



# Climate envelope models suggest spatio-temporal co-occurrence of refugia of African birds and mammals

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## ABSTRACT

**Aim** Studies investigating the theory of tropical refugia for vertebrates have previously focused on a handful of species or a single taxonomic group. We sought to identify the potential location of cross-taxonomic refugia of African birds and mammals in the Last Glacial Maximum, and used historic climate data to hindcast the location of past ranges of species based on their current distributions.

**Location** Mainland sub-Saharan Africa.

**Methods** Using current distributions of 537 mammal and 1265 bird species, we modelled the past distribution of species, taking advantage of recently available reconstructions of climate for the Last Glacial Maximum. Modelled historical ranges were verified individually using standard techniques for evaluating the precision of bioclimatic envelope models. Potential refugia were identified as those areas with a higher overlap of climatically suitable ranges (i.e. levels of species richness) than expected based on randomizing of the modelled past climatically suitable ranges in the sub-Saharan domain and on the level of resource availability (by modelling past species richness patterns as would be expected given the water-energy theory).

**Results** Our models show that during the Last Glacial Maximum areas of high concentration of climatically suitable ranges of birds and mammals tend to aggregate, more than can be accounted for random placement of ranges and resource availability (ecological processes), in the same six areas: Upper Guinea, the Cameroon Highlands, the Congo Basin, the Ethiopian Highlands, the Angola–Namibia area and the south-east part of South Africa.

**Main conclusions** The unusually high aggregation of predicted suitable ranges for birds and mammals in six relatively small geographical areas corresponds to the location of some of the previously suggested refugia. We interpret this – and the similarity of patterns obtained for both birds and mammals – as a strong indication of the existence of refugia in those areas. The results also illustrate the usefulness of bioclimatic envelope models, coupled randomization techniques and macroecological models, for the reconstruction of geographical distribution patterns in the past.

## Keywords

**Africa, bioclimatic envelope models, birds, hindcasting, Last Glacial Maximum, mammals, tropical refugia.**

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## INTRODUCTION

Researchers have long pondered the role of Pleistocene climatic fluctuations in shaping the patterns of species ranges as well as spatial variation in species richness. The most prominent theory in the tropical context is Haffer's refugia theory (Haffer, 1969). This theory, also known as 'forest islands' (Lönnerberg, 1929; Moreau, 1933), suggests that tropical forests were repeatedly fragmented during the cold and arid glacial periods and expanded during the warm and wet interglacials. These refugia enabled tropical lowland fauna to persist during unfavourable climatic periods, with the further argument that spatial isolation of populations also presented opportunities for speciation (Haffer, 1969). Refugia theory has been debated ever since its early days (Endler, 1982) without a consensus being achieved. Most, if not all, of Haffer's perceptions of refugia and how they might have affected contemporary patterns of diversity have been repeatedly and severely criticized (e.g. Colinvaux *et al.*, 2000). Our aim is not to discuss the mechanisms associated with refugia theory but to analytically investigate predicted patterns of expansion and contraction of species ranges through hind-casting modelling techniques using contemporary ranges and palaeoclimatic data from the Last Glacial Maximum. Consensus regarding the location of past refugia and the mechanisms generating them has been elusive, partly because of the difficulties in reconstructing past species distributions, which in turn places obstacles to generating plausible hypotheses for the existence of refugia. For example, simulated glacial vegetation across Africa suggests that tropical broadleaf forest was not severely displaced by expanding grasslands within Central African vegetation (Cowling *et al.*, 2008), while pollen records support the idea of a reduction in forest area in tropical Africa in the Last Glacial Maximum (Maley, 1991; Maley & Brenac, 1998; Anhufo *et al.*, 2006). Furthermore, pollen-based biome reconstructions for this period corroborate that sites in the African tropical highlands, characterized today by evergreen forest, were dominated by steppe and/or xerophytic vegetation (Elena *et al.*, 2000). Pollen records are seldom complete, however, and are restricted to localities where water bodies allow for sedimentation to occur, so there is a possibility that such biases in the data might affect the biological interpretation of the patterns derived from them.

The vertebrate fossil record is even more incomplete and does not fully describe past species distributions. As a result, researchers have used several indirect methods to assess the existence and location of refugia for vertebrates in the tropics. In Africa, these attempts were largely based on inferences from contemporary patterns of distribution. For example, Mayr & O'Hara (1986) identified secondary contact zones between sister species, postulating that potential refugia should occur between these zones. Others have examined diversity patterns, associating areas of high diversity (Diamond & Hamilton, 1980; Crowe & Crowe, 1982; Mayr and O'Hara, 1986) and centres of endemism (Fjeldsø & Bowie, 2008) with refugia.

Another approach has been to investigate patterns of phylogenetically old versus young African bird species, postulating that phylogenetically younger species will occur in areas where speciation occurs, i.e. in refugia (Fjeldsø & Lovett, 1997). More recently, phylogenetic studies of African primates, rodents and birds found support for the existence of refugia, inferring results using molecular techniques (e.g. Roy *et al.*, 2001; Quérrouil *et al.*, 2003; Anthony *et al.*, 2007). However, these studies were restricted to a handful of species and therefore do not represent refugia for entire faunas.

