

## LETTER

## Projected impacts of climate change on a continent-wide protected area network

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### Abstract

Despite widespread concern, the continuing effectiveness of networks of protected areas under projected 21st century climate change is uncertain. Shifts in species' distributions could mean these resources will cease to afford protection to those species for which they were originally established. Using modelled projected shifts in the distributions of sub-Saharan Africa's entire breeding avifauna, we show that species turnover across the continent's Important Bird Area (IBA) network is likely to vary regionally and will be substantial at many sites (> 50% at 42% of IBAs by 2085 for priority species). Persistence of suitable climate space across the network as a whole, however, is notably high, with 88–92% of priority species retaining suitable climate space in  $\geq 1$  IBA(s) in which they are currently found. Only 7–8 priority species lose climatic representation from the network. Hence, despite the likelihood of significant community disruption, we demonstrate that rigorously defined networks of protected areas can play a key role in mitigating the worst impacts of climate change on biodiversity.

### Keywords

Biodiversity, biome, climate change, community disruption, extinction risk, impacts and adaptation, important bird areas, persistence, range shifts, turnover.

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### INTRODUCTION

Networks of protected areas remain our single most valuable resource for conserving global biodiversity (Bruner *et al.* 2001). The majority, however, have been established on a static, present-day snapshot of species' pattern, greatly increasing their susceptibility to anthropogenic drivers of global change (Gaston *et al.* 2006). Climate change in particular represents a key potential threat to their future effectiveness (Burns *et al.* 2003; Hannah *et al.* 2007). Evidence from the paleoecological record of past climate change (Graham & Grimm 1990), together with recent documented changes in species' phenology and distributions (Parmesan & Yohe 2003; Jonzen *et al.* 2006), and modelled

simulations of species' future range shifts (Erasmus *et al.* 2002; Huntley *et al.* 2008), indicate that species' responses to projected climatic change over the coming decades could substantially alter present-day patterns of biodiversity. These shifts are likely to have profound consequences for both individual protected areas and protected area networks as species potentially shift their ranges outside a site's boundaries in response to their individual climatic tolerances (Burns *et al.* 2003), raising the spectre of even greater extinction rates than those currently projected (Thomas *et al.* 2004). However, the converse is also likely to be true, with some species currently outside a site's borders moving in, providing suitable conditions (e.g. habitat) exist. Hence, protected areas that potentially lose a high proportion of

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their current species complement under climate change may well gain a suite of new colonizers in the future. If we are to be proactive in responding to these projected changes through, for example, the development of adaptation strategies aimed at maintaining and improving the effectiveness of protected areas and networks, then it is crucial that we evaluate the projected impacts of climate change on species turnover and persistence across time (and hence the level of community disruption) within those networks.

Several recent attempts have been made to assess the risks posed by climate change to theoretical and/or real-world reserves, using modelled projections of species' future distributional shifts, together with a range of conservation planning tools to assess projected changes in species representation now and in the future (Araujo *et al.* 2004; Hannah *et al.* 2007). However, no assessment of the potential risks to a rigorously defined, existing network, at a pan-continental scale, has yet been made.

The network of Important Bird Areas (IBAs) across sub-Saharan Africa (defined here as sites south of 20° N latitude and excluding islands) represents an ideal system with which to test the resilience of a real-world network to projected climate change. The network comprises a continent-wide series of 863 sites across 42 countries and territories, covering *c.* 2 079 306 km<sup>2</sup> or 7% of the continent. Sites range in size from less than 10 ha to almost 8 million ha (with a median of *c.* 36 000 ha). These sites have been identified as being critical for the conservation of avian biodiversity in the face of the overwhelming threats of habitat loss and fragmentation (Fishpool & Evans 2001). Despite their demonstrated importance, more than 40% currently lack any form of protected status under national or international law. Sites identified as IBAs meet one of four globally standardized criteria: (i) they contain significant numbers of one or more globally threatened species [i.e. those listed as Critically Endangered, Endangered or Vulnerable on the IUCN Red List (<http://www.iucnred-list.org>)]; (ii) they represent a set of sites that together hold a suite of restricted-range or (iii) biome-restricted species; and/or (iv) they hold exceptionally large numbers (i.e. above a given threshold) of individuals of congregatory species (Fishpool & Evans 2001). Together, they support 875 species meeting these criteria (i.e. species that trigger IBA designation), with the network also likely to represent a significant proportion of the region's entire terrestrial breeding avifauna of 1679 species.

Here, we address the specific concern of whether the network will retain its efficacy under projected climatic change. We used the modelled relationship between current climatic variables and the present-day distributions [i.e. the climate envelopes (Pearson & Dawson 2003)] of 1608 bird species, including 815 species meeting criteria 1–3 above (henceforth referred to as 'priority species'), to determine

projected levels of avian community turnover and persistence across the sub-Saharan African IBA network. We utilized two modelling methodologies and three general circulation models (GCMs), across three future time periods (centred on 2025, 2055 and 2085) to represent inherent variability in projections. This also allowed a pragmatic assessment of conservation implications within a timescale relevant to current conservation planning objectives [e.g. post-2010 Convention on Biological Diversity (CBD) targets], as well as providing end-of-century projections that highlight the potential ramifications if serious steps towards mitigation (i.e. CO<sub>2</sub> emissions reductions) are not forthcoming.

We show that while rates of turnover are projected to be substantial in individual IBAs within certain regions, the persistence of individual species across the network as a whole is remarkably high.

