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Predicted impact of climate change on European bats in relation to their biogeographic patterns

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Abstract

There has been considerable recent interest concerning the impact of climate change on a wide range of taxa. However, little is known about how the biogeographic affinities of taxa may affect their responses to these impacts. Our main aim was to study how predicted climate change will affect the distribution of 28 European bat species grouped by their biogeographic patterns as determined by a spatial Principal Component Analysis. Using presence-only modelling techniques and climatic data (minimum temperature, average temperature, precipitation, humidity and daily temperature range) for four different climate change scenarios (IPCC scenarios ranging from the most extreme A1FI, A2, B2 to the least severe, B1), we predict the potential geographic distribution of bat species in Europe grouped according to their biogeographic patterns for the years 2020–2030, 2050–2060 and 2090–2100. Biogeographic patterns exert a great influence on a species' response to climate change. Bat species more associated with colder climates, hence northern latitudes, could be more severely affected with some extinctions predicted by the end of the century. The Mediterranean and Temperate groups seem to be more tolerant of temperature increases, however, their projections varied considerably under different climate change scenarios. Scenario A1FI was clearly the most detrimental for European bat diversity, with several extinctions and declines in occupied area predicted for several species. The B scenarios were less damaging and even predicted that some species could increase their geographical ranges. However, all models only took into account climatic envelopes whereas available habitat and species interactions will also probably play an important role in delimiting future distribution patterns. The models may therefore generate 'best case' predictions about future changes in the distribution of European bats.

Keywords: bats, bioclimatic envelope, climate change, Europe, maximum entropy models, spatial PCA, species distributions

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Introduction

During this first decade of the 21st century, climate change has become a frequently discussed issue, with coverage ranging from the more general media to more specialized scientific publications. A number of species have already been affected by recent climate change, with effects on phenology, geographical range or even local survival documented (Pounds *et al*., 1999; Parmesan & Yohe, 2003; Root *et al*., 2003; Sanz *et al*., 2003; McMahon & Burton, 2005). Recent studies have focused on the potential impact of climate change on global biodiversity (Araújo & Rahbek, 2006), raising great concerns over the future of a range of animal (Araújo *et al*., 2006; Huntley *et al*., 2008) and plant species (McLachlan *et al*., 2005; Kirilenko & Sedjo, 2007).

One of the major impacts of climate change may be the movement of populations from their original locations to new and unoccupied areas. In this process, local extinctions may occur and populations may become highly fragmented (Thomas *et al*., 2004). If these

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situations persist over long periods of time, it is likely that other conservation issues may arise. The extinction of species in their glacial refugia and their survival in unconnected populations may cause depletion of genetic variability and high levels of inbreeding (Ezard & Travis, 2006), thus also compromising the survival of those remaining populations.

When studying species' responses to future climate change, it is important to model several future scenarios, in order to cover how each species responds to a range of climate change projections (Araújo *et al*., 2006; Beaumont *et al*., 2007). The Intergovernmental Panel on Climate Change (IPCC) has developed a set of climate change scenarios that include a wide variety of possible socio-economic projections (Nakicenovic & Swart, 2000). 'Worst case' scenarios generate more severe projections, with annual average temperatures rising up to 5.8 °C by the end of the century in some regions, while other scenarios are less severe. None predicts a decrease in average temperature in comparison with present conditions.

Bioclimatic modelling is the primary tool used when simulating climate change projections (Beaumont *et al*., 2007). Climate envelopes represent the ecological conditions a species requires for its survival without taking into account any biotic interactions, such as competition with other species or other individuals, predation, and changes in food availability (Thomas *et al*., 2004). Several methods have already been developed and assayed to predict distributions under different climates, such as using Pleistocene data to build models for current distribution (Martínez-Meyer *et al*., 2004; Hijmans & Graham, 2006). However, it is usual for future climate change studies to cluster their results by taxa (Araújo *et al*., 2006) or species are simply grouped into a single dataset (Thomas *et al*., 2004). This may result in great variability in the output models, because species with different biogeographical origins may have different responses to climate change. Consequently, when building species richness models we may not detect relevant conservation problems for biogeographic groups that are less representative of the taxa of interest. Furthermore, because mammals are very diverse in terms of body size, morphology and ecology they are not expected to react to climate change in a uniform manner (Scheel *et al*., 1996).

