

Potential impacts of climatic change upon geographical distributions of birds

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Potential climatic changes of the near future have important characteristics that differentiate them from the largest magnitude and most rapid of climatic changes of the Quaternary. These potential climatic changes are thus a cause for considerable concern in terms of their possible impacts upon biodiversity.

Birds, in common with other terrestrial organisms, are expected to exhibit one of two general responses to climatic change: they may adapt to the changed conditions without shifting location, or they may show a spatial response, adjusting their geographical distribution in response to the changing climate. The Quaternary geological record provides examples of organisms that responded to the climatic fluctuations of that period in each of these ways, but also indicates that the two are not alternative responses but components of the same overall predominantly spatial response. Species unable to achieve a sufficient response by either or both of these mechanisms will be at risk of extinction; the Quaternary record documents examples of such extinctions.

Relationships between the geographical distributions of birds and present climate have been modelled for species breeding in both Europe and Africa. The resulting models have very high goodness-of-fit and provide a basis for assessing the potential impacts of anthropogenic climatic changes upon avian species richness in the two continents. Simulations made for a range of general circulation model projections of late 21st century climate lead to the conclusion that the impacts upon birds are likely to be substantial. The boundaries of many species' potential geographical distributions are likely to be shifted ≥ 1000 km. There is likely to be a general decline in avian species richness, with the mean extent of species' potential geographical distributions likely to decrease. Species with restricted distributions and specialized species of particular biomes are likely to suffer the greatest impacts. Migrant species are likely to suffer especially large impacts as climatic change alters both their breeding and wintering areas, as well as critical stopover sites, and also potentially increases the distances they must migrate seasonally.

Without implementation of new conservation measures, these impacts will be severe and are likely to be exacerbated by land-use change and associated habitat fragmentation. Unless strenuous efforts are made to address the root causes of anthropogenic climatic change, much current effort to conserve biodiversity will be in vain.

INTRODUCTION

The past decade has seen general acceptance by the scientific community of the premise that anthropogenic

increases in atmospheric concentrations of radiatively active gases, so-called 'greenhouse gases', have already led to changes in global climate (IPCC 2001) and will continue to do so in the future. As Schneider (1994) foresaw, it was the demonstration that a combination of natural and anthropogenic forcing was

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required in order for a general circulation model (GCM) to successfully simulate the observed climatic changes of the 20th century (Tett *et al.* 1999, Stott *et al.* 2000) that made a crucial contribution to this acceptance of the role of human activities in changing the global climate. Over the same decade it also has become apparent that many species already are responding to the changing climate (Parmesan *et al.* 1999, Parmesan & Yohe 2003, Root *et al.* 2003), and there is a strong suspicion that at least one species has been driven to extinction by climatic change (Pounds *et al.* 1999, Still *et al.* 1999). Already a decade ago, models were being constructed relating species' geographical distributions to climate (Huntley *et al.* 1995, Sykes *et al.* 1996); although at that time attention focused principally upon plant species, the likely implications for the potential future distributions of birds already were being discussed (Huntley 1995).

Scientific advances during the past decade now enable the potential impacts of future climatic changes upon birds, and many other taxonomic groups, to be explored more directly and with greater confidence. Amongst these advances are the very substantial improvements that have been achieved in models of the climate system. Models have finer resolution and improved representations of key processes compared to those of a decade ago, and also make coupled simulations of the general circulations of the atmosphere and oceans, whereas their predecessors generally had very much simplified representations of the oceans. As a result, we can have greater confidence in the projections of future climatic change made using these models. Important new datasets recording species' geographical distributions have become available, including the dataset that underpins *The EBCC Atlas of European Breeding Birds* (Hagemeijer & Blair 1997), as have new compilations of observed climatic conditions (e.g. New *et al.* 1999, 2000). Such datasets have paved the way towards more extensive efforts to model the relationships between species' distributions and climate. A plethora of new approaches has been developed to address this modelling problem (see, e.g. Berry *et al.* 2002, Midgley *et al.* 2002, Pearson *et al.* 2002, Peterson *et al.* 2002, 2004, Peterson 2003); faced with this diversity one worker has advocated applying a suite of alternatives and choosing that model that performs 'best' according to 'expert opinion' (Thuiller 2003). New ways of assessing model goodness-of-fit also have been developed, and greater understanding achieved of the limitations of previous methods that continue to be widely used

(Manel *et al.* 2001). Models have been applied to species from a wide range of taxonomic groups; a systematic comparison of model performance has shown that the approach performs equally well for species from three major taxonomic groups and spanning four trophic levels (Huntley *et al.* 2004). The last decade also has seen important advances in our knowledge of past climatic changes, and in the sensitivity of terrestrial ecosystems to these changes. Ice cores from Antarctica have provided records spanning multiple glacial–interglacial cycles (Petit *et al.* 1999, EPICA community members 2004), whilst long lacustrine sediment records have shown vegetation responding rapidly to the millennial climatic fluctuations of the last glacial stage (Allen *et al.* 1999).

In this paper we aim briefly to review the current state of knowledge with respect to potential future climatic change and how this compares to climatic changes of the recent geological past. We will also briefly consider how species respond to climatic change. We will then outline our approach to modelling the relationships between species' distributions and climate, and illustrate some examples from our recent work modelling the distributions of bird species in Europe and Africa. We will then demonstrate the use of these models to explore the potential impacts of anthropogenic climatic change upon birds, considering the uncertainties inherent in modelling such impacts and focusing upon the robust results that emerge. Finally, we will end with some conclusions with respect to conservation measures that will assist species in adapting to the inevitable changes in climate, as well as emphasizing the need for mitigation measures to limit climatic change.

Climatic change

It is evident both from historical evidence (Lamb 1982, Grove 1988) and from Quaternary geological data (Bartlein 1997, Bartlein & Prentice 1989, Webb & Bartlein 1992) that climatic change is not a new phenomenon, but has always been a feature of the earth system. The earth's climate changes naturally, apparently principally as a result of major volcanic events (Minnis *et al.* 1993), variations in solar output (Karlén & Kuylenstierna 1996) and variations in the earth's orbit around the sun (Hays *et al.* 1976, Berger *et al.* 1984, Imbrie *et al.* 1992), each force operating principally at a characteristic time scale of years, decades or centuries and tens to hundreds of millennia. Over even longer timescales, of millions

to tens of millions of years, tectonic processes apparently have resulted in major changes to the climate system, such as the onset of the Quaternary ice age (Kutzbach *et al.* 1993b, Ruddiman & Kutzbach 1989, 1990, Ruddiman & Kutzbach 1991, Raymo & Ruddiman 1992) or the development of 'super-monsoon' circulation during the time of Pangea or of other 'super-continent' (Kutzbach & Ziegler 1993). The climate system also has inherent instabilities that lead to quasi-periodic fluctuations on time scales ranging from multiannual, in the case of the El Niño–Southern Oscillation (Henderson-Sellers & Robinson 1986, Friedrich & Müller 1992, Cole *et al.* 2000), to millennial, in the case of the Dansgaard–Oeschger cycles during the last glacial stage (Bond *et al.* 1993, Knutz *et al.* 2001, Schulz 2002), and even multimillennial, in the case of Heinrich events that also occurred during the last glacial stage (Andrews 1998, Kirby & Andrews 1999). The underlying mechanisms of these instabilities often are obscure, however, and it has been argued that the 1470-year periodicity of Dansgaard–Oeschger cycles is too regular to be the result of an internal instability of the earth system (Rahmstorf 2003).

These past climatic changes are differentiated from current and projected anthropogenic climatic change in several important ways. First and foremost, anthropogenic climatic change is expected to result in global conditions markedly warmer by 2100, by between 1.4 and 5.8 °C (IPCC 2001), than the recent past; a more recent analysis of modelling results (Stainforth *et al.* 2005) suggests that the upper limit of possible warming may be substantially greater, with the sensitivity of the climate system to a doubling of the pre-industrial atmospheric concentration of carbon dioxide perhaps being as much as 11 °C. Although global climates of the past have at times been substantially warmer, it is necessary to go back well into the Tertiary geological period, 10 million years or more, to find evidence of conditions more than at most 1.5–2 °C warmer in terms of global mean temperature than the recent past (Bartlein 1997). Furthermore, warmer conditions than those of the recent past have accounted for only a small minority of the Quaternary period, occurring during only short parts of a few recent interglacial stages (Shackleton & Opdyke 1976, Imbrie *et al.* 1984, EPICA community members 2004) that are estimated to have global mean temperatures only 1–2 °C warmer than the recent past (Webb & Bartlein 1992, Webb & Wigley 1985). Global climate is thus projected to be at least as warm, by the end of the

present century, as it has been at any time during the evolution as species of most of the world's present diversity of organisms; most probably it will be substantially warmer, the modal projection being a warming of 3.0–3.5 °C by 2100.