Newly available reconstructions of past climates open a potentially new avenue for the identification of the location of refugia based on potential occurrences of species without relying upon the limited fossil record available for the Last Glacial Maximum. We combined these climatic reconstructions with hindcasting of bioclimatic envelope models (Nogués-Bravo, 2009) to yield insights into changes of climatically suitable areas for species over time. This approach permitted us to assess the climatic suitability for individual species in the Last Glacial Maximum directly, thus overcoming the limitations of traditional approaches using current diversity patterns as proxies. It should be noted that species climatic suitability models are subject to a series of assumptions, some of which might limit the ability to successfully transfer distributions in space and time (for discussion see Araújo & Rahbek, 2006; Nogués-Bravo, 2009, and Svenning *et al.*, 2011). For example, a known shortcoming is the lack of equilibrium of species distributions with climate, which causes species to occupy a proportion of the total suitable climate available (e.g. Araújo & Pearson, 2005). When non-equilibrium exists, apparent niche shifts can occur through time (see for review Peterson *et al.*, 2011). That is, species can occupy different portions of their niches because different combinations of climate and biotic interactions exist. Therefore, results based on hindcasting should be interpreted with caution (Nogués-Bravo, 2009).

Acknowledging the above-mentioned issues concerning the assumptions and limitations of the models, we generated patterns of potential species richness by overlaying modelled past climatically suitable ranges of species. We compared this species richness pattern with two other patterns: (1) a mid-domain model generated by simple randomization of the modelled past climatically suitable ranges (cf. Colwell *et al.*, 2004) in the sub-Saharan domain; and (2) a predictive model of past species richness expected if temperature and precipitation at any given time determines the carrying capacity of species co-existences (cf. Hawkins *et al.*, 2003). We interpret areas with a higher range overlap (i.e. species richness) than expected by our mid-domain model or past levels of resources, as areas that may have acted as refugia. We used this pattern-comparison approach to: (1) investigate the possibility that refugia for birds and mammals might have existed in sub-Saharan Africa during the Last Glacial Maximum, (2) identify the geographical location of such potential refugia, and (3) assess whether potential refugia for birds and mammals co-occurred in the same locations.

## METHODS

### Geographical template and scale of the analysis

The study area covers sub-Saharan continental Africa excluding Madagascar and other islands. Climate and species distribution data were sampled within a 2° latitudinal–longitudinal grid, and all analyses were conducted at this resolution. This scale of analyses was imposed by the spatial resolution of the climatic reconstructions available for Africa for the Last Glacial Maximum. Excluded from analyses were coastal cells with less than 50% land, resulting in a total data set of 476 quadrates.

### Species distribution data

The distributions of 1556 birds (Hansen *et al.*, 2007) and 970 mammals (Burgess *et al.*, 2007a) endemic to sub-Saharan Africa were obtained as conservative estimates of extent of occurrence from the Copenhagen Databases of African Vertebrates (<http://www.zmuc.dk/commonweb/research/biodata.htm>). For a description of the methods used to create the databases see Brooks *et al.* (2001) and Burgess *et al.* (2000). These data have been previously used for phylogeographical (Fjeldså *et al.*, 2007; Fjeldså & Bowie, 2008), macroecological (Jetz and Rahbek, 2001; Jetz & Rahbek, 2002), conservation (Balmford *et al.*, 2001; Burgess *et al.*, 2002, 2007b) and climate change studies (Hole *et al.*, 2009; Willis *et al.*, 2009; Garcia *et al.*, 2012). To encompass the entire range of climatic conditions under which the species occur, thus minimizing the risk problems associated with extrapolation of models (e.g. Thuiller *et al.*, 2004; Fitzpatrick & Hargrove, 2009), we restricted our analyses to species restricted to the domain of sub-Saharan Africa. Given that species–climate envelope models have a limited ability to cope with small numbers of occurrences (e.g. Stockwell & Peterson, 2002), we further restricted the analyses to 1265 birds and 537 mammals with more than 10 within-grid-cell records. Exclusion of the most restricted range species might affect the ability to detect refugia in regions with unusually high concentrations of narrow endemic species (e.g. in the Albertine Rift and Eastern Arc mountain regions; see Jetz & Rahbek, 2002).

### Climatic data

Minimum and maximum temperatures and annual precipitation for the Last Glacial Maximum were calculated using an atmospheric ocean coupled general circulation model (AOGCM). The circulation model used in this study is the HadAM3 version of the UK Meteorological Office's Unified Model (Wood *et al.*, 1999). It has a horizontal grid resolution of 2.5° × 3.75° in latitude and longitude with 19 levels in the vertical, and a time step of 30'. The model incorporates prognostic cloud, water and ice, has a mass-flux convection scheme with stability closure and uses mean orography. The model was integrated for the Last Glacial Maximum over 20 simulated years and climatological means were compiled for the final 14 years. The model was initialized from a previous Last Glacial

Maximum simulation and time-series analysis of various climate variables for the entire 20 years' simulation shows that disregarding the first 6 years is sufficient for the climatology of the model to reach a dynamic equilibrium.

The HadAM3 model was initialized with monthly sea surface temperatures derived from the Climate Long-Range Investigations, Mapping and Prediction data set (CLIMAP Project Members, 1981). The distribution of surface ice and water cover for the Last Glacial Maximum was derived from the ICE-4G model (Peltier, 1994). The atmospheric concentration of CO<sub>2</sub> was specified at 200 p.p.m. in agreement with measured values in ice core records (Petit *et al.*, 1999). All other trace gas concentrations were specified at modern levels. The experimental design conforms to recommendations outlined by the Palaeoclimate Modelling Intercomparison Project (PMIP; Joussaume & Taylor, 1999). More recent reconstructions (e.g. Braconnot *et al.*, 2007) show that mid- and high-latitude climates depend strongly on the ice sheet reconstructions (which remain uncertain). However, tropical African climates are less sensitive to such uncertainties and our climate simulations are reasonably robust.