In this study, we focused on the response of 28 European bat species to climate change. Bats constitute one the most diverse mammal groups in Europe yet many species are also threatened (Mitchell-Jones *et al*., 1999). Their diversity comprises several biogeographic groups (Horáček *et al*., 2000) with a widespread distribution in Europe, covering all the major biomes from the warmer Mediterranean to the colder Boreal and Alpine regions. Despite their diversity and wide distribution, bat responses to climate change have been little studied although Burns *et al*. (2003) predicted that bats could be among the taxa most affected by climate change in the United States.

The main aim of this study was to categorize bats into biogeographic groups that currently occupy similar climatic conditions and to predict the response of each biogeographic group to a range of projected climate change scenarios until the end of the 21st century. To achieve these aims, we investigated the impact of climate change on the spatial patterns of species richness for each biogeographic group using bioclimatic envelopes to build predictive models and determined the range shift from their current distribution to their future potential occupied areas.

Methods

Study area

The study area included all of mainland Europe (west of Caucasus), United Kingdom and Ireland, all major Mediterranean islands and part of north Africa, covering land between the coordinates 71°31′N; 33°30′N; 10°45′W; 45°33′E. The study area therefore included the geographical range of all European near-endemic bat species (Mitchell-Jones *et al*., 1999), as well as the range of the most common European species. Europe's climate can be characterized overall as temperate although considerable variations exist, with a Mediterranean climate dominating in the south (with hot summers and mild winters) whereas in the north and in mountainous regions the climate is considerably colder and more humid (Huntley *et al*., 2007).

Species data, climatic variables, future scenarios and spatial conversion

All presence data were obtained from Mitchell-Jones *et al*. (1999) available at the European Environment Agency website (http://eunis.eea.europa.eu). Several cryptic species have been discovered more recently (Barratt *et al*., 1997; Mayer & Helversen, 2001; Ibañez *et al*., 2006; Mayer *et al*., 2007), although data from these species were not included here because their distributions are still poorly understood. In total, 28 bat species were considered for study, assuming a uniform distributional confidence for all of them. Species presence data varied between 71 known locations for *Nyctalus lasiopterus* and 1098 for *Myotis daubentonii* (average 522 ± 322 locations), covering the majority of each species' known distribution in Europe.

Five climatic variables [average temperature (°C), minimum temperature (°C), daily temperature range (°C), relative humidity (%) and monthly precipitation (mm month^{-1})] were chosen to model future bat distribution for four time periods: 1961–1991 (representing present climate), 2020–2030, 2050–2060 and 2090–2100. These variables were downloaded for four IPCC future scenarios as follows. A1FI (where FI stands for fossil fuel intensive) represents a globalized world with intensive economic growth sustained by the intensive use of fossil fuel; the scenario A2 is also driven by economic growth although at regional scale, creating a diversified political and social world; the B1 scenario is clearly the 'greenest' of all projections, with high levels of environmental and social consciousness and a global sustained development; B2 is the 'mixed green bag' scenario, with only a regional steady growth and social awareness (Nakicenovic & Swart, 2000).

For spatial conversion of climatic data, two datasets with monthly data in a compressed format were downloaded from the Tyndall centre (Mitchell *et al.*, 2004): the historical climate dataset (CRU TS 2.1 – http://www.cru.uea.ac.uk/ ~ timm/grid/CRU_TS_2_1.html) spanning from 1901 to 2002 and the future climate dataset (TYN SC 2.0 – http://www.cru.uea.ac.uk/ ~ timm/grid/TYN_SC_2_0.html) with climate prediction grids from 2001 to 2100, both with a resolution of 0.5° (~ 55 km) meaning that we had a total of 5965 cells for the study area. The final map for each variable and scenario is the result of averaging the monthly grids of each analyzed period into a single map.

All operations were automated with a script made in Python programming language and incorporated as a toolbox in ARCGIS 9.2 (ESRI, Redlands, CA, USA).

