“… Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a (Brazilian) forest. … A most paradoxical mixture of sound and silence pervades the shady parts of the wood. The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore; yet within the recesses of the forest a universal silence appears to reign.”

The voyage of the Beagle / Charles Darwin 1845
Graphic and cover design: Søren Fischer Jepsen
Species distributions and climate change
- linking the past and the future

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PhD Thesis
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Preface

This thesis is a result of a three-year PhD project, which was carried out in two academic institutions: the Center for Macroecology, Evolution and Climate, Department of Biology at the University of Copenhagen, and the Biodiversity and Global Change Lab, Department of Biodiversity and Evolutionary Biology at the National Museum of Natural Sciences (CSIC) in Madrid.

The project was funded by an internationalisation stipend from the Danish Agency for Science, Technology and Innovation, and supervised by Prof. Carsten Rahbek at the University of Copenhagen and Dr. Miguel Bastos Araújo at the National Museum of Natural Sciences.

The thesis consists of a synopsis, describing the background and objectives of this thesis and discussing the contribution of this work in a broader perspective, and four chapters, written as scientific papers and reporting the findings of this PhD project. It ends with an appendix, a published paper based on the results from my M.Sc. thesis, from which many of the ideas for this thesis have emerged.

Irina Levinsky

Copenhagen, May 2010
# Table of contents

Acknowledgements ........................................................................................................... 5

Summary............................................................................................................................ 7
Danish summary ............................................................................................................... 9
Spanish summary ............................................................................................................ 11
Hebrew summary ............................................................................................................ 13

Synopsis............................................................................................................................ 15
1. Introduction .............................................................................................................. 15
2. Effects of past climatic changes on biodiversity ...................................................... 16
3. Challenges related to predicting the future .............................................................. 19
4. Outlook  .................................................................................................................... 23

Chapter I - Climate envelope models suggest a spatio-temporal co-occurrence of refugia of African birds and mammals ................................................................. 31
Supplementary material ............................................................................................... 55

Chapter II - Exploring surrogates for the dispersal ability of African starlings ...... 61
Supplementary material ............................................................................................... 81

Chapter III - Sub-Saharan African vertebrates persisted in the Last Glacial Maximum despite loss of their bioclimate envelope .................................................... 83
Supplementary material ............................................................................................... 107

Chapter IV - Rethinking species’ ability to cope with rapid climate change .......... 109

Appendix A – Potential impacts of climate change on the distribution and diversity patterns of European mammals ......................................................... 119
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תודה!
Summary

Climate change is predicted to have a marked impact on biodiversity, and changes in the distributions of numerous species have already been correlated with ongoing climate change. Climatic oscillations, however, were also the rule during the Pleistocene. A look to the past may therefore shed light on the impact of future climate change. In this thesis, I relate past climatic changes and their impact on biodiversity to future climate change.

I first revisit the role of refugia as areas where African birds and mammals survived adverse climatic conditions. I use bioclimate envelope models to reconstruct climatically suitable ranges of the two taxa during the Last Glacial Maximum, and find that these congregated in the same areas, lending support to the refugia hypothesis. I then focus on one taxonomic group of birds, the African starlings, and explore surrogates for their dispersal ability in relation to range size and range filling.

Next, I take a critical view of the tools I use and the assumptions behind them. Bioclimate envelope models are the most widely used tool to forecast the impact of climate change on species distributions, and species that are predicted to have reduced or no climatically suitable range in the future are considered at risk. However, by hindcasting bioclimate envelope models, I find that that several extant species are modelled to have no climatically suitable range in the Last Glacial Maximum, even though we know they existed in that period and persisted until today. This cautions against interpreting uncritical forecasts of reduction in bioclimate envelopes as strong evidence for species extinction due to future climate change. Finally, I discuss how our perception of species’ abilities to cope with future climate change is altered by novel geophysical findings of abrupt climatic changes in the past. Climatic changes in the Pleistocene have generally been regarded as gradual, and therefore not detrimental for biodiversity, while the current rapid climate change is assumed to pose a marked threat. The new studies support the view that abrupt climatic changes were more common in the past, yet species have nevertheless managed to persist. Although this may imply that current climate change may not impose a big threat to biodiversity, habitat fragmentation doubtless alters this view.
Resumé

Klimaforandringer forudsiges at få markant indflydelse på biodiversitet, og ændringer i udbredelsen af adskillige arter er allerede blevet sammenholdt med igangværende klimaforandringer. Klimatiske fluktuationer var dog også fremherskende under Pleistocænen. Et kig tilbage i fortiden kan derfor være med til at kaste lys over de konsekvenser som fremtidens klimaforandringer kan få.

Først reviderer jeg refugiernes rolle som områder hvor afrikanske fugle og pattedyr overlevede ugunstige klimatiske forhold. Jeg anvender bioklimatiske envelope modeller til at rekonstruere klimatisk passende udbredelser for de to taxa under det sidste glaciæle maximum, og resultaterne viser at disse samlede sig i de samme områder hvilket underbygger refugia hypotesen. Jeg fokuserer derefter på en taxonomisk gruppe af fugle, de afrikanske stære, og udforsker mønstre af sprednings-evner i relation til migratorisk status og ændringer i omfanget af deres udbredelser.

Dernæst ser jeg med kritiske øjne på de værktøjer jeg anvender og de bagvedliggende antagelser. Bioklimatiske envelope modellering er blandt de hyppigst anvendte værktøjer til at rekonstruere klimatisk passende udbredelser for arters udbredelse, og de arter der forudsiges at få indskrænket eller ingen passende klimatisk udbredelse i fremtiden betragtes som værende i risiko. Ved at projicere bioklimatiske envelope modeller tilbage i tiden, finder jeg dog at flere nulevende arter modelleredes til at have ingen passende klimatisk udbredelse i det sidste glaciæle maximum, på trods af at vi ved de eksisterede i den periode og vedblev med at eksistere frem til i dag. Dette maner til forsigtighed i forhold til ukritisk at fortolke forudsigelserne af reduktionen i bioklimatisk rum som klare beviser for arters uddøen som følge af klimaforandringer. Til sidst diskuterer jeg hvordan vores opfattelse af arters evner til at håndtere fremtidige klimaforandringer bliver ændret af nye geofysiske beviser for bratte klimaforandringer i fortiden. Klimaforandringer i under Pleistocænen er blevet anset for at være en gradvis proces og derfor ikke synderlig skadelig for biodiversitet, mens de nuværende, hurtige klimaændringer antages at udgøre en markant trussel. Disse nye studier underbygger synspunktet om at bratte klimaforandringer var mere almindelige i fortiden og dog lykkedes det arterne at overleve.
frem til i dag. Selvom dette kunne antyde at de nuværende klimaførandringer ikke udgør den store trussel mod biodiversitet, så ændrer habitat-fragmentering uden tvivl dette synspunkt.
Resumen

Es previsible que la biodiversidad sufra significativos impactos por el cambio climático, y de hecho los cambios en la distribución de numerosas especies en relación al cambio climático en las últimas décadas han sido profusamente estudiadas. Sin embargo, los cambios climáticos no son algo nuevo sino un proceso común en otros periodos, como por ejemplo durante el Pleistoceno. En este sentido, una mirada al pasado podría arrojar luz sobre los impactos futuros del cambio climático en la biodiversidad. En la presente tesis pongo en relación los cambios climáticos pasados y sus impactos en la biodiversidad con los impactos futuros del cambio climático.

Primero, revisito el papel y la localización de los refugios donde las aves y mamíferos africanos sobrevivieron a las oscilaciones climáticas pleistocenas. Para ello uso modelos de distribución de especies, para reconstruir los rangos de distribución de aves y mamíferos en África en el Último Máximo Glaciar. Los resultados muestran que estos refugios coinciden en las mismas áreas para aves y mamíferos, lo que refuerza la hipótesis de los refugios. Posteriormente, estudio específicamente una familia de aves, los estorninos africanos, y exploró los patrones de su capacidad dispersiva en relación a su status migratorio y a cambios en el tamaño del rango geográfico.

En otro de los capítulos, reviso de forma crítica la principal herramienta metodológica usada durante mi tesis, modelos de distribución de especies, y sus bases teóricas. Los modelos de distribución de especies son actualmente una de las herramientas más usadas para predecir el impacto del cambio climático en la distribución de especies. Además, se considera que aquellas especies que sufrirán una reducción completa o substancial de la extensión geográfica de sus condiciones climáticas favorables se consideran en riesgo potencial de extinción. Sin embargo, mis resultados contradicen esa idea ya que cuando predecimos la distribución para algunas especies de aves y mamíferos en África en el Último Máximo Glaciar, los resultados muestran que especies que todavía siguen existiendo no disponían de ninguna condición climática favorable. Estos resultados subrayan la necesidad de ser prevenidos a la hora de interpretar las proyecciones futuras sobre el impacto del cambio climático en la extinción de especies. Finalmente, discuto
como nuestra percepción sobre la capacidad de las especies para tolerar los impactos del cambio climático puede ser alterada por recientes investigaciones en el ámbito geofísico relativas a cambios climáticos abruptos en el pasado. Los cambios climáticos durante el Pleistoceno habían sido interpretados hasta fechas muy recientes como cambios graduales y por lo tanto escasamente peligrosos para la biodiversidad, en contraposición al actual cambio climático. Esos estudios recientes muestran que cambios climáticos abruptos se han producido de forma continuada durante el Pleistoceno, y que aún así muchas especies han sobrevivido a ellos. Aunque esto implica que quizá el cambio climático por sí mismo no impacte muy negativamente en la biodiversidad, la fragmentación del hábitat podría amplificar sus efectos.
שנתונים אקלימיים שונים הלשנים בצרות מאמצות על מגדלי הבולונדר, ומרגישים בתופעתו של המסף הר
של,mid נמסגו בקרבה לleetcodeי אקלים שונים המתרחשים בתוכוח האקלים. דו כי הנחת אקלימי
וגו עלупить בשנורサポート בתקופת הפולפסוקז. מנשל לשבר, אט כל בול לשפר, מרוי על התחילה שטידיי. ב
صعبת בו אני בריתא את נשאו, בין השינויים האקלימיים שתרחשה בשבר ושופעת על מגדלו הבולונדר
לובני שעינו אקלים שטידיי.

ארוש את נרתון המקודש את המקודש של אורי מקלט, (refugia), beishtamgangli ציירימ ווניקס וחבר
בהצלחת שנויה אקלים רעונים. כי נשמה השמדת במדלים של התופעת מטני על מת שלשיה ואת ת事業
התופעת המתחימה אקלים שונים בתיקתיות הושע באלגראל אתᵛאר אחרים عبر תקעצה שקטומית ש. מתמקם
עלילה כי בשני הקבוצת התנועה באזות האזוריים התזה התוכחה וה鄜ות אורי המקולט. בלבל הנני
מתמקדות בפשחת אצות של פריויר, הוריזוניים האפריקהיים, וחקור את דופס יקולת פורו שלвал חמא
לאפרגיני נרというもの בגודל אורי המקולט.

במחושך או מלחץ בתניא בקורותית של כל המקדש בה הוא השמחות גם להנהלת הנמודстроен מחלו
מולדים של התופעת מטני מעמדים כל כפין המחירים במדליון הממסות ולצאת לעצפתות של השגניר
אקלימליים על תופעת המטני. מטני אשר נמסגו בעבוד צפיפות יגוך ואית הصلة של אורים לוחזים
אקלימליים חשבים מעוב במדליון. בניסויים אחרים השם מה שמתמשת במדליון colum על מטני שזרימה של
בויה את מה שנגבים תקלות רבות שלגריאלים האזוריים. ואן מגדלי זהזים של צב שגילון אשר
היעלמות של אורי ה隆重举行 המתחים בתיקתיות והקלטנו, וזף שלמשל העבר את והتشكيلים של🤓י
והם. הצאצאים אנל מעשרים ומפרים מחברים המנסים צמצום של אורי אקלים בוחר את האועדנות להتكامل
לところで של מטני בתקופה שטרויא אקלים. לבסוף, איני הנה את בנייתו בין הוותימ של היסודות
ע سواء אקלימיים בעבר, ובקטובו עירובי א-פריוור הходят לקוטב של שגניר פצואים בקלל
בינה(print, את הנחת המקדס של אל השגניר האקלים שונים בתיקתיות הפיסטיות והדבריות על אל פגוע
במגדלי הבולונדר, בודק שלגניר האקלים שונים של מגדליבסיסם של היסודות. המחקרים
ההיתשים של כרכי שגניר אקלים פצואים והходятנו рецепт החובב העבר ש𝗿פע לע פן
מילים שגניר העולות לדרום לולמי וחלקים. ל哉זור גנשים שלגניר שגניר אקלים נקודים
איננו מורזים אחר הכל גודל למגדלו הבולונדר, או יש לקחת שיחבון fragmented, או האדות ושופעת החרסית והשתפה של
שהגרים האקליםיים ביתו של הקוטב של בתי הגנה.
Synopsis

1. Introduction

1.1 Species distributions and climate change
The geographical ranges of species are shaped by numerous factors, e.g. climatic conditions, dispersal abilities and opportunities, historical events and biotic interactions (Lomolino et al. 2006). However, at broad scales species distributions are largely governed by climatic conditions, and it is well documented that climatic changes affect species distributions. The climatic oscillations of the past have indeed resulted in shifts in the distributions of species (Graham et al. 1996, Grayson 2000, Davis and Shaw 2001, Barnosky et al. 2003). Similarly, the previous century’s rise in mean global temperatures (of approximately 0.7°C, IPCC 2007) has also been shown to correlate with shifts in the distribution of numerous species, both polewards and up in elevation (Parmesan and Yohe 2003, Root et al. 2003, Hickling et al. 2006, Parmesan 2006). This warming is expected to continue in the future, with mean global temperature predicted to increase by 1.8-4° in the coming century (IPCC 2007), and is assumed to result in dramatic consequences for biodiversity (Thomas et al. 2004, Thuiller et al. 2005, Thuiller et al. 2006, Levinsky et al. 2007). However, predicting the future is not an easy task, and constitutes a key challenge for conservation and climate change ecology. Our knowledge is strongly dependent on modelling and the ability of the models to correctly forecast the unknown. Therefore, information on changes in climate and species distributions in the past is invaluable for improving our understanding of the potential impact of future climate change on species distributions (Willis et al. 2007).

1.2 Objectives of the thesis
This thesis attempts to use information on the effect of past climatic changes on species distributions, in order to provide a better understanding of future impacts of climate change on biodiversity. The thesis has three main objectives:
• Shedding light on a classical debate in biogeography concerning the refugia theory for birds and mammals in Africa (Chapter I)
• Inferring dispersal abilities of species from classical and novel proxies (Chapter II)
• Critically evaluating the methods used for the previous analyses and the assumptions behind them (Chapters III & IV)

2. Effects of past climatic changes on biodiversity

2.1 Glacials, interglacials and species distributions
Climatic changes have been the rule in the history of our planet, and climates of the past range from “greenhouse” conditions 100Mya to “ice-house” conditions of, e.g., the Last Glacial Maximum (21Kya) (Ruddiman 2001). The best documented are the climatic oscillations associated with glacial-interglacial cycles of the Pleistocene. These have had clear effects on the distribution and diversity patterns of many taxa (Graham et al. 1996, Grayson 2000, Davis and Shaw 2001, Barnosky et al. 2003). The temperate zones saw vast glaciated areas and species were largely pushed towards the equator (but see recent ideas on "cryptic refugia" in Stewart and Lister 2001). The tropics, on the other hand, experienced reduced temperatures and markedly drier conditions, and pollen data suggest changes in the composition of the vegetation (Maley 1991, Elenga et al. 1994, Maley and Brenac 1998, Anhuf et al. 2006). However, reconstructing past species distributions is difficult as fossil and pollen data are scarce for most species, especially in tropical regions.