### Bioclimatic envelope modelling

Climatically suitable ranges for the Last Glacial Maximum were reproduced by means of hindcasting bioclimatic envelope models. In order to investigate the effects of intermodal variability we fitted an ensemble of forecasts (Araújo & New, 2007) using the BIOENSEMBLES software (Diniz-Filho *et al.*, 2009; 2010). Four different modelling approaches requiring presence only or presence background data were implemented in BIOENSEMBLES – GARP, Domain, Bioclim and Mahalanobis distance –, and we also fitted the maximum entropy (Maxent) model using Maxent software (Phillips *et al.*, 2006; Phillips and Dudík, 2008). Species richness patterns from the Maxent modelling were closest to empirical patterns (see Table S1 and Figs S1 & S2 in Supporting Information) and in order to constrain uncertainties we decided to carry on further analysis using its predictions (see Guisan and Rahbek, 2011, for discussion of model fit with empirical richness data). Notice that matching between observations (of richness) and predictions (of richness) is not a demonstration that the models are superior (Araújo *et al.*, 2005; Araújo & Rahbek, 2006; Peterson *et al.*, 2011). However, choosing the projections maximizing the matching between the two surfaces does constrain commission errors (absences predicted to be present), thus yielding results that are more conservative and more easily interpreted. Maxent is known to provide better adjustments between observed and predicted species distributions (Elith *et al.*, 2006; Phillips *et al.*, 2006), but it might sometimes over-fit species–climate relationships, possibly limiting their transferability (Peterson *et al.*, 2007). Using a small number of predictor variables reduces the risk of over-fitting of the species–climate relationships and might thus allow greater transferability to other spatiotemporal domains (Peterson *et al.*, 2007). We started with six climatic variables – mean annual temperature, mean temperature of the

warmest month, mean temperature of the coldest month, annual precipitation, December–February precipitation and June–August precipitation – and used principal components analysis to identify the three least correlated variables (see also Baselga & Araújo, 2009; Nenzén & Araújo, 2011). The modelling was then carried out using the following climatic variables: mean temperature of the warmest month ( $T_{\text{warm}}$ ), mean temperature of the coldest month ( $T_{\text{cold}}$ ) and annual precipitation ( $P_{\text{ann}}$ ). The Maxent modelling included all background points available in the study area ( $n = 476$ ), with the maximum number of iterations set to 500 and the regularization multiplier to 1 (Phillips *et al.*, 2006).

To characterize uncertainties associated with extrapolation of present-day models into climates in the Last Glacial Maximum that were not present in the calibration data, we mapped the areas with non-analogue climates in the past with respect to the baseline conditions following Araújo *et al.* (2011). The interpretation is that hindcasts made into areas with non-analogue climates are forcefully less reliable than areas with the same range of climatic conditions found in the baseline climate (see also Garcia *et al.*, 2012). Specifically, we map the location and quantify the extent of non-analogue climatic conditions in the Last Glacial Maximum for each variable ( $T_{\text{warm}}$ ,  $T_{\text{cold}}$ ,  $P_{\text{ann}}$ ), non-analogue climates being defined as those exceeding the highest and lowest values recorded for current climatic conditions. We show that the risk of models extrapolating beyond the baseline climate is generally small (Fig. S3), as non-analogue climates occupies only  $1.4 \times 10^6$  km<sup>2</sup>, i.e. 6.2% of the study area. They are restricted to some areas of the Sahel (central regions of Sudan, Chad, the south of Mauritania and Senegal), central Ethiopia and central South Africa.

Hindcasts of species climatic suitability can vary when using different AOGCMs to simulate past climatic conditions, although the greatest source of uncertainty in modelling species range shifts under climate change arises mainly from using alternative methods for bioclimatic envelope modelling, the effect of the AOGCM model being much smaller in the overall uncertainty (Diniz-Filho *et al.*, 2009). AOGCMs may differ slightly in the simulated absolute values of estimated climatic conditions. If those conditions largely differ across AOGCMs for the same period of time (i.e. the Last Glacial Maximum), the potential uncertainty in the modelled ranges associated with the palaeoclimatic reconstruction would be high. On the contrary, the potential uncertainty in the modelled ranges of species associated with palaeoclimatic reconstruction will be small if different AOGCMs simulate climatic conditions within the same range of values. To infer the potential effect of palaeoclimatic reconstruction in our results we assess the geographical location and extent, in the Last Glacial Maximum, of climatic conditions modelled by an alternative AOGCM, Genesis 2, exceeding the highest and lowest values modelled by HadAM3 for the Last Glacial Maximum. We show that differences between AOGCMs are small – those areas with non-analogue climatic conditions make up only 5.3% of the study area (Fig. S4). Non-analogue climatic conditions are located in the Sahel region and South Africa. In other words,

both AOGCMs provide a similar range of climatic conditions for the Last Glacial Maximum.

Model precision was estimated using the area under the curve (AUC) of a receiver operating characteristic curve (for review see Fielding & Bell, 1997). A random draw of 70% of the data was used 10 times to assess the sensitivity of projections to variations in the data for model calibration (yielding a 10-fold cross validation), and thus providing a measure of model stability (Araújo & Guisan, 2006). Mean AUC values across the 10 cross-validated samples were used to determine whether species were retained in the analysis. An AUC of 0.5 indicates that the model fits absence and presence data no better than random predictions, while a value of 1 indicates perfect adjustment of predictions with the data. AUC values above 0.7 are usually seen as indicating useful predictions (Swets, 1988); thus, we included only species with a mean AUC > 0.7 in subsequent analyses. From the original pool of 537 mammal and 1265 bird species, we retained 475 (88%) and 1103 (87%) species with AUC values higher than 0.7.

The modelled probability maps produced by Maxent were converted into binary presence/absence maps using a maximum training sensitivity and specificity threshold, recently identified as one of the best performing thresholds (Liu *et al.*, 2005; but see Nenzén & Araújo, 2011). We subsequently overlaid the binary maps of each taxon to produce potential modelled species richness maps for birds and mammals under current and Last Glacial Maximum climatic conditions.

