Assessing the Impacts of Future Climate Change on Protected Area Networks: A Method to Simulate Individual Species' Responses

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Received: 5 July 2006/Accepted: 28 March 2008 © Springer Science+Business Media, LLC 2008

Abstract Global climate change, along with continued habitat loss and fragmentation, is now recognized as being a major threat to future biodiversity. There is a very real threat to species, arising from the need to shift their ranges in the future to track regions of suitable climate. The Important Bird Area (IBA) network is a series of sites designed to conserve avian diversity in the face of current threats from factors such as habitat loss and fragmentation. However, in common with other networks, the IBA network is based on the assumption that the climate will remain unchanged in the future. In this article, we provide a method to simulate the occurrence of species of conservation concern in protected areas, which could be used as a first-step approach to assess the potential impacts of climate change upon such species in protected areas. We use species-climate response surface models to relate the occurrence of 12 biome-restricted African species to climate data at a coarse (quarter degree-degree latitudelongitude) resolution and then intersect the grid model output with IBA outlines to simulate the occurrence of the species in South African IBAs. Our results demonstrate that this relatively simple technique provides good simulations of current species' occurrence in protected areas.

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Institute of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark We then use basic habitat data for IBAs along with habitat preference data for the species to reduce over-prediction and further improve predictive ability. This approach can be used with future climate change scenarios to highlight vulnerable species in IBAs in the future and allow practical recommendations to be made to enhance the IBA network and minimize the predicted impacts of climate change.

Keywords Biodiversity · Climate change · Climate envelope modeling · Protected area network

Introduction

Over recent decades, species have been declining and becoming extinct, both locally and globally, at an alarming rate (BirdLife-International 2000; Brooks and others 2002; Pimm and others 1995; Thomas and others 2004b). The conservation of biodiversity is therefore an urgent priority and much effort has been put into identifying localities of maximum diversity (Balmford and others 2001; De Klerk and others 2002; Myers and others 2000) and the protection of such areas (De Klerk and others 2004; Muriuki and others 1997).

BirdLife International's Important Bird Areas (IBA) network is a biodiversity conservation network that identifies priority sites for the protection of the global avifauna. As with most conservation networks, algorithms for the selection of priority sites are based entirely upon current species' distributions. Such networks are essential for the urgent protection of species of high priority due to their threat status, restricted distributions, or other factors. However, they make no allowance for the fact that species' ranges are dynamic over time, and thus, alone, these networks may be inadequate for the conservation of species with shifting ranges. Consequently, there is an equally urgent need to identify those sites that will remain important for species over the medium to long term. IBAs predicted to remain resilient to change in the future should be prioritized for protection, and the existing network should be enhanced to minimize the predicted impacts of climate change.

Global climate change is one major factor that has already caused recent alterations in species' ranges (Parmesan and others 1999; Parmesan and Yohe 2003; Root and others 2003; Walther and others 2002; Warren and others 2001) and is likely to become increasingly important in altering species' ranges over the current century (Hill and others 2002; Thomas and others 2004a).

Biodiversity in Africa

Tropical and equatorial ecosystems are noted for their relatively high biodiversity; tropical latitudes also contain a high proportion of the world's "biodiversity hotspots," characterized by their concentrations of endemic species (Myers and others 2000). Of the top 25 global hotspots recognized by Myers and others (2000), four lie in mainland sub-Saharan Africa, while Madagascar represents a fifth. Sub-Saharan Africa plays host to over 1900 bird species, approximately 20% of species globally. Of these, 947 are confined solely to the Afrotropical region, around 340 being of global conservation concern (Fishpool and Evans 2001). In addition to the hotspots of endemism, sub-Saharan Africa has many other areas that harbor local concentrations of biodiversity. The mountainous areas of equatorial east Africa are one such example, with highaltitude cloud forests characterized by a suite of ecologically restricted species found only in these spatially limited habitats. During recent decades, similar cloud forests elsewhere have suffered biodiversity losses, which correspond to regional warming and reduced incidence of cloud formation in the forests, especially during the dry season (Pounds and others 1999). Comparisons of future climate scenarios and current climate have revealed that in the future there is likely to be a substantial loss of climate types in mountain regions of Africa and an increase in novel, no-analogue climates (Williams and others 2007).

