

Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change

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ABSTRACT

Aim To examine the impacts of climate change on endemic birds, which are of global significance for conservation, on a continent with few such assessments. We specifically assess projected range changes in relation to the Important Bird Areas (IBAs) network and assess the possible consequences for conservation.

Location South Africa, Lesotho and Swaziland.

Methods The newly emerging ensemble modelling approach is used with 50 species, four climate change models for the period 2070–2100 and eight bioclimatic niche models in the statistical package BIOMOD. Model evaluation is done using the receiver operating characteristic and the recently introduced true skill statistic. Future projections are made considering two extreme assumptions: species have full dispersal ability and species have no dispersal ability. A consensus forecast is identified using principal components analysis. This forecast is interpreted in terms of the IBA network. An irreplaceability analysis is used to highlight priority IBAs for conservation attention in terms of climate change.

Results The majority of species (62%) are predicted to lose climatically suitable space. Five species lose at least 85% of their climatically suitable space. Many IBAs lose species (41%; 47 IBAs) and show high rates of species turnover of more than 50% (77%; 95 IBAs). Highly irreplaceable regions for endemic species become highly localized under climate change, meaning that the endemic species analysed here experience similar range contractions to maintain climate niches.

Main conclusions The South African IBAs network is likely to become less effective for conserving endemic birds under climate change. The irreplaceability analysis identified key refugia for endemic species under climate change, but many of these areas are not currently IBAs. In addition, many of these high-priority areas that are IBAs fall outside the current formal protected areas network.

Keywords

Bioclimatic niche modelling, BIOMOD, bird conservation, climate change, endemic birds, ensemble modelling, irreplaceability, southern Africa, true skill statistic.

INTRODUCTION

The idea that we can conserve species where they currently exist is unrealistic given recent climate change predictions. Conservationists are in dire need of robust estimates of the impacts of climate change on species, since it is likely that species will move out of the current locations of reserve networks and designated conservation areas or face local extinction (Parmesan & Yohe, 2003; Araújo *et al.*, 2004, 2006; Hannah *et al.*, 2007; Coetzee, 2008a).

Bioclimatic niche models are widely used to estimate the potential impacts of climate change (e.g. Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Thuiller *et al.*, 2008). However, substantial challenges remain in their use and application,

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especially in interpreting between-model differences for the same species and different climate change scenarios (Pearson & Dawson, 2003; Thuiller, 2004; Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Pearson et al., 2006; Austin, 2007). While these models excel at predicting the current distributions of species, it is unclear which models perform the best at predicting future distributions under a changing climate, as modelling projections can vary widely (Thuiller, 2004, 2007; Araújo & Rahbek, 2006; Pearson et al., 2006). A recently emerging alternative method for reducing uncertainty among models is the use of ensemble forecasting, which involves combining multiple bioclimatic niche models (Thuiller, 2004; Araújo et al., 2005, 2006; Araújo & New, 2006). By using a suite of models and many climate change scenarios, combined with ensemble techniques, more robust forecasts can be made with appropriate interpretation (Araújo & New, 2006). In a seminal paper, Araújo et al. (2005) tested the predictive accuracy of bioclimatic models using observed bird species range shifts under climate change in two periods of the recent past. Their study supports the use of ensemble forecasting approaches in climate change modelling research and demonstrates how uncertainty in predictions can be reduced by selecting the most consensual projections (see also Marmion et al., 2009).

Here, we use the newly emerging ensemble modelling approach to examine the impacts of climate change on South African endemic birds, which are of global significance for conservation. We also assess the predicted range changes in terms of the southern African Important Bird Area network. Important Bird Areas (IBAs) are a global network of sites designated by BirdLife International as being important for the conservation of the world's avifauna (Fishpool & Evans, 2001). IBAs are designated using criteria based on the presence of globally threatened, restricted-range or biome-restricted bird species, or the presence of substantial congregations of bird species. IBAs are designed so that they overlap as far as possible with the existing reserve network of the particular region in question (Fishpool & Evans, 2001).

Endemic species are particularly suitable for bioclimatic niche models since: (1) models can capture the entire distributional range of a species in question, and can thus be expected to be more accurate (Thuiller, 2004; Guisan & Thuiller, 2005; Broennimann *et al.*, 2006), and (2) errors are greater for species with larger areas of occupancy and greater extents of occurrence, but endemic species typically have smaller distribution ranges (Araújo & Pearson, 2005; McPherson & Jetz, 2007).