2.2 Tropical refugia
The climatic fluctuations of the Pleistocene have been proposed to shape species ranges and diversity patterns. The most prominent theory in the tropical context is Haffer’s refugia theory (Haffer 1969, also known as "forest islands", Lönnberg 1929), which he based on the contemporary distribution of the chachalaca (Ortalis) superspecies and rainfall patterns in the Amazon Basin. Haffer’s refugia theory suggests that tropical forests were repeatedly fragmented during the cold and arid glacial periods throughout
the Pleistocene and expanded during the warm and wet interglacials. These refugia are thought to have enabled the persistence of the tropical lowland fauna under unfavourable climatic conditions, with the further argument that this isolation also presented opportunities for speciation (Haffer 1969). The refugia theory was challenged from its early days (Endler 1982), with a plethora of competing theories that alternatively may promote speciation, e.g. barriers in the form of rivers and changes in sea level, competitive species interactions or parapatric speciation across steep environmental gradients (see Haffer 1997 for a review).

Although the idea of isolated forest blocks has largely been rejected, there is an overall consensus regarding the existence of refugia for vertebrates in Africa (e.g., Grubb 1982, Mayr and O'Hara 1986, Nichol 1999). In the absence of a good fossil record, numerous methods have been used to assess the existence and location of refugia for vertebrates in Africa. Attempts to identify refugia were largely based on (1) inferences from contemporary patterns of distribution: secondary contact zones between sister species, predicting refugia to lie between these zones (Mayr and O'Hara 1986), diversity patterns, associating refugia with areas of high diversity (Diamond and Hamilton 1980, Crowe and Crowe 1982, Mayr and O'Hara 1986) and centres of endemism, assuming that these reflect speciation centres (Fjeldså and Bowie 2008); (2) the phylogenetic age of African bird species, postulating that phylogenetically younger species will occur in areas where speciation occurs, i.e., in refugia (Fjeldså and Lovett 1997); and (3) molecular phylogenetic studies of African birds, rodents and primates (Roy et al. 2001, Querouil et al. 2003, Anthony et al. 2007- respectively).

The previous studies focused on one taxon or just a handful of species. In order to search for glacial refugia of all endemic African birds and mammals I used hindcasting bioclimate envelope modelling (Nogués-Bravo 2009) (Chapter I). I found that modelled climatically suitable ranges of African birds and mammals during the Last Glacial Maximum were aggregated in specific areas, where richness was higher than expected when taking into account geometric constraints or resources (Fig. 1). This excess of species can be interpreted as refugia, thus supporting the idea that during the Last Glacial Maximum the same refugia existed for both birds and mammals in sub-Saharan Africa.
Six areas emerged as potential refugia: Upper Guinea, the Cameroon Highlands, the Congo Basin, the Ethiopian Highlands, the Angola-Namibia area, and the highest part of the Drakensberg mountain range in South Africa (Fig. 1). These locations largely correspond to the refugia suggested in the literature. Especially the Cameroon Highlands, Upper Guinea and the Congo Basin are well established as forest refugia (Fjeldså and Bowie 2008) and retained forest cover during the Last Glacial Maximum (Cowling et al. 2008). The fact that these areas were potential refugia for both birds and mammals suggests that both taxa reacted similarly to past climate changes, and are presumably governed by the same factors.

Figure 1 - Refugia for birds and mammals in Africa in the Last Glacial Maximum (Chapter I). Deviations of species richness from that expected by geometric constraints or resource availability for mammals (a) and birds (b). Red areas represent a surplus of species, i.e. refugia, and green areas – a deficiency. The upper 50% of the excess are plotted for mammals (c) and birds (d) for better visualisation.
3. Challenges related to predicting the future

Bioclimate envelope models are widely used for predicting the effects of climate change on species distributions (Thomas et al. 2004, Thuiller et al. 2005, Thuiller et al. 2006, Levinsky et al. 2007). These models use information on current geographical ranges of species combined with climatic variables to project climatically suitable ranges onto modelled climatic conditions for the future (Pearson and Dawson 2003). A reduction in the modelled climatically suitable range of a species is assumed to imply a reduction in population size and abundance, and has been interpreted as posing a threat to species’ persistence. Recent studies using bioclimate envelope models suggest that climate change will have marked impacts on biodiversity, with many species projected to experience marked reductions in climatically suitable ranges and some projected to lose their complete climatic envelope in the studied regions (Araújo et al. 2004, Thomas et al. 2004, Thuiller et al. 2006, Levinsky et al. 2007).

3.1 Assessing the ability of species to track climatic changes

Species responses to climate change are typically boiled down to genetic adaptation, dispersal or extinction (Holt 1990). The prevailing consensus, however, is that current climate change outpaces micro-evolutionary processes (Jump and Penuelas 2005), and dispersal is therefore perceived as the most likely response of species to recent climate change. Shifts in the distributions of species have indeed already been shown to correlate with changes in the distribution of numerous species (Parmesan and Yohe 2003).

Understanding the ability of species to disperse is therefore essential for assessing their ability to track climatic changes in the future. However, dispersal is difficult to quantify (Nathan 2001), and empirical data on dispersal ability are limited to few species. Therefore, proxies of dispersal are exceedingly sought after. Previous studies have found positive correlations between dispersal and morphological characteristics such as wing length (Paradis et al. 1998, Skjelseth et al. 2007), wing pointedness and bill depth (Dawideit et al. 2009). In addition, the migratory behaviour of birds has been shown to correlate with dispersal ability, showing that migrants are better dispersers than resident
species (Paradis et al. 1998, Sutherland et al. 2000, Dawideit et al. 2009). Finally, Sylvia warblers with better dispersal ability have larger range sizes (Böhning-Gaese et al. 2006).

I used the African starlings to explore classical and novel surrogates for their dispersal ability (Chapter II). I assessed whether range size and range filling (the proportion of a species’ climatically suitable range that it occurs in) correlate with wing pointedness, migratory status and change in range size over time. The expansion of a species’ range over time may give an indication of its dispersal ability, and the more species expanded their range since the Last Glacial Maximum, the better they should be at tracking their climatic envelope in the future. I found a significant positive correlation between change in range size over time and range filling, and a tendency for partial migrants and nomadic species to have larger range sizes and higher range filling than resident species, suggesting they may be better dispersers.

3.2 How well do the models perform?
Assessing the performance of bioclimate envelope models is key to making reliable forecasts; however, it is not an easy task as there is no data against which forecasts can be tested. A few studies have used independent data to assess model performance on time scales ranging from decades (Araújo et al. 2005a, Araújo et al. 2005b) to millennia (Martinez-Meyer et al. 2004, Martinez-Meyer and Peterson 2006, Varela et al. 2009) with differing results regarding the ability of the models to be transferred in time. For example, models predicted fossil distributions of North American mammals in the Last Glacial Maximum well (Martinez-Meyer et al. 2004), while Varela et al. (2009) find that although their model fits current African distributions of the spotted hyena well, it does not predict European fossils from the Last Interglacial (126Kya). Unfortunately, independent data sets from surveys or fossils are usually only available for a number of well studied temperate species.

Generalising from studies on few species is not easy, and our ability to predict the effects of future climate change on biodiversity remains difficult to assess. To overcome this problem, I explored an alternative approach to obtain insight into the ability of bioclimate envelope models to project distributions of species in time under climate
change (Chapter III). The approach consisted of hindcasting the distributions of extant African mammal and bird species to the Last Glacial Maximum. A substantial reduction or complete loss of climatically suitable ranges would not be expected for species that persisted until today. However, the results showed reductions and complete losses of climatically suitable ranges of the same order of magnitude as predictions for the future (Table 1). The species with no climatically suitable ranges in the Last Glacial Maximum were spatially clustered, partly in areas with no climatic analogues in the Last Glacial Maximum. They were also phylogenetically clustered, occurred in lowland forests and were associated with moist habitats. These associations were not captured by our modelling approach presumably due to scale issues, and may be more important for the persistence of the species than coarse-scale climatic conditions. In addition, the weak prediction ability of the models for these species was not captured by standard evaluation methods. This further cautions against interpreting forecasts of reduction of bioclimate envelopes as extinction risk due to climate change.

### Table 1 - Reductions of climatically suitable ranges in studies using forecasting and hindcasting bioclimate envelope models

<table>
<thead>
<tr>
<th>Time horizon</th>
<th>Geographical extent</th>
<th>Taxon</th>
<th>Lose &gt;50%</th>
<th>Lose 100%</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>2080</td>
<td>Europe</td>
<td>Plants</td>
<td>12-55%</td>
<td>0-2%</td>
<td>Thuiller et al. (2005)</td>
</tr>
<tr>
<td>2100</td>
<td>Europe</td>
<td>Mammals</td>
<td>14-57%</td>
<td>1-9%</td>
<td>Levinsky et al. (2007)</td>
</tr>
<tr>
<td>2050 &amp; 2080</td>
<td>Africa</td>
<td>Mammals</td>
<td>25-60%</td>
<td>0-4%</td>
<td>Thuiller et al. (2006)</td>
</tr>
<tr>
<td>21Kya</td>
<td>Sub-Saharan Africa</td>
<td>Birds</td>
<td>26-29%</td>
<td>1-2%</td>
<td>Chapter III</td>
</tr>
<tr>
<td>21Kya</td>
<td>Sub-Saharan Africa</td>
<td>Mammals</td>
<td>32-34%</td>
<td>2-7%</td>
<td>Chapter III</td>
</tr>
</tbody>
</table>

### 3.3 Is current climate change indeed unprecedentedly rapid?

It has generally been assumed that climatic changes in the Pleistocene were gradual, while contemporary climate warming occurs at an unprecedentedly rapid rate; this is predicted to have dramatic consequences for biodiversity (IPCC 2007). However, recent geophysical studies challenge this view by documenting abrupt increases in storminess and temperature in just a few years at the end of the last glacial (Brauer et al. 2008, Steffensen et al. 2008, respectively), and rapid sea levels rise of 2-3 meters during the last interglacial period (121Kya) (Blanchon et al. 2009). Chapter IV discusses how our perception of species’ ability to cope with future climate change is altered with these
novel findings of abrupt climatic changes in the past. Abrupt climatic changes may have been more common in the past than previously assumed, yet species have nevertheless managed to persist (previously coined the “Quaternary conundrum” by Botkin et al. 2007). Viewed in isolation this may suggest that current climate change will not pose a big threat to biodiversity. However, I argue that even if climatic changes in the past were as fast as the new evidence suggests, species will not necessarily be able to cope, as the habitat today is more fragmented (Fig. 2). Habitat fragmentation impedes short- and long-distance dispersal processes and reduces species’ potential to respond via trait shifts due to lower phenotypic variability across their range. The potential responses of species to changing environments (e.g. dispersal and adaptation) can only be assessed by considering climate change in concert with main drivers of species extinctions within human history, such as habitat destruction, invasive species and diseases.

**Figure 2 - Changes in species’ ranges as a result of climatic changes in a pristine vs. a fragmented landscape.** Species ability to track climatic changes (ignoring adaptation) in (a) a pristine world where species’ ranges may track gradual climatic changes and (b) a world modified by humans, with habitat destruction and fragmentation, where available areas of suitable microclimatic conditions are smaller, reducing the probability of endurance (central panel), as well as that of successful range shifts (right-hand panel). Green indicates suitable habitat, whole circles represent the distribution of a species and dashed circles - its distribution in the previous time step.
4. Outlook

There is little doubt that climate change will affect biodiversity. The big question remains how and to what extent, posing a substantial challenge for conservation planning. We are therefore forced to rely on the only source of information available – knowledge on the effects of climate change on species in the past.

- **Understanding changes in species distributions over time**
  To achieve a better understanding of changes in species distributions over time, data on the past distributions of species is required. Fossil and pollen data may be scarce but data do exist in museum collections, individual published studies and notes scattered around the world. Information on past changes in distributions of extant and extinct species and their population dynamics can also be obtained from ancient DNA (e.g., Haile et al. 2009, Campos et al. 2010), although these are limited to regions with permafrost that presents the degradation of DNA. Phylogeographic studies, although restricted to extant species, may overcome the limitation of data availability related to preservation of fossils and DNA, because they are independent of the climatic conditions at the study site. All these data sources could be combined to get a more complete picture of the past distributions of species. Preferably, a publicly available database with spatial distribution of past occurrences of species could be created. An excellent template for such a database is FaunMap, an electronic database documenting the late Quaternary distribution of mammal species in the United States (http://www.museum.state.il.us/research/faunmap/ ). Studies combining bioclimate envelope models with phylogeography have already provided insights into the role of refugia in promoting speciation (Carstens and Richards 2007, Waltari et al. 2007, Solomon et al. 2008), and studies combing these with ancient DNA are underway.

- **Species responses to climatic changes – looking beyond dispersal**
  Species are assumed to either disperse or adapt as a response of climate change. However, to date, the focus has been on dispersal, and the ability of species to adapt to the changing climate has largely been ignored (in this thesis, as well). For example, bioclimate models assume that species lack sufficient genetic adaptive potential, as
well as phenotypic and behavioural plasticity, to adapt to climates beyond those under which they occur today. However, phenotypic changes have already been documented to correlate with climatic changes. The body mass of the bushy-tailed woodrat (*Neotoma cinerea*), for example, has increased in correlation with the decrease in temperatures in the Late Quaternary in the Colorado Plateau (Smith and Betancourt 1998), and decreased with recent increases in temperature in New Mexico (Smith *et al.* 1998). Although adaptive potential is bound to differ between species, these examples demonstrate that it may be more important than previously assumed, and if dispersal is prevented, key in determining the fate of species in the light of climate change in the future.

**Improving models for the future**

Recent studies have taken bioclimate modelling to the next level by incorporating dispersal abilities (Engler and Guisan 2009) and population models (Brook *et al.* 2009). However, these require detailed information on dispersal, ecology and population dynamics, which is only available for few species. In addition, while incorporating more data into the models improves them, a trade-off exists between precision and generality, so they may perform worse when projected in time. Evaluating the predictive ability of bioclimate envelope models, however, remains a challenge for (see section 3.2). Evaluation methods based on fitting the models to current data do not hold the capacity to correctly reflect prediction ability. Therefore, more independent data on the distribution of species in past is in high demand (see above), as it holds the potential to be applied more systematically to evaluate model predictions.
References


25


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

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Abstract

Studies investigating the theory on tropical refugia for vertebrates have previously focussed 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, using historic climate data to model the location of past ranges of species based on their current distributions. Using current distributions of 537 mammal and 1265 bird species, we model the past distribution of species taking advantage of recently available reconstructions of climate for the Last Glacial Maximum. Modelled historical ranges were evaluated individually using standard techniques for evaluating the performance of species distribution models. Potential refugia were identified by the overlap of climatically suitable ranges (i.e., levels of species richness) beyond the anticipated as a result of geometric constraints alone (by randomising the locations of the modelled past climatically suitable ranges in the sub-Saharan domain), or the expected given resource availability (by modelling species richness patterns as would be expected given the water–energy theory). 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 by geometric constraints (chance) 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 highest part of the Drakensberg mountain range in South Africa. This unusual high aggregation of predicted suitable ranges of birds and mammals in six relatively small geographical areas corresponds in location to 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.
Introduction

Researchers have long pondered on the role of Pleistocene climatic fluctuations in shaping tropical patterns of species ranges and levels of richness. The most prominent theory in the tropical context is Haffer’s refugia theory (1969). This theory, also known as “forest islands” (Lönnberg 1929, Moreau 1933), suggests that during the climatic fluctuations of the Pleistocene, tropical forests were repeatedly fragmented during the cold and arid glacial periods and expanded during the warm and wet interglacials. These refugia were proposed to enable the persistence of the tropical lowland fauna under unfavourable climatic conditions, with the further argument that this isolation also presented opportunities for speciation (Haffer 1969). The refugia theory has been debated ever since its early days (Endler 1982), without a consensus being achieved.