Predicted Climate Change

Global climate is expected to change substantially in the course of the present century, primarily as a consequence of anthropogenic greenhouse gas emissions (Christensen and others 2007). In many regions at tropical and sub-tropical latitudes, the most important changes are likely to

be in precipitation patterns, both spatially and temporally. The recent IPCC Fourth Assessment Report projects that by 2080-99 declines in rainfall will be likely in most subtropical areas, with increases projected in areas of regional tropical precipitation maxima. Intensity of precipitation is also projected to increase, particularly in tropical areas of increasing precipitation, with a tendency for drying of mid-continental areas (Meehl and others 2007). In the case of the African continent, there is a general consensus among GCM simulations indicating modest increases in mean annual precipitation over equatorial Africa, particularly eastern regions. Conversely, northern, southern and parts of western Africa are projected to have reduced precipitation in most models, soil moisture being markedly reduced as a result (Meehl and others 2007). Increases in mean annual precipitation in the equatorial latitudes, however, often mask seasonal shifts. In equatorial east Africa, for example, GCM simulations indicate modest changes in precipitation during June-August but substantial increases in precipitation during December-February (Meehl and others 2007). Temperature increases projected for Africa by 2080-99, while modest compared to high latitudes, are nonetheless 4-5°C higher than temperatures recorded in 1980-99, based on 20 general circulation models and a medium-high emissions scenario (Boko and others 2007), with less warming in equatorial and coastal areas.

Predicting Ranges Using Climate Data

Large-scale distribution patterns of many species, from autotrophs through to top predators have been reliably simulated using climate variables (H-Acevedo and Currie 2003; Huntley and others 2004). The geographical ranges of a majority of the bird species of Europe and Africa can be been modeled well using a limited number of climatic variables (Huntley and others 2006, 2007). There is evidence, both from the Quaternary palaeoecological record (Graham and Grimm 1990; Huntley and others 1997) and from recent observational studies (Parmesan and others 1999; Parmesan and Yohe 2003; Root and others 2003; Walther and others 2002; Warren and others 2001), which shows species responding to environmental changes primarily by shifting their geographical ranges. Simulations of various European plant and animal species' potential future distributions reveal 21st century climate changes may shift species' potential range boundaries >1000 km (Hill and others 2002; Huntley and others 1995; Huntley and others 2008). There is an urgent need to investigate the extent to which ranges of African species might also shift, and to modify conservation management strategies accordingly.

Terrestrial ecosystems of many tropical areas, but especially of Africa, however, are not only threatened by climate change but also are already under considerable pressure from the growing human population. Tropical forest destruction and other human land-use are reducing the extent of the remaining habitat available to support the unique and rich biodiversity of these regions. Desanker and others (2001), while noting that land-use change is and will continue to be "the major driver of land-cover change in Africa," consider that biodiversity losses in Africa are likely to be accelerated by climate change, citing the Afromontane and Cape centers of endemism and biodiversity as particularly vulnerable. Jetz and others (2007) also highlight the likely combined impact of land-use and climate changes on bird species in the tropics. In Britain, the combination of climate change and habitat alteration during the last 30-50 years has had major impacts upon butterfly ranges and abundances. Habitat loss has limited species' ability to shift their ranges in response to climate change (Warren and others 2001). Similar impacts can be expected in the future for many African taxa.

Objective

The overall aim of this study is to assess whether coarse scale climate-envelope modeling approaches can be used as a tool to simulate species' occurrences within networks of priority sites for conservation. If so, such an approach could be used with future climate simulations to forecast species turnover within protected areas and to make practical recommendations to enhance protected area networks to minimize the possible impacts of climate change. This aim is addressed using twelve bird species of sub-Saharan Africa and assessing our ability to predict their current known occurrences in IBAs of South Africa.

Methods

We chose to work on birds in Africa because knowledge of their distribution, biodiversity, and endemism patterns is better than for any other major taxonomic group and because an IBA network has been identified and documented across the region (Fishpool and Evans 2001). Also, the region is predicted to experience substantial climate change during this century; the impacts of which will be exacerbated by intensifying human land-use, rendering correctly targeted conservation efforts vital if a substantial part of extant biodiversity is to survive to the 22nd century. South Africa was chosen as the case study region because of the more complete knowledge of the aviafuna in the region compared to many other parts of Africa. We selected 12 biome restricted bird species (Table 1), two from each of the six major biome types of South Africa (Afro-tropical highland, East African coast, Zambezian, Kalahari-Highveld, Namib-Karoo and Fynbos—Fishpool and Evans 2001).