Of course it can be argued that at least regionally and even globally following major volcanic eruptions, short-term variations of mean annual temperature of such magnitude are commonplace, and thus should cause us no concern. Whilst it is true that such variations in mean annual temperature are an inherent feature of the global climate system, the warming projected is in the long term mean global temperature. Such interannual variability will continue about this increasing mean, and may even have increased magnitude as a consequence of anthropogenic interference with the climate system (Stott *et al.* 2004). Furthermore, there is considerable potential for feedback in the climate system to amplify the warming (Cox *et al.* 2000), perhaps leading to a mean state of the system more like the current El Niño extreme of the ENSO.

The second feature of projected anthropogenic climatic change that is noteworthy is its magnitude. Even at the lower end of the range of possibilities, the change is comparable in magnitude to the extent by which temperatures during the last (Eemian) interglacial may have exceeded those of the post-glacial. Regionally in Europe the warmer conditions of the Eemian were reflected by northward expansions of the ranges of southern species: *Acer monspessulanum* (Montpelier Maple) and *Emys orbicularis* (European Pond Tortoise) both extended their ranges into southern Britain, at least 500 km beyond their present northern limits (West 1968). The modal projected warming of 3.0–3.5 °C, however, is more than twice this magnitude, whilst at the upper end of the range cited by the IPCC (2001) a warming of 5.8 °C is comparable in magnitude to the global warming estimated (Schneider 1989) to have taken place during the transitions from glacial to interglacial conditions that have occurred approximately every 100 000 years during the late Quaternary. These glacial termination events were associated with major rearrangements of the climate system (COHMAP 1988, Kutzbach *et al.* 1993a) and associated changes in terrestrial ecosystems (Jacobson *et al.* 1987, Webb 1987, Wright *et al.* 1993). Any future climatic change of comparable magnitude must be expected to have similar far-reaching consequences.

Finally, the projected warming also is extremely rapid, its rate being arguably without precedent in

the recent geological past. The most rapid large magnitude changes in global mean temperature of the recent geological past occurred during glacial terminations when global mean temperature rose by *c.* 5 °C in 5000–7000 years. Recent evidence from the EPICA ice core (EPICA community members 2004) shows remarkable consistency in the length of time taken for temperature to rise from glacial to interglacial levels during different glacial terminations. This Antarctic evidence is consistent with evidence from tropical ice cores (Thompson *et al.* 1995, 1998a) in indicating progressive warming over several millennia, and contrasts with the oft-cited evidence from Greenland ice cores (see, e.g. Alley 2000) interpreted as indicating that a substantial part of that warming took place in less than a century at the end of the Younger Dryas cold oscillation. The latter evidence clearly indicates very rapid regional climatic changes around the North Atlantic and is paralleled by evidence from marine cores (see, e.g. Austin & Kroon 1996, Kroon *et al.* 1997). The extent to which these rapid changes reflect comparably rapid global changes remains questionable, however, especially in light of ice core evidence from the tropics and Antarctica. Given the well-documented rapid shifts in location of the Polar Front in the North Atlantic during deglaciation (Ruddiman & McIntyre 1981), and current understanding of the causes of the associated rapid changes in North Atlantic circulation (Clark *et al.* 2001, Teller *et al.* 2002), it is probably inappropriate to take records of climatic change from this region as representative of changes in overall global mean conditions. Furthermore, the ‘flickering’ commented upon by Alley (2000) that often precedes these rapid changes, and that is seen also in the marine record (Austin & Kroon 1996, Kroon *et al.* 1997), is most easily explained as a reflection of interannual variability in the mean position of a front, the position of which in shifting past a particular spatial location will result in a very rapid change in prevailing conditions at that location.

Taking a precautionary stance, the rate of global mean temperature increase during glacial terminations may have averaged as little as *c.* 0.01 °C per decade (i.e. 5 °C increase in about 5 millennia); if the rapidity of the warming in Greenland truly reflects global warming, however, then the rate may have been as high as *c.* 0.25 °C per decade (i.e. about half of the overall warming occurring in a century). The rate projected by the IPCC (2001) for the present century is between 0.14 and 0.58 °C per decade. If

the precautionary stance is taken, then projected future global warming is at least an order of magnitude faster than deglacial global warming. On the other hand, if the Greenland records are taken as reflecting global mean warming rates, then the rate of the projected warming is of the same order of magnitude as deglacial warming. In the latter case, however, it then becomes necessary to conclude that ecosystems that showed progressive change over a period of several millennia, lagged substantially behind the rapid deglacial warming. This issue of ‘migrational lag’ has long ago been debated by palaeoecologists (see, e.g. Davis 1981, Webb 1986, Davis & Sugita 1997), however, and the general conclusion now reached is that vegetation sustained a dynamic equilibrium with the changing climate during the transition from the last glacial stage and the early postglacial. This conclusion received particularly strong support from the work of Prentice *et al.* (1991). Notwithstanding this, whether the projected future rate is comparable to deglacial warming or unprecedented, we can expect ecosystems to fail to track such rapid changes. Furthermore, even if we take the optimistic view, that such disequilibrium has occurred before and thus is something to which the global system is adapted, the inevitable conclusion that we must reach, given the palaeoecological record, is that global ecosystems are likely to take several millennia to regain equilibrium with the warming projected for this century.

In reality, however, the situation does not parallel past warming events in one crucial way that has profound implications for the ability of ecosystems to adapt. During past glacial stages, the geographical distributions of many temperate species, although much more limited in extent than their present distributions, coincided with or lay geographically close to the equatorward limits of the species’ postglacial and present distributions. Subsequently, in response to the climatic changes associated with deglaciation, these species extended their distributions into more poleward areas where climate was newly suitable, whilst being able to maintain their equatorward populations in relatively close proximity to their areas of glacial distribution (Bennett *et al.* 1991, Tzedakis *et al.* 2002). This behaviour is reflected clearly in the patterning of genetic variability in such species, greatest variability being found in their equatorward populations where long-term persistence of the species through both glacial and interglacial stages has been associated with an accumulation of genetic variability, whereas populations exhibit

progressively reduced variability with distance from these centres of glacial distribution (Hewitt 1996, 1999). The projected future warming, however, will, as emphasized above, lead to conditions unparalleled for millions of years. If, as seems probable, the equatorward areas of many species' current distributions become no longer suitable, as a result of these unprecedented climatic changes, then whilst the species' advancing range limits probably will lag behind climatic change, their equatorward limits may retreat more or less in equilibrium with climatic change. Such a scenario not only will lead to potentially rapid range reductions for many species, crucially it also will lead at an early stage to the loss of most of their genetic diversity.

Projected climatic change thus, in summary, differs from past changes crucially in its 'destination', leading to a world warmer than it has been for millions of years, and is also expected to take place at a rate that is beyond that with which ecosystems can maintain equilibrium. Such rapid change towards unprecedented conditions is likely to lead to species' distributions being reduced and to loss of most of the genetic diversity in many temperate species. To explore these potential consequences further, however, we now turn to consider how species respond to climatic change.

Species' responses to climatic change

Working from first principles we can argue that species' responses to climatic change will fall into one of two categories (Huntley *et al.* 1997a, 1997b): species may exhibit adaptation, through natural selection of those genotypes best suited to the new climatic conditions; alternatively, they may exhibit a spatial response, shifting their area of geographical distribution in response to the changing climate, allowing species to continue to occupy the range of climatic conditions to which they are adapted. Those approaching the problem from a biological background are more likely to focus upon adaptation (see, e.g. Butterfield & Coulson 1997, Dolman 1997), whereas those approaching from a biogeographical or palaeoecological perspective are more likely to emphasize the spatial response (Huntley & Webb 1989, Graham 1997, Preece 1997, Webb 1997), as Good (1931, 1964) did when he proposed his 'Theory of Tolerance'.

The Quaternary fossil record provides us with evidence that has been interpreted as indicating an adaptive response by at least some species (Hellberg

et al. 2001, Smith *et al.* 1995, Rousseau 1997), although in general such interpretations are based only upon the morphological phenotype of the fossils. Strikingly, in none of the few reported cases interpreted in this way does the range of variation seen amongst the fossils from periods of contrasting environmental conditions exceed the range of variation seen in the species today across the extent of its geographical range. This accords with the argument advanced by Bennett (1990, 1997) that the relatively frequent reversal of direction of the selective pressure exerted by climate during the Quaternary, at least when viewed in relation to evolutionary time scales, has precluded an adaptive evolutionary response as the principal response of organisms to the climatic changes of that period. Only when we examine the responses of organisms to such things as the overall long-term cooling trend of Quaternary climates, or the progressive increase in the extent of grass-dominated vegetation over the same period as a response to climatic drying in some regions, do we find clear evidence of evolution as a primary component of these responses (Lister 1997, Lister & Sher 2001).

