

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

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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; Araújo 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 tropic 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):

$$T_{\min} = 0.006T_C^2 + 1.316T_C - 2.19,$$

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):

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

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.metu.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 bioclimate 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 50×50 km grid. For each bioclimatic variable, we computed the mean value of all $10'$ grid pixels within the quadrature 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:

$$\text{CCSR} = (\text{new_suit} - \text{curr_suit})/\text{curr_suit},$$

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 $0.84 \pm \text{SE } 0.01$ (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. $\text{AUC} > 0.7$) 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 $-0.04 \pm \text{SE } 0.05$) for the B1 scenario and between -1 and 2.46 (mean $-0.05 \pm \text{SE } 0.07$) 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 $-0.50 \pm \text{SE } 0.03$) 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

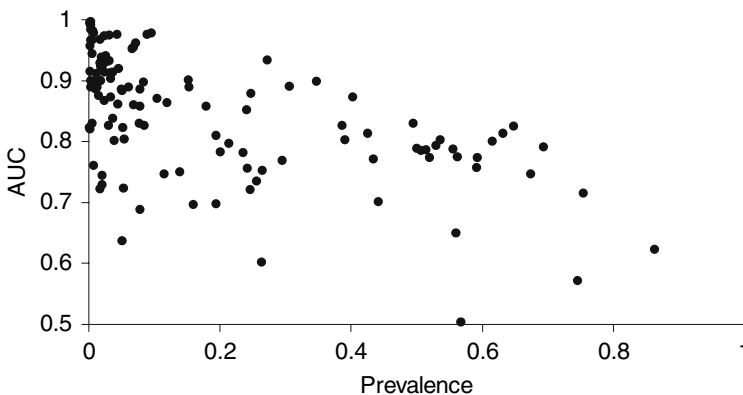


Fig. 1 Area-Under-the-Curve (AUC) values for a plot of sensitivity against 1-specificity for all 120 native, non-volant terrestrial mammals, plotted against prevalence

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

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

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

^E endemic

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)

		Ex	CE	En	Vu	LR	Gain
(a)							
Overall	B1	1 (0.9)	5 (4.5)	11 (9.9)	19 (17.1)	36 (32.4)	39 (35.1)
	A2	1 (0.9)	12 (10.8)	6 (5.4)	33 (29.7)	22 (19.8)	37 (33.3)
Endemic	B1	1 (2.5)	0 (0.0)	6 (15.0)	5 (12.5)	9 (22.5)	19 (47.5)
	A2	1 (2.5)	3 (7.5)	4 (10.0)	6 (15.0)	8 (20.0)	18 (45.0)
>100 quadrates	B1	0 (0.0)	0 (0.0)	7 (10.9)	14 (21.9)	28 (43.8)	15 (23.4)
	A2	0 (0.0)	5 (7.8)	1 (1.6)	27 (42.2)	15 (23.4)	16 (25.0)
(b)							
Overall	B1	6 (5.4)	12 (10.8)	34 (30.6)	32 (28.8)	26 (23.4)	1 (0.9)
	A2	10 (9.0)	28 (25.2)	35 (31.5)	24 (21.6)	13 (11.7)	1 (0.9)
Endemic	B1	2 (5.0)	5 (12.5)	19 (47.5)	11 (27.5)	3 (7.5)	0 (0.0)
	A2	5 (12.5)	19 (47.5)	12 (30.0)	2 (5.0)	2 (5.0)	0 (0.0)
>100 quadrates	B1	0 (0.0)	2 (3.1)	13 (20.3)	24 (37.5)	24 (37.5)	1 (1.6)
	A2	0 (0.0)	10 (15.6)	18 (28.1)	23 (35.9)	12 (18.8)	1 (1.6)

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

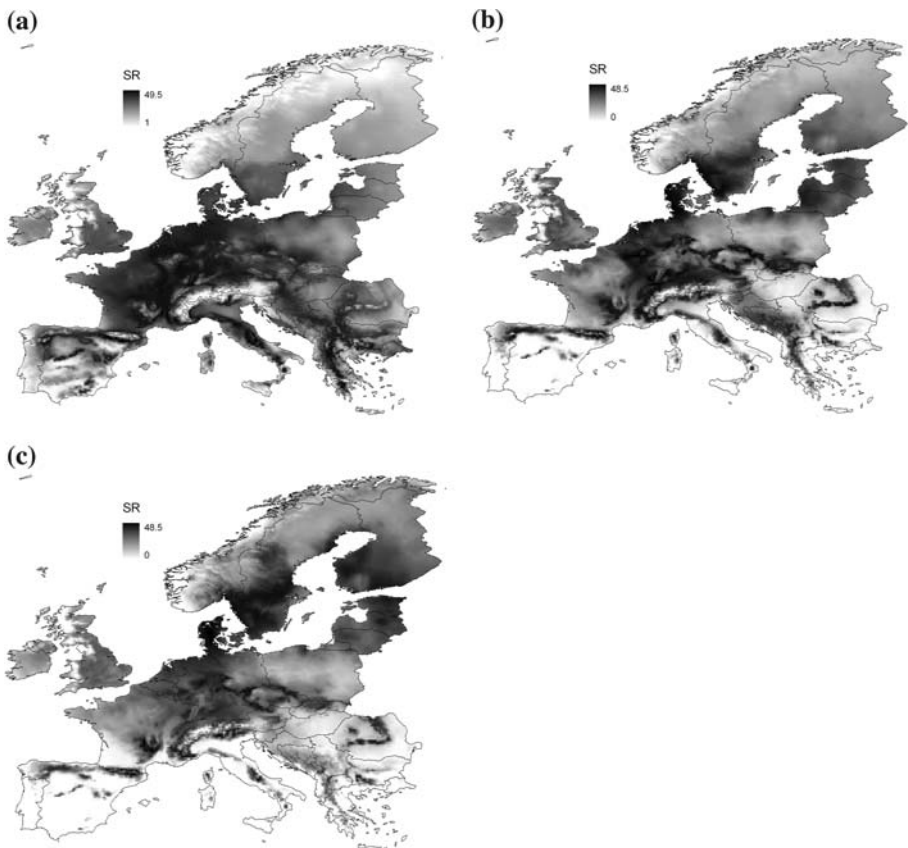


Fig. 2 Modelled potential species richness in Europe at a 10' resolution. Current (a) and future species richness under the mild climatic scenario, B1 (b), and the severe climatic scenario, A2 (c)

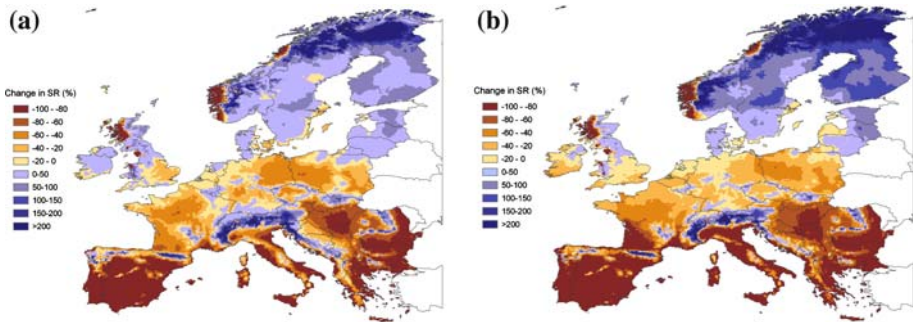


Fig. 3 Modelled changes in mammalian species richness in percentage, under the mild climatic scenario, B1 (a), and severe climatic scenario, A2 (b), in a $10' \times 10'$ resolution

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

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 led 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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