We constructed a geographical information system (GIS) in which a series of spatial data sets were assembled. The GIS incorporates:

- Meteorological data
- Topographical data
- Bird species' distribution data—existing 1° resolution grid data for the whole of sub-Saharan Africa birds (http://www.zmuc.dk/commonweb/research/blueprint-africa.htm), replacing this with 0.5° and 0.25° data where it was available (South Africa, Botswana, Lesotho, Swaziland, Namibia, Zimbabwe, Kenya and Uganda; from Carswell and others 2005; Harrison and others 1997; Lewis and Pomeroy 1989). Note, however, that many of the chosen species are endemic to southern Africa.
- Late 21st century climate change scenarios—developed using output from the Hadley Centre's HadCM3 general circulation model for the 30-year averages of the period approximating to 2055, using a B2a emissions scenario (http://www.ipcc-data.org/sres/gcm_data.html).
- Digitised IBA outlines for South Africa (101 IBAs)

Landuse types within the South African IBAs were extracted from Fishpool and Evans (2001) and were assigned to IUCN level 1 habitat types (http://www.iucnredlist.org/info/major_habitats.html). Habitats used by the bird species were extracted from the seven-volume *Birds of Africa* (Brown and others 1982) and species assigned to relevant IUCN level 1 habitat types.

Using the topographic data, we made elevation-sensitive interpolations of the meteorological data and developed gridded bioclimatic data sets. The relationships between species' ranges and climate were then investigated by fitting species–climate response surfaces ("climate-envelope" models) to the species' distribution and bioclimatic data (see Huntley and others 1995 for details).

Previous work (Huntley and others 2006) suggested that, for African birds, good models of fit required bioclimate variables that incorporated measures of summer and winter temperatures (MTWA and MTCO = mean temperature of the warmest and coldest month respectively), water availability (APET = the ratio of actual to potential evapotranspiration), and seasonal water availability. The seasonal variable we use here is a measure of the intensity of the dry season (DRYINT), derived by summing daily water deficit during the dry season(s); dry season initiation and cessation being defined as when the summed water deficit crossed a threshold value. We used locally weighted regression to fit climate response surfaces for the 12

Table 1 Distribution and modeling success for the twelve sel	and modeling succes	ss for the twelve selec	lected biome-restricted species	stricted specie	S							
Scientific name	Common name	Biome	Number of	Model simulation	Predictive ability in	Predictive ability	Presences correctly	Absences correctly	Predictive size thres	Predictive ability afte size thresholds (TSS)	ter removin 3)	Predictive ability after removing IBAs below size thresholds (TSS)
			IBAs in which species is listed	across Africa (AUC)	IBAs from intersecting grid output and IBA outlines (TSS)	in IBAs after habitat filtering (TSS)	predicted (using habitat filtering) (%)	predicted (using habitat filtering) (%)	<500 ha	<1000 ha	<2000 ha	<10,000 ha
Geronticus calvus	Southern Bald Ibis	Afrotropical Highland	20	0.9999	0.63	0.69	80.00	88.75	0.70	0.68	0.73	0.86
Turdus libonyana	Kurrichane Thrush	Zambezian	27	0.9915	0.64	0.75	96.30	79.10	0.73	0.73	0.74	0.75
Cercomela sinuata	Sicklewing Chat	Namib-Karroo	21	0.9998	0.74	0.77	80.95	95.95	0.82	0.82	0.80	0.82
Lamprotornis corruscus	Black-bellied Glossy-Starling	East African Coast	27	0.9934	0.80	0.86	92.59	93.06	0.84	0.83	0.86	0.80
Pycnonotus capensis	Cape Bulbul	Fynbos	23	0.9998	0.91	0.79	82.61	96.10	0.77	0.82	0.85	0.95
Camaroptera fasciolata	Southern Barred Warbler	Kalahari- Highveld	6	0.9965	0.73	0.73	77.78	95.60	0.74	0.74	0.73	0.70
Phylloscopus ruficapilla	Yellow-throated warbler	Afrotropical Highland	25	0.9902	0.70	0.82	88.00	94.12	0.83	0.82	0.82	0.79
Spizocorys sclateri	Sclater's Lark	Namib-Karroo	4	0.9991	0.50	0.50	50.00	100.00	0.50	0.50	0.50	0.50
Nectarinia veroxii	Mouse-colored Sunbird	East African Coast	22	0.9942	0.88	0.79	81.82	97.44	0.78	0.81	0.84	0.77
Nectarinia talatala	White-breasted Sunbird	Zambezian	25	0.9889	0.59	0.64	88.00	75.81	0.62	0.61	0.66	0.68
Philetairus socius	Social Weaver	Kalahari- Highveld	6	0.9980	0.94	0.95	100.00	94.68	0.94	0.94	0.93	0.91
Serinus totta	Cape Siskin	Fynbos	6	1.0000	0.79	0.91	100.00	91.21	0.91	0.92	0.92	0.91
Model simulations across Africa refer to the grid data at sever absence of the species in the South African IBAs	oss Africa refer to thin the South African	he grid data at several n IBAs	l resolutions (see text) and	al resolutions (see text) and measured using AUC. All other columns of data refer to predictive ability to model the presence	AUC. All o	ther columns	of data refe	er to predi	ctive abilit	y to model	the presence/