Much more abundant evidence from the Quaternary fossil record indicates that spatial responses have predominated, at least amongst terrestrial taxa (Graham & Grimm 1990). Such responses have been documented and discussed for, *inter alia*, plants (Bernabo & Webb 1977, Davis 1983, Huntley & Birks 1983, Huntley 1988, 1991), mammals (FAUNMAP Working Group 1996, Graham 1997), beetles (Ashworth 1997, Morgan 1997) and molluscs (Preece 1997). More recently, such fossil evidence has been supplemented by phylogeographical evidence for species from an even wider range of taxonomic groups, including birds (see, e.g. Holder *et al.* 2000, Kraaijeveld & Nieboer 2000, Liukkonen-Attila *et al.* 2002, Ruegg & Smith 2002, Drovetski *et al.* 2004).

In reality, however, the distinction between adaptive and spatial responses is artificial: both are most usefully viewed as components of the same general response. This can be illustrated by considering a species that exhibits clinal variation across its geographical range as a result of differential selection of warm-adapted and cold-adapted genotypes at the extremities of this cline (Fig. 1). If, after the passage of some interval of time, the climatic conditions to which the species is adapted are found in a different geographical area within the same overall region, the species can be expected to have shifted its overall area of distribution so as to maintain equilibrium

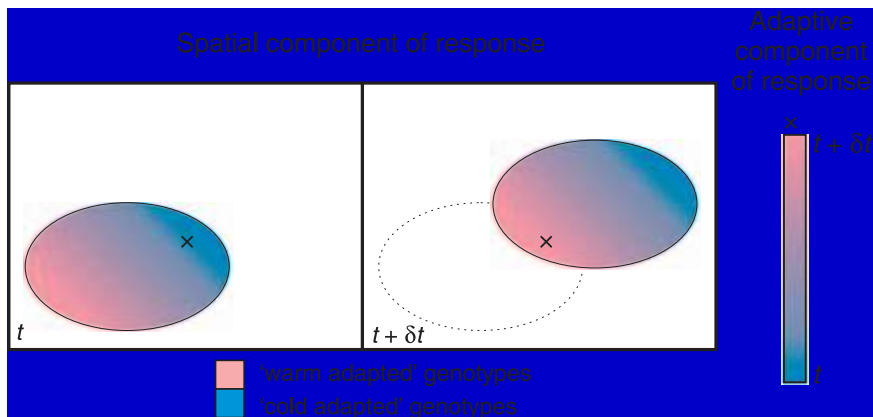


Figure 1. The spatial and adaptive components of a species' response to climatic change.

The rectangular area represents a continental region, within which the species' area of geographical distribution is represented by the shaded ellipse. The shaded ellipse is displaced between times t (left-hand panel) and $t + \delta t$ (right-hand panel) as a consequence of climatic change, its former position at time t being indicated on the panel for time $t + \delta t$ by the dotted outline. The symbol \times signifies a fixed location that falls within the species' geographical distribution at both times t and $t + \delta t$ (see text for further explanation).

with the changing climate. This is the spatial component of the response that would be perceived by a worker examining a sequence of maps of the species' geographical distribution through time. At the same time, however, at any particular location that falls within the species' distribution both initially and after the spatial shift, the climatic change at that location will have resulted in natural selection favouring genotypes differing from those initially dominant in the population at that location. This is now the adaptive component of the response that would be perceived by a worker examining either the genetics or the phenotypic expression of the contrasting genotypes in the local population of the species at one particular locality through time.

Before moving on to consider how we can model the relationships between species' distributions and climate, it is important to note that the Quaternary fossil record also documents the fate of species that have been unable to respond adequately to past climatic changes, i.e. their extinction. Late-Quaternary extinctions are best known amongst the larger terrestrial mammals (Barnosky *et al.* 2004, Stuart 1991, Stuart 1993, Lister & Sher 1995, Stuart *et al.* 2004), including *Homo neanderthalensis* (Stringer *et al.* 2003), but have been documented also amongst trees (Jackson & Weng 1999). Although there has been considerable debate about the potential mechanisms that led to these extinctions, and especially the putative role of humans in relation to the extinctions of large mammals (Alroy 2001, Barnosky *et al.* 2004), it is probable that the rapid climatic changes of the

late Quaternary, and especially those that characterized the last glacial stage and its termination, contributed to many, if not all, of the extinctions of this period. Extinctions as a result of climatic change may arise through a number of mechanisms (Huntley 1999), including the increased likelihood of stochastic extinction of small populations. Where a species experiences an insurmountable spatial discontinuity in the availability of the climatic conditions to which it is adapted, its extinction might be prevented today by artificial translocation. Where the discontinuity in the availability of suitable climatic conditions is temporal, however, then the species' extinction in the wild is certain and only captive breeding stocks might be maintained. Such might be the fate of *Mammuthus primigenius* (Woolly Mammoth) were it still with us today and being faced with the projected rapid warming at high latitudes. Such rapid warming during the last deglaciation led eventually to the effective disappearance of the tundra–steppe habitat to which this species was adapted (Guthrie 2001, Walker *et al.* 2001) and hence to its extinction (Stuart *et al.* 2002), albeit that its global extinction occurred finally only as recently as c. 4000 years ago (Vartanyan *et al.* 1993).

MODELS

Modelling relationships between species' distributions and climate

Given the predominant spatial component of species' response to climatic change, within which the

adaptive component can be considered to be subsumed at least to the extent that novel combinations of climatic conditions do not arise, the potential impacts of projected climatic change upon species can be simulated using models relating their geographical distributions to climatic variables. As mentioned above, a plethora of techniques now is available for the fitting of such models. In selecting an appropriate technique to apply, however, several issues need to be considered. Of these, the first is the nature of the species' distribution data available for the taxonomic group and region to be modelled. In particular, an important distinction must be made between data that record only species' presences, usually for point locations from which museum specimens or other records have been obtained, and data that record both presences and absences of a species, most frequently for the cells of some regular grid. In our work modelling the distributions of bird species in Europe and Africa we have used data of the second type, selecting our modelling approach appropriately.

The data for Europe were made available to us by the European Bird Census Council and are those that were used to prepare the maps presented by Hagemeyer & Blair (1997). These data record the presence and absence of species breeding in Europe for the cells of a *c.* 50 km UTM grid. In addition, for each species grid squares reporting neither presence nor absence are distinguished from those reporting absence, i.e. grid squares where the species was sought but not found. In modelling each species we have used only those squares reporting presence or absence, although when simulating the species' present distribution we have extrapolated our model spatially to predict presence and absence of the species in 'no data' grid cells for which the climatic conditions fall within the range of climatic conditions to which the model is fitted. The data for Africa come from the compilation made by the Zoological Museum, University of Copenhagen, Denmark (Burgess *et al.* 1998, Brooks *et al.* 2001). These data record presence and absence of species in the cells of a 1° longitude × latitude grid. To date we have restricted the scope of our work to sub-Saharan Africa and to species breeding in the region.

The climatic data that we have used also differ between the two regions, although in both cases we have as far as possible used only data relating to the period 1961–90. For Europe, we have interpolated monthly values of temperature, precipitation and insolation for the cells of the EBCC UTM grid from

the 0.5° longitude × latitude global compilation of New *et al.* (1999). For Africa, we used the monthly temperature and precipitation values interpolated to a 3' longitude × latitude grid by Corbett & O'Brien (1997). Insolation data were not available from Corbett & O'Brien (1997), however; they were therefore interpolated for the geographical mid-points and mean elevation of the 3' cells using elevation-sensitive spline surfaces (Hutchinson 1989) fitted to a dataset derived from the meteorological station data compilation of Leemans & Cramer (1991) with additional data points added by W. Cramer (unpubl. data).