## MATERIALS AND METHODS

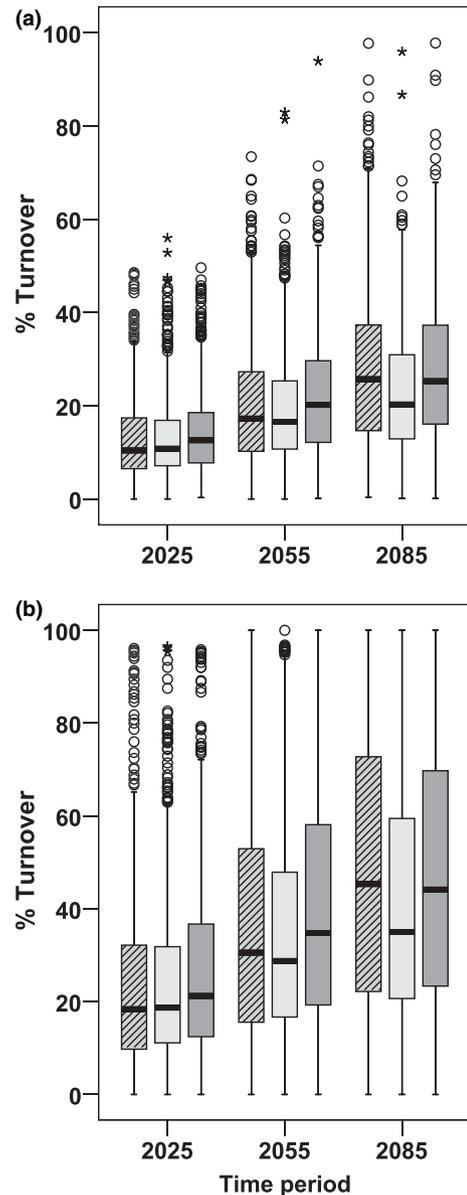
### General approach

To forecast current and potential future avian community composition of individual IBAs, we first derived climate envelope models for all 1608 species at 1° resolution across sub-Saharan Africa, using two modelling methodologies [species–climate response surfaces (CRS) and generalized additive models (GAM) – see Climate envelope modelling approach below]. We then projected these species models onto individual climates [representing the present and the three future scenarios (GCMs) and time periods] for each IBA and used the modelled probabilities of occurrence to generate current and potential future *expected* species inventories. We carried out a rigorous validation of these current expected inventories by comparing them against *observed* inventories (i.e. species lists for individual IBAs derived from long-term monitoring) for a subset of IBAs, which indicated our approach is robust. We define species turnover for each IBA as the sum of colonizers (species for which the IBA becomes climatically suitable in the future) and emigrants (species for which the climate becomes unsuitable) divided by the total species number for which the IBA is climatically suitable in the present plus the total species number for which the IBA is climatically suitable in the future (calculated individually for the 2025, 2055 and 2085 time periods for each of the three GCMs) (Diamond 1969). We define species persistence for each IBA as the proportion of species for which the climate is suitable in the present that also retain suitable climate space in the future. To represent the variability inherent in our ensemble of future climate scenarios, values are expressed as the range across the three GCMs. We also use *ensemble turnover* and *ensemble persistence* where pertinent, defined

simply as the mean of the three GCMs. As both modelling methodologies (CRS and GAM) produced qualitatively and quantitatively similar results, for clarity we present only the results of analyses based on the more robust methodology (CRS). However, figures equivalent to Figs 1 and 2, but presenting the results obtained using GAMs, are available as Supporting Information for comparison (Figs S1 and S2).

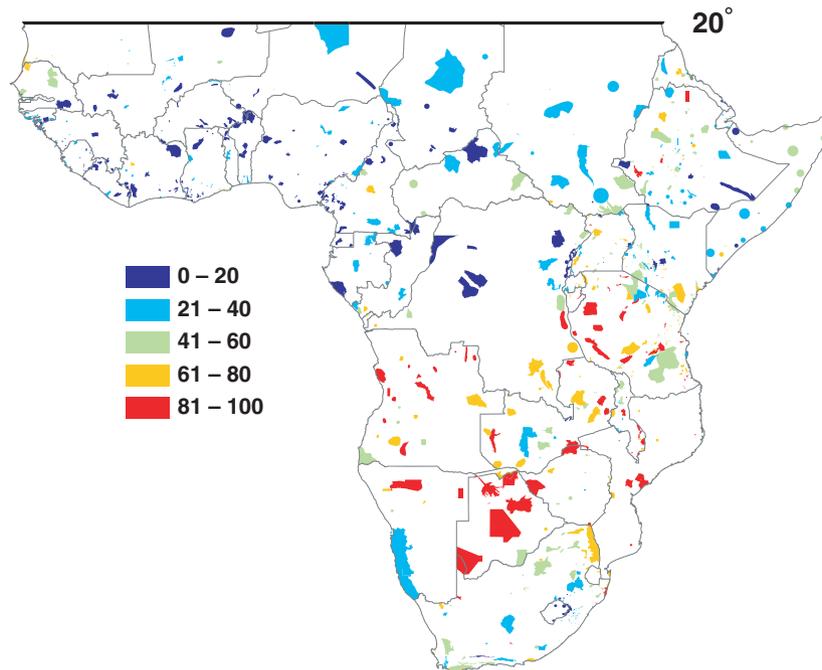
### Species' distributions and current climate data