Determination of bat biogeographic groups

In order to determine bioclimatic regions occupied by assemblages of bat species a spatial principal components analysis (sPCA) was calculated using current climatic variables, where each pixel in the map was the dependent variable and climatic values constituted the independent variables (Sillero *et al.*, 2009). First, we chose which variables to include in the sPCA through analysis of their correlation matrix to avoid multicolinearities. Afterwards, each pixel was scored from the obtained sPCA components (or axis) and was represented in a composite map where each chosen component had a RGB colour (available as supporting information, Fig. S1). Consequently the colour of each pixel was a representation of the vectorial location within the sPCA. Additionally, species' locations were intersected with the previous composite map and obtained values of the sPCA axes were then used to calculate a PCA for the 28 bat species in study and subsequently determine biogeographic group for each species. All subsequent modelling and projections were done using this biogeographic grouping of species. All spatial and geographical statistics were done in ARCGIS 9.2 using the PCA extension in the toolbox. The PCA for the 28 bat species was calculated in SPSS v15.0 (SPSS Inc., Chicago, IL, USA).

Modelling procedure and testing

We chose to model using a presence-only technique since we do not have reliable absence data and the elusive and nocturnal behaviour of bats adds even more uncertainty to absences. We used a maximum entropy modelling technique (MAXENT 3.2.1; http://www.cs.princeton.edu/ ~ schapire/maxent) that seems to have very good performance when compared with other methods (Elith *et al.*, 2006) for past, present and future conditions, even when sample size is low (Elith *et al.*, 2006; Hijmans & Graham, 2006; Martínez-Freiría *et al.*, 2008). MAXENT is a machine-learning process that uses a statistical mechanics approach and estimates the range of a species by finding the maximum entropy distribution (i.e. closest to the uniform) given the constraint that the expected value for each variable closely matches the empirical average of the set of occurrence data (Phillips *et al.*, 2006).

Models were run in autofeatures with a maximum of 1000 iterations and were tested with receiver operated characteristics (ROC) plots to evaluate their predictive ability. The area under curve (AUC) of the ROC analysis provides a single measure of model performance (Liu *et al.*, 2005) and ranges from 0.5 (randomness) to 1 (perfect discrimination), where a score higher than 0.7 is considered a good model performance (Fielding & Bell, 1997). Seventy-five percent of the presence data was randomly chosen to train the models while the remaining 25% was used to test them. We calculated the average value of AUC for all species within each biogeographic group as well as their maximum and minimum values. In addition, the percentage of each variable's contribution to the model was determined.

Combining different species models and thresholds definition

The output maps from MAXENT classify each pixel with a probability of occurrence between 0 and 1. The threshold value above which the species is considered present was selected in the ROC plot as the point where the sum of sensitivity and specificity is maximized (Liu *et al.*, 2005). Afterwards, according to these thresholds all maps were reclassified to display areas of probable presence and absence for the species. Subsequently, the binary maps from each species' biogeographic group were added, thus producing species richness maps for each modelled scenario and time period. All analysis was carried out in ARCGIS 9.2.

Analysis of each biogeographic group's occupied area

In order to determine if predicted suitable areas in the future would increase or decrease in relation to current potential areas, we calculated the ratio between each future projection and the present potential occupied area and converted this ratio into a percentage of variation in relation to the latter value. Similarly, we wanted to know if in the future projections bats would still occupy their present distribution. For this we calculated the proportion of projected suitable area that overlapped with the current distribution. Results were then averaged for each biogeographic group and scenario with maximum and minimum values also determined. We also used Mann–Whitney *U*-tests to check if the predicted areas occupied in the future that overlapped with the present distribution varied significantly among the biogeographic groups.