Consensus 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 Africa 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 and Brenac 1998, Anhuf et al. 2006). Furthermore, pollen based biome reconstructions for this period corroborate that sites in the African tropical highlands, characterised today by evergreen forest, were dominated by steppe or xerophytic vegetation (Elenga 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 represent past species distributions. As a result, researchers have turned to other sources of information 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 and Hamilton 1980, Crowe and Crowe 1982, Mayr and O'Hara 1986) and centres of endemism (Fjeldså and Bowie 2008) with refugia.

Another approach has investigated phylogenetically old vs. young African bird species, postulating that phylogenetically younger species will occur in areas where speciation occurs, i.e., in refugia (Fjeldså and Lovett 1997). More recently, phylogenetic studies of African birds, rodents, and primates found support for the existence of refugia using molecular techniques (Roy et al. 2001, Querouil et al. 2003, Anthony et al. 2007 - respectively). However, these studies were restricted to one taxon or just a handful of species and therefore do not represent refugia for entire faunas.

Newly available reconstructions of past climates allow shedding light on the location of refugia without relying upon the limited fossil record available for the Last Glacial Maximum. We combined these climatic reconstructions with hindcasting of bioclimatic envelope models, to yield insights into changes of climatically suitable ranges of 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. That is, based on overlaying the modelled past climatically suitable ranges of species, we compared the level of aggregation of such ranges with the expected level of species richness given a null model (i.e., the Mid-Domain Model, Colwell et al. 2004) and given climatic resources conditions (i.e., the water-energy model, Hawkins et al. 2003). We interpret areas with a higher range-overlap (i.e., species richness) than expected by chance or resources levels, as areas that may have acted as refugia. We used this approach to (1) investigate the possibility that refugia of 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 <50% land, resulting in a total data set of 476 grid cells.

Species distribution data
The distributions of 1556 birds (Hansen et al. 2007) and 970 mammals (Burgess et al. 2007b) 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 previously been used for phylogeographical (Fjeldså et al. 2007, Fjeldså and Bowie 2008), macroecological (Jetz and Rahbek 2001, Jetz and Rahbek 2002), conservation (Balmford et al. 2001, Burgess et al. 2002, Burgess et al. 2007a) and climate change studies (Willis et al. 2009, Hole et al. 2009). To encompass the entire range of climatic conditions under which the species occur, we restricted our analyses to species endemic to the domain of sub-Saharan Africa. Given that bioclimatic envelope models do not perform well for species with a small number of occurrences (Stockwell and Peterson 2002), we further restricted analyses to 1265 birds and 537 mammals with more than 10 grid cell records.

Climatic data
Minimum and maximum temperatures and annual precipitation for the Last Glacial Maximum were calculated using a General Circulation Model. 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 min. 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 LGM over 20 simulated years and climatological means were compiled for the final 14 yr. Time-series analysis of various climate variables for the entire 20 yr simulation shows that disregarding the first 6 yr allows the climatology model to reach full equilibrium.

The HadAM3 model was initialised 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 LGM was derived from the ICE-4G model (Peltier 1994). The atmospheric concentration of CO₂ was specified at 200 ppm 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 and Taylor 1999).

**Bioclimatic envelope modelling**

Climatically suitable ranges for the Last Glacial Maximum were reproduced by means of hindcasting climate envelope modelling. We used the Bioensembles software (Rangel et al. 2009, Diniz et al. 2009) to implement four different modelling approaches – GARP, Domain, Bioclim, Mahalanobis distance, and the maximum entropy software Maxent (Phillips et al. 2006, Phillips and Dudik 2008). Maxent performed best (see supplementary material Table S1, Fig. S1 and Fig. S2) and we decided to carry out further analysis using its predictions. Maxent often predicts current species distributions better than other climate envelope modelling methods (Elith et al. 2006, Phillips et al. 2006), but it might sometimes over-fit species–climate relationships, possibly limiting its transferability (Peterson et al. 2007). Using a small number of predictor variables reduces the risk of over-fitting of the species–climate relationships and may 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 component analysis to identify the three least correlated variables. 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 regularisation multiplier to 1 (Phillips et al. 2006).

Model accuracy was estimated using the area under the curve (AUC) of a receiver operating characteristic curve (Metz 1978, Fielding and Bell 1997). A random draw of 70% of the data used 10 times to assess the sensitivity of projections to variations in the data for model calibration (yielding a 10-fold cross validation), thus providing a measure of model stability (Araújo and 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 $>0.7$ 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). 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.

Null model: Predicting levels of species richness based on geometric constraints

Some grid cells 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). To take this into account when attempting to identifying potential refugia based on unusual aggregation of overlapping ranges in the past, 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, i.e., we followed the advice on using the empirical data in the randomisation analyses of Colwell et al. (2004). 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. This gives us a null-model prediction of number of species per grid cell. By subtracting this figure from the species richness generated by overlaying the modelled past climatically suitable ranges, we identified areas with higher richness than expected given geometric constrains.

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 temporal-invariant state of equilibrium with climate (Hawkins et al. 2003). To identify areas of unusual high aggregation of species beyond the level expected given the potential equilibrium of species richness with available resources, we simulate expected patterns of species richness during the Last Glacial Maximum using the historic climate data on temperature and precipitation. We first identified the function describing the relationship between contemporary species richness and contemporary 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 BioGeoSim (Gotelli et al. 2007) to predict the spread and occurrence of species ranges in a climatic heterogeneous landscape, where probabilities of species occurrence are highest in grid cells exhibiting relatively high temperature and precipitation. This generates a prediction of the historical pattern of species richness if it were fully determined 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.

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). Spatial-statistical analyses were carried out using SAM 3.0 (Rangel et al. 2006, spatial analysis in macroecology http://www.ecoevol.ufg.br/sam/).

**Results**

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

Modelling the individual ranges of species using Maxent performed better than the other climate envelope models (see Methods). Overlaying contemporary modelled ranges modelled by Maxent generates a similar species richness pattern for birds and mammals that, in contrast to the other modelling approaches (see supplementary material Table S1 and Fig. S1), resembles the empirical pattern of species richness (mammals: Pearson’s $r=0.797$, $p=0$, Dutilleul’s adjusted $p<0.01$; birds: Pearson’s $r=0.776$, $p=0.001$, Dutilleul’s adjusted $p<0.001$) (Fig. 1a–d). One deviation from the empirical pattern in the richness map generated by the Maxent modelling, however, is an additional peak in species richness south of the Congo basin. Overlaying the Maxent hindcasted ranges for the Last Glacial Maximum generates 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 (Fig. 1a–f).
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).
Historical patterns of species richness and geometric constraints

The null model 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 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 null-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 higher than expected-by-chance levels of richness in the Congo Basin and Cameroon Highlands, the Ethiopian highlands, Upper Guinea, the Namibian-Angolan area, and the Drakensberg mountain range in South Africa. One exception is that the Eastern Arc Mountains slightly stand out 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 as determined by, and in equilibrium with, historic level of water–energy were significantly correlated with Last Glacial Maximum species richness modelled by Maxent (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 identical to the null-model residual pattern, highlighting the same six areas with unusually high level of species richness (Fig. 2c-d). The similarity of the residual plots originates from the the fact that both the null 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 unusual high level of richness in tropical vertebrates (Jetz and Rahbek 2001, Jetz et al. 2004, Rahbek et al. 2007).
Figure 2 - Last Glacial Maximum species richness residual maps for mammals and birds endemic to sub-Saharan Africa (see text for details). Null-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).

Discussion

We showed that individually modelled climatically suitable ranges of African birds and mammals in the Last Glacial Maximum were aggregated in specific areas, where richness was higher than expected when taking into account geometric constraints or resources (water–energy), and interpret this excess of species surpassing the amount expected as refugia. That the areas of unusually high level of aggregation of species are similar for birds and mammals strengthens the idea that certain areas in the past were maintaining a higher degree of suitability and perhaps stability (with regard to habitat and/or climate) than the surrounding regions. Furthermore, the cross-taxon congruence suggests that both
birds and mammals reacted similarly to past climate changes, and that overall their geographical ranges are presumably governed by the same factors. Six areas with 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 highest part of the Drakensberg mountain range in South Africa. Reconstructions of forest cover in that time period (Cowling et al. 2008) suggest that four of the refugia - the Cameroon Highlands, the Congo Basin, the Angola-Namibia area and the highest part of the Drakensberg mountain range in South Africa - experienced forest cover during the Last Glacial Maximum. The highlands and the Congo Basin are forested today as well, while the Angola-Namibia area may have been able to sustain a denser vegetation cover as it experienced higher precipitation than today (Fig. 3b,d). The remaining two refugia, Upper Guinea 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).

The geographical locations where we identified a surplus of species during the Last Glacial Maximum largely correspond to the refugia suggested in the literature. Especially the Cameroon Highlands, Upper Guinea and the Congo Basin are well established as forest refugia. For example, studies of marine pollen cores (Dupont et al. 2000) suggest that rainforest could grow south or southwest of the Guinean mountains, southwest of the Cameroon Highlands and in Gabon and Congo throughout the last glacial. Along the rest of the coast of the Gulf of Guinea, rainforest occurred in patches, and dry forest and savannah vegetation replaced the rain forest over large areas (Dupont et al. 2000).

The same areas have also been suggested as refugia based on contemporary distribution and diversity patterns of birds and mammals (Diamond and Hamilton 1980, Crowe and Crowe 1982, Mayr and O'Hara 1986, Fjeldså and Lovett 1997). Crowe and 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. They 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: the Upper Guinea, 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. In addition, high endemism in these postulated refuges and allopatric taxa, that have never come to secondary contact provide further support their argument.

![Δ Maximum temperature](a) ![Δ Annual precipitation](b)

![Δ Maximum temperature](c) ![Δ Annual precipitation](d)

Figure 3 - Deviations of Last Glacial Maximum climate from contemporary climate. Maximum temperature (°C, a) and annual precipitation (mm, b) and their equivalent in percentages (c,d).

Refugia, centres where species have persisted unsuitable conditions in the surrounding area, may exhibit high levels of endemism, if species have not had time or means for dispersal. The areas indentified in this study as potential refugia do correspond to some extent to the bird endemism centres recognised by Fjeldså & Bowie (2008): the Cameroon Highlands, the Angolan Highlands, the Eastern Arc, the Albertine Rift, the
Kenyan Highlands, the Ethiopian Highlands and the Malawi rift and southern Africa (corresponding to our Drakensberg mountain range). For mammals, Grubb (1982) identifies three major endemism centres for larger forest African 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). The high endemism of birds and mammals found in the Cameroon Highlands may suggest that this area served as diversification centre for both taxa, while the Ethiopian and Kenyan Highlands may have been such for birds.

Some of the locations we identified differ from previous findings of endemism centres and postulated refugia. The most pronounced discrepancies include previous suggestion that the Eastern Arc Mountains served as an assemblage of refuges for birds (Fjeldså and Lovett 1997) and the Albertine Rift as a refuge for mammals (Grubb 1982). We only find a weak signal of richness excess in the Eastern Arc Mountains, and none in the Albertine Rift. On the other hand, the Ethiopian plateau and the Namibian-Angolan areas have not been suggested to be refugia previously, but stand out in our analysis. The Ethiopian Plateau is a centre of endemism for birds (Fjeldså and Bowie 2008), which supports a possible role of that area as a refugium. In the case of the Namibian-Angolan areas, the discrepancy may arise from the fact that much of the refugia literature is confined to forest-associated species, while our study includes both forest and savannah species. Thus, this area may represent a richness centre of savannah species during the Last Glacial Maximum. Interestingly, although the general tendency in Africa during the Last Glacial Maximum was of reduced precipitation, the Angolan-Namibian area actually experienced higher precipitation rates than today (Fig. 3). This higher precipitation may have transformed the local habitats, resulting in savannah-like conditions, enabling the persistence of savannah-related species in the Last Glacial Maximum. Reconstructions of Last Glacial Maximum forest cover show denser vegetation cover in this area (Cowling et al. 2008), supporting this idea.

A number of studies use phylogenetic information to assess geographic locations with high speciation (Fjeldså and Lovett 1997, Fjeldså and Bowie 2008). True relictual species (restricted range species representing ancient small clades) have high
concentrations in areas that are postulated to have been refugia (Fjeldså and 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. Fjeldså and Bowie (2008) assume that contemporary distributions of species must reflect, to some extent, their ancestral distribution, and conclude that the main Guineo-Congolian rainforest acts mainly as a ‘museum’ while the Cape and the montane/forest mosaics in Tanzania are characterised high lineage persistence as well as local differentiation. Our analysis, though not assessing the role of speciation, supports the idea that the rainforests may have helped species persist under the unfavourable glacial climatic conditions, i.e. serving as some sort of museum.

Our modelling approach, climate envelope modelling, involves several assumptions (Pearson and Dawson 2004, Nogués-Bravo 2009), including: (1) Species’ climatic niches remain stable over time. Although the time scale we use extends over of thousands of years, previous studies show some concordance between fossils and model results suggesting that the climatic niches of species may retain some degree of constancy over time. Examples include the woolly mammoth (Nogués-Bravo et al. 2008), North-American mammals (Martinez-Meyer et al. 2004) and North-American plants (Martinez-Meyer and Peterson 2006). (2) Species experience no dispersal limitations. In a period of thousands of years, it is likely that dispersal did not pose a 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. To minimize potential biases caused by violations of this assumption, we included only species with a high correspondence between empirical ranges and their potential climatically suitable ranges (high AUC values). (4) Species possess no potential for evolutionary adaption to the changing climate. The latter assumption is likely simplistic considering the time frame involved, representing the most problematic assumption behind the modelling approach in this study, and should therefore be kept in mind when interpreting our results.

We reconstruct a potential picture of bird and mammal diversity patterns during the Last Glacial Maximum in sub-Saharan Africa, representing the largest effort in number of hidcasted species, approaching whole-taxon level analyses. Our results point to areas with
an excess of species above that expected by chance or resource availability, suggesting that common refugia for mammals and birds existed in that period. Climate envelope models do not come without assumptions, but they do provide us with a new perspective on the refugia debate, complementing insights from previous studies focusing on contemporary diversity patterns.

Acknowledgements

We thank Steven Phillips for add-ons for Maxent and Louis Hansen for help with the species distribution data. IL, DNB, and CR thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate MBA and DNB were partially funded by BIOIMPACTO (FBBVA).
References


Supplementary material

We used the ensemble forecasting software Bioensembles (Diniz et al., 2009; Rangel et al., 2009) to implement four different model approaches – GARP, Euclidean distance, Bioclim, Mahalanobis distance and the maximum entropy software Maxent (Phillips et al. 2006, Phillips and Dudik 2008), and produce climatically suitable ranges for current climatic conditions. The models were based on three 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 modelled suitability maps were then converted into binary presence/absence maps using a maximum training sensitivity and specificity threshold. Subsequently, all climatically suitable ranges were overlaid to produce species richness maps for mammals and birds (Fig. S1), and these were correlated with the empirical species richness (Table S1). For both taxa, the species richness patterns produced by Maxent models showed the highest correlation to the empirical species richness (Fig. S1, Table S1, Fig. S2). Maxent also demonstrated the closest fit to the unity of slope (Fig. S2), suggesting that its models show the least over-prediction of the model approaches we examined. As Maxent clearly performed best, we decided to use its predictions for further analyses.