The impacts of climate change on biodiversity in South Africa are predicted to be severe, and are already occurring (e.g. Foden *et al.*, 2007). For example, focusing on only six southern African bird species, Simmons *et al.* (2004) predicted a 40% mean loss of climatically suitable area for these species in the region by 2050. Many African IBAs are predicted to experience a major loss of species as bird distributions change in response to changing climate (Hole *et al.*, 2009). Our study provides an important contribution, given the lack of information on the impacts of climate change on biodiversity in the Southern Hemisphere (IPCC, 2007).

DATA AND METHODS

Species and climate data

Species locality data were obtained from the Southern African Bird Atlas Project database (SABAP; Harrison *et al.*, 1997). SABAP data were collected mainly between 1987 and 1992 by observers visiting quarter-degree grid cells ($0.25^{\circ} \times 0.25^{\circ}$, *c*. 676 km²; hereafter grid cells). We assumed that a species was absent from grid cells where it was not recorded, as done by others (van Rensburg *et al.*, 2004). For the modelling analysis we selected endemics with > 90% of their distributions within South Africa, occupying > 20 grid cells and excluding those species where taxonomic uncertainties exist – 50 species fulfilled these criteria (Hockey *et al.*, 2005); see Appendix S1 in Supporting information). In total we used 18,658 records in 2000 grid cells.

Mean values of six climatic predictor variables were derived from the Climate Research Unit (CRU) monthly means climate data (New *et al.*, 2002) for the period 1961–90. The climate variables included: annual temperature (°C), temperature of the coldest month (°C), temperature of the warmest month (°C), annual precipitation (mm), precipitation in the warmest month (mm) and precipitation in the coldest month (mm). The choice of variables reflects energy and water constraints on the distribution range of birds and the availability of suitable variables obtained from the various climate change models. These variables impose known constraints on species distributions as a result of widely shared physiological limitations (e.g. Lennon *et al.*, 2000; van Rensburg *et al.*, 2002; Araújo *et al.*, 2005).

Southern Africa is especially vulnerable to climate change, but few regional climate models (RCMs) have been applied to the region and throughout the world (Tadross *et al.*, 2005). We used four climate change models, including RCMs and downscaled global climate models (MM5, PRECIS, HadCM3, CCAM – details follow) to capture the variability in the underlying assumptions of the climate processes that are represented in the models. While a variety of emissions scenarios reflect different projected anthropogenic emissions rates, the climate change models that we used follow the 'business as usual' A2 Special Report on Emission Scenarios (SRES) scenario, which assumes that global carbon emissions will continue unhindered (Nakicenovic & Swart, 2000).

Both MM5 (a fifth-generation mesoscale model; Tadross *et al.*, 2005) and the Providing REgional Climates for Impacts Studies model (PRECIS) are RCMs that have been produced at a spatial resolution of 50 × 50 km and are nested within 10 years of control and future integrations of HadAM3H (Jones *et al.*, 2004). The current climate calibration for PRECIS spans the period 1970–79 whereas the current climate calibration of MM5 is 1975–84. Future climate projections are for 2070–80 and 2090–2100 for MM5 and PRECIS, respectively. The performances of MM5 and PRECIS have been assessed over the southern African domain and been shown to be relatively credible (Hudson & Jones, 2002; Tadross *et al.*, 2005). HadCM3 is a coupled ocean–atmosphere general circulation model devel-