We used comprehensive distributional data for all terrestrial bird species breeding in sub-Saharan Africa, provided by the Zoological Museum of the University of Copenhagen (Jetz & Rahbek 2002). Data for 1608 species (the entire breeding avifauna of 1679 species minus 71 species recorded from fewer than five grid cells for which modelling was impractical), including 815 priority species, were available as presence-absence in the 1963  $1^\circ \times 1^\circ$  latitude-longitude (*c.* 111 km  $\times$  111 km at the equator) cells encompassing the continental land-mass south of latitude  $20^\circ$  N. Taxonomy followed that of BirdLife International (full taxonomy available at [http://www.birdlife.org/datazone/species/downloads/BirdLife\\_Checklist\\_Version\\_0.xls](http://www.birdlife.org/datazone/species/downloads/BirdLife_Checklist_Version_0.xls)). Digitized IBA boundaries were provided as a GIS polygon coverage by BirdLife International. We used all IBAs within the region that contain a significant terrestrial (as opposed to marine) component and for which a spatial extent has been defined (803 of 863 IBAs). Mean monthly temperature and precipitation data for sub-Saharan Africa were obtained from a global dataset (Hijmans *et al.* 2005; <http://www.worldclim.org>) as  $2.5'$  resolution grids, representing the period 1950–2000 (*i.e.* the present).  $1^\circ$  resolution grids for each monthly variable were derived by ranking the  $2.5'$  cells comprising each  $1^\circ$  cell by elevation, omitting the upper and lower quartiles of  $2.5'$  cells, then calculating the mean of the remainder. By calculating variables in this manner, the resulting values were representative of mean conditions in each cell and were not distorted by inclusion of atypical values from areas of extreme high/low elevation. We chose seven bioclimatic variables *a priori* for their previously demonstrated utility in modelling the climate envelopes of a wide range of bird species in Europe and Africa (Huntley *et al.* 2006): mean temperature of the coldest month; mean temperature of the warmest month; an estimate of the ratio of actual to potential evapotranspiration; wet season duration; wet season intensity; dry season duration; and dry season intensity. The latter four variables were chosen to reflect seasonality in moisture availability (for definitions and derivations see Huntley *et al.* 2006). For each species, we then used the first three variables along with one of the four seasonality variables for modelling [the procedure for selection of the fourth variable for each



**Figure 1** Projected turnover within 803 IBAs for: (a) whole avian communities and (b) priority species. Plots are for three future time periods and for three future climate scenarios: hashed bars represent HadCM3; white bars GFDL-R30 and dark-grey bars ECHAM4. For each box-plot: the black line indicates the median; ends of the box are the lower and upper quartiles; circles represent 'outliers' (*i.e.* values  $\geq 1.5 \leq 3$  box lengths from the ends of the box; asterisks are 'extreme' values (*i.e.*  $> 3$  box lengths away); whiskers represent maximum and minimum values, not including outliers or extreme values.

species is described in detail elsewhere (Huntley *et al.* 2006)]. Models were fitted using only four variables because we could not identify a biologically plausible basis for including additional variables and because the additional



**Figure 2** Spatial pattern of projected percentage ensemble turnover of priority species within Important Bird Areas (IBAs) by 2085. Ensemble turnover of priority species for each individual IBA is calculated as the mean species turnover for the three future climate scenarios (i.e. the three GCMs) for the time period 2085. Absolute percentage turnover for each IBA is placed into one of five classes, with warmer colours representing higher projected turnover.

explanatory power of even the fourth variable was often small (Huntley *et al.* 2006).

### Future climate change ensemble

Projections of future climate change were obtained from transient simulations of three GCMs: HadCM3 (Gordon *et al.* 2000), ECHAM4 (Roeckner *et al.* 1996) and GFDL-R30 (Knutson *et al.* 1999), for the intermediate SRES B2a emissions scenario and for three time periods; 30 year averages approximating to 2025, 2055 and 2085 ([http://www.ipcc-data.org/sres/gcm\\_data.html](http://www.ipcc-data.org/sres/gcm_data.html)). The three GCMs used have an equilibrium sensitivity for global mean temperature close to the mean for the nine models included in the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (Cubasch *et al.* 2001). With respect to simulated precipitation, however, GFDL-R30 is relatively wet, HadCM3 is close to the mean for all nine models, while ECHAM4 is relatively dry, thereby enabling us to represent a principal element of uncertainty in future projections within our ensemble. For each GCM, temperature and precipitation anomalies between present and future time periods were interpolated to 2.5' resolution and applied to the values of the Worldclim present-day climate. 1° grids were then generated as above, before calculating values for each bioclimatic variable.

### Climate envelope modelling approach

The climate envelope of a species represents the modelled statistical association between its present-day distribution and current climatic variables (Pearson & Dawson 2003). This model can be transposed from climate space into geographic space, allowing estimation of the species' current distributional area. Future distributions can then be estimated by projecting this relationship onto scenarios of climate change, assuming that current relationships between climate and distribution are retained.