species and assessed their goodness of fit using the area under the curve of a receiver operating characteristic, (AUC) (Manel and others 2001). AUC values vary between 0.5-1 with higher values signifying better model fit. Modeled suitability values for each species in half and quarter degree cells across southern Africa were then converted to presence/absence predictions, using a threshold cut-off value that maximized model-fit, as used elsewhere (Huntley and others 2004, 2006). We then intersected this presence-absence grid with the South African IBA outlines to simulate presence-absence in each IBA. If any half-degree cell that intersected an IBA was modeled as climatically suitable for a species then the species was simulated to occur in that IBA. In addition, as this method takes no account of the habitat available within an IBA, we incorporated a simple algorithm that modified our predictions for IBAs that were simulated as climatically suitable for a species, depending upon whether or not the IBA contained any habitats with which the species was associated. Finally, as some species might require a minimum area to maintain a viable population, we undertook a further analysis that incorporated the habitat algorithm but which considered only those IBAs above a threshold area. This was repeated four times using different thresholds to exclude IBAs each time, the threshold values being <500 ha, <1000 ha, <5000 ha, and <10000 ha. Each of the above analyses produced predicted presence or absence data for the 12 species in all of the South African IBAs. The ability to simulate successfully the species in IBAs was assessed by producing a 2×2 contingency table for each species and assessing the concordance between the modeled and recorded presence (as recorded in Fishpool and Evans 2001—but see discussion) using the True Skill Statistic (TSS, Allouche and others 2006), a prevalence independent measure of fit. TSS values vary between 0–1, with 1 representing perfect agreement.

In order to demonstrate the potential for this method to simulate changes in species' occurrences within IBAs in the future, we applied the climate envelope models for two species to the HadCM3 B2a climate predictions for 2055 and then used the resultant simulated presenceabsence grid, along with the habitat algorithm, to simulate

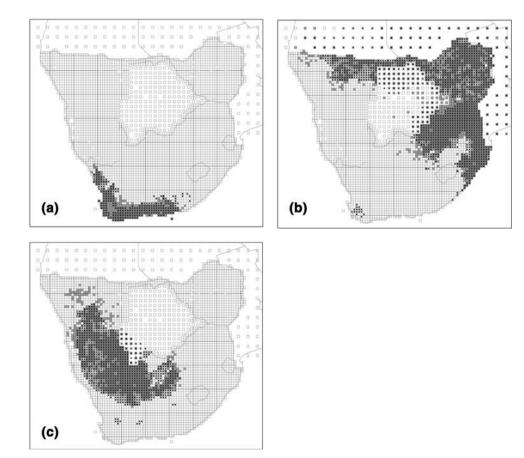


Fig. 1 Examples of recorded species occurrence and climate-envelope simulated occurrence for (a) *Pycnonotus capensis*, (b) *Nectarinia talatala*, and (c) *Philetairus socius* in southern Africa. Open white cells indicate no recorded occurrences, grey cells indicate

recorded occurrences, and smaller black squares represent cells modeled as climatically suitable for each species. Cells are positioned at the center of quarter, half or one degree cells, dependent upon the resolution of data available in different regions

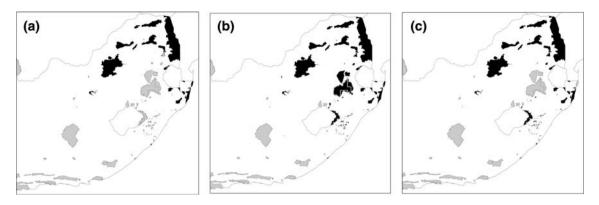


Fig. 2 (a) The recorded occurrence of *Nectarinia talatala* in IBAs of eastern South Africa and the simulated distribution using (b) a simple intersection of the species' climate envelope simulation (TSS = 0.59)

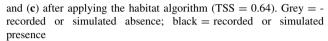
potential changes in occupancy of IBAs between now and 2055.