Rather than fitting models to the raw climatic variables, few of which have any readily comprehended mechanism by which they might limit species' distributions, we computed from the interpolated climatic variables a series of bioclimatic variables that have well-established mechanisms by which they may limit species' distributions. These bioclimatic variables fall into three categories. The first, and simplest, are representative of temperature extremes: The mean temperatures of the coldest and warmest months were used as proxies for the extreme annual temperatures, because the latter are reported by only a small proportion of meteorological stations and thus are not available in the interpolated datasets. The second category are temperature sum estimates derived from the monthly mean temperature data: the annual temperature sum above a threshold value of 5 °C was calculated following Prentice *et al.* (1992). The third category are estimates of moisture availability; these are derived from the monthly climatic values for temperature, precipitation and insolation using a bucket model (Cramer & Prentice 1988) that requires also an estimate of soil water capacity. We used for this purpose the global soil water capacity dataset developed by Prentice *et al.* (1992). In addition to estimating the overall annual ratio of actual to potential evapotranspiration (Priestley-Taylor's α), we also used daily values of the ratio of precipitation to potential evapotranspiration (P/PE) to estimate the length and 'intensity' of wet and dry seasons for the African dataset. The seasonal intensities were computed as the sum of the daily values of (P/PE - 0.5) for the relevant season, with dry season intensities thus being negative and wet season intensities positive. For the African data we used the values of these bioclimatic variables computed for the 3' cells to estimate values for each cell of the 1° longitude × latitude grid for which the bird data were available. In order to provide an estimate for the modal elevation of each 1° cell we

ranked the 400 3' cells in each 1° cell by elevation and computed the mean of the values for the cells ranked 176th to 225th, i.e. the 'middle 50' with respect to elevation.

Some of these bioclimatic variables can have direct effects upon birds, leading to limits upon their distributions. Temperature extremes, for example, readily can impose limits directly through the physiological tolerances of the species; the intensity of a wet season may operate directly by limiting opportunities to feed, that of a dry season by limiting access to surface water for birds that require to drink. Others of the bioclimatic variables, however, are more likely to operate indirectly by affecting various interactions with other species that impact upon the focal species and affect its ability to breed. The mean temperature of the coldest month in their European breeding area is not directly experienced by sub-Saharan migrants, for example, but may easily determine the availability of food or suitable habitat, or the prevalence of a parasite.

The modelling approach that we have used is that of fitting species–climate response surfaces that describe the probability of occurrence of a species throughout the space defined by a small number of bioclimatic variables (Huntley *et al.* 1995, Thompson *et al.* 1998b). We have fitted these surfaces using locally weighted regression (Cleveland & Devlin 1988) because this makes no assumptions about the form of the relationship between a species' probability of occurrence and the bioclimatic variables. This approach also enables the surface to reflect the often complex interacting effects of the bioclimatic variables upon the species' distribution. This approach also requires an a priori decision as to which variables are to be included in the model. For European species we reasoned that winter cold, seasonal warmth and moisture availability were likely to be the primary determinants of species' distributions; these had already been shown to be important determinants both of individual plant and butterfly species' distributions in the region (Huntley *et al.* 1995, Hill *et al.* 2003) and of the potential broad-scale vegetation cover (Prentice *et al.* 1992). We experimented with alternative variables representing these three constraints, using them in combinations of three or four, in the latter case using two seasonal warmth variables, temperature sum and warmest month temperature. Although a few species were marginally better fitted by some other combination of variables, or by the addition of a fourth variable, the best-fitting model for the majority of species was obtained using the

three variables, coldest month mean temperature, annual temperature sum above 5 °C and the annual ratio of actual to potential evapotranspiration (Huntley *et al.* in press). Model fit was assessed using the area under the curve (AUC) for a receiver operating characteristic plot (Manel *et al.* 2001, Huntley *et al.* 2004), whilst for the purpose of representing the model results as simulations of species presence/absence the optimum threshold probability of occurrence was evaluated as that which optimized the value of Cohen's κ (Cohen 1960, Huntley *et al.* 1995). Models were considered to have a good fit if $AUC \geq 0.9$; 89% of models fitted for European species and 84% for African species achieved this threshold, with > 60% in each case having $AUC \geq 0.95$ (Huntley *et al.* in press, S.G. Willis, Y.C. Collingham, G. Hilton, C. Rahbek & B. Huntley, unpublished).

In the case of Africa, we reasoned that seasonal temperatures and moisture availability were likely to be the primary constraints upon species' distributions. We therefore experimented with combinations of three or four of the variables representing these aspects of the climate (S.G. Willis, Y.C. Collingham, G. Hilton, C. Rahbek & B. Huntley, unpublished). In contrast to the situation in Europe, we found that models using four variables had a better goodness-of-fit for the majority of species (92%) and also that models fitted using warmest month mean temperature to reflect seasonal warmth consistently performed better than those fitted using the annual temperature sum above 5 °C. The best performing models thus consistently used the coldest and warmest month mean temperatures plus the annual ratio of actual to potential evapotranspiration, along with a seasonal moisture availability variable. Which of the latter variables gave the best fitting model, however, varied systematically, with species of the moist and equatorial forest regions generally fitted best by a model using the length or intensity of the wet season, whereas species of the semi-arid and savanna regions were generally best fitted by a model using the length or intensity of the dry season (S.G. Willis, Y.C. Collingham, G. Hilton, C. Rahbek & B. Huntley, unpublished).

For both continents the majority of species gave models with a high goodness-of-fit (Huntley *et al.* in press, S.G. Willis, Y.C. Collingham, G. Hilton, C. Rahbek & B. Huntley, unpublished); species that were not modelled successfully predominantly were those with very few recorded presences, although species restricted to areas of very diverse relief also were poorly modelled because the mean elevations of the grid squares in which they were recorded, and hence

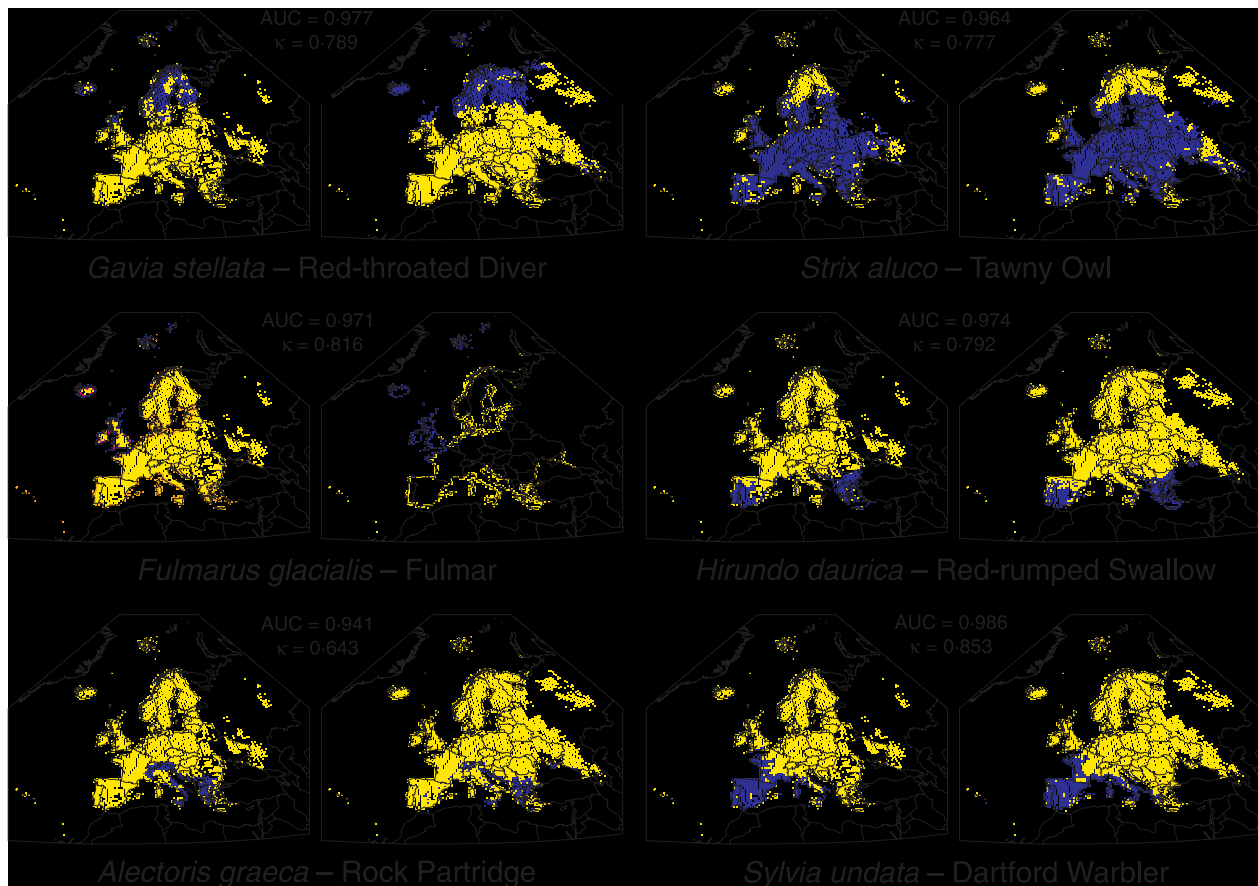


Figure 2. Observed and simulated distributions for six European species. In each case the left-hand map is the observed present breeding distribution as recorded by Hagemeyer & Blair (1997), whilst the right-hand map is the breeding distribution simulated by the species–climate response surface. The model goodness-of-fit is indicated in each case by the values of Cohen's κ and of the area under the curve (AUC) for a receiver operating characteristic plot. The model for *Fulmarus glacialis* was fitted using only coastal grid squares; therefore only presence or absence in such squares is simulated. Blue symbols indicate recorded or simulated presence; yellow symbols indicate recorded or simulated absence; orange symbols on the map of *F. glacialis* indicate the coastal squares from which it is absent and which were included in the model.