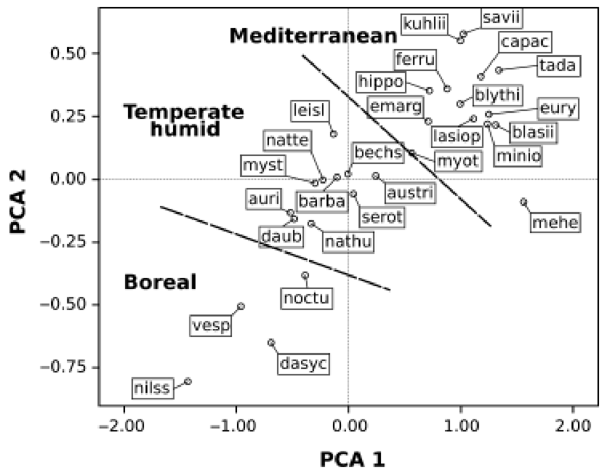

Fig. 1 PCA plot of the 28 bat species in study using the same three climatic variables as in the sPCA (see Suplementary material S.1). The dashed lines separate each biogeographic group. *Rhinolophus blasii*: blasii; *Rhinolophus euryale*: eury; *Rhinolophus ferrumequinum*: ferru; *Rhinolophus hipposideros*: hippo; *Rhinolophus mehelyi*: mehe; *Myotis bechsteinii*: bechs; *Myotis blythii*: blythi; *Myotis capaccinii*: capac; *Myotis dasycneme*: dasyc; *Myotis daubentonii*: daub; *Myotis emarginatus*: emarg; *Myotis myotis*: myot; *Myotis mystacinus*: myst; *Myotis nattereri*: natte; *Pipistrellus kuhlii*: kuhlii; *Pipistrellus nathusii*: nathu; *Hypsugo savii*: savii; *Nyctalus lasiopterus*: lasiop; *Nyctalus leisleri*: leisl; *Nyctalus noctula*: noctu; *Eptesicus nilssonii*: nilss; *Eptesicus serotinus*: serot; *Vespertilio murinus*: vesp; *Barbastella barbastellus*: barba; *Plecotus auritus*: auri; *Plecotus austriacus*: austri; *Miniopterus schreibersii*: minio; *Tadarida teniotis*: tada.

Results

Determination of biogeographic groups

The sPCA was calculated using three climatic variables: average temperature, daily temperature range and precipitation (PCA matrix available as Table S1). The other two climatic variables were not included in this analysis because they were highly correlated with the other variables used (correlation matrix values higher than 0.9 between relative humidity and precipitation and between minimum temperature and daily temperature range) and explained less of the variation than the input variables with which they were correlated.

We produced a map (available as Fig. S1) that combined two sPCA components (with 93.67% of cumulated variance explained, first axis score = 1.8 and second axis score = 1.01). A PCA was then plotted for the 28 bat species under study by intercepting each species' distribution with the sPCA axes (Fig. 1). In this plot we can distinguish the three biogeographic groups that can be linked to the bioclimatic regions identified in the sPCA map (available as Supplementary data S.1). We can group four species in the Boreal biogeographic zone, 10 in the Temperate Humid Zone (hereafter called Temperate) and 14 in the Mediterranean (Fig. 1).

Predictive modelling, validation and testing

ROC plots exhibited very similar AUC values between training and test data although values were slightly lower for the latter (Table 1). Moreover, all AUC values (including registered minimums) show that the models had a very good predictive power with AUC values always higher than 0.79.

Analysis of variable importance

The most relevant variables for the three biogeographic groups were different, hence ecological factors limiting bat distribution differed for each group (Table 1). There is some variability within the Boreal group but, overall, average temperature and relative humidity were the most relevant variables for modelling the distribution of this group as well as minimum temperature. The Temperate group had the greatest variability of all biogeographic groups. Nevertheless, minimum temperature and relative humidity had the greatest importance while average temperature and monthly precipitation seem also important for some of these bats. For the

Mediterranean biogeographic group, average temperature, relative humidity and monthly precipitation were the most important factors limiting distribution, while minimum temperature (which was very important for the other two groups) had no relevance for delimiting the distribution of these bats.

