.020
Sensitivity	0.981 ± 0.011	0.964 ± 0.023	0.983 ± 0.010
Specificity	0.981 ± 0.010	0.963 ± 0.026	0.983 ± 0.010

AUC, area under the relative operating characteristic curve; TSS, true skill statistic.

Table 2 Median predicted range shifts and changes (5–95% quantiles) according to the variables used and the dispersal scenario

	Climate variables	Habitat variables	Climate and habitat variables
Range shift (km) (total dispersal)	378 (157–729)	97 (16–360)	335 (116–739)
Range shift (km)	329 (129–654)	88 (15–333)	289 (97–643)
Range change (total dispersal)	−8% (−61–+72%)	−1% (−35–+17%)	−11% (−59–+45%)
Range change	−12% (−62–+45%)	−1% (−36–+14%)	−14% (−59–+36%)

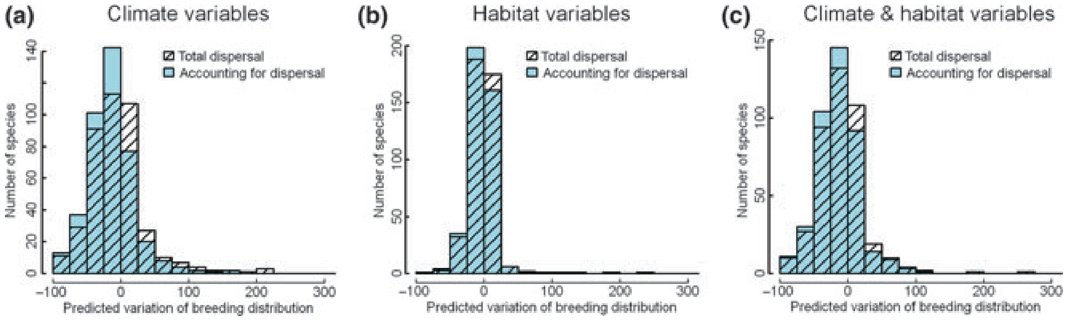


Fig. 2 Predicted variations of breeding distribution according to the variables used and to the dispersal scenario.

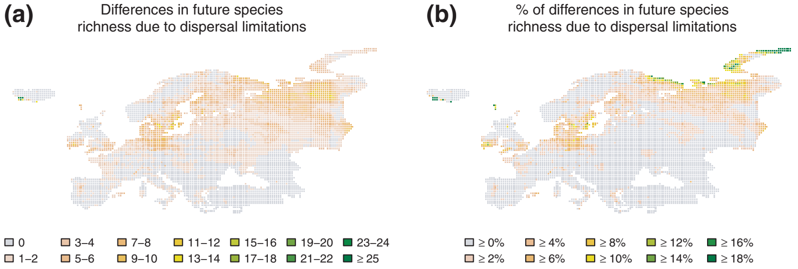


Fig. 3 Difference in future species richness due to dispersal limitations.

expected to shift mainly in a northward direction, while eastern species were expected to shift either northwards or eastwards. When species distributions were modeled with habitat variables only, most of the shifts were very small, and interestingly, most of the eastern species were expected to shift westwards.

Predicted changes in species richness

Predicted changes in species richness depended on the variables used for modeling (Fig. 5). When using climate variables only, southeastern Spain, Greece, southern Turkey, and the north coast of the Black Sea were expected to face the largest decrease in species richness. Large increases in species richness were predicted in northern Russia and Scandinavia, Iceland, parts of Great Britain, northwestern Iberia, northern Turkey, and the Alps. When using climate and habitat variables, the predicted change in species richness was very similar to that obtained when using climate variables only, but with smaller decreases in southern Spain. With habitat variables only, predicted changes in species richness were smaller and differed in their spatial structure. There were only a few pixels for which the species richness was expected to decrease by more than 30%, and only a few in the south of Europe. Species richness was predicted to increase by more than 30% in northern Russia, Ireland, and western France.

Discussion

Climate, habitat or mixed models

As in previous studies, current distributions of European breeding birds were more accurately modeled with climate variables than with habitat variables at a large spatial scale (Thuiller *et al.*, 2004; Luoto *et al.*, 2007). Nevertheless, the predictive accuracy of the

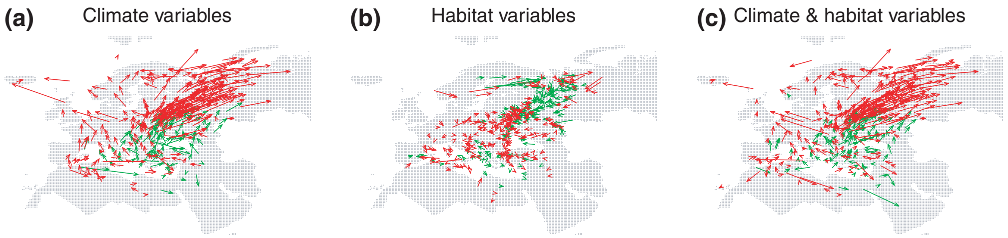


Fig. 4 Predicted range shifts according to the variables used. Shift of species whose range is predicted to increase or decrease are depicted in green and red, respectively.