### Mid-domain model: expected level of range-overlap based on randomization of ranges

Some quadrats may contain more species than others simply because of geometric constraints (i.e. the mid-domain effect, MDE) (Colwell *et al.*, 2004; Rahbek *et al.*, 2007). In order to take this into account when attempting to identify potential refugia based on an unusual aggregation of overlapping ranges in the past, we followed the advice on using the empirical data in the randomization analyses of Colwell *et al.* (2004). We simulated the placement, spread and dispersal of Last Glacial Maximum climatically suitable ranges for species (as modelled by Maxent). This generates a prediction of the continental-wide pattern of species richness during the Last Glacial Maximum, conditioned solely on the shape of the continent and given the empirical number of species and their modelled Last Glacial Maximum range-size-frequency distribution. The modelling was carried out using the BioGeoSim software (Gotelli *et al.*, 2007) as developed and used in Rahbek *et al.* (2007). Specifically, we used the spreading dye function of Jetz and Rahbek (Jetz and Rahbek, 2001) with 1000 iterations and 500 replications, assumed continuous ranges and set the contiguous pattern to four.

The spreading dye model works as follows (Jetz & Rahbek, 2001): For each species, a ‘starting’ cell is chosen randomly and the species’ range is then produced by repeated ‘expansion’ in steps of one cell added per time in a random direction from a randomly chosen edge of all already occupied cells until

the final range size is reached. Cells qualifying for 'expansion' must be adjacent in a horizontal or vertical (i.e. a cardinal) direction, not yet occupied by the species. This process is repeated for all species. The result is a mid-domain model prediction of number of species per quadrat. By subtracting this figure from the number of species generated by overlaying the modelled past climatically suitable ranges from the Maxent modelling, we identified areas with higher richness than expected on average by randomization of ranges given geometric constraints.

### Resources: predicting levels of species richness based on water–energy dynamics

In low latitudes, species richness often correlates with energy and water availability, and is believed to be in a temporally invariant state of equilibrium with climate (Hawkins *et al.*, 2003; Fisher *et al.*, 2011). To identify areas with an unusually high aggregation of species beyond the level expected given the potential equilibrium of species richness with available resources, we simulated expected patterns of species richness during the Last Glacial Maximum using the historic climate data for temperature and precipitation. We first identified the function describing the relationship between current species richness and current water–energy. We used the first principal component of a principal component analysis of  $T_{\text{warm}}$  and  $P_{\text{ann}}$ , which accounted for 89% of the variation in species richness. Applying the reconstructed climate data for the Last Glacial Maximum to this function, we used the approach of Rahbek *et al.* (2007) and the software BIOGEO SIM (Gotelli *et al.*, 2007) to predict the spread and occurrence of species ranges in a climatically heterogeneous landscape, where probabilities of species occurrence are highest in quadrats exhibiting relatively high temperature and precipitation.

The predicted water–energy model works as follows (cf. Rahbek *et al.*, 2007): for each species, a 'starting' cell is chosen stochastically, based on the environmental probability maps. The probability map is calculated as the probability of species occurrence proportional to the function found to best describe statistically the water–energy fit with species richness. Thus, initial occurrence was more likely in some grid cells than others based on their level of water–energy. Having selected an initial cell, the placement of each species range was completed by choosing subsequent cells from among the set of terrestrial cells bordering (by sides or corners) the cells already occupied by that species, with the choice again guided probabilistically by the values of the water–energy probability map in those cells. The result is a pattern reflecting the historical pattern of species richness if it were fully determined by, and in equilibrium with, levels of temperature and precipitation. Again, by subtracting the obtained predicted figure of historical species richness from the level of richness based on hindcasted ranges, we identified areas with higher richness than expected given water–energy dynamics in the Last Glacial Maximum.