the interpolated climate of these grid cells, was extremely variable. Species restricted to coastal breeding sites also were poorly modelled if the entire continental region was used to develop models; such species are absent from many inland grid cells with climates similar to those of the coastal grid cells where they do occur. Very good models could be fitted for the majority of coastal species, however, if data only from coastal grid cells was used. The examples shown in Figs 2 and 3 illustrate the performance of models fitted for European and African species, respectively.

Simulating potential impacts of anthropogenic climatic change

Given a model that successfully simulates a species' present distribution using a limited number of

bioclimatic variables, the potential impacts of any particular scenario of projected future climatic change upon that species' distribution can be simulated. In order to do this, monthly values of the climatic variables must first be interpolated for each grid cell of the mapped area for any particular scenario of projected future climate; these interpolated values then can be used to calculate the projected future values of the bioclimatic variables used in modelling the species' distribution. These values in turn can be used to simulate the species' potential future distribution were it to maintain equilibrium with the projected changed climate.

The procedure for interpolation of the monthly values of the climatic variables that we have adopted is designed to minimize the influence upon the projected future scenario of any biases in the particular

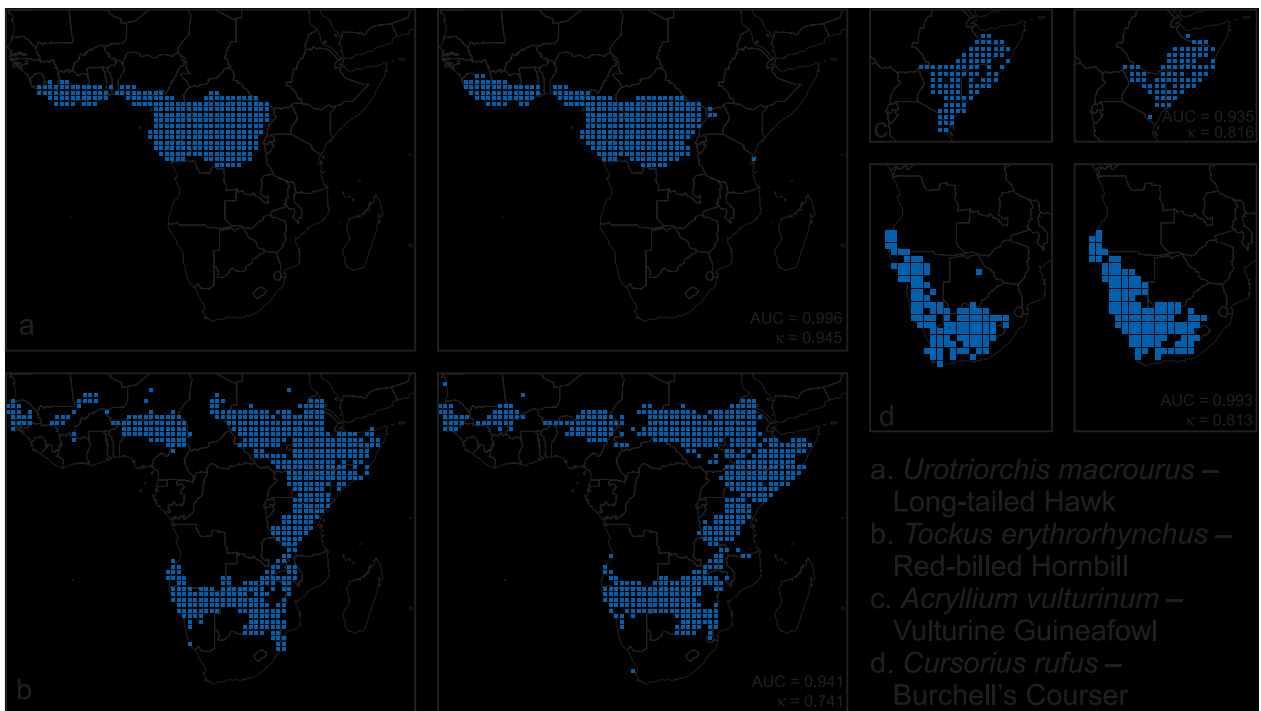


Figure 3. Observed and simulated distributions for four African species. In each case the left-hand map is the observed present distribution as recorded in the Zoological Museum, University of Copenhagen database, whilst the right-hand map is the distribution simulated by the species–climate response surface. The model goodness-of-fit is indicated in each case by the values of Cohen's κ and of the area under the curve (AUC) for a receiver operating characteristic plot. Blue symbols indicate recorded or simulated presence; absence of a symbol indicates a lack of any recorded presence on the maps of observed distributions, assumed to equate to absence, and simulated absence on the maps of simulated distributions.

GCM, whilst also maximizing the retention of information about fine-scale patterns in the present climate that relate to such things as topography, proximity to the coast or the influence of large inland water bodies. For each GCM scenario that we have used we have calculated the mean monthly temperature and precipitation values for the 3-year periods 1961–90 and 2070–99 in the GCM transient simulation for the SRES B2 emissions scenario (Nakicenovic & Swart 2000)¹ for each cell of the GCM grid. We then calculated the anomalies between these two periods, using the difference ($T_{2070-99} - T_{1961-90}$) for the temperature variables and the proportion ($P_{2070-99} \div P_{1961-90}$) for the precipitation variables. Spline surfaces (Hutchinson 1989) were then fitted to

¹The B2 scenario relates to 'a world in which the emphasis is on local solutions to economic, social, and environmental sustainability', in which global population continues to increase, but at a decreasing rate, levels of economic development are intermediate and technological change is diverse. It is a relatively 'optimistic' scenario, resulting in more moderate levels of climatic change than do scenarios closer to 'business as usual'.

describe the variation in the anomaly values for each of the temperature and precipitation variables with respect to longitude and latitude, and these spline surfaces used to interpolate anomaly values for the geographical mid-points of the cells of the grid with respect to which the species' distribution data used in our initial modelling are recorded. These interpolated anomaly values were then either added to (temperature) or multiplied by (precipitation) the values interpolated for these grid cells from the observed climatic data for the period 1961–90 and used to fit the species–climate response surfaces.

We applied this procedure to the output from three separate GCMs selected from the nine included by the IPCC in their ensemble projections (Cubasch *et al.* 2001), namely the HadCM3 (Gordon *et al.* 2000), GFDL_R30_c (Knutson *et al.* 1999, hereafter referred to as GFDL) and ECHAM4/OPYC3 (Roeckner *et al.* 1996, hereafter referred to as ECHAM4) models. These three models were chosen because they all produce projections of global mean warming by 2100 close to *c.* 2.5 °C, the modal value