To investigate potential variability in future projections arising from modelling methodology (Thuiller 2004), we developed 1° resolution models (based on the same datasets and species-specific bioclimatic variable combinations) using two techniques: (i) CRS, a methodology that uses locally weighted regression to fit a response surface to species' presence-absence data. It makes no assumption about the general form of the relationship between a species' probability of occurrence and each bioclimatic variable, and any extrapolation of the fitted model is highly conservative. Previous work has shown it to be effective in modelling the distributions of a range of taxa (Huntley *et al.* 2004); (ii) GAM, a generic methodology, implemented in the statistical package R2.5.1 (<http://www.r-project.org>). While a wide range of modelling methodologies can be

utilized to characterize the climate envelope of a species (e.g. Elith *et al.* 2006), there is considerable debate over which methodology(ies) are 'best' and even how 'best' is defined. As a result, some researchers advocate a model ensemble approach [*sensu* the use of an ensemble of climate change scenarios (Araujo & New 2007)]. There is, however, currently no systematic approach for choosing, for example, which of the many modelling methodologies to incorporate into the ensemble; how to select candidate independent variables from the essentially unlimited pool of abiotic and biotic variables that exists; how to weight different models' contributions according to how 'well' they represent a species' distribution in the present; or how to assess a particular model's ability to extrapolate onto potentially novel climates in the future. Hence, rather than attempting to combine arbitrarily the results of the two modelling methodologies, we assessed the ability of each to simulate the observed inventories of 64 IBAs. Paired *t*-tests on both our assessment metrics [sensitivity and true skill statistic (TSS) – see IBA modelling approach] for the 64 IBAs indicated that CRS performed consistently better (on sensitivity:  $t = 2.451$ ,  $P < 0.05$ ; on TSS:  $t = 2.621$ ,  $P < 0.05$ ). Hence, all analyses presented herein are based on the CRS modelling approach (see Figs S1 and S2 for a comparison using GAMs).

Validation of CRS models for species recorded from  $> 20$   $1^\circ$  grid cells was carried out through *K*-fold partitioning, with projection performance assessed using the values obtained for the area under the curve (AUC) of a receiver-operating characteristic plot (Fielding & Bell 1997) ( $K = 100$ , with replacement; models calibrated on a 70% random sample of the observed data; projection accuracy evaluated on the remaining 30%). We fitted models for 1401 species; 89% of species exhibited *K*-fold partitioned AUCs  $\geq 0.9$  [ $0.952 \pm 0.035$ ; median  $\pm$  standard deviation (SD)] indicating high model performance (Swets 1988) (no species had a *K*-fold partitioned AUC  $< 0.7$ ) [median omission and commission error rates (Fielding & Bell 1997) across all 1401 full models (i.e. using all observed data for each species)  $\pm$  SD =  $0.163 \pm 0.103$ ;  $0.023 \pm 0.046$  respectively]. For the 207 species recorded from 20 or fewer  $1^\circ$  grid cells, validation was carried out, for each species, via a jack-knifing approach. Taking the observed data, the first of the 1963  $1^\circ$  grid cells comprising sub-Saharan Africa was dropped. A model was then fitted on the remaining data and used to simulate the probability of occurrence in the dropped cell. The dropped cell was then replaced and the process repeated with the next cell and so on until all 1963 cells had been dropped in turn. Projection accuracy was then assessed via AUC through comparing the observed distribution with the simulated probabilities of occurrence across all 1963 cells. Eighty-three per cent of species exhibited a jack-knifed AUC  $\geq 0.9$  ( $0.986 \pm 0.075$ ;

median  $\pm$  SD) again indicating high-model performance [median omission and commission error rates across all 207 full models  $\pm$  SD =  $0.286 \pm 0.161$ ;  $0.001 \pm 0.002$  respectively].

### IBA modelling approach

Our IBA modeling approach had two key objectives: the first was to reduce any potential bias caused by the mismatch in scale between the species' models (generated at  $1^\circ$  resolution) and many of the smaller (or very large) IBAs. This precluded determining a species' presence or absence within an IBA based simply on the intersection of each IBA polygon with each species'  $1^\circ$  modelled distribution. The second was to retain the distinctive climatic character of each IBA to maximize our ability to predict its species' assemblage. For topographically diverse IBAs and those with a large spatial extent, this precluded generating a simple mean climate, because such an approach would even out the climatic variability inherent across large elevational and/or latitudinal gradients. To meet these two objectives, we therefore characterized one or more bioclimates for each individual IBA and used these, together with our species'  $1^\circ$  models, to simulate directly each species' presence or absence in each IBA. This was achieved using a spatial intersection, within a GIS, of the IBA polygons, a generic  $1^\circ$  grid and  $2.5'$  grids for each of the seven bioclimatic variables and for elevation, according to the following procedure: (i) Each IBA polygon was intersected with the  $2.5'$  elevation grid (together with the seven bioclimatic variable grids) to determine the identity of the  $2.5'$  cells comprising each IBA and the elevational range of those cells. (ii) Each IBA polygon was then intersected with the generic  $1^\circ$  grid to determine the IBA's spatial extent. (iii) If the IBA's component  $2.5'$  cells spanned an elevation  $\leq 600$  m and its extent was  $\leq 1^\circ$  of longitude or latitude, then the value of each bioclimatic variable for that IBA (i.e. its bioclimate) was computed based on its component  $2.5'$  cells, in the same manner as described previously (see Species' distributions and current climate data). (iv) If the IBA's extent was  $> 1^\circ$  of longitude or latitude, the IBA polygon was split into two or more sub-polygons (i.e. with each laying entirely within a single  $1^\circ$  cell). Values for each bioclimatic variable were then computed based on the  $2.5'$  cells comprising each sub-polygon as described previously, thereby generating two or more bioclimates for that IBA. (v) However, if the elevational range of either the full IBA polygon or a sub-polygon exceeded 600 m, then the component  $2.5'$  cells were stratified into two or more elevational bands, where the number of bands was determined as: one plus the integer portion of the result of dividing the elevational range in metres by 600. A 600-m threshold was chosen on the basis of the mean temperature lapse rate (*c.*  $6^\circ \text{C km}^{-1}$ ) and

the magnitude of the uncertainty typical of interpolated climatic values ( $c. \pm 1^\circ\text{C}$  for temperature variables). Application of this threshold resulted in elevational bands between 300 and 600 m, with the mean temperature for adjacent bands thus generally differing by an amount comparable with or greater than the inherent uncertainty in the interpolated values. Bioclimatic values were then computed based on the component  $2.5'$  cells comprising each elevational band, of each IBA polygon or sub-polygon, as described previously, and thereby potentially generating multiple bioclimates for that IBA. (vi) Finally, the  $1^\circ$  models for all 1608 species were projected onto each IBA's bioclimate(s), for the present and for all time periods and GCMs.