### Comparison of results from macroecological models with those from species distribution hindcasting models

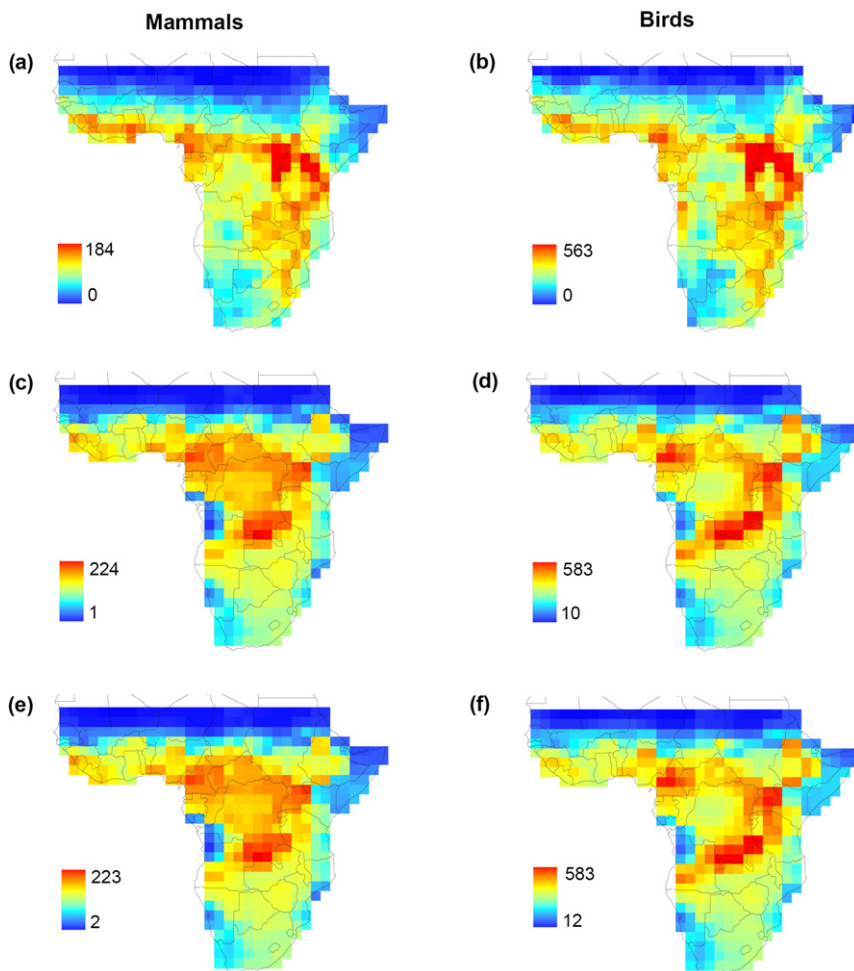
Macroecological models, such as the mid-domain model and the water–energy model used in our analyses, face a series of statistical issues (e.g. noticeable spatial autocorrelation, non-independence and intercorrelation in data, variables and among models, and model testing) and conceptual issues (i.e. how to test the models) that continue to spur debate and remain unresolved (Rahbek *et al.*, 2007; Gotelli *et al.*, 2009). In particular, the mid-domain model has been the focus of much debate (see, for example, the critique by Zapata *et al.*, 2003, Hawkins *et al.*, 2005, and Currie and Kerr, 2008, and replies by Colwell *et al.*, 2004, 2005). Given the lack of consensus in the literature, we conduct the analyses of these models in alignment with the procedure proposed by the proponents of the models. The purpose of our study is not to test these macroecological models or to discuss their relative merits but to test if they could potentially affect the main results of the species distribution hindcast models. Henceforth, with this purpose in mind and to ensure full transparency in light of the aforementioned debate, we present the results in three ways: (1) the simple species richness pattern generated by the species distribution hindcasting models, (2) the pattern after subtracting the pattern of species richness predicted by the mid-domain model, and (3) the pattern after subtracting the pattern of species richness generated by the water–energy model.

Data manipulation and mapping were performed using R 2.5.1 (R Development Core Team, 2007, <http://www.r-project.org/>) and ArcGIS® 9.2 geographic information system software and its spatial analysis extension ArcGIS Spatial Analyst (ESRI, Redlands, CA, USA). Spatial-statistical analyses were carried out using SAM 3.0 (Rangel *et al.*, 2010, spatial analysis in macroecology <http://www.ecoevol.ufg.br/sam/>). To correct for spatial autocorrelation in the Pearson correlation analysis between the empirical pattern of species richness and the pattern modelled by Maxent, we calculated the effective number of degrees of freedom according to Dutilleul's method (Dutilleul, 1993; Legendre *et al.*, 2002). We followed the same approach for the Pearson correlations between the modelled patterns of species richness for the Last Glacial Maximum, generated both by the randomization procedure and by the water–energy model, with the derived species richness map of overlaying modelled ranges of species in the Last Glacial Maximum using Maxent.

## RESULTS

### Comparison of modelled patterns of contemporary and Last Glacial Maximum species richness

Modelling the individual ranges of species using Maxent yielded greater adjustments between observed and predicted richness than the other species–bioclimate envelope models (see Table S1 and Fig. S1). The correlations between the empirical pattern of



**Figure 1** Species richness patterns of 475 mammals and 1103 birds endemic to sub-Saharan Africa. Empirical species richness (a, b), and species richness based on overlaying species climatically suitable ranges modelled by Maxent for current climatic conditions (c, d) and for Last Glacial Maximum climatic reconstructions (e, f).

species richness and the richness pattern modelled with Maxent was Pearson's  $r = 0.797$  for mammals ( $P = 0$ , Dutilleul's adjusted  $P < 0.01$ ) and Pearson's  $r = 0.776$  for birds ( $P = 0.001$ , Dutilleul's adjusted  $P < 0.01$ ) (Fig. 1a–d). One deviation from the empirical pattern in the richness map generated by the Maxent modelling is an additional peak in species richness south of the Congo Basin. Overlaying the Maxent hindcasted ranges for the Last Glacial Maximum generated a pattern of species richness that is more aggregated than the modelled pattern for today, with major richness peaks in the Congo Basin and Cameroon Highlands (Fig. 1e, f). These modelled species richness patterns for mammals and birds in the Last Glacial Maximum are highly concordant.

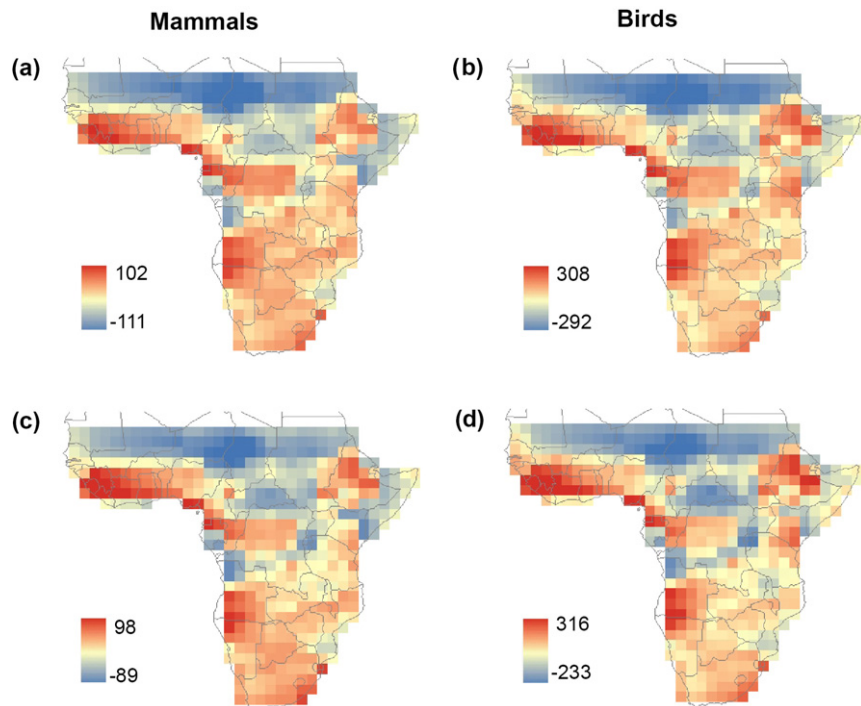
### Historical patterns of species richness and geometric constraints