Results

The "climate envelope" models simulating the recorded ranges of the species across Africa produced a very good agreement with the recorded ranges for all 12 species (as assessed from the AUC values and the interpretation of Thuiller and others (2006)—see Fig. 1 for examples and Table 1 for AUC values).

When the half degree predictions for presence-absence were intersected with the IBA outlines there was a very good agreement between those IBAs that contained the species and the model predictions (Mean TSS of 0.74, Table 1, Fig. 2b). The only exception was *Spizocorys sclateri*, which had a low TSS value compared to the other species. This was the most restricted species, only occurring in four IBAs, of which only two were modeled as being climatically suitable by the climate-envelope model.

After applying the habitat algorithm there was an improvement in TSS values for nine of the 12 species, no improvement for two species, and a decrease for one species (mean TSS of 0.78). S. sclateri was one of the species with no improvement in model fit. However, the only errors in its original model were as a result of simulating unsuitable climate in two IBAs (errors of omission). Such errors cannot be improved by applying the habitat algorithm, which can serve only to reduce incorrectly simulated presences (errors of commission) in IBAs with no suitable habitat. For the species (Nectarinia veroxii) with reduced TSS values after applying the habitat algorithm, the total number of incorrectly assigned IBAs (i.e., errors of commission plus omission) actually declined (7 incorrect predictions which decreased to 6 for N. veroxii after applying the algorithm). The decrease in TSS is an artifact



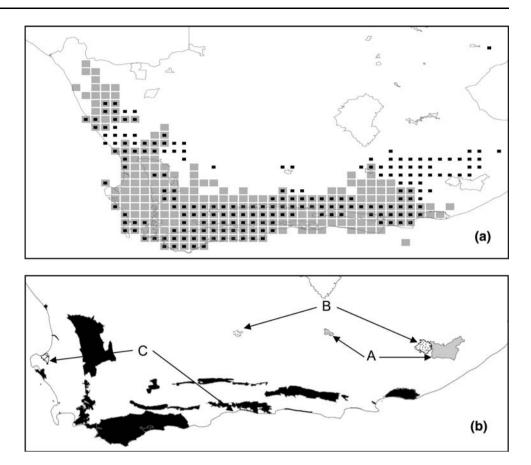
of the way in which the statistic is calculated. Because *N. veroxii* is absent from more IBAs than it is present in, changes in the distribution of errors between commission versus omission cause the TSS value to decrease.

Overall, the combined climate-envelope-habitat algorithm (CE-HA) method proved excellent in predicting species' occurrences in IBAs, correctly simulating on average 86% of recorded presences and 92% of absences (Table 1, Fig. 2). This approach produced significantly better predictions than did intersecting using only the climate-envelope simulations (paired t-test on TSS values, comparing values for each species' predictions with and without the habitat algorithm: n = 12, t = 2.50, p < 0.05). Applying the habitat algorithm reduced errors of commission by 46% on average (average error of commission across the species was 12% before applying the algorithm and 6.5% after).

We also applied the CE-HA method to subsets of IBAs that excluded smaller IBAs, to determine whether predictive ability of the method was improved by excluding smaller protected areas (Table 1). The predictive ability of the method did not increase significantly when smaller IBAs were excluded, using any of the four area thresholds (paired t-test comparing TSS values for each species' predictions when using all IBAs with TSS values produced when smaller IBAs were excluded: excluding IBAs < 500 ha, t = 0.15; excluding IBAs < 1000 ha, t = 0.00; excluding IBAs < 2000 ha, t = 1.66; excluding IBAs <10,000 ha, t = 0.34. n = 12, p > 0.05 in all cases). Geronticus calvus was the only species for which excluding smaller IBAs systematically improved the predicted distribution. After excluding IBAs with areas < 10,000 ha, the number of IBAs correctly predicted (in terms of either presence or absence) increased to 98%, up from 87% using the CE-HA approach but including all IBAs.