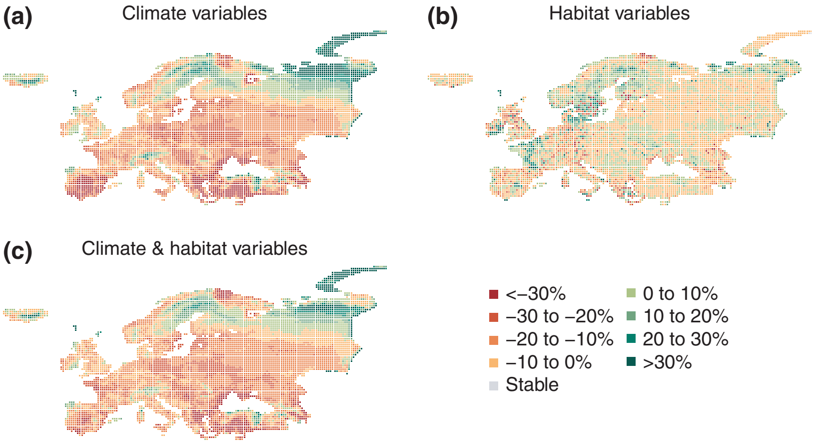


Fig. 5 Predicted variation in species richness according to the variables used.

models was very good, even when using habitat variables only (Table 1). Besides, land-use changes are known to induce changes in abundance (Jiguet *et al.*, 2007) and distribution in birds (Vallecillo *et al.*, 2009). Therefore, land-use scenarios should be considered whenever possible to predict the potential effects of global changes on the fate of a species. The ability of variables to accurately predict a current species distribution, depending mainly on the spatial resolution, is different from their ability to predict future distribution changes. However, land-use changes are rarely considered when predicting future species distributions, and predicted changes have not been compared with SDMs, depending on whether they consider land-use variables or not. Interestingly, predicted future changes in species distributions were very different in that respect. Indeed, future habitat changes are not only the result of climate change, but of a preferential destruction of some habitats and a general increase in fragmentation as well. Future predicted range shifts were also three to four times smaller when using habitat variables only than with climate variables, probably because habitats are expected to change at a lower rate than climate, and rarely follow a directional spatial trend at a very large spatial scale. In our study, we used land-use variables representing the proportion of a 0.5°×0.5° grid cell covered by nine habitat classes. Such a resolution was probably too rough to precisely account for habitat factors, and other types of habitat parameters such as fragmentation or heterogeneity could play an important role in shaping the niche of a species. Besides, in cases where bird species are strongly dependent on a few tree species, habitat classes are not precise enough to account for changes in species composition within a specific habitat class. The better accuracy of current distributions modeled with both climate and habitat variables and contrasted future predictions with climate or habitat variables only emphasized that both types of variables should be considered when modeling current and future species distributions.

Accounting for dispersal

Under scenarios of environmental changes, differences between predicted and actual future species distributions probably arise from changes in species interactions and dispersal abilities. Although a few studies have considered intermediate dispersal scenarios (e.g., Peterson *et al.*, 2002), the two extreme scenarios (null or full dispersal) that are generally considered – due to a lack of knowledge about true species-specific dispersal ability – are one of the critical drawbacks of most existing SDMs (Higgins *et al.*, 2003; Pearson, 2006; Thuiller *et al.*, 2008). Here, we proposed a new method using means and standard deviations of natal dispersal for several bird species to obtain more realistic projections for the 409 breeding birds across Europe. Data were available for 75 species only, so we assumed that values of phylogenetically closely related species would provide reasonable estimates of actual values for all other species with missing data (Appendix S1). This is a reasonable assumption given that among the 75 species for which natal dispersal was estimated, phylogenetically closely related species had very similar values. Nevertheless, for some species with missing data, estimated natal dispersal could be an overestimation or underestimation of their actual value. We preferred to use natal dispersal estimates since they were always larger than breeding dispersal estimates in Paradis *et al.* (1998). Since we considered the dispersal ability of a species over a 50-year period, the estimated potential of dispersal in remote islands such as Iceland or the Faroe is probably misleading since the necessary dispersal ability to reach Iceland from northern Great Britain would have to be over only one generation.

The reduction of potential future breeding distribution due to dispersal limitations was very high for several species. For example, in the case of the Barnacle goose (*Branta leucopsis*), dispersal abilities reduced the potential future breeding range by 42%, which led to a predicted variation in the future range of −48% instead of only −10%. In the same vein, for Baillon's Crake (*Porzana pusilla*), taking dispersal ability into account reduced the potential future breeding distribution by 31%, which led to a predicted future range variation of −32% instead of only −2%. For 27 species, the predicted future range variation switched from positive to negative as a result of dispersal limitations. For example, for the Great Bustard (*Otis tarda*), the predicted range variation under full dispersal hypothesis was +28%, whereas it decreased to −17% when dispersal was taken into account. Nevertheless, for most species considered in this study, future predictions that take dispersal into account were very close to their full dispersal predictions as summarized by the difference in predicted future species richness between the two dispersal scenarios (Fig. 3). Therefore, the full dispersal hypothesis may be realistic for some groups such as birds that have considerable dispersal abilities combined with short mean generation times for most species. Nevertheless, differences in predicted future species richness due to dispersal limitations are not homogeneous in all parts of Europe: the difference is not negligible in southern Ireland and in the region including Denmark, northern Germany, and southern Sweden, since these regions are probably out of reach for some southern species. Differences are also not negligible in northern Russia and northern Finland, probably out of reach for some central species.