Determination of bat diversity hot-spots from present to 2100

Currently, the highest species richness of bats in Europe is mainly located in the peninsulas of southern Europe and in southern France (Fig. 2a). Species richness within the Boreal group is concentrated in the northeast of Europe with species from this group being almost absent from southern Europe (Fig. 2b). Species richness in the Temperate group is clearly focused in central Europe and the United Kingdom, although high levels of richness also occur in the northern areas of the peninsulas in southern Europe (Fig. 2c). Despite not being the most species-rich group, the Temperate group is clearly the most widespread group, occupying the greatest area in Europe. As expected, the Mediterranean group had the highest species richness in the southern European peninsulas and in north Africa (Fig. 2d). This group had the largest number of species

Table 1 Average (minimum–maximum) percentage contribution of each variable for the predictive modelling in each biogeographic group and average (minimum–maximum) training and test area under the curve (AUC)

	Boreal	Temperate	Mediterranean
Daily temperature range (°C)	7.75 (5.59–9.7)	7.59 (5.48–10.11)	5.8 (3.76–8.42)
Average temperature (°C)	**33.98** (22.13–47.21)	**18.39** (11.07–27.29)	**24.59** (19.1–30.16)
Minimum temperature (°C)	**19.61** (8.07–31.63)	**24.84** (16.35–33.01)	4.82 (2.62–7.22)
Monthly precipitation (mm)	13.2 (11.54–15.09)	**21.9** (19.04–24.67)	**18.99** (16.44–22.02)
Relative humidity (%)	**25.47** (20.92–31.62)	**28.27** (23.07–34.82)	**45.79** (40.43–51.86)
Training AUC	0.86 (0.83–0.92)	0.84 (0.8–0.91)	0.9 (0.84–0.95)
Testing AUC	0.83 (0.77–0.91)	0.83 (0.79–0.91)	0.88 (0.8–0.94)

Most important variables are in bold.

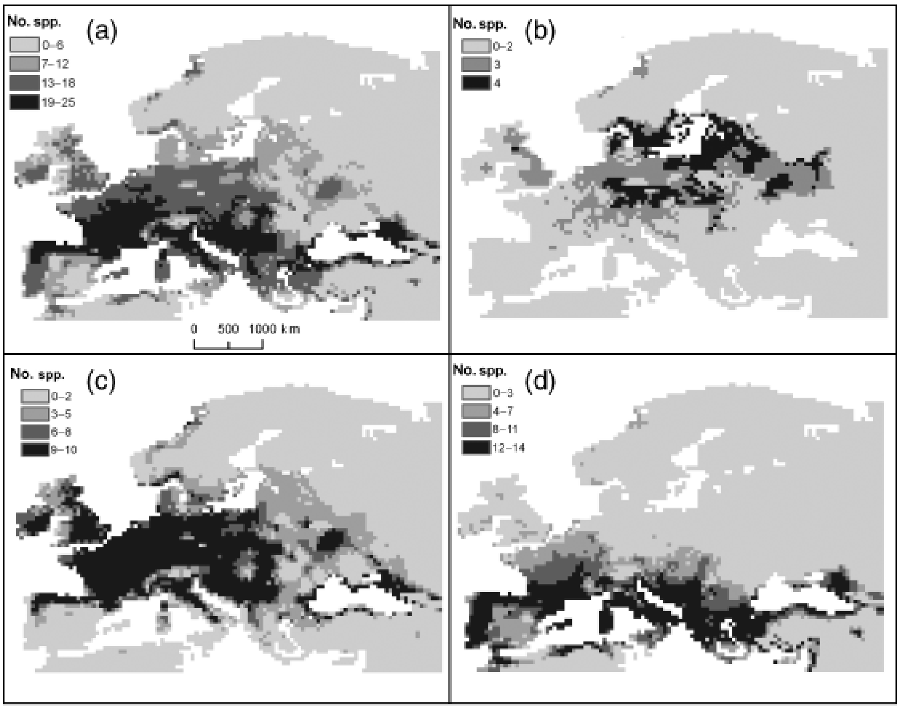

Fig. 2 (a) Predicted total European species richness for present distribution and for each biogeographic group: (b) Boreal, (c) Temperate and (d) Mediterranean.