To express the probabilities of occurrence simulated by each model as presence or absence of the species, we applied the threshold probability that maximized Cohen's  $\kappa$  for the  $1^\circ$  model (Cohen 1960; Huntley *et al.* 2006). Expected species inventories for each IBA were then generated according to each species' presence or absence as defined by this threshold. Where an IBA consisted of  $> 1$  bioclimate, a species was regarded as present if its probability of occurrence exceeded the threshold in at least one of the bioclimates characterized for that IBA.

Despite our best efforts, some errors of omission (false negatives) and commission (false positives) are inevitable when projecting species'  $1^\circ$  models onto the bioclimate(s) of individual IBAs; commission errors in particular are likely, because a species has a much higher likelihood of being absent from an IBA for non-climatic reasons (e.g. lack of suitable habitat) than from a  $1^\circ$  cell. To validate our approach, we therefore compared our expected inventories for the present with observed species inventories for individual IBAs where sufficient monitoring has occurred such that observed inventories are likely to be largely (although never entirely) complete. Comparison of modelled with observed inventories for 64 IBAs in five relatively data-rich countries indicates our approach is robust; (median sensitivity  $\pm$  SD =  $88 \pm 11\%$ ; median Hansen–Kuiper discriminant [or TSS (Allouche *et al.* 2006)]  $\pm$  SD =  $0.721 \pm 0.137$ ; see Table S1). Note that this analysis also provides a further independent validation of our CRS models for all species.

## RESULTS

Across all IBAs in the network, projected turnover of both whole avian communities (i.e. all bird species modelled to be present within an IBA) and the subset of priority species clearly increases with time period, as climate change becomes more pronounced towards the end of the century (Meehl *et al.* 2007) (Fig. 1). Variability is also evident across our ensemble of future climate scenarios, notably between

the wet GCM (GFDL-R30) and the two drier GCMs (HadCM3 and ECHAM4). However, Jaccard similarity coefficients, generated across all modelled IBA inventories for whole avian communities, indicate a high degree of concordance among GCMs, across all three time periods (Table S2). Hence, despite some variability in turnover, absolute species composition within individual IBAs exhibits a high degree of consistency between GCMs, further increasing confidence that our modelled projections are robust.

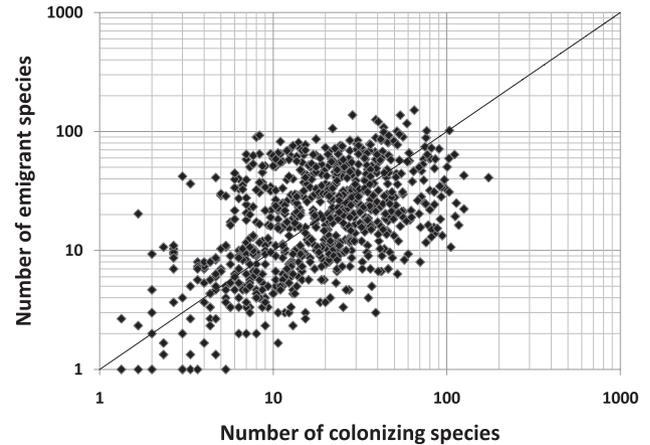
Median projected turnover across all IBAs for whole avian communities is 10–13% by 2025, rising to 20–26% by 2085, and for priority species, 18–21% rising to 35–45%. Consistently higher turnover in this group is likely a result of the tendency for range- and biome-restricted species to show greater sensitivity to climate change, arising from their comparatively narrow climatic niches, in contrast to more widespread and generalist species (Thuiller *et al.* 2005). This is reflected by a significantly smaller overlap between the present and projected 2085 ranges of the 815 priority species, in comparison with the remaining 793 species (median overlap for priority species = 31.5%; non-priority species = 56.3%;  $t = 12.6$ ,  $P < 0.001$ ; analysis based on each species'  $1^\circ$  modelled distribution for the present and ensemble mean distribution across GCMs for 2085). However, turnover is distributed unevenly across the continent. Areas of high ensemble turnover for 2085 show a similar spatial pattern for both whole avian communities (Fig. S3) and priority species (Fig. 2) but are far more pronounced in the latter. Areas of high ensemble turnover for priority species are evident as a swathe running east–south-east across southern Africa, from Angola and northern Namibia, to Mozambique, and north–north-east from north-eastern South Africa to the Ethiopian Highlands. The Horn of Africa and west coast of Senegal also exhibit substantial turnover. Ensemble persistence (Fig. S4) follows a similar, but inverse, geographical pattern (compare Fig. 2 with Fig. S4). As an illustration of this regional disparity, of the 58 IBAs within Botswana, Zimbabwe and Zambia [a region of relatively low ensemble persistence comprising large elements of the Kalahari-Highveld and Zambezi biomes (Fishpool & Evans 2001)], 83% are projected to retain suitable climate space for more than half of their current whole avian community complement by 2085, with 24% retaining suitable climate space for more than half of their complement of priority species. This contrasts with 100% and 95% respectively for the 64 IBAs found within Nigeria, Cameroon and the Central African Republic [a similar-sized region of relatively high ensemble persistence, composed primarily of the Sudan-Guinea Savanna and Guinea-Congo Forest biomes (Fishpool & Evans 2001)].