The modelled pattern of species richness for the Last Glacial Maximum, generated by randomly overlaying the modelled past climatically suitable ranges from the Maxent modelling, and taking into account the size and shape of the sub-Saharan domain, was not significantly correlated after controlling for spatial autocorrelation using Dutilleul adjusted  $P$ -values, with

the derived species richness map of overlaying modelled ranges of species in the Last Glacial Maximum using Maxent (mammals, Pearson's  $r = 0.583$ ,  $P < 0.001$ , Dutilleul's adjusted  $P = 0.085$ ; birds, Pearson's  $r = 0.556$ ,  $P < 0.001$ , Dutilleul's adjusted  $P = 0.1$ ). Subtracting the mid-domain-modelled Last Glacial Maximum richness pattern from the Maxent-modelled Last Glacial Maximum richness pattern generated a residual species richness pattern showing concordance among mammals and birds (Fig. 2a, b), with levels of richness in the Congo Basin and Cameroon Highlands, the Ethiopian Highlands, Upper Guinea, the Namibia–Angola area and the Drakensberg mountain range in South Africa all higher than expected by chance. One exception is that the Eastern Arc Mountains stand out slightly as an area with richness levels higher than expected by chance, only for birds.

### Historical patterns of species richness and water–energy

Predicted patterns of species richness in the Last Glacial Maximum if determined by, and in equilibrium with, historic levels of water–energy were significantly correlated with Last Glacial Maximum species richness modelled by Maxent



**Figure 2** Last Glacial Maximum species richness residual maps for mammals and birds endemic to sub-Saharan Africa (see text for details). Mid-domain modelled species richness subtracted from Maxent modelled species richness (a, b) and water–energy modelled species richness subtracted from Maxent modelled species richness (c, d).

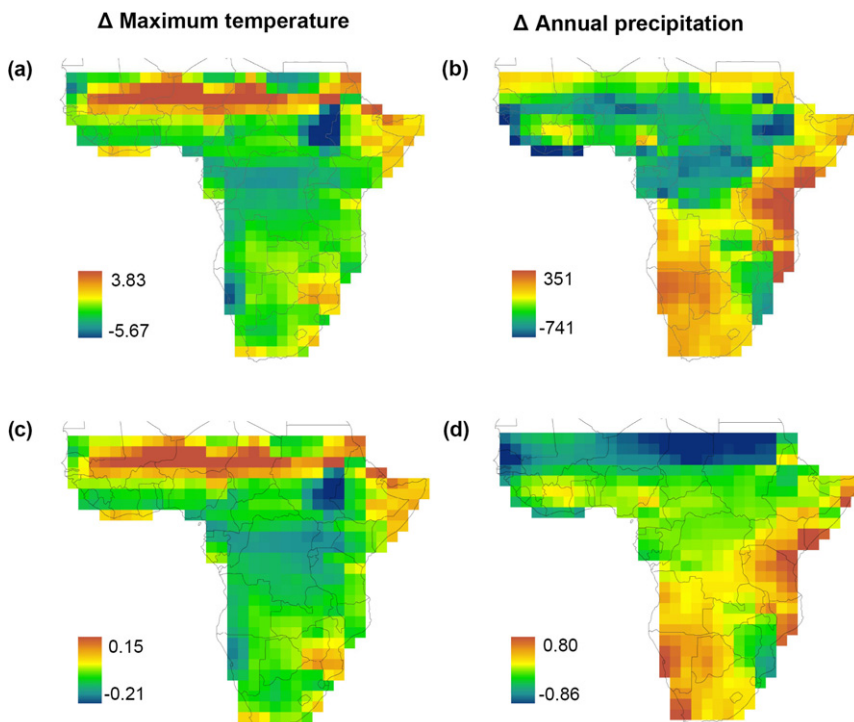
(mammals, Pearson's  $r = 0.719$ ,  $P < 0.001$ , Dutilleul's adjusted  $P = 0.019$ ; birds, Pearson's  $r = 0.694$ ,  $P = 0$ , Dutilleul's adjusted  $P = 0.025$ ). Subtracting the water–energy-modelled pattern of richness from the Maxent-modelled pattern of richness generated a residual species richness pattern similar to the one resulting from subtracting the mid-domain modelled pattern of richness, highlighting the same six areas with an unusually high level of species richness (Fig. 2e,f). The similarity of the residual plots originates from the fact that both the mid-domain model and the water–energy model predict species richness patterns of larger-ranged species well, but not the geographical placement and richness of smaller-ranged species that are responsible for unusually high level of richness in tropical vertebrates (Jetz & Rahbek, 2001; Jetz *et al.*, 2004; Rahbek *et al.*, 2007).