Fragmentation is known to affect the dispersal rate of a species (Collingham & Huntley, 2000; Dewhirst & Lutscher, 2009; Willis *et al.*, 2009; Kinezaki *et al.*, 2010). In our study, we used natal dispersal values that were estimated primarily in Great Britain (Paradis *et al.*, 1998), so these data were representative of dispersal in habitats similar to those found in Great Britain. The dispersal ability of birds could be higher or lower, depending on the degree of fragmentation of the habitat. Habitat fragmentation is all the more important to consider when predicting future distributions since it is expected to increase because of anthropogenic activities. Therefore, even though our predictions account for dispersal ability, they are still likely to overestimate future species distributions. Moreover, natal dispersal will probably be smaller at range margins than at the center of species distributions, and studies aimed at comparing natal dispersal at range margins with natal dispersal in the center of the distribution would be very informative and help to improve the accuracy of predicted future distributions. Indeed, from 1975 to 2004, North American birds only expanded their ranges at a rate of 1.48 km/yr at their northern margins (La Sorte & Thompson, 2007), which is less than the values considered in our study, even though global warming over the past 30 years was less than what is expected for the next 50 years (IPCC 2007). Range shifts should therefore be smaller than expected and range changes even worse than expected. Spatially explicit models coupled with species population dynamics would also help improve the accuracy of future distribution predictions (Keith *et al.*, 2008; Anderson *et al.*, 2009; Midgley *et al.*, 2010).

Predicted shifts and variations of species distribution

Huntley *et al.* (2008) proposed an extensive review of the potential impacts of climate change on European breeding birds. Our work is an extension and an update using data from the entire western Palaearctic range of European species, scenarios of both climate and habitat changes and the dispersal abilities of species. These updated scenarios emphasize that global changes are expected to be a major concern for more than 40 bird species whose range is expected to decrease by more than 50% by 2050, with 100 more species expected to lose between 25% and 50% of their current breeding range. The mean predicted range change for the 409 species studied was a 14% decrease. Species interactions among birds could be modified in the future, but the consequences of future changes in species interactions on their respective distributions are difficult to forecast. Moreover, birds also interact with other taxonomic groups within ecosystems (diet and predation, parasitism, competition) with potentially different shifts (Both *et al.*, 2006). The future occupancy of a predicted species distribution area outside of the one currently occupied will therefore depend on more factors than climate and habitat conditions alone. The future impacts of global changes on the distribution of species could then be larger than predicted in this study.

Predicted changes in species richness

The scenario of limited dispersal predicted richness patterns globally similar to those obtained with a full dispersal scenario (Fig. 3), but differences may be more obvious at the local level. In fact, southern European species will not be able to reach the north of central Europe, northern Russia or Iceland, except for a restricted area in the southwestern part of Iceland. The predicted increase of species richness in that part of Iceland is nevertheless probably too optimistic, as the dispersal model used here is not suitable for remote islands. In most of Europe, bird species richness is expected to decrease. Nevertheless, predicted changes are not uniformly distributed and it is expected that northern Europe will gain species by 2050, following the poleward range shift of numerous species. Nevertheless, other parts of Europe should see their species richness increase. This should be the case in parts of Great Britain, in northwestern Iberia, in northern Turkey, and in the Alps. It should be noted that the predicted patterns of species richness variations were obtained by excluding bird species currently breeding only in North Africa and/or the Middle East. It is therefore possible that the breeding range of some of these species would be predicted to expand to Southern Europe (Barbet-Massin *et al.*, 2010). Thus, if able to colonize, these species would contribute to the future species richness of Southern Europe and lessen the predicted decrease in species richness there. Even though the spatial pattern of the predicted changes of taxonomic diversity of European birds can be very helpful to develop adaptive management and conservation strategies (Hannah *et al.*, 2007), functional and phylogenetic diversities were also both advocated as two important facets of diversity respectively for ensuring the provision of goods and services (Diaz *et al.*, 2007) and for representing an evolutionary history of conservation interest (Knapp *et al.*, 2008; Thuiller *et al.*, 2011). Thus, if different from the predicted changes of species richness, estimating changes of phylogenetic and functional diversity would be complementary.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean and standard deviation of natal dispersal (km) used in the study (last two columns) as well as the values from Paradis *et al.* (1998).
Appendix S2. Relationship between the range change predicted with climate variables and the range change predicted with habitat variables. The number of points falling in each quarter (with a change above 5%) is indicated. Empty and full points stand for species whose range change modeled with both climate and habitat variables is positive or negative, respectively.
Appendix S3. Direction of the predicted range shifts according to the variables used.