Breeding bird populations have been declining in Europe during the past few decades, with long-distance migrants being especially affected (Sanderson et al. 2006). Few studies have investigated the impact on migrant species due to changing climate conditions along migration routes on stopover sites and wintering grounds (Tøttrup et al. 2008). The potential impacts of climate change on the breeding ranges of European birds have been estimated recently (Huntley et al. 2008), and changes in migration phenology have been reported in numerous species (Jonzén et al. 2006). However, we still need to study the potential impacts on winter ranges. La Sorte & Thompson (2007) reported recent poleward shifts in the winter ranges of North American birds. It is thus likely that a changing climate in Africa will affect the winter distribution of trans-Saharan migrants, potentially affecting their conservation status.

Here, we estimated the potential impacts of climate change on the winter distributions of 64 species of Afro-Palaearctic trans-Saharan migrant passerines. We used various climatic scenarios (IPCC 2007) in an ensemble forecasting framework (Araújo & New 2007) to account for climate prediction and modelling uncertainties. We first explored the potential changes in range size and position, considering either full or no dispersal ability of species between present and future ranges. We then synthesized potential impacts by mapping predicted changes in species richness of these migrant species.

2. MATERIAL AND METHODS
(a) Bird and climate data
For each migrant species, we used recorded localities obtained from museum specimens, ringing records and field observations (see the project website www.macrolecology.dk/africamigrants). We considered records obtained south of 24°N latitude (south of the Sahara) from 1st November to 29th February, to be sure they concerned wintering not migrating birds. A total of 16 638 primary records were used, reduced to 9797 records when combined at a 0.5° × 0.5° grid cell resolution, leaving 6–1201 grid cell records per species. Pseudo-absences were selected randomly, outside the suitable area of the surface range envelope model (appendix 2, electronic supplementary material).

Future climate projections were derived from five general circulation models (GCMs; BCM2, ECHAM5, HadCm3, MRI-CGCM3, 2-HI and MK3) and three recent special reports on climate scenarios (SRES) (A1B, R1 and A2 when available). We used monthly mean predictions taken from IPCC (2007), for time intervals 1961–1990, 2011–2030, 2046–2065 and 2080–2099. GCMs represent physical processes in the atmosphere, ocean, cryosphere and land surface. SRES reflect the potential impacts of different assumptions about demographic, socio-economic and technological development on the release of greenhouse gases. We interpolated these values onto a 0.5° × 0.5° grid over Africa and the Arabian Peninsula for a total of 11 275 grid cells. For distribution modelling, we used eight climatic variables: (i) annual mean temperature, (ii) mean temperature of the warmest month, (iii) mean temperature of the coldest month, (iv) temperature seasonality, (v) annual precipitation, (vi) precipitation of the wettest month, (vii) precipitation of the driest month, and (viii) precipitation seasonality. The use of climatic variables only simply be proxies for the major habitats and these habitats may not be able to track the climate change.

(b) Ensemble forecast
We modelled present and possible future distributions using nine climate suitability models (Thuiller 2003; Phillips et al. 2006; details are given in appendix 1 of the electronic supplementary material). Each model was first calibrated using a 70 per cent random subset of the data, and then evaluated with the remaining 30 per cent using a threshold-independent method, the area under...
the relative operating characteristic curve (AUC). Data splitting was performed five times, from which we calculated an average AUC. The final runs of the models for obtaining the range predictions used 100 per cent of the data.

For each species and time period, we obtained 45 (9 models × 5 GCMs) present and 108 (9 models × 12 (GCMs × SRES)) future modelled distributions. The consensus distribution was obtained with an ensemble forecast approach, by selecting the outputs of the five modelling techniques with the best AUC scores, and by further calculating the unweighted mean distributions (Marmion et al. 2009; appendix 1, electronic supplementary material) for the corresponding 25 (5 models × 5 GCMs) present or 60 (5 models × 12 (GCMs × SRES)) future distributions. For every species, the mean AUC of all models ranged from 0.757 to 0.987 (mean = 0.930 ± 0.04). The mean AUC of the models used for consensus distributions ranged from 0.840 to 0.996 (mean = 0.962 ± 0.03; appendix 3, electronic supplementary material). To transform the probabilistic consensus distribution to a presence/absence distribution, we preserved the occurrence probabilities for pixels above the sensitivity–specificity sum maximization threshold, and set to zero the occurrence probability for pixels under the threshold.

(c) Winter range extents and shifts

The range was calculated for each species’ consensus distribution, by summing the probabilities of the filtered distribution, weighting each pixel by its area and accounting for the latitudinal variations. The latitude and longitude of the range centroids were also estimated from the filtered distribution, using probabilities as weights. For each species, the distance between present and future range centroids was calculated as a measure of range shift. We further calculated the area ratio between future and present ranges as a measure of the potential impact on range size; this measure assumes that each species is capable of dispersing completely from the present to the future range. We finally calculated the ratio between the overlap of present and future ranges and the present range; this measure assumes that no species is capable of any dispersal into new areas predicted to be climatically suitable in the future. We used a generalized least-squares phylogenetic comparative method (appendix 6, electronic supplementary material) to test for a correlation between the ratio of range sizes, the range overlap or the range shift with the present range size and the latitude and longitude of range centroid. To map the potential evolution of species richness of these migrant birds, we considered the extreme two cases presented above where dispersal is either full or null. Given that all the investigated bird species are migratory, the full dispersal ability is certainly closer to the reality. Species richness per grid cell was obtained by summing the number of species predicted as present.