## DISCUSSION

We have shown that modelled ranges of African birds and mammals in the Last Glacial Maximum were aggregated in areas where richness was higher than expected if ranges were placed randomly across the study area, or if they were in equilibrium with water and energy. We interpret these areas with an unusually high aggregation of species as past areas of refugia. That the areas with an unusually high level of aggregation of species in the past were similar for birds and mammals, strengthens the idea that certain areas maintained higher suitability and perhaps stability (with regard to habitat and/or climate) than the surrounding regions. Furthermore, the cross-taxonomic congruence suggests that both birds and mammals reacted similarly to past climate changes, and that, overall, their geographical ranges are presumably governed by similar factors.

Six areas with an unusually high level of aggregation of species emerged: Upper Guinea, the Cameroon Highlands, the Congo Basin, the Ethiopian Highlands, the Angola–Namibia area and the south-east part of South Africa. Reconstructions of forest cover for that time period (Cowling *et al.*, 2008) suggest that three of the refugia – the Cameroon Highlands, the Congo Basin and the south-east part of South Africa – experienced dense forest cover during the Last Glacial Maximum. The highlands and the Congo Basin are forested today as well. The remaining three refugia, Upper Guinea, the Angola–Namibia area and the Ethiopian Highlands, occur in areas that contained low forest cover during the Last Glacial Maximum (Cowling *et al.*, 2008), presumably because they experienced colder and drier conditions (Fig. 3). Pollen records for the Angolan coast during the LGM suggest a vegetation of open savanna with few trees in the lowlands, and an open landscape with Afro-Alpine vegetation at high altitudes. During the Last Glacial Maximum, the region was far less forested than during the Holocene (Dupont & Behling, 2006).

The geographical locations where we identified a higher number of species than expected given our mid-domain and water–energy models during the Last Glacial Maximum largely correspond to the refugia suggested in the literature. The Cameroon Highlands, Upper Guinea and the Congo Basin in particular are well established as forest refugia. For example, studies of marine pollen cores (Dupont *et al.*, 2000) suggest that rain forest could grow south or south-west of the Guinean mountains, south-west of the Cameroon Highlands and in Gabon and Congo throughout the Last Glacial Maximum. Along the rest of the coast of the Gulf of Guinea, rain forest occurred in patches,



**Figure 3** Deviations of Last Glacial Maximum climate from present climate. Maximum temperature ( $^{\circ}\text{C}$ , a) and annual precipitation (mm, b) and their equivalent in percentages (c, d).

and dry forest and savanna vegetation replaced the rain forest over large areas (Dupont *et al.*, 2000).

The same areas have also been suggested as refugia based on present-day distribution and diversity patterns of birds and mammals (Diamond & Hamilton, 1980; Crowe & Crowe, 1982; Mayr and O'Hara, 1986; Fjelds  & Lovett, 1997). Crowe & Crowe (1982) examined current diversity patterns of Afrotropical passerine and non-passerine birds and suggested several refugia: an area in Upper Guinea, the Cameroon Highlands, the Albertine Rift, the Kenyan Highlands and the Angolan Highlands. Although the pollen record has shown open vegetation for the Angolan region, it also suggests some Afromontane forest with *Podocarpus* and *Ilex mitis* occurring at intermediate altitudes (Dupont & Behling, 2006). Crowe & Crowe (1982) interpret areas of Africa with higher bird diversity than their environmental variation would predict as bearing a historical signal, and suggest that these areas may have acted as forest refugia for birds during dry phases in the geological past. Mayr and O'Hara (1986) also find support for refugia in Africa in three classical locations: Upper Guinea and the western and eastern Congo Basin. They examine the position of contact zones between African bird subspecies and find that these occur between postulated refugia, as expected by the refugia hypothesis as formulated by Haffer (1969). In addition, high endemism in these postulated refugia and allopatric taxa that have never come into secondary contact, provide further support their argument.

Refugia taken as centres where species have survived unsuitable conditions in the surrounding area often exhibit high levels of endemism; this is more likely when species had no sufficient time or means for dispersal. The areas identified in this study as

potential refugia do correspond to some extent to the centres of endemism recognized by Fjelds  & Bowie (2008): the Cameroon Highlands, the Angolan Highlands, the Ethiopian Highlands and the south-eastern part of Africa. For mammals, Grubb (1982) identifies three major centres of endemism for larger African forest mammals: the Western (corresponding approximately to the area that comprises Liberia) the West Central (i.e. the Cameroon Highlands) and the East Central (the Albertine Rift).

Some of the locations we identified differ from previous findings of centres of endemism and postulated refugia. The most pronounced discrepancies include previous suggestions that the Eastern Arc Mountains served as an assemblage of refuges for birds (Fjelds  & Lovett, 1997) and the Albertine Rift as a refuge for mammals (Grubb, 1982). We only find a weak signal of excess richness in the Eastern Arc Mountains, and none in the Albertine Rift. One likely explanation for the discrepancy between our results and the expected location of these two African refugia is that the Eastern Arc Mountain, and to a lesser degree the Albertine Rift, are characterized by having unusually large numbers of species with extremely small ranges (Jetz & Rahbek, 2001; Jetz *et al.*, 2004). Given limitations in our modelling approach, these species – species with fewer than 10 grid cell records – had to be removed from the analysis (see Methods).