References


Table S1 - Correlations between empirical and modelled species richness patterns for Sub-Saharan mammals and birds.

<table>
<thead>
<tr>
<th>Bioclimat envelope model</th>
<th>Pearson's r</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bioclim</td>
<td>0.570</td>
<td>0.32</td>
</tr>
<tr>
<td>Euclidean distance</td>
<td>0.560</td>
<td>0.31</td>
</tr>
<tr>
<td>GARP</td>
<td>0.661</td>
<td>0.44</td>
</tr>
<tr>
<td>Mahalanobis distance</td>
<td>0.515</td>
<td>0.27</td>
</tr>
<tr>
<td>Maxent</td>
<td>0.802</td>
<td>0.64</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bioclim</td>
<td>0.521</td>
<td>0.27</td>
</tr>
<tr>
<td>Euclidean distance</td>
<td>0.512</td>
<td>0.26</td>
</tr>
<tr>
<td>GARP</td>
<td>0.637</td>
<td>0.41</td>
</tr>
<tr>
<td>Mahalanobis distance</td>
<td>0.467</td>
<td>0.22</td>
</tr>
<tr>
<td>Maxent</td>
<td>0.798</td>
<td>0.64</td>
</tr>
</tbody>
</table>
Figure S1 - Contemporary empirical and modelled species richness of Sub-Saharan of mammals (a) and birds (b).
Figure S1 - Continued.
Figure S2 - Correlations between empirical and modelled species richness patterns of Sub-Saharan mammals (a) and birds (b), for the five modelling approaches. The red lines depict the unity of slope, i.e., $y = x$. 

(a) Mammals:
(b) Birds:

**Figure S2** - Continued.
Exploring surrogates for the dispersal ability of African starlings

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Abstract

Dispersal is important, especially in the light of climate change when species may have to track their moving climatic window. However, dispersal is difficult to quantify and surrogates are therefore urgently needed. Here we explored three potential surrogates for the dispersal ability of African starlings: wing pointedness, migratory status and change in range size over time, by correlating them with range size and range filling. We found no correlation between wing pointedness and range size and range filling. Although non-significant, we found that migratory species had larger range sizes and higher range filling. This suggests that migratory species (here, defined as partial migrants or nomads) are better dispersers than resident species, which is especially interesting when considering that none of the African starlings are true migrants. The change in range size over time was significantly correlated with both range size and range filling, suggesting that species that have expanded their ranges more since the Last Glacial maximum are better dispersers and may be better at tracking climatic changes in the future, as well.
Dispersal is fundamental to our understanding of range shifts and expansions, and is particularly relevant in the light of climate change (Loarie et al. 2009), as inter-specific variation in dispersal ability may reflect a disparity in species’ ability to track their moving climatic envelope. Dispersal ability has been predicted to explain much of the variation in range sizes among species (Gaston 2003, but see Lester et al. 2007). For example, from a significant relationship between species geographic range size and eco-morphological traits related to flight ability in *Sylvia* warblers, it has been concluded that dispersal determines range size (Böhning-Gaese et al. 2006), suggesting that a species’ range size in turn may reflect its dispersal ability. However, range size alone does not account for the fact that species have limitations as to where their populations can be expected to persist because of each species’ specific physiological and ecological requirements. As a result, previous studies have not accounted for an important driver of range size variation, i.e., the ecological tolerances of species. Evaluating the area that a species could occupy given its ecological constraints (termed its potential range, Gaston 2003) relative to its realised range (current observed range) can provide a better indication of dispersal ability. The ratio of the realised range to the potential range, i.e., the range filling, can thus be used to assess to what degree species occupy their potential ranges (Gaston 2003, Svenning and Skov 2004).

Dispersal is an extremely challenging parameter to quantify directly (Nathan 2001), and data on the dispersal ability of birds are sparse for most species, with the exception of a few temperate ones (Paradis et al. 1998, Sutherland et al. 2000, Dawideit et al. 2009). Generalising from these to other species, including tropical ones, is questionable, and researchers have therefore sought after simple surrogates for dispersal ability. One proposed surrogate for dispersal is the migratory behaviour of birds, i.e., whether they are residents, short- or long-distance migrants, for which previous studies suggest contradicting relationships with dispersal ability. In general, migratory species are thought to be better dispersers (Paradis et al. 1998, Sutherland et al. 2000), yet some studies suggest that migrants tend to have smaller geographical breeding ranges than residents. For instance, the continents of the Old and New World have relatively fewer
terrestrial migratory passerine species in common than resident species (Böhning-Gaese et al. 1998). Migratory species were also found to be less likely than residents to have breeding ranges that include both sides of the Eurasian continent, i.e. Scandinavia and eastern Siberia (Bensch 1999). However, Thorup (2006) examined the winter ranges of birds in the South American, African and Indian landmasses and showed that there are more long-distance migrants that have colonized two or more of these regions than short-distance migrants and particularly residents. These results support the notion that long-distance migrants indeed have a superior capacity to disperse, and therefore also tend to have larger ranges.

Dispersal ability is also thought to be reflected in some morphological characters of birds. Dawideit et al. (2009) studied 47 British passerine species and found that Kipp’s distance, a measure of wing pointedness, and bill depth may provide good surrogates for natal dispersal. Kipp’s distance also correlated closely with migratory distance of stonechats (Saxicola torquata) (Baldwin et al. 2010).

Changes in species distributions over time may also provide an approximation of the ability of species to disperse. The expansion of a species’ range from one time period to the next should reflect the distance a species can move over that particular time scale. Contemporary distributions could be compared to survey data from another period or to the distributions of fossils, but these are seldom available. Another approach could be to use hindcasting bioclimate envelope modelling (Nogués-Bravo 2009) to assess the size of past distributions of species, where one could assess dispersal ability by assuming that species whose ranges expanded more had to disperse farther and are therefore better dispersers.

Here, we explore three surrogates for the dispersal abilities of African starlings. We assume that range size and range filling reflect dispersal ability, and correlate those with three surrogates for dispersal ability: (1) Wing pointedness (Kipp’s distance), expecting species with more pointed wings to be better dispersers, and therefore to have larger range sizes and higher range filling; (2) migratory status, expecting migrants to be better dispersers and thus to have larger ranges and higher range filling; and (3) a measure of
change in range size from the Last Glacial Maximum to today, assuming that the more a species’ range has expanded, the farther it has dispersed and the better its dispersal abilities; we expect species that have greatly expanded their range since the Last Glacial Maximum to have a larger contemporary range size and higher range filling than a species whose range has expanded less.

Materials and 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 <50% land, resulting in a total data set of 476 grid cells.

Distribution data
The distributions of 51 African starlings endemic to sub-Saharan Africa were obtained 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).

Morphological measurements
We measured morphological traits of 25 of the 51 African starlings included in this study. Kipp’s distance and wing length were measured on skins of the 25 African starling species represented at the Zoological Museum, University of Copenhagen. For each species, measurements were taken from 1-10 individuals (mean 5.72). When possible, we strove to have an equal representation of both sexes. Kipp’s distance is defined as the distance between the tip of the first secondary and the tip of the longest primary on a folded wing. Kipp’s distance was standardised by wing length (bow to tip, measured on a flattened wing). Kipp’s distance has been shown to correlate with natal dispersal distance.
and migration in 47 British passerine bird species (Dawideit et al. 2009), and is here used as a surrogate for dispersal ability.

**Migratory status**

The migratory status of the starlings was extracted from The Birds of Africa (Fry and Keith 2000). The starlings were classified into two groups according to their migratory status. One group included all resident species and the other partially migratory and nomadic species, hereafter referred to as migrants.

**Phylogeny**

Two recent molecular phylogenetic studies investigated relationships among starlings (Zuccon et al. 2006, Lovette and Rubenstein 2007). Although the two studies differ in the taxa included in the analysis and in the genes used, the resulting topologies are highly congruent. The trees were combined into a supertree from which the non-African species were then pruned. The resulting topologies included 44 out of 47 African species recognised by Feare and Craig (1999). The few missing taxa were added to the supertree following the results of an ongoing project on the species limits and relationships among the African starlings (D. Zuccon et al., unpublished data). The same results also indicate that some polytypic species in the genera *Cinnyricinclus*, *Lamprotornis* and *Onychognathus* are subdivided in clearly genetically distinct and reciprocally monophyletic clusters, corresponding with traditionally defined subspecies. All these clusters were treated as distinct species and included in the final supertree.

**Climatic data**

Minimum and maximum temperatures and annual precipitation for the Last Glacial Maximum were calculated using a General Circulation Model. The General 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 min. 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 yr. Time-series analysis of various climate variables for the entire 20 yr simulation shows that disregarding the first 6 yr allows the climatology model to reach full equilibrium.

The HadAM3 model was initialised 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$_2$ was specified at 200 ppm 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 and Taylor 1999).

**Climate envelope modelling**

Climatically suitable ranges for the Last Glacial Maximum were estimated by means of hindcasting climate envelope modelling (Nogués-Bravo 2009). We used the maximum entropy software Maxent (Phillips and Dudik 2008, Phillips et al. 2006), and three climatic variables: mean temperature of the warmest month, mean temperature of the coldest month and annual precipitation. 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 regularisation multiplier to one (Phillips et al. 2006). 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).
**Range filling and change in range size over time**

Based on the modelled climatically suitable ranges for each species, we calculated the range filling and the change in range size from the Last Glacial Maximum to today. *Range filling* was calculated as the proportion of a species’ modelled climatically suitable ranges that its current empirical ranges fills. *Change in range size* was defined as the number of grid cells that a species range gained or lost over time, i.e., the change from the climatically suitable range in the Last Glacial Maximum to the contemporary empirical range.

Assuming that a species’ climatically suitable range in the past reflects its maximum possible range, we explored which starlings are potentially better dispersers based on changes in their range sizes since the Last Glacial Maximum. This analysis was restricted to the 11 starlings that had smaller past climatically suitable ranges than their current empirical geographical ranges, indicating an expansion in range size over time. Species whose climatically suitable ranges in the Last Glacial Maximum were larger than their contemporary empirical ranges were excluded, as their actual range change since the Last Glacial Maximum is not known with certainty. If they filled the complete climatically suitable ranges, their range size may have contracted, but if it did not it may have expanded or stayed unchanged.

**Figure 1** - Possible values of range filling and changes in ranges. Grey shading denotes the range of possible values for a given proportion of the domain that the range of a species covers.
The measure of range filling (the proportion of the modelled climatically suitable range that a species’ empirical range constitutes) is constrained by the proportion of the domain that the empirical range covers. The modelled climatically suitable range cannot exceed the size of the domain, hence if a species’ range covers a large proportion of the domain, its range filling will be high by definition, while a species with a small range may have either a low or a high range filling (Fig. 1a). Further, the analysis of changes in range size over time was restricted to species whose ranges expanded. The change in range size is therefore limited by the size of the contemporary range, since if the contemporary range size is small, the expansion can only have been small, as well, while if the contemporary range size is large – the expansion may have been either small or large (Fig. 1b). When range size is translated into proportion of the domain (i.e., divided by 476), the two limitations can be combined to illustrate the potential array of range filling values for a given change in range size (Fig. 1c).

Statistical analyses
We tested for relationships between the three potential measures of dispersal ability and range size and range filling using univariate regression. Since related species are expected to be more similar in morphological traits due to evolutionary constraints, they do not constitute independent data points (Felsenstein 1985, Harvey and Pagel 1991, Freckleton et al. 2002). We therefore repeated the analyses with phylogenetically independent contrasts (Purvis and Rambaut 1995), using the “crunch” algorithm of the CAIC package for R to control for phylogenetic non-independence (Orme et al. 2009). As our phylogeny was undated, branch lengths were set to one; polytomies were randomly resolved with internal branch lengths of zero. To better approximate a normal distribution, range size was log-transformed, while range-filling and standardised Kipp’s distance were square-root transformed.

Data manipulation and statistical analyses were performed using R 2.9.1 (R Development Core Team 2007, http://www.r-project.org/), and mapping using the ArcGIS™ 9.2 geographic information system software and its spatial analysis extension ArcGIS Spatial Analyst (ESRI, Redlands, CA).

Results
**Kipp’s distance**

The ecomorphological surrogate, Kipp’s distance, did not correlate with the range sizes of the African starlings (Fig. 2a) or their range filling (Fig. 2b). There was no significant relationship with either using univariate regression, or accounting for phylogeny did not change the results (Table 1).

![Figure 2](https://via.placeholder.com/150)

**Figure 2** - The relationship between standardised Kipp’s distance and range size (# grid cells) and range filling (see Table 1 for the results of the regression analysis).

**Table 1** - Results of univariate regression analyses for the square-root transformed Kipp’s distance vs. the log-transformed range size and square-root-transformed range filling of African starlings (n=25). In *italics*, the equivalent when accounting for phylogeny.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Estimate</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Range size (log transformed)</td>
<td>-0.655</td>
<td>0.013</td>
<td>0.909</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>-4.045</td>
<td>1.244</td>
<td>0.278</td>
<td>0.059</td>
</tr>
<tr>
<td>Range filling (square-rooted)</td>
<td>1.189</td>
<td>0.932</td>
<td>0.344</td>
<td>0.039</td>
</tr>
<tr>
<td></td>
<td>1.008</td>
<td>1.342</td>
<td>0.260</td>
<td>0.063</td>
</tr>
</tbody>
</table>
**Migratory status**

Of the 51 African starling species, 24 were resident and 27 were classified as migratory, i.e. were partial migrants or nomadic. Resident species tended to have smaller ranges and lower range filling than the migrants (Fig. 3), but this tendency was only nearly significant (Table 2). Accounting for phylogeny gave non-significant relationships with much increased $p$ values.

![Box plots](a) and (b)

**Figure 3 - The relationship between migratory status and range size and range filling** (see Table 2 for the results of the analysis of variance). Note that the category migratory consists of species that are partial migrants or nomadic.

**Table 2 - Results of analysis of variance for migratory status vs. the log-transformed range size and square root-transformed range filling of African starlings (n=51).** In *italics*, the equivalent when accounting for phylogeny.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Range size (log transformed)</td>
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<td>0.059</td>
</tr>
<tr>
<td></td>
<td>0.187</td>
<td>0.667</td>
</tr>
<tr>
<td>Range filling (square-rooted)</td>
<td>3.562</td>
<td>0.065</td>
</tr>
<tr>
<td></td>
<td>0.017</td>
<td>0.896</td>
</tr>
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</table>
Range filling

The African starlings generally had small ranges (median 31 grid cells, range: 3-132) that constituted a relatively small proportion of the Sub-Saharan domain (median 0.065, range 0.006-0.277, Fig. 4). Range filling values varied considerably between species and ranged between 0.022 and 0.902 (median 0.368). The range filling of 16 African starling species was above the mean possible (i.e., lay above the red line in Fig. 4). These were generally species with larger range sizes that covered a higher proportion of the domain.

Figure 4 - Range filling vs. the proportion of the domain that the empirical range constitutes. In the small graph, the grey shading represents the range of potential possible range filling values for a given proportion of the domain. In the larger, the black line delimits the area corresponding to the grey area in the small one. The red line represents the mean of the possible range of range filling values.
**Change in range size**

The change in range size from the Last Glacial Maximum to today ranged between -273 and 64 grid cells (median -79). The range sizes of 11 of 51 African starling species had expanded since the Last Glacial Maximum, while the range size of 40 had contracted. We found a significant positive correlation ($r^2=0.679$, $p=0.002$) between the change in range size of the 11 species that expanded their range size since the Last Glacial Maximum and their range filling, but none had a larger range filling than the mean of the possible range (i.e., none lay above the red line in Fig. 5).