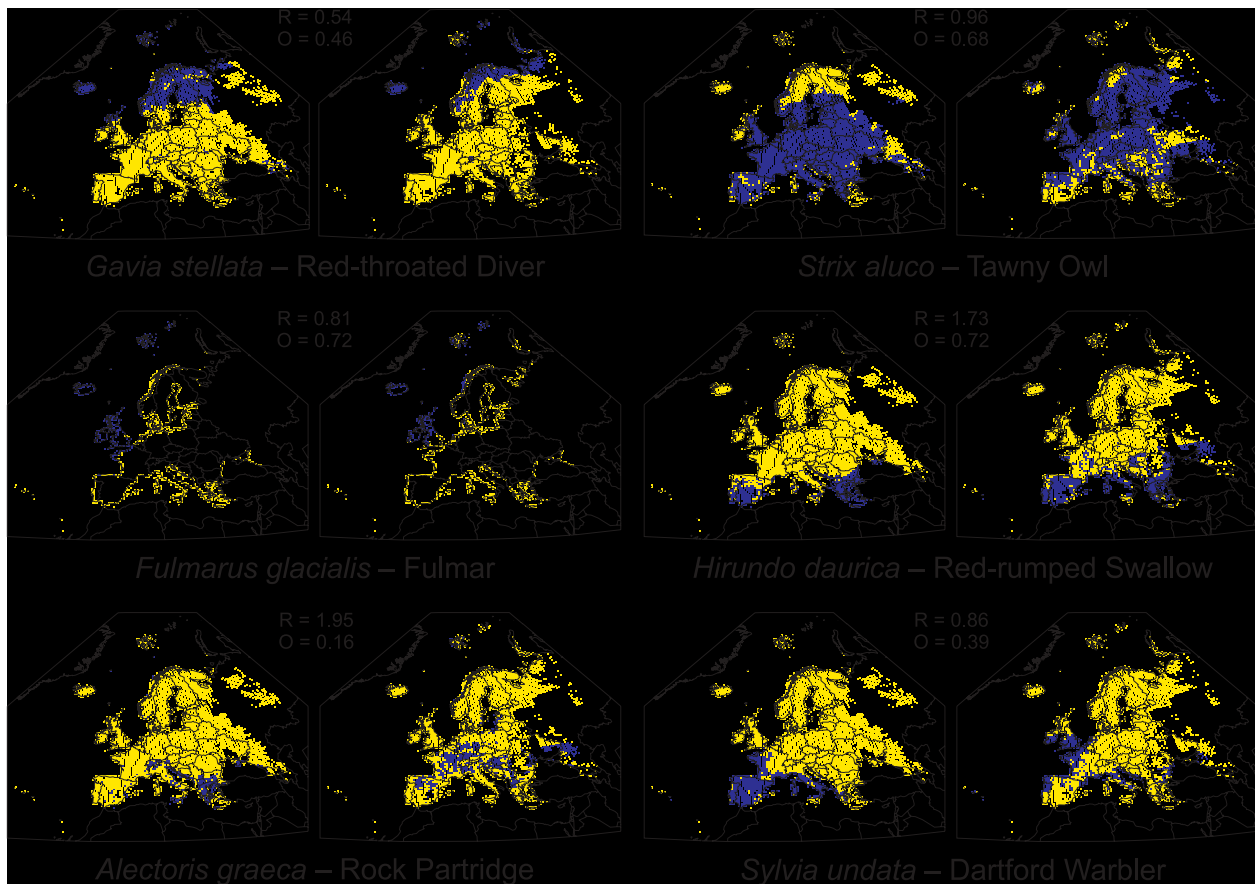


Figure 4. Simulated present and potential future distributions for six European species. In each case the left-hand map is the breeding distribution simulated for the present climate, whilst the right-hand map is the breeding distribution simulated for a potential future climate scenario for 2070–99 derived from the HadCM3 simulation for the SRES B2 emissions scenario. The relative extent of the potential future distribution (R) and the extent of the overlap between the potential future and present distributions (O), both expressed as a proportion of the extent of the species' present distribution, are indicated for each species. Blue symbols indicate simulated presence; yellow symbols indicate simulated absence.

for the nine GCMs included by Cubasch *et al.* (2001), but are representative of the 'dry' (ECHAM4), 'medium' (HadCM3) and 'wet' (GFDL) groups into which the nine models fall with respect to their projections of change in global precipitation by 2100. This contrast with respect to their precipitation projections was considered likely to be particularly important in relation to projections of the potential impacts of future climatic change upon birds in Africa, where seasonal patterns of moisture availability had proved to be important in successfully modelling species' distributions. In practice it turned out that the three scenarios also differed substantially in the magnitude, although not in the general spatial patterns, of the climatic changes that they project for Europe by 2100.

Figures 4 and 5 illustrate the nature and magnitude of the simulated impacts of future climatic change upon the potential distributions of the species, the model fits for which are illustrated in Figs 2 and 3. These examples serve to illustrate the general patterns that we find and that can be summarized as follows. First, the magnitude of the projected climatic change is such that species' potential distributions are shifted substantially, with many European species' range boundaries potentially shifting by 1000 km or more and potential range boundary shifts of more than 500 km also seen amongst African species. Secondly, the rate of the projected climatic change causes the boundaries of species' potential distributions to shift at rates much faster, in many cases faster by more than an order of magnitude,

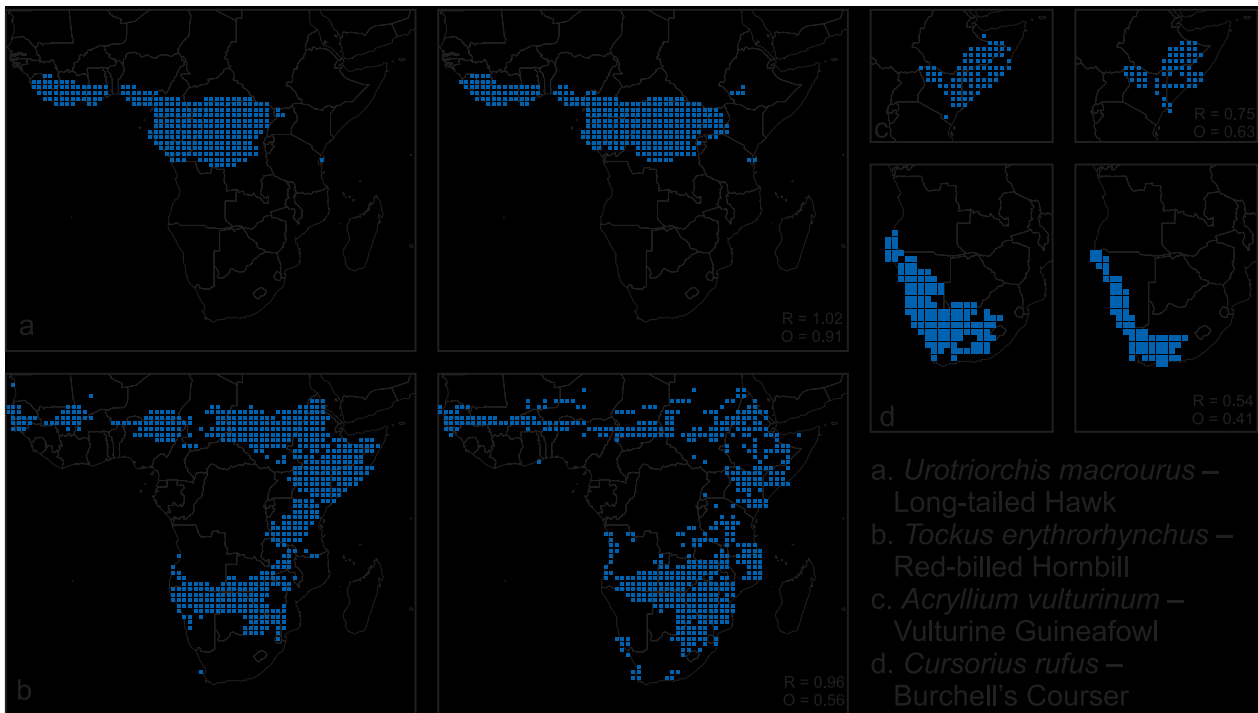


Figure 5. Simulated present and potential future distributions for four African species. In each case the left-hand map is the distribution simulated for the present climate, whilst the right-hand map is the distribution simulated for a potential future climate scenario for 2070–99 derived from the HadCM3 simulation for the SRES B2 emissions scenario. The relative extent of the potential future distribution (R) and the extent of the overlap between the potential future and present distributions (O), both expressed as a proportion of the extent of the species' present distribution, are indicated for each species. Blue symbols indicate simulated presence; absence of a symbol indicates simulated absence.

than the rates of range boundary change observed in the palaeoecological records from the late Quaternary period. The very rapid rates of future potential range boundary shifts are likely to be faster than many species are able to realize such range boundary changes. Finally, the 'destination' reached already by climatic change by the end of the present century, which it must always be remembered would not be the final 'destination' of the climatic change to which the globe would be committed by that time under the B2 scenario, is reflected by a general northward and/or eastward shift of species' potential distributions in Europe: northern species' potentially become even more restricted to high latitudes and/or elevations; southern species in many cases potentially become more extensive; common species of the extensive zone of broad-leaved forests potentially extend their ranges into the Boreal zone at the expense of the species today found exclusively in that zone. Although the situation in Africa is more complex, a number of general patterns do emerge that are reflected by the examples chosen for illus-

tration: Species of southern Africa potentially become more restricted, their distributions contracting towards the Cape; species restricted to the Horn of Africa also potentially become more restricted, their distributions again contracting within that region; species of the semiarid zone, as well as most of those found in East Africa, especially those of montane habitats, potentially become more restricted as many arid areas expand and montane habitats become more restricted or even displaced from lower elevation ranges; species associated primarily with equatorial and moist tropical forest habitats are relatively unaffected, their distributions being potentially little altered.