**Table 1** Projected change in IBA representation of priority species

Biome	No. species	Median % change in IBA representation by:		
		2025	2055	2085
Afrotropical Highlands	178	-16	-29	-41
East African Coast	35	10	18	17
Fynbos	8	-10	-48	-61
Guinea-Congo Forests	263	8	11	15
Kalahari-Highveld	13	-7	-15	-17
Lake Victoria Basin	12	-24	-34	-36
Namib-Karoo	22	-22	-46	-63
Sahara-Sindian	13	-3	6	37
Sahel	16	-7	5	4
Somali-Masai	113	-6	-11	-19
Sudan & Guinea Savanna	53	26	49	70
Zambezian	61	-13	-24	-33
(Not biome restricted)	28	-10	-26	-34
Total/median change	815	-7	-15	-19

Projected change in IBA representation of priority species categorized by biome [787 of the 815 priority species are restricted to one of the 12 biomes defined across sub-Saharan Africa (Fishpool & Evans 2001)]. Percentage change in representation is defined as the change in the number of IBAs a species is projected to occur in, between the present and future time period, expressed as a percentage of the number of IBAs a species is projected to occur in at present, and averaged across the three GCMs.

The spatial character of these turnover patterns becomes even clearer through examination of the projected change in IBA representation of priority species (defined here as the change in the number of IBAs in which a species is projected to occur, between the present and the future, averaged across GCMs), categorized by biome (Table 1). Of the 12 broad biome-types, species of the Namib-Karoo, Fynbos and Afrotropical Highland biomes are projected to lose the greatest IBA representation by 2085 (-63, -61 and -41% respectively), while species of the Sudan & Guinea Savanna and Sahara-Sindian biomes in contrast are projected to increase their representation within IBAs by on average 70 and 37% respectively (note that the latter biome also extends into Asia; our results refer only to the African component). Moreover, these changes in representation are projected to become apparent even in the relatively short time window to 2025 (Table 1). Such patterns are likely to result from the shifts in, and disappearance of, extant climates, together with the probable generation of novel



**Figure 3** Relationship between the number of projected emigrants and number of projected colonizers within individual Important Bird Areas (IBAs), for priority species. 'Number of emigrant species' is the number of priority species (averaged across the three GCMs) for which an IBA is projected to become climatically unsuitable by 2085 (+1 to allow logarithmic transformation); 'number of colonizing species' is the number of priority species (averaged across the three future climate scenarios) for which climatic conditions are projected to become suitable by 2085 (+1 to allow logarithmic transformation). Black line represents no net change in overall species number within an IBA (i.e. number of colonizers = number of emigrants).

climatic conditions, across Africa (rather than extant climates simply shifting to regions that are under-represented by the current IBA network) and is supported by recent evidence indicating that disappearing climates will be concentrated in tropical mountain regions and the poleward sides of continents (Williams *et al.* 2007). Our results therefore suggest that these changes could lead to substantial reductions in range and a consequently elevated extinction risk for species within these climatic zones (Sekercioglu *et al.* 2008).

Nevertheless, median projected persistence for whole avian communities (i.e. the persistence of all bird species modelled to occur currently within an individual IBA) across all IBAs in the network is notably high (74–80%), even for late 21st century (i.e. 2085) projections and remains substantial for priority species (55–68%). Furthermore, those IBAs projected to lose suitable climate space for the largest numbers of priority species are also projected to experience most new priority species' colonizations (Fig. 3). This likely reflects the representation of a diversity of climatic conditions within those IBAs, resulting from their tendency to be located in areas of relatively high relief [altitudinal range within IBAs correlates positively with numbers of both emigrant (Spearman's  $\rho = 0.312$ ,  $n = 803$ ,  $P < 0.001$ ) and colonizing priority species ( $\rho = 0.250$ ,

$n = 803$ ,  $P < 0.001$ ], and hence the presence of relatively large numbers of priority species, whose diverse climatic requirements can be met. While such topographically related climatic diversity will also characterize the future climates of those IBAs, the regional-scale changes associated with climate change will likely modify all local climates within those IBAs. As a result, the climatic niches of many species currently present will disappear, while conditions will become suitable for many others to colonize.

Persistence at the level of the individual species meanwhile is remarkably high; of the 815 priority species triggering IBA designation, 714–746 (88–92%) are still projected to retain suitable climate space in one or more of the IBAs for which they are currently trigger species, by 2085. Of the remaining priority species, suitable climate space for 62–93 will become newly available in one or more IBA(s) elsewhere within the network. Only 7–8 priority species are projected to lose all suitable climate space from the network under late 21st century climate change.