**Figure 5 - Change in range size from the Last Glacial Maximum to today (contemporary empirical range size minus modelled climatically suitable range in the Last Glacial Maximum) vs. empirical range.** Only species whose ranges have expanded over this time period are plotted. In the small graph, the grey shading represents the range of potential range filling values for a given change in range size. In the larger, the black line delimits the area corresponding to the grey area in the small one. The red line represents the mean of the possible range of range filling values. Note that the lines cross the x axis at 1 and not at 0, as the minimum empirical range possible for a change in range size is 1.
Discussion

Returning to our initial three expectations regarding the potential surrogates of the dispersal ability of African starlings, we found that: (1) Wing pointedness was not correlated with either range size or range filling; (2) the migratory status of the starlings showed a tendency for migrants to have larger ranges and higher range filling, yet this was not significant; and (3) starlings with ranges that have expanded more since the Last Glacial Maximum had significantly larger range sizes and higher range filling than species whose range has expanded less.

Kipp’s distance
We found no significant correlation between Kipp’s distance and range size or range filling, contradicting previous studies which found a positive relationship between the two (Baldwin et al. 2010, Dawideit et al. 2009). However, we only had measurements available for half of the African starling species, and a complete representation may result in a different pattern. In addition, a potential correlation could be masked because wing pointedness is also related to habitat association (Dawideit et al. 2009), and forest species tend to have more rounded wings while species associated with open habitat tend to have more pointed wings. However, for the African starlings Kipp’s distance was not higher for species associated with open habitats than for those associated with closed habitats (results not presented).

Migratory status
We found no significant relationship between migratory status and range size or range filling. However, there was a clear tendency for resident starlings to have smaller ranges and lower range filling. Phylogenetic analyses indicate that this relationship may be conserved within clades, since the tendency was nearly significant across species but vanished when controlling for phylogenetic non-independence. These findings corroborate previous findings that migratory species have larger range sizes, which may suggest that they are better dispersers (Dawideit et al. 2009, Thorup 2006). However, while none of the African starlings are true migrants, the previous studies, finding significant correlations between migratory status and dispersal, include short- or long
distance migrants. The fact that we find a trend suggests that even the difference in dispersal ability between resident and nomadic/partially migratory species is enough to affect range size and range filling.

*Change in range size*
We expected that species whose ranges had expanded more since the Last Glacial Maximum would be better dispersers than species whose ranges expanded less, and indeed found such a relationship. This suggests that the change in range size over time may be used as a surrogate for dispersal ability. A clear limitation of this approach, however, is that it can only be used for species whose ranges have expanded over time. This resulted in a relatively small sample size, as only eleven species expanded their ranges since the Last Glacial Maximum, representing 20% of the African starlings.

To conclude, we explored two conventional and one novel surrogate for dispersal in African starlings. Both the new surrogate, the change in range size over time, and to a certain extent the migratory status of the species, have the potential to reflect dispersal ability, and therefore may mirror a species’ ability to track future climatic changes.

**Acknowledgements**
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References


Supplementary material

Table S1 – summary of variables included in the analysis: migratory status, empirical range size (# of grid cells), change in range from the Last Glacial Maximum to today (empirical range size minus modelled range size for the Last Glacial Maximum, # of grid cells), range filling (empirical range size divided by modelled range size for today), mean Kipp’s distance (mm) and mean wing length (mm).

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<th>Range filling</th>
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Table S1 – Continued.

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Sub-Saharan African vertebrates persisted in the Last Glacial Maximum despite loss of their bioclimate envelope

Irina Levinsky$^{1,2}$, Miguel B. Araújo$^{2,3}$ & Carsten Rahbek$^{1}$

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Abstract

Bioclimatic envelope modelling is a widely applied tool for forecasting climate change impacts on species distributions and potential risk of extinction, despite critique that the predictive power of such models is limited when transferred in space and time. Here, we use such models to hindcast climatically suitable ranges of extant sub-Saharan African bird and mammal species onto the Last Glacial Maximum (21,000 years ago), to assess their predictive ability. We found that models predict a reduction of 50% in the climatically suitable range for approximately 30% of the birds and mammals, but more interestingly also a complete loss for 1-2% of the birds and 2-7% of the mammals. These results are similar in magnitude to predictions of future loss of climatically suitable ranges and species using the same modelling approach. However, the species predicted to have lost their entire climatically suitable range in the Last Glacial Maximum persisted until today. The contemporary empirical ranges of these species are spatially clustered in lowland rainforests, which in part had no climatic analogue in the Last Glacial Maximum, suggesting that the association with moist habitats is key to the poor description of these species’ climatic envelope. This association may not be reflected in the coarse-scale used in this study, or, alternatively, the climatic conditions in the rainforest may not be described accurately by general circulation models. Our results serve to caution against interpreting uncritical modelled forecasts of reductions in bioclimatic envelopes as strong evidence of species extinctions due to future climate change, and call for a focus on improving models for tropical forest areas.
**Introduction**

Bioclimatic envelope models are widely used for predicting the effect of climate change on species distributions (Kerr and Packer 1998, Peterson *et al.* 2002, Erasmus *et al.* 2002, Skov and Svenning 2004, Meynecke 2004, Thomas *et al.* 2004, Thuiller *et al.* 2005, Thuiller *et al.* 2006, Levinsky *et al.* 2007). These models use information on current geographical ranges of species combined with climatic variables to approximate their climatically suitable ranges in the future (Pearson and Dawson 2003). A reduction in the modelled climatically suitable range of a species is assumed to imply a reduction in population size and abundance, and has been interpreted as evidence that climate change poses a threat to species persistence (e.g., Thomas *et al.* 2004, Thuiller *et al.* 2005). Studies relying on bioclimatic envelope models typically conclude that climate change will have a marked impact on biodiversity, with many species projected to experience substantial reductions in their climatically suitable ranges, and some projected to lose their entire climatic envelope (Araújo *et al.* 2004, Skov and Svenning 2004, Thomas *et al.* 2004a, Thuiller *et al.* 2005, Levinsky *et al.* 2007). It is, however, increasingly recognised that evaluating the performance of models forecasting biodiversity change is not an easy task (Manel *et al.* 2001, Araújo *et al.* 2005a, Araújo and Guisan 2006, Peterson *et al.* 2007). A few studies have used independent data from a different time period to evaluate the predictions of the models (Araújo *et al.* 2005a, Araújo *et al.* 2005b, Mitikka *et al.* 2008), but these are seldom available. When they are available they are often on a short time scale (max. 20 years), and it is difficult to assess their performance for longer time spans. Alternatively, one could hindcast climatically suitable ranges onto past climates (Araújo and Rahbek 2006, Willis *et al.* 2007, Nogués-Bravo 2009), and compare projections with fossil or pollen data (Martinez-Meyer *et al.* 2004, see e.g. Martinez-Meyer and Peterson 2006, Varela *et al.* 2009). However, the fossil record for most species is limited and subject to various potential issues sampling biases. Additionally, model evaluation requires larger sample sizes, representatively distributed across the spatial extent of the study area, than are usually available. Generalising from studies on few species to be valid for biodiversity per se is difficult. Henceforth, our ability to predict the effect of future climate change on biodiversity remains difficult to assess.
Here, we explore an alternative approach to obtain insight into the ability of models to project the distributions of species in time under climate change. Using data on contemporary species distributions and climate, we model the bioclimatic envelope of species and project it onto maps of historic climate to reconstruct climatically suitable range of extant African mammals and birds in the Last Glacial Maximum. For the extant species projected to have lost their entire bioclimatic envelope, we ask whether there are patterns in a) co-occurrences of current ranges, b) habitat-association and c) taxonomical clustering. Based on these results, we discuss how well the commonly used bioclimatic envelope models provide accurate predictions of species extinctions, based on the notion of loss of species climatic envelopes.

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 <50% land, resulting in a total data set of 476 grid cells.

Species distribution data
The distributions of 1556 birds (Hansen et al. 2007) and 970 mammals (Burgess et al. 2007b) 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 previously been used for phylogeographical (Fjeldså et al. 2007, Fjeldså and Bowie 2008), macroecological (Jetz and Rahbek 2001, Jetz and Rahbek 2002), conservation (Balmford et al. 2001, Burgess et al. 2002, Burgess et al. 2007a) and climate change studies (Hole et al. 2009, Willis et al. 2009). To encompass the entire
range of climatic conditions under which the species occur, we restricted our analyses to species endemic to the domain of sub-Saharan Africa. Given that bioclimatic envelope models do not perform well for species with a small number of occurrences (Stockwell and Peterson 2002), we further restricted analyses to 1265 birds and 537 mammals with more than 10 grid cell records.

Climatic data
Minimum and maximum temperatures and annual precipitation for the Last Glacial Maximum were calculated using a General Circulation Model. The general 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 $2.5^\circ \times 3.75^\circ$ in latitude and longitude with 19 levels in the vertical, and a time step of 30 min. 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 LGM over 20 simulated years and climatological means were compiled for the final 14 yr. Time-series analysis of various climate variables for the entire 20 yr simulation shows that disregarding the first 6 yr allows the climatology model to reach full equilibrium.

The HadAM3 model was initialised 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 LGM was derived from the ICE-4G model (Peltier 1994). The atmospheric concentration of CO$_2$ was specified at 200 ppm 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 and Taylor 1999).

Bioclimatic envelope modelling
Climatically suitable ranges for species in the Last Glacial Maximum were hindcasted using the Bioensembles software (Rangel et al. 2009, Diniz et al. 2009) implementing three different modelling approaches: Euclidean distance, Bioclim and Mahalanobis distance. In addition, we also used the maximum entropy software to implement Maxent
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 component analysis to identify the three least correlated variables: mean temperature of the warmest month, mean temperature of the coldest month and annual precipitation. These variables were subsequently implemented in the four modelling approaches, to produce maps of contemporary and Last Glacial Maximum climatically suitable ranges for each species.

The species specific maps of modelled climatically suitable range were converted into binary presence/absence maps using a threshold based on maximum training sensitivity and specificity, that has recently been identified to perform well (Liu et al. 2005). The change in the size of the climatically suitable range was calculated in percentages, as the change from the present to the past for each species, estimating contraction or expansion over time. Studies modelling potential impacts of future climate change on species distributions assess changes in climatically suitable ranges from the present to the future in the same manner.

Some extant species were projected to have lost their entire bioclimatic envelope, i.e., modelled to have no climatically suitable range in the Last Glacial Maximum (see the results section), hereafter referred to as disappearing species. For these species, we ask whether there are patterns in a) co-occurrences of current ranges, b) habitat-association and c) taxonomical clustering.

Model performance
Model accuracy was estimated using sensitivity and specificity. Sensitivity describes the ability of the model to correctly predict the grid cells where a species is present, and is calculated as the percentage of correctly predicted true positives (Manel et al. 2001). Specificity describes the ability of the model to correctly predict the grid cells where a species is absent, and is calculated as percentage of correctly predicted true negatives (Manel et al. 2001).
**Taxonomic clustering and phylogenetic signal**

We visually inspected whether there was a tendency for the disappearing species to be taxonomically clustered within orders. Orders followed the most recent global mammalian taxonomy (Wilson and Reeder 2005). As taxonomy is only a rough reflection of evolutionary history, we also used a phylogeny for all African mammalian species in our dataset to test whether disappearing species were phylogenetically clustered, which would indicate that they are more related than expected by chance (Harvey and Pagel 1991, Freckleton et al. 2002). The phylogeny was extracted from a global supertree of 5020 mammalian species (Bininda-Emonds et al. 2007, Fritz et al. 2009). Our measure for phylogenetic signal in binary traits was D (Fritz and Purvis 2010); disappearing species were coded as 1. D ranges from 0 to 1, where 1 reflects a random distribution of the measured trait across the tips of the tree, and 0 a perfect phylogenetic signal expected if the trait evolved under a Brownian motion threshold model. There is no species-level phylogeny for all African bird species available so far, so D was computed for the mammals alone.

**Non-analogue climates**

We searched for climates that occur today but did not exist in the Last Glacial Maximum, to examine whether the disappearing species had no climatically suitable ranges in the Last Glacial Maximum because the climatic combinations they occur under today did not occur in that period. We computed non-analogue climates following a similar procedure to the one described by Fitzpatrick and Hargrove (2009). They suggest a simple approach to identify non-analogue climates, by calibrating a model on the entire study area and projecting it onto a climatic conditions from a different time period. We applied a similar method to identify areas with climatic conditions that did not occur in the Last Glacial Maximum. We used the Raster Calculator in the Spatial Analyst extension for ArcMap 9.2 to compute the minimum and maximum values and percentiles 97.5 and 2.5 of the distribution of the three climatic variables used for modelling the species: mean temperature of the warmest month, mean temperature of the coldest month and annual precipitation for the Last Glacial Maximum. This method models all combinations of Last Glacial Maximum climatic conditions found within the study area, and when
projected onto contemporary climatic conditions, reveal regions containing non-analogue climates (i.e., as areas of predicted absence).

Results

The changes in climatically suitable ranges from today to the Last Glacial Maximum are fairly consistent across the four modelling approaches (Table 1), with comparable figures for birds and mammals. Approximately 30% of all birds and mammal species are projected to have lost at least 50% of their climatically suitable range. Interestingly, the models projected that 1-7% of the species should have had no climatically suitable range in the Last Glacial Maximum (Table 1). A total of 45 birds and 53 mammals were predicted by at least one of the four models to have lost all of their climatic suitable area (see supplementary material Table S1 for the complete list). Among the two bird and five mammal species predicted to have lost their complete range by all four models are, e.g., the Congo sunbird (*Nectarinia congensis*), bob-tailed weaver (*Brachycope anomala*), Allen’s swamp monkey (*Allenopithecus nigroviridis*), Bonobo (*Pan paniscus*), and Slender-tailed squirrel (*Protoxerus aubinnii*).

**Table 1 - Changes in climatically suitable ranges of African birds and mammals when projected onto reconstructed Last Glacial Maximum climate.** Number (and percentage) of species whose climatically suitable ranges are modelled to have been markedly smaller during the Last Glacial Maximum.

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<td>179 (33%)</td>
<td>38 (7.1%)</td>
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<tr>
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<td>23 (4.3%)</td>
</tr>
<tr>
<td>Maxent</td>
<td>183 (34%)</td>
<td>12 (2%)</td>
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Figure 1 - Current empirical distributions of African mammals and birds. Species richness of all mammals (a) and birds (b), and of the species predicted to have no climatically suitable range in the Last Glacial Maximum, using the four modelling approaches (c-j).
Size and geographical position of empirical ranges

Species modelled to have no climatically suitable ranges in the Last Glacial Maximum have noticeable smaller contemporary ranges (mean range size 19.48 ± 1.27 and 16.06 ± 0.74 for 44 species of birds and 53 mammals, respectively), compared with species modelled to maintain a range over time (mean range size 80.86 ± 2.18 and 68.9 ± 3.30 for 1221 species of birds and 484 mammals, respectively). Although the exact species predicted to have lost their climatic ranges largely differ between the four modelling approaches (see supplementary material Table S1), richness patterns based on their contemporary ranges are similar for birds and mammals and consistent across the four model approaches (Fig. 1c-j). Richness peaks in the lowland forests of the Congo basin and Upper Guinea. The Congo Basin, the Somali peninsula and parts of the Sahel experienced have no climatic analogue in the Last Glacial Maximum, and experienced lower precipitation amounts and lower temperatures (Fig. 2).