For Europe we have examined the potential impacts upon the breeding distributions of all those birds that are native to the region as breeding species, doing so for each of the three GCM scenarios (Huntley *et al.* in press). Such a synthesis reveals further general features of the potential impacts upon avian species richness that arise from the potential impacts upon the individual species. First,

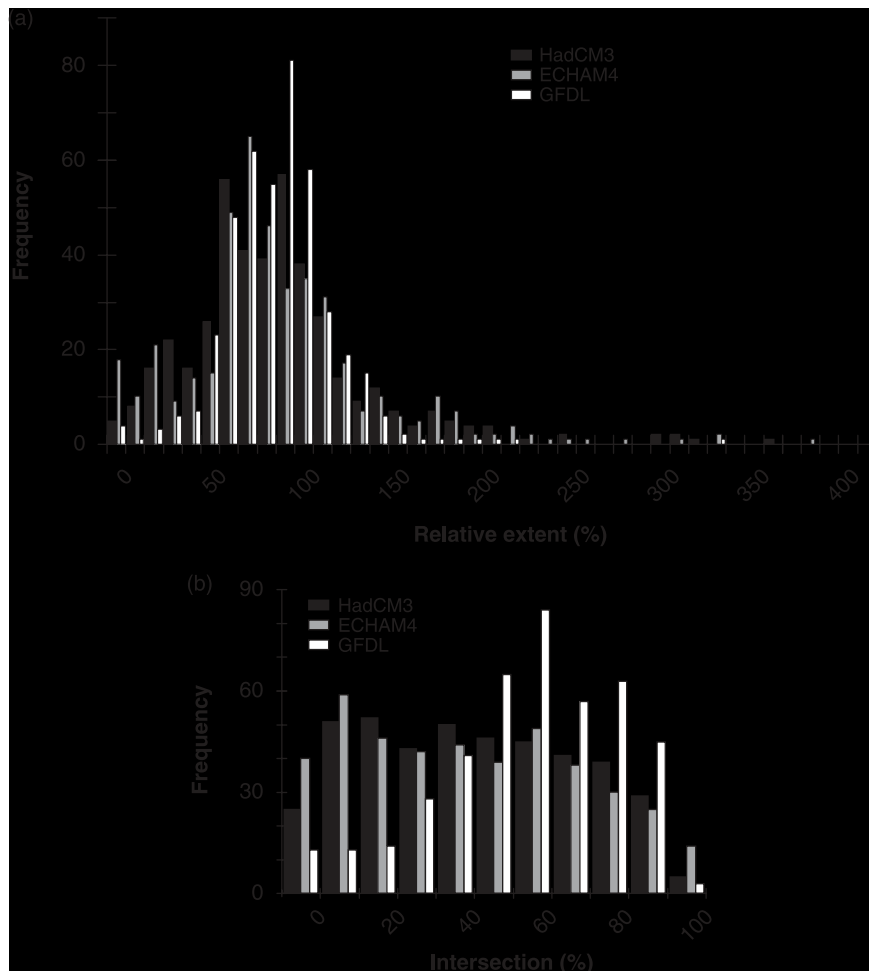


Figure 6. (a) Frequency plot of relative extent of potential future breeding distributions of European birds; (b) Frequency plot of intersection between potential future and present breeding distributions. Relative extent is the extent of the simulated potential future breeding distribution expressed as a percentage of the simulated present breeding distribution; intersection is the percentage of the simulated present breeding distribution that is simulated also to be occupied under the potential future climate scenario.

in addition to being displaced, the potential future distributions of species are on average reduced in extent compared to their present distributions: For the HadCM3 scenario the potential future distribution of 426 European breeding species is on average only 81.1% of the extent of their distributions as simulated for the present climate (81.0% for ECHAM4; 81.4% for GFDL), with the majority of species' potential future distribution being between 50% and 80% of the extent of their present distribution (Fig. 6a). Secondly, the extent of the potential displacement of species' distributions is such that the overlap between their potential future distribution for the HadCM3 scenario and that simulated for the present climate is on average only 39.7% of

the extent of their present distribution (37.9% for ECHAM4; 52.8% for GFDL), with a greater number of species having no potential overlap than having an overlap > 90% (Fig. 6b). As a consequence of the potential spatial displacement of species' distributions the area of highest avian species richness, expressed as the number of species potentially breeding in an individual c. 50 km grid cell, potentially shifts north-eastwards (Fig. 7). In parallel with this, and as a result of the overall average reduction in the extent of individual species' distributions, the overall average avian species richness is reduced by 8.6% for the HADCM3 scenario even if we make the optimistic assumption that all species fully realize their potential changes in distribution; if we make the pessimistic

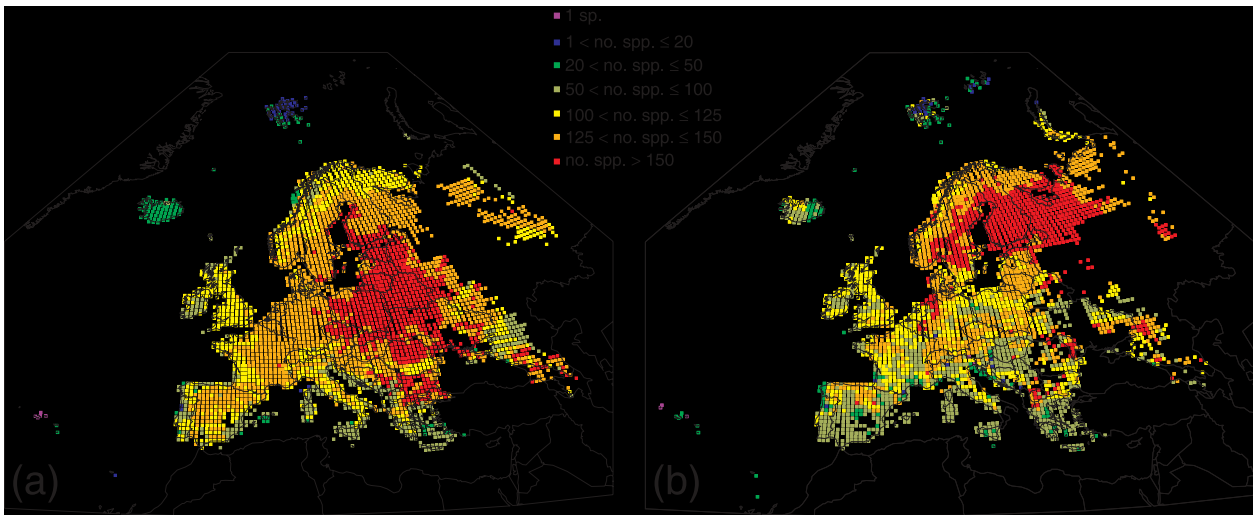


Figure 7. Simulated present and potential future diversity of European breeding birds. The left-hand map (a) shows the number of species simulated breeding in each grid square for the present climate, whilst the right-hand map (b) shows the number of species simulated as potentially breeding in each grid square for a potential future climate scenario for 2070–99 derived from the HadCM3 simulation for the SRES B2 emissions scenario.

assumption that species persist only in the area of intersection between their present and potential future distributions, where suitable climatic conditions persist, then the overall average species richness declines to 60% of its present value (Huntley *et al.* in press). Although this analysis does not take into account the potential for species found today in North Africa to extend their range into southern Europe in response to the potential future climatic changes, an examination of the numbers of species involved, and their ecological characteristics, suggests that they will not alter the general pattern of declining species richness in southern Europe (Huntley *et al.* in press).