oped by the Hadley Centre for Climate Prediction (Gordon et al., 2000), and empirically downscaled to a regional resolution by Hewitson (2003). An evaluation of this downscaling (Hewitson & Crane, 2005) shows that key climate patterns are captured. The current climate calibration for HadCM3 spans the period 1970-99 and the future climate projection is for 2071-2100. The Conformal-Cubic Atmospheric Model (CCAM) is a variable-resolution model (here used at 50×50 km) applied to sub-Saharan Africa by Engelbrecht et al. (2009). Its predecessor, DARLAM, has been used in bioclimatic niche modelling (Olwoch et al., 2008). Following Tadross et al. (2005), anomaly values for temperature-related variables for each climate change model (meaning the difference between that particular climate model's current modelled and future modelled output) were added to an observed climate baseline. For rainfall, we used a proportional adjustment, calculated from the current and future modelled outputs, and multiplied the proportional change with the observed rainfall data. This approach is considered robust and follows best-practice guidelines (see Tadross et al., 2005; IPCC-TGICA, 2007). Although climate change models and baseline climate data have differing temporal scales of projections and differing baseline current climate calibrations, these models represent the most recent available climate change data for southern Africa at an appropriate spatial resolution. There is substantial overlap in the range of future conditions predicted by these models, so predictions are not completely disjunct due to these mismatches. Our aim is a broad-scale first assessment of climate change impacts, using a best-practice ensemble technique, and as such we consider this limitation acceptable.

The 50 \times 50 km resolution climate change datasets were matched to the atlas data grid cells by using standard procedures in ArcGIS version 9.1 (ESRI, 2008). We resampled 50 \times 50 km cells, without interpolation, to a 1 \times 1 km raster dataset. We then summarized the data to the 0.25° grid cell bird atlas data using a moving window summary procedure. Since the 0.25° grid cells and the 50 \times 50 km cells datasets did not share the same origin in their coordinate systems, these cells did not overlap in a regular fashion. Exploratory data analysis (unpublished) showed that our procedure, on average, produced results that are more faithful to the original climate patterns' 50 \times 50 km cells than the more common kriging spatial interpolation technique.

Modelling methods

Bird distributions were predicted using eight models in the bioclimatic niche modelling package called BIOMOD (Thuiller, 2003), within the R environment (R Development Core Team, 2006). BIOMOD enables many bioclimatic models to be run simultaneously on a large suite of species. Models included: (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) classification tree analysis (CTA), (4) feedforward artificial neural networks (ANN), (5) generalized boosted models (GBM; also known as boosted regression trees, BRT), (6) random forests (RF), (7) mixture discriminant analysis (MDA), and (8) multivariate adaptive regression spline (MARS). GLM, GAM, CTA and ANN are described and disClimate change and southern African Important Bird Areas

cussed in Thuiller (2003). In a recent test of 16 niche models (Elith *et al.*, 2006), including GBM, MARS, GLM, GAM and CTA, the GBM models performed best. MDA (Hastie & Tibshirani, 1996) and RF (Breiman, 2001) were also added as promising newer modelling techniques which are gaining acceptance in the literature (e.g. Broennimann *et al.*, 2007).

Model evaluation

Models were calibrated using a 70% random sample of the observed data, and model performance was assessed using the remaining 30% of the data. We evaluated model projections between observed species presences and absences and projected distributions by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Fielding & Bell, 1997; Thuiller, 2003). Prediction accuracy is considered to be no better than random for AUC values of <0.5, poor when they are in the range 0.5–0.7, and useful in the range 0.7–0.9. AUC values that are greater than 0.9 are considered to be excellent (Swets, 1988).

The kappa statistic has been widely used for model evaluation (Thuiller, 2003; Araújo *et al.*, 2005; Pearson *et al.*, 2006), but has recently been shown to be particularly sensitive to prevalence (Allouche *et al.*, 2006). We used the recently introduced true skill statistic (TSS) as it is has all of the advantages of kappa but is not sensitive to prevalence (Allouche *et al.*, 2006). The TSS is more often used to assess the accuracy of weather forecasts and compares the number of correct forecasts minus those attributable to random guessing with that of a hypothetical perfect forecast. It uses a confusion matrix (Fielding & Bell, 1997) to calculate sensitivity plus specificity minus one. The following ranges were used to interpret TSS statistics: values from 0.2 to 0.5 were poor, values from 0.6 to 0.8 were useful, and values larger than 0.8 were good to excellent.

Probability of occurrence for each species was transformed to presence–absence values in BIOMOD by estimating an optimum threshold maximizing the percentage of presence and absence correctly predicted for ROC curves and by calculating the best probability threshold by maximizing the TSS statistic for the evaluation data. Overall we obtained 64 projections for each of the 50 species modelled, thus 2400 projections in total (eight models by four climate change models by two methods of transformation to presence/absence for 50 species).