Figure 2 - Non-analogue climates depicted in climatic and geographic space. Deviations of annual precipitation and maximum temperature in the Last Glacial Maximum from contemporary climate (a). Red dots represent quadrates where disappearing species occur today (see Fig. 1). Areas that today exhibit climatic conditions that had no analogue in the Last Glacial Maximum (b). Black represents the maximum and minimum values of the three climatic variables used in the models while grey represents percentiles 2.5 and 97.5.
Model performance

Interestingly, the performance of the models for the disappearing species was overall better than that of species retaining a range (Table 2). With the exception of sensitivity values for Euclidean distance, mean sensitivity and specificity values for the disappearing species were consistently higher than for the species that retained a range.

Table 2 - Model evaluation. Mean values of sensitivity and specificity for birds (a) and mammals (b) that were modelled to have no climatically suitable range in the Last Glacial Maximum, compared with the species that retained one, and their respective Kolmogorov-Smirnov test. Bold figures are significant (* p<0.05, *** p<0.001). Note that in the case of sensitivity for Euclidean it means that values for disappearing species are lower.

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<tr>
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Taxonomic clustering

The disappearing species were taxonomically clustered and 10/24 (42%) of the orders of birds and 6/15 (40%) of the orders of mammals were represented. The disappearing species constituted 3.5% of all birds, but the Strigiformes, Cuculiformes, Galliformes, Psittaciformes, Caprimulgiformes, Musophagiformes and Piciformes were all represented by a higher proportion of the overall species pool of birds (Table 3a). For mammals, the disappearing species comprised 9.7%, while Primates and Soricomorpha were represented by a substantially higher proportion (Table 3b). We found a weak but significant phylogenetic signal in the mammals that had no climatically suitable range in the Last Glacial Maximum (D=0.807, p=0.003). As there is no species-level phylogeny for all African bird species available so far, D could not be computed for the birds.
**Habitat association**

Most disappearing species that were modelled to have no climatically suitable range in the Last Glacial Maximum are associated with forest, representing 87% of the birds (Sinclair and Ryan P. 2003) and 91% of the mammals (Kingdon 1997), while 60% of the birds and 85% of the mammals have a clear association with moist habitats - riverine, swamp or gallery forest.

**Table 3 - The proportion of the each order that the disappearing birds (a) and mammals (b) constitute.**

<table>
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<tr>
<th>(a) Order</th>
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<th>(b) Order</th>
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Discussion

Our four hindcast modelling approaches all generated predictions of significant contraction for both birds and mammals, with 26-34% of the species’ modelled climatically suitable ranges reduced by >50% in the Last Glacial Maximum and 1-7% to disappear completely (see Table 1). The magnitude of these modelled changes is of the same as for studies using these approaches to predict the effect of future climate changes on species distributions (Araújo et al. 2004, Thomas et al. 2004a, Thuiller et al. 2006, Levinsky et al. 2007). For example, using bioclimatic envelope models Thuiller et al. (2006), assessing the impact of climate change on African mammals, found that when no dispersal of species was assumed, 10–15% of the mammals were projected to become critically endangered or extinct by 2050 and between 25% and 40% by 2080. Assuming unlimited dispersal, proportions dropped to approximately 10–20% by 2080. Similarly, for European mammals, Levinsky et al. (2007) found that when assuming unlimited or no dispersal, models predicted a level of 1–9% species extinction due to a complete loss of their climatically suitable range, while 32–78% would be severely threatened (lose > 30%). Using the same logic and approach as in these studies, and considering that the extant species in this study were generated before the Last Glacial Maximum period, species with disappearing ranges in the Last Glacial Maximum should be expected to be extinct today. The fact that they did not, supports the view of several authors that estimating range dynamics including extinction, under climate change, requires that bioclimatic envelope models are combined with spatially-explicit types of population viability analysis (Anderson et al. 2009, Brook et al. 2009).

The disappearing species were taxonomically clustered towards specific orders, and we found a phylogenetic signal in the disappearing mammals. This suggests that the disappearing species share common traits that make them more susceptible to be modelled to have no climatically suitable range in the Last Glacial Maximum, presumably related to their close association with forest and water. The most affected orders of mammals were primates, which are arboreal and forest dwelling, and Soricomorpha, who prefer moist habitats (Kingdon 1997), and one of the most affected orders of birds were the Cuculiformes, which are mostly arboreal (Fry et al. 1988).
Recent studies aiming to assess Late Quaternary extinctions in temperate regions have used bioclimate envelope models in combination with fossil records and projected them to current climates, with contradicting outcomes. On the one hand, the climatic suitable range of the woolly mammoth shows a contraction ca. 6,000 years ago, corresponding to its final extinction (Nogués-Bravo et al. 2008). On the other hand, of eight North American mammalian species that went extinct at the end of the Pleistocene, models based on Last Glacial Maximum fossils generally predicted an increase in climatically suitable ranges under current climate (Martinez-Meyer et al. 2004).

Models did not predict species to disappear because they performed worse than models for species that retained a range over time, as evaluated by standard evaluation measures such as sensitivity and specificity (Table 2). In fact, the species with no climatically suitable ranges in that period had exceptionally high values of sensitivity and specificity across modelling approaches. This suggests that evaluation methods, assessing the overlap of the modelled climatically suitable range with the empirical data, may be misleading. The limited ability to of bioclimatic envelope models to predict changes in ranges in time or space, despite acceptable results of model fit, has previously been discussed in the literature (Araújo et al. 2005a, Randin et al. 2006, Peterson et al. 2007, Duncan et al. 2009, Varela et al. 2009). Varela et al. (2009) used current distribution of the of the spotted hyena, Crocuta crocuta, to project its climatic suitability onto climatic reconstructions of the Last Interglacial (126,000 ya). They, too, find that although the model fits current distribution data well, the projection for the Last Interglacial did not cover European fossils from that period, suggesting that model fit is not a good measure of predictive ability (as suggested by Peterson et al. 2008). Assessments of the prediction ability of models for the future become extremely difficult if the standard means of evaluation do not mirror prediction ability.

Contemporary empirical ranges of the species that were modelled to have no climatically suitable ranges in the Last Glacial Maximum occur today in areas, such as the Congo Basin and the Somali peninsula, where both precipitation and temperature were lower in the Last Glacial Maximum, and that did not have climatic analogues in that period. The disappearing species identified by this study that appear to cluster in such
areas may therefore have persisted under different climatic conditions than today. They may also be more restricted by the availability of moist habitats, as most of them are associated with riverine, swamp or gallery forest. Most mammals that were modelled to have no Last Glacial Maximum distributions were associated with swamp forest, and most birds were associated with riverine habitats. It is likely that the species are modelled to have no climatically suitable range because this water-association was not captured by the climatic variables and the resolution used in our models. Alternatively, current distributions of species may not encompass the whole range of climatic conditions where species may be able to persist, i.e., species may not occupy their complete climatic niche (Araújo and Guisan 2006). Indeed, studies on invasive species found that native range occurrences generally under-predict the invasive potential of species, suggesting that species hold broader climatic tolerances than empirical realised niches reflect (Fitzpatrick et al. 2007, Broennimann et al. 2007), and this may have been the case for the past, as well. Finally, the models assume that populations are homogenous (Pearson and Dawson 2004), yet they may hold some phenotypic variability, enabling them to persist under different climatic conditions in the Last Glacial Maximum. Regardless of the explanation, our results demonstrate that species may be able to persist even if bioclimatic envelope models predicts that they cannot, and they may occur in a different geographical area than those predicted by the models suggesting that other important factors determining geographical range sizes and positions are missing from the models.

Contemporary empirical geographical ranges of the disappearing species all occurred in the Guineo-Congolian lowland rainforest. Cowling et al. (2008) simulated vegetation cover in the Last Glacial Maximum, and suggest that tropical broadleaf forest within central Africa was reduced and the outer extent of closed forest decreased. While the eastern part of the Congo Basin experienced such reductions, the western part retained a dense forest cover. Forests canopy may act as a buffer against the climatic conditions outside the forest. For example, diurnal temperature and humidity variation inside coastal forests is lower than that in adjacent woodlands (Burgess and Clarke 2000), which creates more stable conditions. Similarly, the remaining forest in the Congo Basin in the Last Glacial Maximum may have buffered the climatic oscillations in the past and maintained appropriate climatic conditions for the disappearing species. Finally, general
circulation models may not be precise in forested areas. General circulation models are calibrated on data from meteorological stations (Ruddiman 2001) and there are no meteorological stations within the rainforest (Weather for Sailors http://www.sailwx.info/wxobs/stationpick.phtml), so calibration in these areas may be skewed. If the modelled present climatic conditions are biased, our models are calibrated on climatic conditions that do not mirror the true climatic conditions where the species occur, not reflecting the climatic niches of forest species. The projection of a disappearing range for the Last Glacial Maximum is then meaningless. Caution should therefore be taken when using bioclimatic envelope modelling for forecasting species that occur in forested areas.

Our study shows that model predictions of complete loss of climatically suitable range does not necessarily imply the extinction of species. Disappearing species were spatially aggregated and associated with areas of lowland rainforest, implying that bioclimatic envelope models may be particularly sensitive to modelling rainforest taxa and suggesting that and projections of forest species should be considered carefully. Species with small ranges were excluded from this analysis as they have too few records to be modelled well. These species generally occur on tropical mountains and constitutes a significant proportion of biodiversity. If models currently perform poorly for mountain forests, where most of biodiversity occurs, a focus on improving models for tropical forest areas is needed.

Acknowledgements

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References


Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, 399, 429-436.


Supplementary material

Table S1 - Birds and mammals that were modelled to have no climatically suitable range in the Last Glacial Maximum. Bold font denotes species that were modelled to disappear in all four modelling approaches.

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**Table S1 – Continued.**
Rethinking Species’ Ability to Cope with Rapid Climate Change

Christian Hof\textsuperscript{1,2*}, Irina Levinsky\textsuperscript{1,2*}, Miguel B. Araújo\textsuperscript{2,3} & Carsten Rahbek\textsuperscript{1}

* Both authors have contributed equally to the manuscript

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Planet Earth has undergone severe climatic changes in the past, most recently during the glacial-interglacial cycles of the Pleistocene. It has generally been assumed that climatic changes during and after the Pleistocene were gradual, while contemporary climate warming occurs at an unprecedentedly rapid rate, a factor predicted to have dramatic consequences for biodiversity [1]. However, recent geophysical studies are now challenging this view. Based on high resolution Greenland ice core data, Steffensen et al. [2] showed that moisture source temperature changed up to 4°C per year near the end of the last glacial period (14,700yr B.P.). Brauer et al. [3] reported an abrupt increase in storminess within a single year in Western Germany during the Younger Dryas cold climate period (12,700yr B.P.), and linked this event to the inception of deglaciation [see also 4]. Rapid changes are also not restricted to periods of deglaciation, and sea levels around the Yucatán Peninsula underwent a rapid rise of 2-3 meters (most likely approximately 36 mm per year) during the last interglacial period (121,000yr B.P.) [5]. Although the existence of abrupt historic climate change has previously been acknowledged [6], these new studies not only support the view that abrupt climatic changes might have been more common than expected, they also document on a much finer temporal resolution that they occurred over much shorter time periods. These new geophysical findings have profound implications for climate research and pose a challenge to existing paradigms in climate change impact studies, in particular for researchers modelling the effect of current and future climate change on biodiversity.

Studies assessing the impact of climate change on biodiversity tend to adopt the view that past climatic changes were gradual rather than abrupt. The most recent report of the Intergovernmental Panel of Climate Change (IPCC) recognises that rapid climatic changes occurred in the past, but states that “it is very likely that the global warming of 4°C to 7°C since the Last Glacial Maximum occurred at an average rate about ten times slower than the warming of the 20th century” [1, p. 435]. This perception is based upon the fact that Earth’s temperature has increased by 0.74°C from 1906 to 2005 and that sea levels have risen 3.1 mm per year in the decade between 1993 and 2003 [1]. Climate projections for the end of the century (2090-2099) range from a global mean temperature increase of 1.8-4°C to a sea level rise of 0.18-0.59 m [1]. This focus on the velocity of climate change during the last century has presumably given rise to the view that past climatic changes
Figure 1 - Changes in species’ ranges as a result of climatic changes. A-C represent a pristine world prior to human impact on habitat continuity and D-F a world modified by humans, both excluding adaptation as a determining factor. Species’ ranges may track gradual climatic changes (A). If the climatic changes were extremely rapid, as suggested by recent studies (see text), species may (B) endure in small areas of suitable microclimates within the current ranges and expand when suitable climatic conditions return, or (C) endure in small areas of suitable microclimates within the current ranges, and thereafter track suitable climate conditions. D-F correspond to A-C in a world of habitat destruction and fragmentation, where the available area containing suitable microclimatic conditions is smaller, which reduces the probability of endurance (central panel), as well as the probability of successful range shifts (right-hand panel). Green indicates suitable habitat, whole circles represent the distribution of a species and dashed circles - its distribution in the previous time step.
were much slower, and thus that the current and anticipated “extraordinary” rate of future
global warming is predicted to have a significant effect on Earth’s biodiversity [e.g. 7]. In
this context, it is worth noting that the rapid climate change in the Quaternary period
(spanning approximately 2.5 million years ago to the present) did not cause a broad-
spectrum mass extinction; instead, it appeared to primarily affect a few specific groups,
mainly large mammals and European trees [8]. The fact that relatively few taxa became
extinct, compared to periods of mass extinctions, indicates that most extant species exposed
to contemporary climate change must have coped successfully with the abrupt climatic
changes of the past.

Species responses to climate change are usually synthesised as genetic adaptation,
der展示了 genetic adaptation, dispersal and extinction [9]. The prevailing consensus, when modelling the effects of
cclimate change on species distributions, is that current climate change simply outpaces
micro-evolutionary processes so there is no time for evolutionary adaptation [10].
Dispersal, on the other hand, has been widely identified as one of the most likely responses
of species to recent climate change, usually via range shifts from lower to higher latitudes
and altitudes [11], and it is also regarded as the main response of species to past climatic
changes. However, if abrupt climate changes of the past are factored into our thinking
about species responses to climate change, then species dispersal as a strategy to cope with
the shifting of climatic zones (Fig. 1 A) becomes less probable. Likewise,
microevolutionary adaptations comprising small-scale changes in genetic diversity in a
population over a few generations are even more difficult to imagine as a potential
response to rapidly changing historical climate regimes.

The fact that extant species did not become extinct as a result of the drastic, rapid
climatic changes at the end of the last glacial indicates that species must have used other
strategies to cope with changing climate, rather than shifting their geographical
distributions or changing their genetic make up. Another possibility is that adaptation might
have been a consequence of pre-existing phenotypic variability in the populations. In other
words, intraspecific variation in physiological, phenological or morphological traits might
that have allowed species to cope with rapid climatic changes within their range [12].
Alternatively, retreats to nearby pockets of suitable microclimates (Fig. 1 B, C), permitting
species to endure adverse climatic conditions could have played a role for various taxa and regions [13].

The recent reports on the exceptionally rapid climatic changes in the Late Quaternary and the fact that extant species have coped successfully with past climatic changes give rise to the question of whether estimates of extinction risk due to current and future climate change are inflated. When addressing this question one should bear in mind that the ability of species to cope with fast climate change is different today than it was in the past, with current landscapes and ecosystems severely modified by humans [14]. These modifications include land-use change and concomitant habitat destruction, degradation, and fragmentation at large spatial scales, which impose severe pressures on species. They also have a marked impact on species’ potential strategies to cope with climate change, thus increasing the negative impact of climate change per se. First, these land-use changes may reduce the possibilities of species to survive climatic changes in suitable microclimatic pockets. Smaller and fewer habitat patches contain, by definition, fewer microclimatic areas suitable for the endurance of species during climatic changes (Fig. 1 D-F). Second, smaller habitat patches sustain smaller populations, which show lower genetic and phenotypic variability [10] – a pre-requisite for rapid adaptive responses. Thus, habitat fragmentation reduces a species’ potential to respond with trait shifts due to lower phenotypic variability across its range. Furthermore, fragmentation also impedes short- and long-distance dispersal processes (Fig. 1 D-F) [15], reducing dispersal probability, which further reduces genotypic and phenotypic variability [16] and in turn the ability of species to adapt to changing environmental conditions.