Figures 3a and 4a show simulations of range shifts that could occur for *Pycnonotus capensis* and *Nectarinia*

Fig. 3 (a) The recorded current distribution (grey cells) and simulated regions of suitable climate by 2055 (using the HADCM3 B2 scenario) (black squares) for Pycnonotus capensis across southern South Africa; (b) Simulated change in climate suitability in IBAs between the present and 2055, using the combined climate modeling and habitat algorithm approach: black shading = suitable now and in 2055; grey shading (A) = simulated suitable in both periods but currently unoccupied; stippling (B) = simulated climaticallysuitable only in the future; cross hatching (C) currently present but simulated unsuitable by 2055



talatala by 2055 under a HadCM3 B2a climate change scenario. In a best case scenario, each species would occupy all of the areas simulated to be climatically suitable in the future, whereas under a worst-case scenario they would persist only in those areas of overlap, where climate was simulated to be suitable in both periods. In the case of P. capensis range extent under a best case scenario would be similar to its current extent but in a worst case scenario would decline considerably. By contrast N. talatala would remain in much of its range even under a worst case scenario and could become considerably more widespread in a best-case scenario. Applying the CE-HA method to this future scenario suggests there would be rather limited change in IBA occupation between now and 2055, though under a best case scenario both species would have some potential to colonise new IBAs (Figs. 3b, 4b). Of the two species highlighted, only P. capensis is projected to disappear from any IBAs.

Discussion

The agreement between modeled and observed grid data is very good, suggesting that at a large spatial scale, the ranges of African birds can be modeled using a small number of climatic variables. This fits with other studies in various biogeographic regions that have related the range extents of taxa at a coarse scale to climate. By intersecting the quarter degree climate suitability simulations with IBA outlines, we found an excellent agreement with recorded occurrences, although there remained a limited tendency to incorrectly simulate presences in unoccupied IBAs. However, these errors of commission may be exaggerated as, for a biome-restricted species to be recorded in an IBA (in Fishpool and Evans 2001) it must occur at a site in sufficient numbers or with sufficient regularity to trigger selection (Fishpool and Evans 2001). Hence, it may be that some IBAs simulated as suitable for a species, but in which we record it as absent, might actually hold a small number of individuals or irregularly hold individuals. The simple "climate-envelope-" IBA intersection method produced good predictive ability for all but three species. These three included G. calvus, the only species where individuals require a large home range, and S. sclateri, the most restricted of the 12 species and a rather nomadic species.

We found that the errors of commission in the simple intersection models were significantly reduced using the habitat-matching algorithm and that this did not increase errors of omission greatly. This combined CE-HA method provides a relatively simple means of simulating species current distribution in IBAs and potentially provides a means of simulating those protected areas that will remain

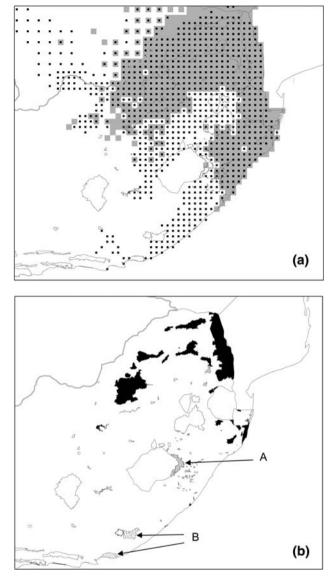


Fig. 4 (a) The recorded current distribution (grey cells) and simulated regions of suitable climate by 2055 (using the HADCM3 B2 scenario) (black squares) for *Nectarinia talatala* across eastern South Africa; (b) Simulated change in climate suitability in IBAs between the present and 2055, using the combined climate modeling and habitat algorithm approach: black shading = suitable now and in 2055; grey shading (A) = simulated suitable in both periods but currently unoccupied; stippling (B) = simulated climatically suitable only in the future; cross hatching. No currently occupied areas are simulated unsuitable by 2055

suitable for species in the future, or which will become newly suitable for species. It is possible that by using more detailed habitat definitions for both species and IBAs, we would be able to further improve simulations. This combined climate-habitat modeling approach, though useful for considering likely changes in species ranges over the short to medium term future, will become less useful in the long term, as the habitats themselves are likely to alter with a changing climate. In addition, the future simulations provide information only on where suitable climate/habitat occurs in the future, with no assessment of the likelihood of a species being able to move to newly suitable protected areas, yet this is a very important factor (Menendez and others 2006). To get a more realistic estimate of the impacts of climate change on protected area networks, it would be necessary to additionally incorporate changes in vegetation types over time and the likelihood of species traversing areas between protected areas, using methods such as least-cost pathways in linked dynamic population-habitat-climate models. However, for most species, our ability to parameterize such models is lacking; therefore, simple methods such as that presented here are the only means of providing an initial measure of the likely impacts of climate change for many species.