Consensus model

To calculate our consensus climate change projection, a principal components analysis (PCA), which identifies linearly covarying projections (e.g. Thuiller, 2004), was run in R (R Development Core Team, 2006). Following Araújo *et al.* (2005), data for the PCA were the future predicted species richness data, per grid cell, obtained from the two transformation methods, for each modelling combination (64 combinations in total). PCA has been used successfully in ensemble forecasting (Thuiller, 2004; Araújo *et al.*, 2005; Thuiller *et al.*, 2005; Marmion *et al.*, 2009). The first principal component (PC1) is equal to a line that goes through the central tendency of all sets of model projections and minimizes the square of the eigen distance of each set of projections to that line. PC1 is as close to all of the data as possible and is thus the consensus axis (Araújo et al., 2005). Component loadings in PCA (the weights given to individual model projections within each component) represent the relative contribution of each projection within components. We selected individual modelling combinations which had the overall highest component loading, from the first principal component which best summarized the overall pattern of variation in climate change projections. In our case, the first nine models had the highest and equal component loadings, and we selected these for the consensus forecast (following Araújo et al., 2005; Appendix S2). Nonetheless, where to place the cut-off from the PCA loading for the selected models is essentially arbitrary. The species richness data per grid cell, thus the projected range change data from the nine models, were averaged using the 'bounding box' technique (Araújo & New, 2006). Model agreement occurs where at least half the models (\geq 5; the median) agree. Thus species presence is predicted if at least five or more models predict species presence - hereafter called the consensus forecast (see Appendix 1 for PCA loadings of consensus models; all results are in Appendix S2).

Data analysis

To account for differences in species dispersal abilities, we considered two scenarios of range change. We assumed that species could either fully disperse to all new suitable areas (full dispersal) or alternatively that they will be unable to disperse to any of the new suitable areas, so would only persist in areas they currently find suitable (no dispersal). This assumption cannot predict whether species would actually establish in new suitable areas under the full dispersal scenario. It is a broad assumption that is commonly used, and represents two opposing extremes of how climate change may affect species ranges, based only on the dispersal abilities of species (Thomas et al., 2004; Thuiller et al., 2005). The realized patterns will necessarily somewhere fall between these two extremes. We calculated both of these scenarios for all species within the consensus forecast, and thus have a consensus forecast under no dispersal and a consensus forecast under full dispersal.

To estimate the climatically suitable space gained or lost per species under the consensus forecast, we calculated the percentage of grid cells gained or lost and the percentage range change under no dispersal and full dispersal assumptions. For each grid cell, under a full dispersal assumption only, we calculated species turnover using T = 100(L + G)/(SR + G); where T = turnover, L = number of grid cells lost, G = number of grid cells gained and SR = current species richness of that grid cell (Thuiller *et al.*, 2005). A turnover value of 0 indicates that the assemblage of species is predicted to remain the same in the future (i.e. no loss or gain of species) and a value of 100 indicates that the assemblage of species in that grid cell is completely different (i.e. the species loss equals the initial species richness).

Irreplaceability is a widely used measure of conservation importance, and aims to achieve representativeness, meaning that all designated biological features are represented. Here we use it mainly as an exploratory analysis, to identify regions with unique endemic species assemblages that are vulnerable to climate change and to identify regions that may form refugia in future. For instance, if species contract their ranges into similar regions, the irreplaceability of that region will increase under future change scenarios. Irreplaceability is defined as the likelihood that a given site will need to be protected to achieve a specified set of conservation targets (e.g. Margules & Pressey, 2000). Its value ranges from 0 to 1, where a value of 1 indicates an entirely biologically distinct and totally irreplaceable site, thus containing species that only occur in that site. We calculated irreplaceability using both the current distribution data and the consensus forecast for the 50 endemic species using the C-Plan systematic Conservation Planning System, Version 3.11 (Pressey et al., 2009); http://www.uq.edu.au/~uqmwatts/cplan. html). C-Plan is designed to support conservation planning decisions. The system calculates the irreplaceability value of landscape elements in terms of characteristics such as species composition, vegetation types and land-use types. C-Plan calculates and displays the irreplaceability of each site in a region as a guide to its importance for the regional conservation goal. We set targets at one, so that each species would be represented in at least one $0.25^{\circ} \times 0.25^{\circ}$ grid cell and investigated the overlap of this pattern with the IBA network.