The fact that extant species have demonstrably survived rapid, historic climatic changes is good news. It suggests that species’ ability to cope with drastic climate change is better than hitherto recognized, perhaps due to the phenotypic variability of populations, or to their ability to survive in microclimatic pockets in a heterogeneous landscape. In other words, species are probably more resilient to climatic changes than typically anticipated in most assessments of the effect of contemporary climate change on biodiversity [17]. To understand the potential responses (e.g. dispersal and adaptation) of species to changing environments, we call for unified framework that considers climate change together with
the main drivers of species extinctions, such as habitat destruction, invasive species and diseases. The development of such a framework imposes a challenge for climate change biologists and conservationists focusing on how to effectively mitigate the biodiversity crisis and ecosystem changes caused by global changes of land-use and climate.
References


Potential impacts of climate change on the distributions and diversity patterns of European mammals

Irina Levinsky · Flemming Skov · Jens-Christian Svenning · Carsten Rahbek

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Abstract The Intergovernmental Panel on Climate Change (IPCC) predicts an increase in global temperatures of between 1.4°C and 5.8°C during the 21st century, as a result of elevated CO₂ levels. Using bioclimatic envelope models, we evaluate the potential impact of climate change on the distributions and species richness of 120 native terrestrial non-volant European mammals under two of IPCC’s future climatic scenarios. Assuming unlimited and no migration, respectively, our model predicts that 1% or 5–9% of European mammals risk extinction, while 32–46% or 70–78% may be severely threatened (lose > 30% of their current distribution) under the two scenarios. Under the no migration assumption endemic species were predicted to be strongly negatively affected by future climatic changes, while widely distributed species would be more mildly affected. Finally, potential mammalian species richness is predicted to become dramatically reduced in the Mediterranean region but increase towards the northeast and for higher elevations. Bioclimatic envelope models do not account for non-climatic factors such as land-use, biotic interactions, human interference, dispersal or history, and our results should therefore be seen as first approximations of the potential magnitude of future climatic changes.

Keywords Climate change · Europe · mammals · Terrestrial · Bioclimatic envelope models · Distributions · Species richness

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Abbreviations
IPCC Intergovernmental panel on climate change
CCSR Change in climatically suitable range
GDD Growing degree days
PET Potential evapotranspiration
ROC Receiver operating characteristic
AUC Area under the curve

Introduction

The last century’s increase in global temperatures has affected ecosystems and a wide array of taxa, (Hughes 2000; McCarty 2001; Walther et al. 2002; for a review see Walther et al. 2005). The observed changes include the timing of seasonal events (Crick et al. 1997; Parmesan and Yohe 2003; Root et al. 2003; Tøttrup et al. 2006) and shifts in geographic distributions—polewards (Thomas and Lennon 1999; Parmesan and Yohe 2003; Austin and Rehfisch 2005; Hickling et al. 2005) as well as towards higher elevations (Wilson et al. 2005). The Intergovernmental Panel on Climate Change (IPCC) predicts an additional increase in global temperatures of between 1.4°C and 5.8°C during the 21st century as a result of elevated CO₂ levels (Anon. 2001). These future climatic changes are expected to have a significant impact on biodiversity (Pearson and Dawson 2003), and a number of modelling studies have been initiated in order to predict potential impacts on the distribution of plants (Skov and Svenning 2004; Thuiller et al. 2005a) and animals (Kerr and Packer 1998; Peterson et al. 2002; Erasmus et al. 2002; Meynecke 2004). Bioclimatic envelope models are widely applied in climate change research (Erasmus et al. 2002; Berry et al. 2002; Midgley et al. 2002; Araujo et al. 2004; Skov and Svenning 2004; Elith et al. 2006), although the validity of these has recently been questioned (Davis et al. 1998; Pearson and Dawson 2003; Thuiller 2004; Hampe 2004; Ibáñez et al. 2006; Araújo and Rahbek 2006). If they are applied with care, however, such models may be viewed as a useful first approximation of the potential impact of climate change on the distribution of species.

In this study, we evaluate the potential effects of two of IPCC’s climatic scenarios (Anon. 2001) on the distribution of native terrestrial European mammals using bioclimatic envelope models. We examine (1) to what degree the current distribution of mammals is likely to undergo modification (contraction or expansion), and (2) in what manner climate change will affect spatial patterns of mammalian species richness in Europe. We follow the practice in the current literature (Thomas et al. 2004; Thuiller et al. 2005a) and consider two contrasting assumptions concerning migration abilities: (a) species are unable to disperse at all on the time scale considered (i.e. no migration), and (b) species have no constraints with respect to dispersal and establishment (i.e. universal migration). For most species, reality is likely to fall between these extremes. We calculate changes in climatically suitable areas under both migration assumptions and changes in spatial patterns of species richness under the assumption of universal migration.
Materials and methods

Scale of the analysis

The study area extends from 11°W 34°N to 32°E 72°N, and comprises of the British Isles and continental Europe, excluding Russia, Belarus, Ukraine, Moldova, Asia Minor and North Africa. We used equal area mapping units of 50 × 50 km, based on the Universal Transverse Mercator projection and the Military Grid Reference System for the model building, while all model predictions were computed at a 10′ × 10′ resolution. For the rest of this paper, we refer to the study area described above as Europe, the basic mapping units of 50 × 50 km as quadrates, and the 10′ × 10′ units as pixels.

Data

Current distributions of the 120 non-volant, terrestrial mammal species native to Europe were obtained from ‘The Atlas of European Mammals’ (Mitchell-Jones et al. 1999), including occurrences caused by intra-European introductions. The following mammal orders were represented: Artiodactyla (N = 12 species), Carnivora (N = 20), Insectivora (N = 25), Lagomorpha (N = 7) and Rodentia (N = 56). In order to accurately compare species distributions with current climate, only distribution data collected since January 1st 1970 were included in this study. Nomenclature follows Mitchell-Jones et al. (1999).

The three key bioclimatic variables, growing degree days (GDD), absolute minimum temperature, and water balance, were derived from monthly mean temperature and precipitation values following Skov and Svenning (2004). These factors can affect mammals’ distributions directly or indirectly, through their impact on trophic interactions such as predation and herbivory (Andrewartha and Birch 1954).

The absolute minimum temperature is an important factor controlling the distribution of mammals. All endotherms have a thermal neutral zone within which little or no energy is expended on temperature regulation (Vaughan et al. 2000). Especially below that zone, a disproportionately large amount of energy must be used for thermal regulation. Furthermore, as plants and invertebrates do not tolerate temperatures below a certain threshold, low temperatures affect the availability of food resources for mammals and thereby indirectly their distribution. The theoretical absolute minimum temperature was calculated according to the following regression equation based on observations from a large number of climate stations (Prentice et al. 1992):

\[
T_{\text{min}} = 0.006T_{C}^2 + 1.316T_{C} - 2.19,
\]

where \( T_{C} \) is the minimum temperature of the coldest month.

The amount of energy available for plant growth influences productivity, i.e. resource availability for herbivorous and, thereby indirectly also, carnivorous mammals. The length of the growing season and the influx of solar energy are captured by the index of GDD (Prentice et al. 1992; Beerling et al. 1995; Pearson et al. 2002) and represent heat availability for plant growth. GDD is computed as:

\[
\text{GDD} = \sum \max\{0, (T_{m} - T_{t})\},
\]

where \( T_{m} \) is the mean daily temperature (interpolated from monthly averages), and \( T_{t} \) is a threshold value indicating the lowest temperature for growth. In this study we use a \( T_{t} \) of 5°C.
Water balance is a measure of available moisture for plant growth and thereby also influences resource availability for mammals. However, it also represents the amount of water available for drinking. Here, water balance was computed as the monthly difference between precipitation and potential evapotranspiration (PET). These monthly values were then summed per year. Monthly PET was calculated following Lugo et al. (1999):

$$\text{PET} = 58.93 \times \frac{T_{(\text{above}0^\circ\text{C})}}{12}$$

All climatic variables were calculated from data sets based on monthly values of mean temperature and precipitation for 1961–1990 (current climate) or projected for 2070-99. The climate data, generated by the coupled atmosphere-ocean circulation model, HadCM3 (Pope et al. 2000; Gordon et al. 2000), were provided by the Hadley Centre for Climate Prediction and Research (www.meto.gov.uk/research/hadleycentre) and The Tyndall Centre for Climate Change Research (www.tyndall.ac.uk) at a spatial resolution of $10' \times 10'$.

We used two of the IPCC’s climatic scenarios (Anon. 2001), namely the “mild” B1 scenario, describing a world with reduced use of natural resources and the use of clean and resource-efficient technologies, and the more severe “business as usual” A2 scenario, where the greenhouse gas emission rate continues to increase.

The fuzzy envelope model

We modelled species-climate relationships using the fuzzy climatic envelope model of Skov and Svenning (2004), a modified version of the standard rectilinear climatic envelope (Guisan and Zimmermann 2000). This model is specifically designed to provide a conservative estimate of climate change sensitivity, modelling species tolerances as simple non-interactive threshold responses to a limited set of key bioclimatic parameters (Skov and Svenning 2004). As a consequence it relies less on the equilibrium assumption than the many other bioclimatic envelope models that focus on optimising the fit between the observed and predicted occurrences (Guisan and Thuiller 2005). The fuzzy model is described in detail in Skov and Svenning (2004). It first computes a suitability value on a continuum from 0 to 1 that represents the degree to which a given pixel belongs to the species’ envelope with regard to each individual climatic variable. Then, the full fuzzy envelope based on all three bioclimatic variables is calculated as the degree to which a pixel belongs to the individual envelope for all three bioclimatic variables, represented by the minimum suitability with respect to the three individual bioclimatic variables (Skov and Svenning 2004).

In order to define the climatic envelope for each species, we related environmental variables on a $10'$ grid to species distribution data on a $50' \times 50$ km grid. For each bioclimatic variable, we computed the mean value of all $10'$ grid pixels within the quadrate boundaries. All quadrates where a species occurred were selected, and the species’ bioclimatic envelope was estimated as the percentiles described above for the quadrates’ bioclimatic mean values. The model was used to produce suitability surfaces scaled from 0 to 1 for each species under current climate and future climatic scenarios (i.e. its potential distribution). Future potential distributions were computed by applying a species’ bioclimatic envelope model to the 2070-99 climate data for scenarios B1 and A2, respectively.

Model evaluation

To increase the robustness of our suitability estimates we chose to analyse only those species where the fuzzy envelope model provided a good fit to the data. For these species it
is safer to assume that climate is among the dominant range controls. In order to evaluate the fit of the modelled suitabilities to the observed present distribution for each species, we used threshold-independent receiver operating characteristic (ROC) curves (Metz 1978; Fielding and Bell 1997). The ROC analysis involves the calculation of sensitivity and specificity values. Sensitivity is defined as the number of true positive predictions for a species (true positives) divided by the total number of positive observations, while specificity is defined as the number of true negative predictions divided by the total number of negative observations (Metz 1978). The Area Under the Curve (AUC) of a plot of sensitivity against 1-specificity (false negative fraction) at every given probability of occurrence provides a measure of the predictive ability of a model; an AUC of 0.5 indicates that the model performs no better than random predictions, while a value of 1 indicates perfect predictions. AUC values >0.7 indicate useful applications (Metz 1978; Swets 1988). AUC was calculated using the Analyse-it® statistical software add-in (Analyse-it Software, Ltd, Leeds, UK) for Microsoft Excel®. Only species with an AUC value above 0.7 were included in the subsequent analyses (see Results).

Analysis of maps

For each species we recorded the suitability under current climate and future climatic scenarios for each pixel \((10' \times 10')\), within its present distribution range (no migration) as well as across Europe (universal migration). These values were then used to calculate the change in climatically suitable range (CCSR) under the B1 and A2 scenarios, as follows:

\[
\text{CCSR} = \frac{\text{new}_\text{suit}}{\text{curr}_\text{suit}}-\frac{\text{curr}_\text{suit}}{\text{curr}_\text{suit}};
\]

where new_suit is the modelled climatically suitable area (i.e. total suitability sum) for the species under a given climatic scenario, and curr_suit is the species’ current modelled climatically suitable area. Suitability across Europe was used when assuming universal migration, while suitability within the species’ present distribution was used when assuming no migration.

In accordance with the method described by Thuiller et al. (2005a), the CCSR was used to assign each species to an International Union for Conservation of Nature and Natural Resources (IUCN) threat category (IUCN 2001) for each climatic scenario. The following thresholds were used: Extinct covers species with a projected range loss of 100%, critically endangered species have a projected range loss of >80%, endangered species have a projected range loss of 50–80% and vulnerable species have a projected range loss of 30–50%.

For species occurring beyond Europe the full range of tolerated climates may not be represented in our data set. Consequently, we carried out a supplementary analysis that included only species endemic to Europe. However, as endemic and other narrowly distributed species are less likely to be in equilibrium with current climate than widespread species, a separate analysis was conducted using just the widespread species (>100 occurrences).

Current and future potential species richness were computed by summing all suitability values under the universal migration assumption and were interpreted as estimates of the species-holding capacity of each grid cell (ignoring biotic interactions).

All spatial operations and modelling were carried out using the ArcGIS™ 9 geographic information system software, and its spatial analysis extension, ArcGIS Spatial Analyst (ESRI, Redlands, CA).
Results

Model evaluation

The bioclimatic models had a mean AUC of 0.84 ± SE 0.01 (min. 0.503, max. 0.997). Of the 120 study species, 111 species (93%) had models that were useful for predicting their current occurrences (i.e. AUC > 0.7) and were used in the subsequent analyses. Plotting the AUC values against species prevalence (Fig. 1) shows that narrowly distributed species were better predicted than widespread species.

Species distribution ranges

Assuming universal migration, both losses and gains in climatically suitable area are expected to occur, and the trends appear to be similar for the two climatic scenarios. Changes in climatically suitable ranges (CCSR) vary between $-1$ and 2.05 (mean $-0.04 ± SE 0.05$) for the B1 scenario and between $-1$ and 2.46 (mean $-0.05 ± SE 0.07$) for the A2 scenario. One endemic species (0.9% of the 111) is predicted to lose all its climatically suitable range (i.e. become extinct) in both future climatic scenarios (Table 1).

A gain in climatically suitable area is calculated for 35% and 33% of the 111 species, under the B1 and A2 scenarios, respectively (Table 2a). On the other hand, under the B1 scenario, 32% of the 111 species are predicted to become threatened (lose > 30% of their current distribution), as compared to 47% under the A2 scenario (Table 2a). The threatened fraction for the endemic and the widespread species are predicted to be similar to the overall fraction under B1, whereas only 35% of endemic species, but as many as 52% of the widespread ones are predicted to become threatened under A2 (Table 2a).

Gain in climatically suitable area is predicted for 48% and 45% of the endemic species under the B1 and A2 scenarios, respectively, but only for 23% and 25% of the widespread species (Table 2a).

Based on the assumption of no migration, CCSR values range between $-1$ and 0.17 (mean $-0.50 ± SE 0.03$) for the B1 scenario, and between $-1$ and 0.04 (mean $-0.64 ± 0.03$) for the A2 scenario. Six species (i.e. 5% of the 111 species), three of them

![Fig. 1](https://example.com/fig1.png)

**Fig. 1** Area-Under-the-Curve (AUC) values for a plot of sensitivity against 1-specificity for all 120 native, non-volant terrestrial mammals, plotted against prevalence.
endemic to Europe, are predicted to become extinct under the mild B1 climatic scenario, and ten species (9% of the 111), five of them endemic to Europe, under the severe climatic scenario (A2) (see Table 1). All species predicted to be lost in the mild climatic scenario are rodents, and correspond to 1% of all rodents included in this study. Under the severe climatic scenario, our model predicts a potential loss of 13% of European rodents (seven species), 8% of European Artiodactyls (one species) and 8% of European Insectivores (two species) included in the study.