The general pattern of reduction in the extent of species' distributions also has implications with respect to a general increase in the threat of extinction faced by species, especially those of more restricted distribution and those endemic or near-endemic to Europe (Thomas *et al.* 2004). Those species at greatest risk of regional extinction throughout Europe are those 19 species that have zero potential future distribution extent for at least one future climate scenario, with a further 10 species that have potential future distribution extents $\leq 10\%$ of their present distribution for at least one future climate scenario only marginally less threatened, although none of these 29 species is endemic or near-endemic to Europe. However, those species that have zero or only a small overlap between their potential future and

present distributions also are potentially threatened. If a species is prevented from realizing an expansion into newly climatically suitable geographical areas, but is at the same time unable to persist in areas of its present distribution that are no longer within the range of climatic conditions that it currently occupies, then it may only persist in that part of its potential future distribution that overlaps its present distribution. Such species might be unable to realize an expansion into newly climatically suitable geographical areas for a number of reasons, including: geographical isolation of the newly climatically suitable area from the present distribution; ecosystem inertia, especially in the vegetation component of ecosystems, resulting in the absence of suitable habitat or prey in the newly climatically suitable area; limited dispersal capabilities coupled to habitat fragmentation and isolation of habitat patches, especially in heavily anthropogenically altered landscapes such as prevail already across much of Europe and are projected to extend across most of sub-Saharan Africa by the end of the present century (IMAGE Team 2001). Of the European species modelled, 11 have zero overlap between their potential future and present distributions in Europe for all three future climate scenarios explored; these include the endemic *Loxia scotica* (Scottish Crossbill) that thus must be considered to be at extreme risk of global extinction as a result of climatic change. A further 33 species have zero overlap for at least one of the three future

climate scenarios examined; these again include endemic species, *Aquila adalberti* (Spanish Imperial Eagle) and *Sylvia sarda* (Marmora's Warbler), that thus also must be considered to be at high risk of global extinction as a result of climatic change. Turning to those species with non-zero but small overlaps between the potential future and present distributions, 65 additional species have overlaps of $\leq 10\%$ of the extent of their present distribution for at least one of the three future climate scenarios explored. This group too includes species endemic to Europe, amongst them being *Alectoris graeca* (Rock Partridge), *Cyanopica cyanus* (Azure-winged Magpie), *Passer × italiae* (Italian Sparrow) and *Serinus citrinella* (Citril Finch), all of which must be considered to be at heightened risk of global extinction as a result of climatic change. In total, c. 25% of the species breeding in Europe today have potential future distributions, or overlaps between their potential future and present distributions, that are $\leq 10\%$ of the extent of their present distributions; all of these species must face increased threat as a result of climatic change. Further details, including lists of all these species and discussion of each, are given in Huntley *et al.* in press).

Finally, although they have not yet been modelled in full, it can be predicted that the impacts upon migratory species are likely to be even more severe than those upon resident species. This may at first seem counter-intuitive, given the ability of migrant species to shift their areas of distribution with the seasons, and the ability of many migrants to traverse large areas of unsuitable habitat or to make substantial sea crossings. However, migrant species suffer all of the same potential impacts upon the location and extent of their breeding distribution as residents, whilst also suffering similar potential impacts upon the location and extent of their non-breeding distribution. In addition, many migrant species are critically dependent upon stopover sites used to 're-fuel' during migration; such sites will also be impacted by climatic change, including the consequent sea-level rises, in many cases potentially being altered so that they are no longer usable by migrants as stopovers. In the case of trans-Saharan, and especially trans-equatorial migrants that breed in Europe, our modelling of potential impacts of climatic change upon African birds, coupled to the simulated potential impacts upon their European breeding distributions, leads us to expect the overall distance that many species will be required to cover between their breeding and non-breeding distributions to be increased. This

is likely to have serious implications for at least some species in terms of their physiological capacity for migratory flight: If this is coupled with the loss of a critical stopover site the results for a species might be catastrophic. In the case of many Arctic breeding shorebirds and waterfowl, they will face reductions in the extent of their breeding distributions, and increased migration distances from their present nonbreeding areas as their breeding distributions are displaced polewards. Some, of course, may be able to winter in more northerly sites as a result of climatic change; others, however, that at present winter in the southern hemisphere, are likely to face considerable increases in their migration distances if their wintering distribution also is shifted to higher southern latitudes. Many of these species also depend upon coastal wetland sites, either as areas of non-breeding distribution or as critical stopover sites; these wetlands are likely to be at risk from projected sea-level rise (IPCC 2001), as well as from projected climatic change, adding further to the future threats to these species (Rehfishch & Crick 2003).

CONCLUSIONS

Given the accumulating evidence of recent climatic changes, and of the contribution of anthropogenically increased atmospheric concentrations of greenhouse gases to these changes (Tett *et al.* 1999, Stott *et al.* 2000), and given also the continuing emissions of greenhouse gases to the atmosphere by humankind, some degree of further climatic change is inevitable. Even if the internationally agreed target of limiting global mean warming to no more than 2 °C (Grubb *et al.* 1993) is achieved, this will result in conditions at least as warm, probably warmer, than at any time during the Quaternary, and probably for several million years. As a result it is imperative that conservation strategies, that at present are to a very large extent framed against a paradigm of a 'static' world, be adapted to this 'dynamic' world. This has a number of implications. Firstly, whilst the present network of protected areas will continue to be a necessary part of these strategies, reliance upon these alone will not be sufficient. It will be necessary to ensure that species are afforded protection wherever they shift to in response to climatic change, including the majority of the landscape that is not and will not be within protected areas. It also is essential and urgent that steps be taken to render the landscape, especially in areas that are heavily anthropogenically altered, more 'permeable' to species that are

attempting to respond to climatic change by adjusting their distributions to the new conditions. This means ensuring that patches of a diverse range of seminatural habitats – including woodlands, heathlands, wetlands and bodies of freshwater – are retained within the landscape where they exist already, or are created where they do not. It is unlikely to be necessary for the majority of species that areas of suitable habitat are continuous across the landscape in the form often envisaged as ‘corridors’, but they will require ‘stepping stones’ that are sufficiently close together that they lie within the species’ normal dispersal capability and thus readily can be reached. The importance of such a ‘fine-grained’ landscape, and of the availability of suitable habitat patches, to sustain distribution responses to changing environmental conditions has been demonstrated using models of the dispersal process that underpins these responses (Collingham *et al.* 1996, Collingham & Huntley 2000, Hill *et al.* 2001). Finally, the basis upon which protected areas initially are identified and, more importantly, upon which their protected status is or is not maintained, must be fundamentally revised. Many current protected areas have achieved their status because of the presence of particular rare or threatened species. Following climatic change, that has been predicted to result in > 40% of the global land area no longer experiencing climatic conditions sufficiently similar to maintain ecosystems of the same biome as that by which they are currently occupied (Alcamo & Kreileman 1996), a large proportion of protected sites are unlikely any longer to harbour the species that led to their designation (S.G. Willis, Y.C. Collingham, G. Hilton, C. Rahbeck & B. Huntley, unpublished). This must not be seen as a basis for removing protection from these areas; they may have lost some species but they will have gained others, and as extensive areas of natural or seminatural habitats, they will be extremely important nodes in the overall network of sites essential if some reasonable fraction of global biodiversity is to be conserved as climate changes. In addition, in selecting new sites to add to this network of protected areas, consideration should be given to including sites that offer a diverse range of physical habitats, even if they do not at present harbour any rare or threatened species; such sites offer the greatest scope to sustain a wide diversity of species (Hunter *et al.* 1988). Given the great uncertainty that prevails about exactly what the magnitude and character of future climatic changes will be, such sites represent an important insurance or ‘bet hedging’ component

of future biodiversity strategies. We may not be able to predict for which particular species they will prove to be important, but their inherent physical diversity increases the probability that they will be of importance for at least some rare or threatened species. Of course, we also must ensure that less common physical habitat types, especially wetlands, continue to be protected, and should aim to increase the number of such sites within the protected area network.

Although such adaptation of conservation strategies to the new circumstances of climatic change is urgent and essential, it also is imperative that measures are adopted to limit climatic change. If greenhouse gas emissions continue unabated throughout this century, then not only will climatic change by 2100 inevitably be of greater magnitude than the target of no more than 2 °C warming (IPCC 2001) but climatic change will continue far into the future, reaching an eventual equilibrium that may threaten not just a large component of global biodiversity, but potentially also the integrity of ecosystems and of the services that they provide, and upon which human society is fundamentally dependent. It is thus necessary that steps be taken globally to reduce human activities that lead to increased greenhouse gas levels in the atmosphere, especially the use of fossil fuels in ways that release carbon dioxide to the atmosphere. Energy will inevitably continue to be required, but there is great scope to improve the efficiency with which energy is used, as well as to adopt a diverse range of renewable energy sources that do not contribute to climatic change and that also do not in themselves pose other threats to the environment, for example contamination by radionuclides. On- and off-shore wind turbines, water turbines driven by tidewater flows, biofuels, biomass crops and photovoltaics will all have a role to play. If the impacts of climatic change upon birds and other components of global biodiversity are not to become catastrophic before the end of the present century, then available renewable energy technologies must be adopted as a matter of urgency, whilst other alternatives to carbon-based fuels must be researched for adoption in the longer term.

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