Following others (e.g. Margules & Pressey, 2000; Reyers, 2004) we considered sites with both high vulnerability and high irreplaceability as the highest priority sites for conservation action, here in terms of climate change. IBAs in South Africa, Lesotho and Swaziland were digitized in ArcGIS version 9.1 (ESRI, 2008) using data from Barnes (1998) and conspicuous geographical features (n = 122). Islands were excluded. Species lists for each IBA were obtained by intersecting the IBA layer with the current and consensus forecast grid cell data. Species loss per IBA due to climate change as calculated in the present analysis was standardized from 0 to 1 by dividing all species loss values by the overall highest species loss value. Coetzee (2008b) comprehensively analysed the current and future land-use threats to southern African IBAs. To complement their analysis, and to form part of an integrated assessment on global change threats to IBAs, we used their database of irreplaceability values for all IBAs, calculated for 655 bird species across South Africa. Species loss per IBA due to climate change is plotted against these irreplaceability values for each IBA, forming a comprehensive picture on the threat from climate change, at least in terms of their endemic bird assemblages. These two-dimensional plots of IBAs are used to identify those currently irreplaceable IBAs of national importance that are likely to be most affected by the threat of climate change via endemic species loss per IBA.

RESULTS

In general models had good agreement between observed data and current modelled predictions (Table 1). When the calibration data were used, RF models appeared to overfit the data. Based on the evaluation set, GBM, RF and GAM models

Table 1 Area under the curve (AUC) and true skill statistics (TSS) for the 50 bird species for each model (min = minimum, me = mean and max = maximum values of AUC or TSS statistics). Calibration refers to the 70% dataset used to fit the models, Evaluation is the 30% dataset used to evaluate the fitted models, and Original combines both (Calibration + Evaluation) datasets.

AUC	Calibration			Evaluation			Original		
	Me	Min	Max	Me	Min	Max	Me	Min	Max
GLM	0.94	0.77	0.99	0.93	0.75	1.00	0.94	0.76	0.99
GAM	0.95	0.80	0.99	0.94	0.77	1.00	0.95	0.80	0.99
CTA	0.92	0.75	0.98	0.87	0.71	0.96	0.91	0.75	0.96
ANN	0.95	0.85	1.00	0.93	0.82	0.99	0.95	0.84	0.99
GBM	0.98	0.90	1.00	0.94	0.80	1.00	0.97	0.87	1.00
RF	1.00	1.00	1.00	0.94	0.79	1.00	0.99	0.96	1.00
MDA	0.93	0.79	0.99	0.91	0.75	0.99	0.93	0.78	0.98
MARS	0.95	0.83	0.99	0.93	0.77	1.00	0.94	0.82	0.99
TSS	Calibration			Evaluation			Original		
GLM	0.78	0.43	0.94	0.78	0.43	0.98	0.77	0.43	0.93
GAM	0.80	0.50	0.95	0.79	0.43	0.99	0.79	0.47	0.95
CTA	0.77	0.50	0.94	0.68	0.38	0.87	0.74	0.46	0.88
ANN	0.81	0.54	0.96	0.77	0.47	0.97	0.79	0.52	0.95
GBM	0.87	0.65	0.99	0.77	0.45	0.99	0.83	0.59	0.98
RF	1.00	1.00	1.00	0.78	0.43	0.99	0.92	0.83	0.99
MDA	0.74	0.47	0.91	0.71	0.36	0.93	0.73	0.43	0.90
MARS	0.79	0.53	0.95	0.76	0.42	0.99	0.78	0.49	0.94

GLM, generalized linear model; GAM, generalized additive model; CTA, classification tree analysis; ANN, feed-forward artificial neural networks; GBM, generalized boosted model; RF, random forests; MDA, mixture discriminant analysis; MARS, multivariate adaptive regression spline.

appeared overall to be the best performing bioclimatic models, followed closely by the GLM, MARS and ANN techniques (Table 1).