Table 1 European mammals predicted to become extinct (i.e. to have a bioclimatic suitability = 0 in all 10 × 10 pixels) under the mild (B1) and severe (A2) climatic scenarios under the assumption of no migration

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Climatic scenario</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cretan spiny mouse</td>
<td>Acomys minous</td>
<td>B1, A2</td>
</tr>
<tr>
<td>European bison</td>
<td>Bison bonasus</td>
<td>A2</td>
</tr>
<tr>
<td>Cretan white-toothed shrew</td>
<td>Crocidura zimmermann</td>
<td>A2</td>
</tr>
<tr>
<td>Romanian hamster</td>
<td>Mesocricetus newtoni</td>
<td>B1, A2</td>
</tr>
<tr>
<td>Balkan pine-vole</td>
<td>Microtus felteni</td>
<td>A2</td>
</tr>
<tr>
<td>Tatra vole</td>
<td>Microtus tatricus</td>
<td>B1, A2</td>
</tr>
<tr>
<td>Mouse-tailed dormouse</td>
<td>Myomimus roachi</td>
<td>B1, A2</td>
</tr>
<tr>
<td>Persian squirrel</td>
<td>Sciurus anomalus</td>
<td>B1, A2</td>
</tr>
<tr>
<td>Southern birch mouse</td>
<td>Sicista subtilis</td>
<td>B1, A2</td>
</tr>
<tr>
<td>Taiga shrew</td>
<td>Sorex isodon</td>
<td>A2</td>
</tr>
</tbody>
</table>

Bold face indicates that extinction is even predicted under universal migration as well

endemic to Europe, are predicted to become extinct under the mild B1 climatic scenario, and ten species (9% of the 111), five of them endemic to Europe, under the severe climatic scenario (A2) (see Table 1). All species predicted to be lost in the mild climatic scenario are rodents, and correspond to 1% of all rodents included in this study. Under the severe climatic scenario, our model predicts a potential loss of 13% of European rodents (seven species), 8% of European Artiodactyls (one species) and 8% of European Insectivores (two species) included in the study.

Table 2 Predicted change in climatically suitable range (CCSR) for native terrestrial European mammals (N = 111), endemic species (N = 40) and species currently represented in >100 quadrates (N = 64), under the mild (B1) and severe (A2) climatic scenarios, assuming universal (a) and no migration (b). Species were categorised into IUCN’s threat categories Extinct (Ex), Critically Endangered (CE), Endangered (En), Vulnerable (Vu) and Low Risk (LR)

<table>
<thead>
<tr>
<th></th>
<th>Ex</th>
<th>CE</th>
<th>En</th>
<th>Vu</th>
<th>LR</th>
<th>Gain</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall</td>
<td>B1</td>
<td>1 (0.9)</td>
<td>5 (4.5)</td>
<td>11 (9.9)</td>
<td>19 (17.1)</td>
<td>36 (32.4)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>1 (0.9)</td>
<td>12 (10.8)</td>
<td>6 (5.4)</td>
<td>33 (29.7)</td>
<td>22 (19.8)</td>
</tr>
<tr>
<td>Endemic</td>
<td>B1</td>
<td>1 (2.5)</td>
<td>0 (0.0)</td>
<td>6 (15.0)</td>
<td>5 (12.5)</td>
<td>9 (22.5)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>1 (2.5)</td>
<td>3 (7.5)</td>
<td>4 (10.0)</td>
<td>6 (15.0)</td>
<td>8 (20.0)</td>
</tr>
<tr>
<td>&gt;100 quadrates</td>
<td>B1</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>7 (10.9)</td>
<td>14 (21.9)</td>
<td>28 (43.8)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>0 (0.0)</td>
<td>5 (7.8)</td>
<td>1 (1.6)</td>
<td>27 (42.2)</td>
<td>15 (23.4)</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall</td>
<td>B1</td>
<td>6 (5.4)</td>
<td>12 (10.8)</td>
<td>34 (30.6)</td>
<td>32 (28.8)</td>
<td>26 (23.4)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>10 (9.0)</td>
<td>28 (25.2)</td>
<td>35 (31.5)</td>
<td>24 (21.6)</td>
<td>13 (11.7)</td>
</tr>
<tr>
<td>Endemic</td>
<td>B1</td>
<td>2 (5.0)</td>
<td>5 (12.5)</td>
<td>19 (47.5)</td>
<td>11 (27.5)</td>
<td>3 (7.5)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>5 (12.5)</td>
<td>19 (47.5)</td>
<td>12 (30.0)</td>
<td>2 (5.0)</td>
<td>2 (5.0)</td>
</tr>
<tr>
<td>&gt;100 quadrates</td>
<td>B1</td>
<td>0 (0.0)</td>
<td>2 (3.1)</td>
<td>13 (20.3)</td>
<td>24 (37.5)</td>
<td>24 (37.5)</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>0 (0.0)</td>
<td>10 (15.6)</td>
<td>18 (28.1)</td>
<td>23 (35.9)</td>
<td>12 (18.8)</td>
</tr>
</tbody>
</table>

Numbers represent of species in each category, while numbers in parenthesis represent the percentages of all species included in the analysis
Under the B1 scenario, 70% of the mammals are expected to become threatened, while 24% are expected to experience low range reductions or gains (Table 2b). Under the A2 scenario the effects are expected to be more severe: 78% of the species are expected to become threatened and only 13% to experience just a low reduction or gain in range (Table 2b). The threatened fraction of the endemic species is higher than the overall one (93% and 95% under B1 and A2, respectively), while it is lower for widespread species (61% and 80%, respectively) (Table 2b).

Species richness

Changes in spatial patterns of potential mammalian species richness have only been computed for the universal migration assumption. Our model predicts that future potentially species-rich areas will be found in montane and northern regions, while southern, lowland regions are expected to become depleted of mammalian species (Fig. 2).

Predicted changes in potential species richness range from a total loss (up to 39.8 or 42.8 species) to a gain of up to 1670% (26.4 species) or 1913% (31.2 species) under the B1
and A2 scenarios, respectively. Although, the consequences are more extreme under the severe climatic scenario (A2) changes in potential species richness under both scenarios show similar trends (Fig. 3). The greatest decreases are expected to occur in southern Europe, where parts of the Iberian, Italic and Greek peninsulas, as well as the majority of the Mediterranean islands are conditionally expected to lose up to 100% of current potential species richness. The most pronounced increases are predicted to occur in Fennoscandia, the Pyrenees and the Alps, with gains of over 200% (Fig. 3).

Discussion

Mammal species with distributions extending beyond Europe are problematic to model as they might have broader climatic niches than estimated by our model. Especially species with ranges expanding to the Middle East or Africa, e.g. golden jackal (*Canis aureus*), marbled polecat (*Vormela peregusna*) and wildcat (*Felis silvestris*), all of which are predicted to become threatened by our model, probably have greater tolerances to higher temperatures and drought than modelled here and might in reality be able to thrive in our modelled ‘barren’ southern Europe in the future. As 50% of the species predicted to become extinct by our model are non-endemic to Europe, the results of the overall analysis, covering all 111 mammal species, should be considered with caution. However, the endemic species, represented by their complete climatic niche, were found to be more vulnerable to climate change (under the no migration assumption) than the rest of the species considered, probably due to their smaller distributions (Schwartz et al. 2006). Endemic species were also predicted to gain more climatically suitable area compared to non-endemic species (under the universal migration assumption). Endemic species generally have smaller distributions, and thus a change of a few quadrates proportionately increases or reduces their distribution more than that of widespread species.

Our analyses considered only species that were well predicted by our model, and the ROC evaluation demonstrated that our model conditionally describes species distributions very well, as over 90% of the mammals included in the study received high AUC scores. A low predictive ability may indicate departures from equilibrium with current climate or limitations to the model’s ability to correctly describe the species’ bioclimatic niche. Species with low prevalence generally had better modelling performance than species with high prevalence, corresponding to the findings of some recent studies (Segurado and

![Fig. 3 Modelled changes in mammalian species richness in percentage, under the mild climatic scenario, B1 (a), and severe climatic scenario, A2 (b), in a 10° × 10° resolution](image-url)
Araújo 2004; Luoto et al. 2005). Luoto et al. (2005) suggest that the effect of range size on model performance is caused by the fact that more is known about the ranges of rare species than of many common ones, and that areas containing rare species may be more attractive and therefore experience local over-sampling. However, this pattern may also merely appear due to the fact that the fewer quadrates contributing to the model’s envelope, the narrower it becomes, i.e. the climatic conditions become very specific, even if the small range is mainly caused by non-climatic limitations. Subsequently, these conditions may only be found in the original geographic distribution. For example, the Cretan spiny mouse (Acomys minous) occurs only in three quadrates and the likelihood of finding the exact same combination of climatic conditions elsewhere is low. This is substantiated by the very small current potential distribution predicted for this species. We did not exclude species with small ranges from this study because of their predisposed vulnerability, despite the fact that this strategy has been followed by other workers (Thuiller et al. 2005a, b). However, caution should be taken when interpreting the predictions of the model where small-ranged species are concerned.

Change in species ranges

Our model predicts that up to 10% of all European mammals may risk extinction within 100 years due to global climate change, while up to 25% of the species may become critically endangered. Less threatened species are not expected to be lost immediately, but reductions in habitat area and population size may lead to delayed extinctions (see e.g., Brooks et al. 1999). Range losses are likely to lead to reductions in population size, exposing species to the possibility of genetic drift. Even a small loss of suitable area can result in extinctions of local populations (McCarty 2001), especially when dispersal possibilities are limited.

Our model also predicts that more than a third of all native European mammals will gain climatically suitable area as a result of climate change, when assuming universal dispersal. However, a species may not be able to colonise a climatically suitable area if other habitat requirements are not fulfilled; European trees and forest herbs are predicted to track future climate change only to a limited degree (Skov and Svenning 2004; Svenning and Skov 2004). This limited mobility of plants may slow down or even hold back the migration of certain herbivorous mammals. Similarly, a spatial mismatch between insectivores and their prey might cause a further decline in the predator populations. For example, in the British Isles a poleward shift in the northern distributions of various beetles, woodlice and spiders has been associated with climate change (Hickling et al. 2006). A mismatch between the distributions of these and the ones of e.g. common shrew (Sorex araneus) and pygmy shrew (Sorex minutus), may affect the food availability of the shrews as their diet largely relies on these invertebrates. Moreover, many species may not be able to track of the changing climate due to limited dispersal ability, presence of natural barriers, biotic interactions and/or anthropogenic habitat fragmentation caused by urbanisation or agriculture. Southern species inhabiting the Mediterranean peninsulas will have difficulties moving northwards due to East-West oriented mountain ranges such as the Pyrenees, Alps and Carpathians, while species inhabiting Mediterranean islands will face even greater barriers and presumably not benefit from gains in climatically suitability on the European mainland at all. In addition, biotic interactions, notably competition or hybridisation, may hinder mammals from occupying new climatic suitable areas (Case et al. 2005).
The gain in climatic suitability predicted by our model under the no migration assumption for one species, the sibling vole (*Microtus rossiaemeridionalis*), is not a gain in area, but rather the climatic suitability of the pixels within its current distribution is predicted to increase.

Changes in potential species richness

Our model predicts noticeable changes in potential mammalian species richness over Europe due to climate change. As a result of shifts in species ranges, northwards and towards higher elevations, future species-rich areas are predicted to concentrate around northern and montane regions. Our predictions, showing changes in ranges to be particularly significant in mountain ranges, are corroborated by other studies (Hannah et al. 2002; Thuiller et al. 2005a). In southern Europe, our model predicts species losses from Mediterranean peninsulas and islands. It is essential to emphasise that the model considers Europe to be an isolate. In reality it is possible that species from adjacent regions such as the Middle East might be able to immigrate and fill out these newly available areas. Additionally, the climatic conditions predicted for southern Europe are warmer than today’s, and as a result none of our species envelopes encompass them. Similarly, water balance values beyond the range observed today are likely to cause the predicted loss of all mammals from the western coasts of Norway and Great Britain, and hence may be a model artefact.

Mammals have shown differential responses to climate changes in the past (Graham et al. 1996). The future range contractions and expansions predicted here, as well as the possible arrival of new species from outside Europe may create novel species assemblages, which could contribute to a high temporal species turnover in future communities as a result of new species interactions (e.g. competition and predation). The scope of this study does not permit the quantification of turnover, but in the light of the high turnover resulting from climate change found for mammals in fossil records (Graham et al. 1996; Barnosky et al. 2003), it is not unlikely that near-future climate change will result in similar or even higher rates.

Model limitations

Bioclimatic envelopes are essentially static models relating current distributions to climatic variables. As a result, non-climatic factors influencing species distributions, e.g. land-use, biotic interactions, human interference, dispersal and history, are not accounted for. These assumptions have lead to speculations regarding the validity of bioclimatic models (Davis et al. 1998; Pearson and Dawson 2003; Hampe 2004; Ibáñez et al. 2006; Araújo and Rahbek 2006). The fuzzy envelope model used also assumes some degree of equilibrium with contemporary climate (albeit to a lesser extent than many other models). In Europe, clear departures from species-climate equilibrium are found for many tree species (Svenning and Skov 2004). Furthermore, Araújo and Pearson (2005) concluded that assemblages of reptiles and amphibians in Europe are relatively further from equilibrium than plants and birds. Hence, mammals may not occupy all currently climatically suitable areas in Europe either. In fact, successful human introductions of many mammal species beyond their native range within Europe provide direct support for this possibility, e.g., mouflon (*Ovis ammon*), rabbit (*Oryctolagus cuniculus*), brown hare (*Lepus europaeus*),
and fat dormouse (*Glis glis*) (Mitchell-Jones et al. 1999). Finally, bioclimatic models assume species to lack sufficient genetic adaptive potential or phenotypic or behavioural plasticity to adapt to climates beyond those under which a given species occurs today. However, phenotypic changes have already been documented to correlate with climatic changes. The body mass of the bushy-tailed woodrat (*Neotoma cinerea*), for example, has increased in correlation with the decrease in temperatures in the Late Quaternary in the Colorado Plateau (Smith and Betancourt 1998), and decreased with recent increases in temperature in New Mexico (Smith et al. 1998). On the other hand, the models ascribe all population the same ecological span as the whole species including for example, different sub-species. In reality, individual populations are likely to be more specialised and have more limited ecological tolerance and adaptive capability than the species as a whole.

**Conclusion**

The results of this study should be considered a first approximation of the potential impact of climatic change and the resulting patterns, rather than an accurate prediction of future species distributions. However, this study, encompassing all native European mammals, emphasises the potential severity of climate change, especially for the endemic species, which should be taken into account in conservation planning. Species richness centres are predicted to shift, and new areas may need to be protected in order to ensure the persistence of European mammals. Management options include maintaining a network of suitable habitats in the European landscapes to support persistence as well as facilitate the migration of mammals to new climatically suitable areas. Detailed guidelines for conservation, however, should be based on analyses on a finer scale, especially where the more sensitive heterogeneous mountainous regions are concerned. Ideally, these models should incorporate local population dynamics, dispersal limitations, landscape characteristics as well as human interference. However, such models may become very restricted, highly complicated, and difficult to build due to lack of detailed ecological knowledge.

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