Removing the smallest IBAs from our analyses did not improve the predictive ability of the models, with the exception of the model for *G. calvus*. Occurrence of *G. calvus* in IBAs was predicted successfully for all of the larger IBAs. Removing the smaller IBAs led to improved predictions, with accuracy increasing as progressively larger IBAs were removed. The small IBAs that were incorrectly predicted to be occupied were all sites in KwaZulu-Natal, and are all largely surrounded by agriculture. As *G. calvus* can forage up to 20 miles from breeding sites (Brown and others 1982), it may well depend upon large IBAs to protect suitably large areas of grassland habitat.

Our results suggest that caution should be used if applying this method to species with large home ranges or where the needs of a minimum viable population exceed the size of a protected area. This method is also inappropriate for species whose current range cannot be related to climatic factors, such as species that now survive only in a limited part of their potential range due to factors such as habitat destruction or persecution.

Although the future simulations of range extent for the two species shown in this article did not alter dramatically, other species have been simulated to shift their range substantially, with varying degrees of overlap between present and predicted future ranges (see e.g., BirdLife International 2004). In the most extreme cases there is no overlap between current and simulated future range, meaning that a species would have to alter its entire range in response to climate change or face extinction. The degree to which best versus worst case scenarios are likely to be realized will depend very much upon the mobility of the individual species and the occurrence of suitable habitat in regions becoming climatically suitable.

In order to simulate the potential effects of climate change on species protection within IBAs, the first step will be to predict where suitable climate for species is likely to exist, within IBAs, under future climate scenarios. This will give a crude estimate of how robust the current network is likely to be under a best- or worst-case scenario. At a finer temporal resolution, decadal predictions of climate over the next 100 years might highlight particular timeperiods when occurrence of suitable climate and areas of suitable habitat are incompatible.

Comparing simulated future ranges for species of conservation concern using several different climate change scenarios will allow some basic generalizations to be made. For example, are some reserve types more robust to changing climate, or are particular regions or habitats more prone to climate change effects? Such an approach would also provide some idea of species' potential future distributions. By identifying regions robust to climate change we can give confidence in continued management of such areas for the suite of species they currently contain. Other IBAs may need to have management prescriptions altered over time to allow for colonization by new species of conservation concern. To preserve the efficacy of protected area networks in regions where climate is predicted to change substantially (and ranges to move corresponding large distances), it may be necessary to consider a more extensive system of conservation management, in addition to IBAs, to allow for a natural, dynamic alteration of ranges in future.

Overall, the method we have developed here works very well as a means of simulating the current species component of the South African IBAs and could prove a very useful technique in simulating potential consequences of future climate change over the short to medium term in other regions or other protected area networks.

The techniques, if applied across all species, could permit a preliminary assessment of the extent to which networks of reserves designated on the basis of present patterns of biodiversity and endemism are likely to be sufficient to achieve biodiversity conservation in a world experiencing rapid climate change and a basis for developing conservation strategies that will facilitate ecosystems to adapt naturally to climate change. Such assessments may have very far-reaching significance in relation to the obligations of numerous states to conserve biodiversity.

Acknowledgments We are indebted to numerous people for the provision of data used in this project. BirdLife International personnel have been invaluable in providing data and advice throughout the project. The African BirdLife partners have provided much of the IBA data and maps needed to produce the IBAs GIS; we are especially grateful to Achilles Byaruhanga, Steven Evans, Alfred Owino, Ade Majekodunmi, Tim Dodman, Kenna Kelly, Pete Leonard, Neil Burgess, and Simon Blyth. Paul Britten, Ian Tarplee, and Hannah Williams of RSPB deserve many thanks for digitizing IBA maps. Fine scale distribution data was kindly made available for Uganda, Kenya, and Southern Africa by, respectively, Makerere University (Institute of Environmental & Natural Resources), National Museum of Kenya, and the Avian Demography Unit, University of Cape Town (www.aviandemographyunit.org). This work was supported by RSPB funding. Debbie Pain and Lincoln

Fishpool provided useful comments on an early draft of this article. The article was much improved by the comments of the anonymous referees and the guest editor, Ole Mertz.