The first principal component (PC1 or consensus axis) explained 46.8% of model variation. The nine consensus models were selected from the first axis of the PCA and included outputs from MM5, PRECIS and CCAM climate change models, GBM and CTA bioclimatic niche models and both ROC and TSS binary transformation outputs (Appendix 1). Patterns in predicted species richness changes were broadly similar across the different regional circulation models, as the similar component loadings show (Appendix 1). Overall, GBM best summarized the overall patterns in range change for all models used, followed by CTA models.

The majority of species (31 species; 62%) lose climatically suitable space. Using the consensus forecast, the 50 endemic species modelled show a median loss of climatically suitable space of 12% under full dispersal and 26% under no dispersal (standard deviations of 208.7% and 72.5%, respectively). Irrespective of the dispersal scenario analysed, five species (Cape clapper lark, pied starling, African rock pipit, southern black korhaan and sicklewinged chat) are predicted to lose at least 85% of their climatically suitable ranges (Appendix S1). Sixteen species (32%) are predicted to lose more than 50% of their climatically suitable ranges under full dispersal assumptions. Nineteen species (38%) are predicted to show a gain in climatically suitable space (Appendix S1).

Climate change is predicted to have large impacts on species richness patterns, as substantial changes in species distributions are predicted under both the full dispersal (Fig. 1b) and no dispersal (Fig. 1c) assumptions. The north-western and central regions of South Africa are predicted to lose all climatically suitable space for all species modelled. Under a no-dispersal assumption, these patterns remain similar, although species loss is more acute especially in the north-eastern region of the country. Much of South Africa is predicted to experience high rates of species turnover (Fig. 1d). However, no species are predicted to go 'extinct', meaning that there is at least some suitable climatic space remaining under climate change for all species assessed.

The IBA network currently captures 31 (97%) out of a total of 32 grid cells with irreplaceability values over 0.5. Following predicted range changes, the IBA network would capture 53 (83%) out of a total of 64 grid cells with irreplaceability over 0.5 (Fig. 1f). This means that under climate change there are many more grid cells with higher irreplaceability values, and that a greater proportion of these would fall outside of the current IBA network. In contrast to the currently observed patterns, irreplaceability patterns for endemic species under the consensus forecast become highly localized towards the Western Cape and north-eastern highlands of Lesotho and parts of the Drakensberg mountain range (Fig. 1f). Importantly, the options for conserving those species nationally decrease. A total of 436 (out of 691) grid cells within the IBA network (64%) have reduced irreplaceability under the consensus forecast under full dispersal (future irreplaceability – current irreplaceability = negative).

Highly irreplaceable IBAs that are greatly threatened by climate change (Fig. 2) are identified in Appendix S3. In terms of climate change, these are the 11 IBAs (9%) that need renewed attention for conservation prioritization. The predictions suggest that some species (29; 58%) will no longer occur in the IBAs which they currently find suitable. In total, 47 (41%) of IBAs lose some species, while 37 (29%) show no change and 39 (30%) gain some species. A large number of IBAs also show more than 50% species turnover (77%; 95 IBAs).

DISCUSSION

The impacts of climate change are likely to be severe, as endemic species richness patterns are predicted to undergo large shifts by 2070–2100 (Fig. 1). All of the five species that are predicted to undergo a loss of more than 85% of their climatically suitable spaces (irrespective of dispersal ability) are currently listed as 'not threatened' using IUCN criteria (Appendix S1; IUCN, 2006). This emphasizes the need for threatened species lists to incorporate vulnerability to climate change (Bomhard *et al.*, 2005; IUCN, 2006). Our predictions indicate that bird ranges



Figure 2 Important Bird Area (IBA) irreplaceability values plotted against projected species loss. Sites with higher irreplaceability values (H as opposed to L, i.e. low) can be viewed as having higher conservation value. The horizontal axis depicts the degree to which the conservation targets at a site are vulnerable to species loss caused by climate change. Priority sites in terms of climate change are those with high irreplaceability and under high threat (HH). These 11 IBAs are in identified in Appendix S3. Note that many IBAs are not highly irreplaceable, but are highly threatened by climate change (the LH quadrant).