### Caveats

The availability of species' distribution data is a key constraint when conducting regional studies across entire taxa, necessitating our use of 1° resolution distributional data for model development. As a result, there is a potential mismatch in scale between our species' models built at 1° resolution (a cell of  $c. 111 \times 111$  km) and the many much smaller IBAs (smallest IBA considered is  $c. 10$  ha). We attempt to reduce any effect of this mismatch by projecting all 1608 individual species' models onto distinct climates characterized for each IBA at a much finer resolution. Nevertheless, at the scale of the smallest IBAs there is undoubtedly the potential for local meso/microclimate to diverge from interpolated values representative of the regional macroclimate, because of, for example, local topography, lake effects or proximity to the coast. For the 64 IBAs for which observed inventories are available, however, no evidence is apparent of the systematic bias in expected species' inventories that such divergence would generate. More important is the narrower range of habitats likely to be found in an IBA that is substantially smaller than the 1° cell in which it lies; this probably accounts for the observed tendency for expected species' inventories of the 64 IBAs to include species not found in their observed species' inventories (i.e. errors of commission due to an IBA being climatically suitable for a particular species, but lacking suitable habitat).

Second, in calculating our estimates of turnover, persistence and representation, we make the transparent assumption that all species will be able to realize their respective range shifts and colonize all IBAs in which the climate is projected to become suitable, as well as losing representa-

tion within IBAs for which the climate is projected to become unsuitable. In reality, however, it is unlikely for many species that projected climatic shifts within a protected area will lead to the *immediate* loss of, or colonization by, that species. Adaptation, for example, may permit future persistence under new climates (Thomas *et al.* 2001; Skelly *et al.* 2007). Phenotypic plasticity and metapopulation lag could result in a climatically induced extinction debt (Hanski & Ovaskainen 2002) in some regions, over and above that elicited by habitat loss and fragmentation (Nagelkerke *et al.* 2002). Hence, as climate change proceeds, some species could become committed to localized extinction even in apparently intact habitats. Conversely, but as importantly, realized colonization rates of individual species will be dependent upon realized shifts in critical habitat types and resources (e.g. prey species) (Graham & Grimm 1990) (likely to be a particularly important factor for habitat/resource specialists), species-specific dispersal ability and landscape permeability (Mendez *et al.* 2006). While these uncertainties will tend to reduce the rate of realized community disruption (i.e. by apparently reducing turnover and increasing persistence) in comparison with our projections, other factors may actually lead to higher rates than our projections indicate. For example, interactions between climate change and other drivers of global change (e.g. disease, invasive species) could result in local extinctions of species within an IBA *before* the changes in mean climatic conditions that actually affect those species have occurred (Dukes & Mooney 1999; Pounds *et al.* 2006). Indeed, such interactions are likely to increase in occurrence as 'extreme' climatic events become more common (Meehl *et al.* 2007), thereby exacerbating realized community disruption.

Quantifying these inherent uncertainties with our existing level of knowledge is clearly unfeasible. Our projections therefore simulate the *committed* (*sensu* Thomas *et al.* 2004) community disruption under climate change, whereas realized disruption within individual IBAs may occur over longer (or shorter) time periods, dependent upon these uncertainties. Nevertheless, we contend that our results are demonstrably robust. Under an assumption of zero (or very slow) dispersal, for example, representation of priority species (in terms of the number of IBAs in which a species is projected to be found in the future, in relation to the number of IBAs in which it currently triggers designation) would be projected to decline on average by 51–56%, with important ramifications for species' representation targets, particularly at regional and local scales. However, persistence at the level of individual species would remain notably high, because almost 90% of priority species are projected to retain suitable climate space within at least one IBA in which they currently trigger designation (i.e. no shifts in range are necessary).

Furthermore, the range shifts required to reach newly suitable IBAs, while substantial in a minority of cases, are far less so for the majority of species. For each of the 1608 species, we calculated the minimum geodesic distance between the centroid of each IBA projected to become newly climatically suitable for that species in the future (2085), and the centroid of the nearest IBA projected to be currently occupied. The median distance (across all 1608 species, and within a species, across all IBAs projected to become climatically suitable, averaged across GCMs) was 136.3 km (range = 18.8–5988 km). Hence, the median distance a species will have to shift each year from an IBA in which it is currently projected to occur, to occupy all newly climatically suitable IBAs by 2085, is *c.* 2 km. Despite this figure masking a wide range of variability across individual species, it suggests that the rates of turnover we project are potentially achievable and hence that our results represent a realistic scenario of community disruption as a consequence of 21st century climate change.

## DISCUSSION

Our results provide novel and unique support, at a pan-continental scale and across an entire taxon, for the broadly held, but until now largely untested contention that individual protected areas and entire networks will be committed to substantial community disruption as climate change proceeds. These impacts will not be random, but will instead differentially affect individual species, groups of species and entire regions, and hence the protected areas within them, to greatly varying extents. The potential for substantial impacts of climate change in some tropical regions is in contrast to recent work suggesting that human-induced changes in land-use are the principal threat to avian communities in tropical and sub-tropical regions (Jetz *et al.* 2007). While in no way diminishing the proximate nature of the threat of anthropogenic habitat loss, our results highlight the risks of ignoring shifts in species' ranges in response to climate change and indicate that climate change is likely to be as great a threat to avian conservation in Africa as it is in higher latitudes, such as Europe (Huntley *et al.* 2008).

Such disruption would have profound implications for community stability and function [e.g. through loss or disruption of species-mediated ecological processes (Duffy 2003) and the generation of 'no-analogue' communities (Williams & Jackson 2007)], protected area management [e.g. representation targets (Margules & Pressey 2000)], and the maintenance of ecosystem services (Hector & Bagchi 2007). Moreover, our projections indicate that these impacts could become apparent on a timescale relevant to current conservation planning objectives (i.e. by 2025), with ramifications for post-2010 CBD targets. Meanwhile, by

the late 21st century, a majority of IBAs within regions of highest projected turnover will no longer retain suitable climate for many of the species for which they were designated, but will instead potentially offer refuge to an entirely new species complement.