In contrast, the Ethiopian Plateau and the Angola–Namibia area have not been referred to as refugia previously, but they stand out in our analysis. However, the Ethiopian Plateau is a well-known centre of endemism for birds (Fjelds  & Bowie, 2008), which is consistent with our inferences that the area might have had a role as a past refugium. In the case of the



Angola–Namibia area, the discrepancy might arise from the fact that much of the refugia literature is confined to forest-associated species, while our study includes both forest and savanna species. Indeed, based on analysis of the fossil record, the area has been reported as being covered by open vegetation types during the Last Glacial Maximum. (Dupont & Behling, 2006), which is consistent with the hypothesis that the area might have then been a centre of richness for savanna species. Interestingly, although the general tendency in Africa during the Last Glacial Maximum was of reduced precipitation, palaeoclimatic reconstructions indicate that the Angola–Namibia area had higher precipitation rates than today (Fig. 3). The same inference was made with geophysical proxies of climatic conditions in the region during the Last Glacial Maximum (Gasse *et al.*, 2008), although drier climatic conditions also occurred in some areas of the Angola–Namibia region (Gasse *et al.*, 2008). Consistent with these results, modelling approaches at coarse scale (see Cowling *et al.*, 2008) have suggested that increased forest cover compared with today's cover might be due to increased moisture in the region. However, those results seem to contradict evidence from the pollen record that the area was covered with open savanna vegetation (Dupont & Behling, 2006). This contradiction might be the result of the different scales at which pollen studies and modelling studies are usually carried out, but may also be due to major geographical and methodological gaps, and a number of unresolved issues in palaeoecological knowledge about sub-Saharan Africa, as recently highlighted by Gasse and colleagues (2008).

A number of studies use phylogenetic information to assess geographical locations with high speciation (Fjelds  & Lovett, 1997; Fjelds  & Bowie, 2008). True relictual species (species with a restricted range representing ancient small clades) have high concentrations in areas that are postulated to have been refugia (Fjelds  & Bowie, 2008), peaking in the Cameroon–Gabon area and the upper Congo Basin towards the Albertine Rift, with smaller aggregates in eastern Africa, notably within the Eastern Arc Mountains and the Cape Floristic Region. Fjelds  & Bowie (2008) assume that current distributions of species must reflect, to some extent, their ancestral distribution, and conclude that the main Guineo-Congolian rain forest acts mainly as a 'museum' while the Cape and the montane/forest mosaics in Tanzania are characterized by high lineage persistence as well as local differentiation. Our analysis, though not assessing the role of speciation, supports the idea that the rain forests may have helped species survive the unfavourable glacial climatic conditions, i.e. they serve as some sort of museum.

The bioclimatic envelope models used herein involve several assumptions (Pearson & Dawson, 2004; Nogu s-Bravo, 2009; Peterson *et al.*, 2011; Svenning *et al.*, 2011):

1. Species climatic niches remain stable over time. Although the time-scale of this study extends over thousands of years, previous studies show consistency between fossils and model results, thus inviting the interpretation that climatic niches of species have a degree of predictability through time. Examples include the woolly mammoth (Nogu s-Bravo *et al.*, 2008), North American mammals (Mart nez-Meyer *et al.*, 2004),

and North American plants (Mart nez-Meyer and Peterson, 2006).

2. Species experience no dispersal limitations. In a period of thousands of years in a continent with few mountain ranges, it is likely that dispersal might not pose a major restriction but the dispersal ability of individual species is poorly known.
3. Species distributions are in equilibrium with climate at the scale of the analyses. Although little can be done to address this assumption, the fact that models were fitted for species whose ranges are restricted to Africa alone minimizes the problem.
4. Species possess no potential for evolutionary adaptation to the changing climate. Mammals and birds have relatively large generation times and although behavioural adaptations are common, especially among species with higher cognitive abilities (Sol, 2009), there is no evidence that major changes in the physiological tolerances to the climatic variables used herein occurred for the modelled species in the time frame involved.
5. The existence of non-analogue climates poses challenges to the ability of models to successfully hindcast species distributions. For example, a portion the Ethiopian refugium coincides with areas with non-analogue climates in the Last Glacial Maximum with respect to the baseline conditions, although in this case it occurs for only one out of the three climatic variables used to model species climatic envelopes.

We used a novel approach based on the combination of bioclimatic envelope models and analytical mid-domain models and predictive models of macroecology, to reconstruct a potential picture of bird and mammal diversity during the Last Glacial Maximum in sub-Saharan Africa. Our results identify areas with more species than expected by chance (i.e. stochastic randomization of ranges) or more species than expected given historic levels of resource availability. Results are thus consistent with the suggestion that refugia for mammals and birds existed in the Last Glacial Maximum, and reveal some areas that probably hosted some of these refugia. Previous studies using bioclimatic envelope models have shown that the approach is useful for characterizing past refugia (e.g. Waltari *et al.*, 2007; Svenning *et al.*, 2008; Vega *et al.*, 2010), thus complementing approaches that focus merely on the analysis of current diversity patterns (e.g. Svenning & Skov, 2007; Ara ujo *et al.* 2008), metrics of climate change (e.g. Nogu s-Bravo *et al.*, 2010; Ohlem ller *et al.*, 2012) or phylogeographical patterns (e.g. Waltari *et al.*, 2007; Vega *et al.*, 2010). We suggest here that the combination of these bioclimatic models with macroecological analytical tools can provide further insight into the existence and location of refugia.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Figure S1** Current empirical and modelled species richness of sub-Saharan of mammals and birds.

**Figure S2** Correlations between empirical and modelled species richness patterns of sub-Saharan mammals and birds for the five modelling approaches.

**Figure S3** Distribution of non-analogue climates in the Last Glacial Maximum with respect to the baseline conditions.

**Figure S4** Distribution of climatic conditions for the Last Glacial Maximum, based on HadAM3, exceeding the highest and lowest values recorded for the Last Glacial Maximum climatic conditions based on an alternative atmospheric ocean coupled general circulation model (HadCM3).

**Table S1** Correlations between empirical and modelled species richness patterns for sub-Saharan mammals and birds for the five modelling approaches.

## BIOSKETCH

**Irina Levinsky** is interested in biogeography and biodiversity conservation. More specifically, she is interested in the factors governing the geographical distributions of species and the potential impacts of global change on biodiversity. Irina has recently defended her PhD entitled 'Species distributions and climate change – linking the past and the future', at the University of Copenhagen.

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