0.4 0.5 0.6 0.7

Projected species loss in Important Bird Areas

0.9

0.8

Figure 1 (a) Current species richness of the 50 bird endemic species assessed. (b) Modelled future bird species richness based on a consensus forecast created from 16 models and four climate change models for the period 2070-2100 under a full dispersal assumption. (c) Modelled future bird species richness based on an identical consensus forecast constrained by a no-dispersal assumption, meaning that species will only occupy areas that are both currently suitable and predicted to be suitable in future. (d) Bird species turnover per grid cell. (e) Current irreplaceability patterns for 50 endemic bird species (Important Bird Area locations are in black). (f) Future irreplaceability patterns based on a consensus forecast under a full dispersal assumption. South Africa (SA), Lesotho (LS) and Swaziland (SW) are indicated in grey. White squares indicate the absence of all species analysed.

(j

Species turnover

will probably shift eastward, southward and toward the escarpment regions in the interior of the country. Regions in the arid north-west of the region show particularly high rates of species range change, consistent with other studies for the region on a range of taxa (plants, reptiles, invertebrates, mammals: Erasmus et al., 2002; Midgley et al., 2002; Broennimann et al., 2006; Foden et al., 2007). This region is predicted to have a climate unlike anything currently experienced in South Africa and none of the endemic birds considered here are likely to find it suitable. There is a pronounced east-west aridity gradient in South Africa with a decline in bird species richness in that direction. This is largely in response to primary productivity, in turn determined by energy and water availability (van Rensburg et al., 2002). For South Africa, consensus climate change models predict the entire country to become warmer, with an increase in precipitation in the east and decreased precipitation in the western parts. There is variation in the ability of the models to predict the boundary between the areas of rainfall increase and decrease. This decline in precipitation for the north-western part of the country (IPCC, 2007) suggests that predicted bird responses are a realistic reflection of the impacts of climate change.

In the long term, the current South African IBAs network is predicted to become less effective for conserving endemic birds due to range shifts induced by climate change. For example, current large protected areas, among them the Kruger National Park, and proposed conservation areas like the Grassland Biosphere Reserve (both of which are IBAs) are likely to be greatly

0

0

0.2 0.3

0.1

affected by climate change (Appendix S3). Given the rapidly increasing observed rates of global CO_2 emissions (Raupach *et al.*, 2007), it is likely that the resulting patterns of local climate change will continue to result in reduced effectiveness of priority conservation areas, IBAs included. This again reaffirms that a drastic decrease in global carbon emissions is necessary to safeguard species. Failing that, it underscores the need for protected area management, and IBA design, to incorporate climate change because the geographical areas that are currently important for conservation are very likely to change (Lee & Jetz, 2008).

Modelling results suggest that climate change decreases the climatically suitable ranges of many of the endemic species analysed. This increases the irreplaceability of the regions which remain suitable for them, since they are the only sites still harbouring those assemblages. This observation explains Fig. 1(f); irreplaceability patterns for endemic species under the consensus forecast become highly localized. This trend is disconcerting, as it means there are fewer opportunities for conservation as the bioclimatically suitable space for many species is condensed into an ever smaller area. It can be argued that these 'irreplaceable refugia' are key sites for conservation attention, as they retain the bioclimatically suitable space for many of the endemics analysed. Some IBAs are located in these regions, but those IBAs only have a small proportion of their total area under formal protection, so their conservation status is uncertain (see Appendix S1). These irreplaceable refugia are located mainly along the escarpment regions across southern Africa, emphasizing the crucial role of altitudinal gradients and mountainous regions as buffers against climate change. Dispersal abilities and unfavourable land use will determine the extent to which these refugia are utilized, but these predicted range shifts serve as hypotheses for further testing and monitoring, not only for the region but also to test ideas concerning altitudinal shifts in species ranges.

Irreplaceability is a frequently used measure of conservation importance (Margules & Pressey, 2000), but it has rarely been used in conservation assessment analyses that incorporate climate change, perhaps because it is subject to a variety of caveats. Irreplaceability is dependent on how species are distributed throughout the landscape, so an area that contains several range-restricted species will have a high irreplaceability. Therefore, the irreplaceability analyses used in this study may be particularly sensitive to modelling outputs, since relatively small changes in the predicted species distributions will have a concomitant large effect on the irreplaceability value. The results should be seen as indicative of broad trends, without focus on particular irreplaceability values. However, if interpreted as done here, we suggest that irreplaceability is potentially useful in identifying key areas that are especially vulnerable to climate change and is useful for identifying those regions that may possibly form refugia in future.