Perhaps the greatest conservation challenge we face therefore, is to facilitate the movement of species across the wider landscape, while ensuring the continued viability of individual protected areas, which often represent the last remnants of intact or semi-intact habitat within a region. The unique scale of our analysis, in terms of both number of species and geographical extent, highlights the urgent need for regionally focused, adaptive management approaches, targeted in the first instance towards regions of greatest projected turnover and lowest projected persistence. For the sub-Saharan African IBA network, these results will help to prioritize those strategies across regions and provide the basis of a framework for targeting adaptive management options. Such strategies should include: (i) increasing the number and size of protected areas to maximize the representation of the range of environmental conditions found in a region (Coulston & Riitters 2005), rather than simply maximizing the representation of individual species; (ii) increasing permeability within a matrix dominated by human land-use [e.g. through the provision of stepping stones and active management of current land uses to render them less inimical to biodiversity (Fischer *et al.* 2006)]; (iii) habitat restoration, where feasible, of critical habitat types to facilitate range-shifts, in particular for globally threatened and/or restricted-range species; (iv) regional or pan-continental species representation targets, that reflect the potential magnitude of species' range shifts; and (v) adequate monitoring to assess the efficacy, and inform the adaptive component, of management actions (Sutherland 2006). We would suggest that the latter is particularly crucial when dealing with a threat such as climate change, where uncertainty is high (Meehl *et al.* 2007). However, additional research is now urgently required to build on and refine the broad-scale analyses presented here. Regionally focused studies at a finer grain are needed to inform specific adaptive management actions at the level of individual IBAs and the surrounding landscape, where differing regional contexts and species' assemblages may necessitate novel solutions. Where finer-scale data for individual species are lacking, efforts to collect such data must be given greater importance. Without such data, the development, prioritization and targeting of adaptive management options cannot be effectively coupled with land cover and other fine-scale processes that define species' distributions at management-relevant scales.

More generally, a paradigm shift to explicitly incorporate climate change into the designation and management of

protected areas and networks is a clear and pressing need. For example, the establishment of protected areas based solely on the premise that they will retain their current species complement must be re-evaluated, from both a conservation and legal perspective. Where new colonizers are species of conservation concern, these must be included in flexible management strategies, while difficult decisions are likely to have to be made where management practices currently seek to maintain a species in an area that may cease to be climatically suitable. Despite some recent innovative proposals (e.g. Pyke & Fischer 2005; Williams *et al.* 2005), there is the very real risk of doing too little, too late, with the price of delayed action, both in terms of cost and effectiveness, potentially prohibitively high (Fuller *et al.* 2007; Hannah *et al.* 2007).

Our analyses are based on future projections of climatic change from the IPCC Third Assessment Report (Cubasch *et al.* 2001). However, if we had been able to use the latest projections from the Fourth Assessment Report (Meehl *et al.* 2007) it is unlikely that our conclusions would differ. Mean global-projected changes in temperature and precipitation for a given SRES emissions scenario are almost identical in the two reports, while across sub-Saharan Africa regional patterns and magnitudes of mean-projected change are also broadly similar (Christensen *et al.* 2007). Of more concern, however, is that the time-scale for our projections is likely to prove conservative if the current CO<sub>2</sub> emissions trajectory continues. Emissions growth rate since 2000 has been greater than for even the most fossil-fuel intensive of the IPCC emissions scenarios and currently most closely resembles the A1FI storyline of the A1 scenario family (Raupach *et al.* 2007), with a projected temperature increase in the range of 2.4–6.4 °C (in comparison with 1.4–3.8 °C for the B2 scenario family used here) (IPCC 2007). Should this trend continue, then it is likely that our projections for avian turnover and persistence for 2085, will be manifest on a shorter time-scale, perhaps as early as 2055.

Despite these concerns, however, our projections indicate that the sub-Saharan African IBA network is manifestly robust, at least under medium-term projections of climatic change. Although predicated on the presence of under half of the region's avifauna, it includes the climatic niches of all 1608 species (all species modelled are projected to be currently found in one or more of the 803 IBAs). Further work is required to determine whether comparable representation would have been achieved had the network been established on the basis of some target other than the conservation of current patterns of diversity and, to a lesser extent, process (i.e. is the network's climatic robustness simply a function of its area?). Given that the network comprises just 7% of the land surface of Africa, however, it is likely that in fulfilling its remit, the network samples a

majority of Africa's unique, as well as generic climates, facilitating climatic representation of priority species, even under an ensemble of late 21st century climate change scenarios. We contend therefore that the effective conservation of much of the planet's biodiversity under climate change will depend upon rigorously defined networks of protected areas, displaying functional connectivity, at regional and continental scales.

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#### SUPPORTING INFORMATION

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

**Figure S1** Projected turnover using an alternative modelling approach.

**Figure S2** Spatial pattern of projected ensemble turnover of priority species using an alternative modelling approach.

**Figure S3** Spatial pattern of projected ensemble turnover of whole avian communities.

**Figure S4** Spatial pattern of projected ensemble persistence of priority species.

**Table S1** Accuracy of expected compared with observed IBA inventories.

**Table S2** Similarity between projected future species inventories.

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