References

- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232
- Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P, Rahbek C (2001) Conservation conflicts across Africa. Science 291:2616–2619
- BirdLife-International (2000) Threatened birds of the world. Lynx Edicions & BirdLife, Barcelona, Cambridge
- BirdLife International (2004) State of the World's birds 2004: indicators for our changing world. BirdLife International, Cambridge, UK
- Boko M, Niang I, Nyong A, Vogel C, Githeko A, Medany M, Osman-Elasha B, Tabo R, Yanda P (2007) Africa. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 433–467
- Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16:909–923
- Brown LH, Urban EK, Newman K (1982) The birds of Africa: volume I. Academic Press, London
- Carswell M, Pomeroy D, Reynolds J, Tushabe H (2005) The bird atlas of Uganda. BOU, Oxford
- Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Koli RK, Kwon W-T, Laprise R, Rueda VM, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 847–940
- De Klerk HM, Crowe TM, Fjeldsa J, Burgess ND (2002) Biogeographical patterns of endemic terrestrial Afrotropical birds. Diversity and Distributions 8:147–162
- De Klerk HM, Fjeldsa J, Blyth S, Burgess ND (2004) Gaps in the protected area network for threatened Afrotropical birds. Biological Conservation 117:529–537
- Desanker P, Magadza C, Allali A, Basalirwa C, Boko M, Dieudonne G, Downing TE, Dube PO, Githeko A, Githendu M, Gonzalez P, Gwary D, Jallow B, Nwafor J, Scholes R (2001) Africa. In: White KS (ed) Climate change 2001: impacts, adaptation, and vulnerability. Cambridge University Press, Cambridge, pp 487–531
- Fishpool LDC, Evans MI (2001) Important bird areas in Africa and associated islands: priority sites for conservation. Birdlife International/Lynx Edicions, Barcelona
- Graham RW, Grimm E (1990) Effects of global climate change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 5:289–292
- H-Acevedo D, Currie DJ (2003) Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. Global Ecology and Biogeography 12:461–473
- Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, ParkerV, Brown CJ (1997) The atlas of southern African birds. vols 1,2. BirdLife South Africa, Johannesburg

- Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to 20th century climate warming: implications for future ranges. Proceedings of the Royal Society of London Series B-Biological Sciences 269:2163–2171
- Huntley B, Berry PM, Cramer W, McDonald AP (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography 22:967–1001
- Huntley B, Cramer W, Morgan AV, Prentice HC, Allen JRM (eds) (1997) Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota. NATO ASI Series I: global environmental change. Springer-Verlag, Berlin
- Huntley B, Green RE, Collingham YC, Hill JK, Willis SG, Bartlein PJ, Cramer W, Hagemeijer WJM, Thomas CJ (2004) The performance of models relating species geographical distributions to climate is independent of trophic level. Ecology Letters 7:417–426
- Huntley B, Collingham YC, Green RE, Hilton GM, Rahbek C, Willis SG (2006) Potential impacts of climatic change upon geographical distributions of birds. Ibis 148:8–28
- Huntley B, Collingham YC, Green RE, Willis SG (2007) A climatic atlas of European breeding birds. Lynx Edicions, Barcelona
- Huntley B, Collingham YC, Willis SG, Green RE (2008) Potential impacts of climatic change on European breeding birds. PLoS ONE 3:e1439. doi:10.1371/journal.pone.0001439
- Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on global diversity of birds. PLoS Biology 5(e157):1–9
- Lewis A, Pomeroy D (1989) A bird atlas of Kenya. Balkema, Rotterdam
- Manel S, Williams HC, Ormerod SJ (2001) Evaluating presenceabsence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38:921–931
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge
- Menendez R, Gonzalez-Megias A, Hill JK, Braschler B, Willis SG, Collingham YC, Fox R, Roy DB, Thomas CD (2006) Species richness changes lag behind climate. Proceedings of the Royal Society of London Series B-Biological Sciences 273:1465–1470

- Muriuki JN, DeKlerk HM, Williams PH, Bennun LA, Crowe TM, VandenBerge E (1997) Using patterns of distribution and diversity of Kenyan birds to select and prioritize areas for conservation. Biodiversity and Conservation 6:191–210
- Myers N, Mittermeiner RA, Mittermeiner CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. Science 269:347–350
- Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 398:611–615
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004a) Extinction risk from climate change. Nature 427:145–148
- Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004b) Comparative losses of British butterflies, birds and plants and the global extinction crisis. Science 303: 1879–1881
- Thuiller W, Broennimann O, Hughes G, Alkemade JM, Midgley GF, Corsi F (2006) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology 12:424–440
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69
- Williams JW, Jackson ST, Kutzbach JE (2007) Projected distribution of novel and disappearing climates by 2100AD. Proceedings of the National Academy of Science, 104:5738–5742