While an ensemble of models can be seen as a rapid and useful approach for investigating broad-scale patterns of the impacts of climate change, it is no substitute for creating 'better' models. Our approach still suffers from the same methodological problems that have been dealt with comprehensively elsewhere (e.g. Pearson & Dawson, 2003; Opdam & Wascher, 2004;

Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Araújo & New, 2006; Araújo & Rahbek, 2006; Broennimann et al., 2006; Austin, 2007; Thuiller, 2007). Also, we report broad patterns - but species responses are likely to be idiosyncratic, which is rarely addressed in ensemble modelling studies (Araújo et al., 2005; Thuiller et al., 2005). There is added uncertainty introduced between and within climate change models (Beaumont et al., 2007). Here, however, pattern generation remains similar across models, reaffirming that the consensus forecast represents an adequate representation of the likely impacts of climate change. Ideally, alternative emission scenarios need to be incorporated to explore development and energy policy trajectories, but such data are currently not available for the region. However, given the currently increasing observed rates of global CO2 emissions (Raupach et al., 2007), on which the 'business as usual' A2 SRES scenario is based, our analysis is by no means an overestimate as this scenario is considered as reasonably credible in the future (Broennimann et al., 2006). Our analysis also uses climate change data over a relatively long time-scale. It could be argued that shorter time periods or the incorporation of projected 'time slices' may be more appropriate for conservation assessments since many other proximal factors will also affect species in the near future. In our case the choice of datasets mainly reflects the lack of more appropriate data and, given this limitation, it is important to see our study as a 'conservation assessment' and not as a 'conservation planning' study. Nonetheless, this analysis gives an indication of likely changes in the coming decades.

The use of ensemble modelling methods in this study provides an improvement over earlier modelling techniques in reducing uncertainty and increasing accuracy by selecting the most consensual projections (Araújo *et al.*, 2005). The message from our analysis is clear. We have identified key IBAs that are particularly vulnerable to climate change and reiterate that climate change will have large impacts on endemic birds in South Africa. Consequently, it is essential to explore and refine methods for incorporating the impacts of climate change into conservation plans.

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SUPPORTING INFORMATION

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

Appendix S1 All endemic species modelled (n = 50).

Appendix S2 Component loadings of the principal components analysis (PCA) of the 64 model combinations from the consensus forecast.

Appendix S3 Impact of climate change on Important Bird Areas (IBAs), using distributional range shifts of 50 endemic birds.

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BIOSKETCHES

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Appendix 1 Component loadings of the principal components analysis (PCA) of the 64 model combinations from the consensus forecast for 50 endemic bird species from 16 models and four climate change models. Only the first nine highest loading models are shown here (all the modelling results are displayed in Appendix S2). Model names follow the convention climate change model, niche model and evaluation method e.g. CCAM.GBM.ROC refers to the CCAM climate change model, the GBM niche model and the ROC transformation method. See text for details on models and transformations.

Model	PC1	PC2	PC3	PC4	PC5
Cumulative variance explained (%)	46.78	52.93	56.74	58.86	60.25
CCAM.GBM.ROC	-0.138	0.077	-0.073	0.042	-0.005
MM5.GBM.ROC	-0.138	0.077	-0.073	0.042	-0.005
PRECIS.GBM.ROC	-0.138	0.077	-0.073	0.042	-0.005
CCAM.GBM.TSS	-0.138	0.084	-0.068	0.038	-0.020
MM5.GBM.TSS	-0.138	0.084	-0.068	0.038	-0.020
PRECIS.GBM.TSS	-0.138	0.084	-0.068	0.038	-0.020
CCAM.CTA.TSS	-0.137	0.066	-0.007	0.041	-0.008
MM5.CTA.TSS	-0.137	0.066	-0.007	0.041	-0.008
PRECIS.CTA.TSS	-0.137	0.066	-0.007	0.041	-0.008

CCAM, conformal-cubic atmospheric model; MM5, fifth generation mesoscale model; PRECIS, Providing REgional Climates for Impacts Studies; GBM, generalized boosted model; CTA, classification tree analysis; ROC, receiver operating characteristic; TSS, true skill statistic.