3. RESULTS

Under the total dispersal hypothesis, we found that 35, 38 and 37 species out of a total of 64 should undergo a reduction in their winter range by 2030, 2065 and 2100, respectively (appendices 4 and 7, electronic supplementary material). There is an increase in the variation of winter range size over time: only one species is predicted to experience a more than 50 per cent reduction by 2030, whereas 11 and 16 species should face such a reduction by 2065 and 2100, respectively. By 2100, there should be a median variation (difference between future and present ranges divided by the present range) of −13 per cent in range sizes, with a maximum increase of 980 per cent for Locustella naevia and a maximum decrease of 97 per cent for Ficedula albicolis and Ficedula semitorquata (appendix 8, electronic supplementary material). Under the null dispersal hypothesis, the median variation in winter range size should be a 28 per cent decrease by 2100.

By 2100, the range centroids are predicted to have shifted by 500 ± 373 km (range 57–1410; figure 1). Most species whose winter range is predicted to decrease are predicted to shift latitudinally, whereas most species whose winter range is predicted to increase are predicted to shift longitudinally. Thus, these predicted shifts are strongly spatially structured, and they depend upon whether the winter range is predicted to decrease or increase (see appendix 6 in the electronic supplementary material and table 1). In generalized least-squares models, we found a negative effect of longitude on the ratio of range size, on range overlap and on range shift, and a positive effect of latitude on range overlap. With spatial effects accounted for, we found a positive effect of present range size on range overlap and a negative effect on range ratio and range shift.

4. DISCUSSION

By 2100, 37 out of 64 long-distance migrant passerines are predicted to suffer a winter range reduction, even assuming that species are capable of full dispersal. Under such conditions, 16 species would lose more than half of their range size, two of them losing almost all suitable wintering conditions. The predicted variations in distributions are highly spatially structured; we predict larger distributional reductions for species wintering in eastern or southern Africa, while those wintering in western Africa are predicted to extend their ranges eastwards. In agreement with previous studies (La Sorte & Thompson 2007; Huntley et al. 2008), we predict mostly poleward distributional shifts for species presently wintering in the Southern Hemisphere; however, species presently wintering in West Africa would shift eastward since they are limited northward by the Sahara. Large potential impacts of climate change are predicted for range-restricted species with limited dispersal ability, as they face the smallest overlap between present and future predicted ranges and the largest shifts.

When looking at overall species richness, predicted changes by 2100 (figure 2) show some similarities to those predicted for mammals (Thruiller et al. 2006),
especially a large decrease in the western parts of southern Africa, although they are clearly different from those obtained for African breeding birds (Jetz et al. 2007). Presently, Afro-Palaearctic migrant passerines winter preferentially in a belt stretching from Senegal to Ethiopia and from Sudan southwards through Kenya and Tanzania (Wisz et al. 2007). This distribution corresponds largely with their preferred dry Acacia and moist broadleaved savannah habitats (Salewski & Jones 2006). Consequently, low species-rich areas are found in rainforest habitats at equatorial latitudes and in desert-like habitats, e.g. most of Namibia. Assuming full dispersal ability, a reasonable assumption for migratory birds, our distribution models predict large decreases in species richness in the initially species-rich East African region. The presently species-poor western part of southern Africa is predicted to lose even more of its species. Under the hypothesis of null dispersal, the charts did not show any major relative differences in patterns. Finally, our simulations do not predict present sub-Saharan wintering climatic conditions to appear north of the Sahara, making it unlikely that sub-Saharan migrant species could substitute habitat loss south of the

Table 1. Results of generalized least-squares models conducted on the predicted ratio of range sizes, the predicted range overlap (both log transformed) and the shift, explained by latitude, longitude and size of the predicted present range (effects of predictors are adjusted to each other).

<table>
<thead>
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<th>predictor</th>
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<th>range shift</th>
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<td>6.07</td>
</tr>
<tr>
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<td>present range size</td>
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<td>0.001</td>
<td>3.66</td>
</tr>
</tbody>
</table>

Figure 2. Predicted species richness of migrant passerines in Africa under future climatic scenarios (by 2100): (a) future predicted species richness under the hypothesis of full dispersal ability between predicted present and future ranges; (b) present predicted species richness (1990); (c) future predicted species richness under the hypothesis of null dispersal ability; (d, e) present variations in species richness corresponding to (a) and (c), respectively.

Sahara with expansions of distributions north of the Sahara. Further studies of long-distance migrants should also consider the effects of predicted changes in land cover on future distributions.