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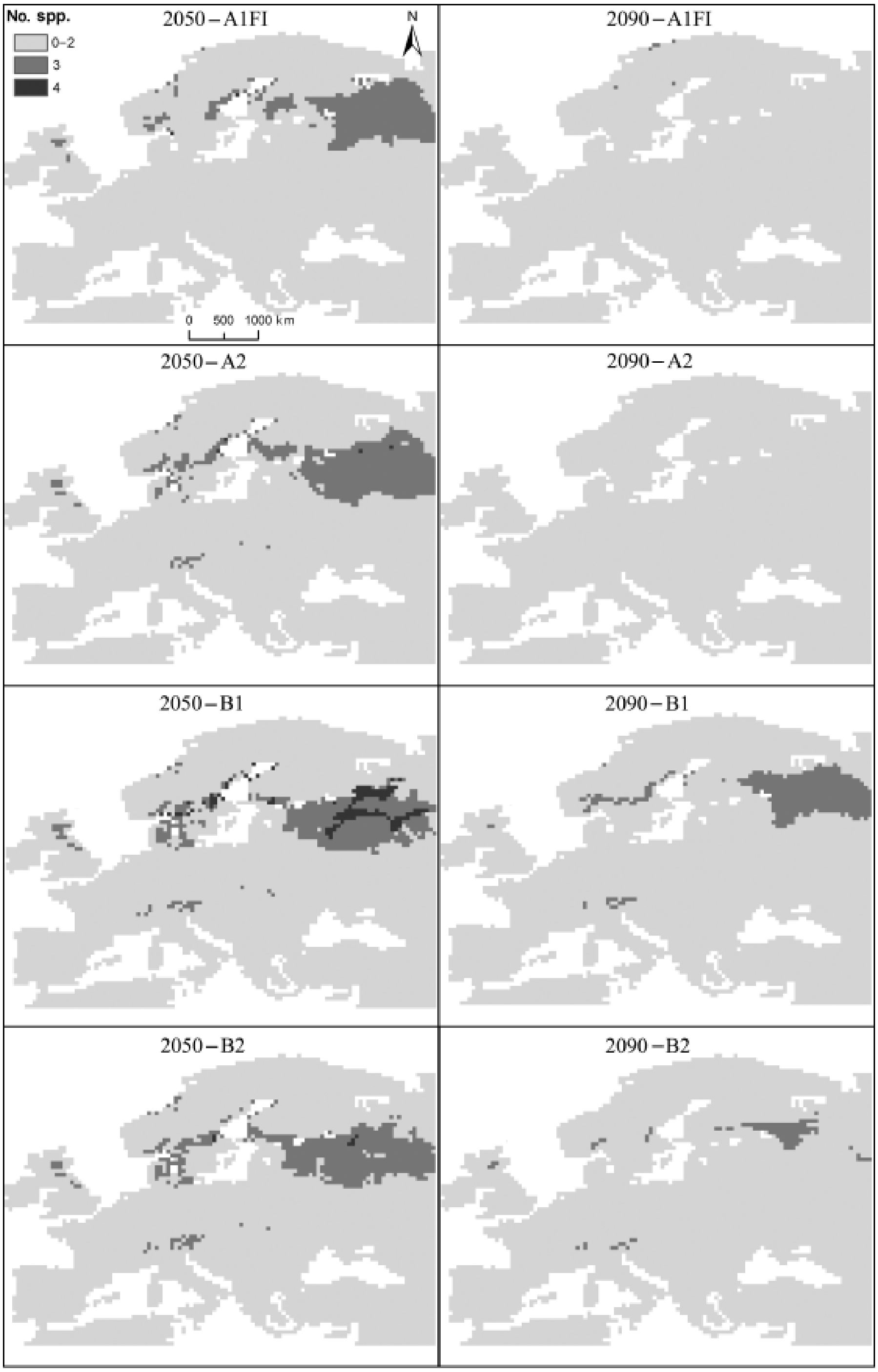

Fig. 3 Modelled potential distribution of bat diversity for the Boreal biogeographic group for two time periods (2050–2060 and 2090–2100) and four IPCC scenarios (A1FI, A2, B1 and B2). See Fig. 1 to check which bat species were included in this group.

altogether although it does not occupy the largest area.

The modelling projections for each biogeographic group produced very different outcomes. The distribution of species richness in the Boreal group was strongly affected by climate change. Distribution patterns moved in a north–east direction (Fig. 3) and scenarios A1FI and A2 had the greatest impact on bats. Although scenarios B1 and B2 had less dramatic effects, bat diversity nevertheless suffered considerable losses. Under scenario B2 it was predicted that an area connecting Scandinavia to the European mainland may be

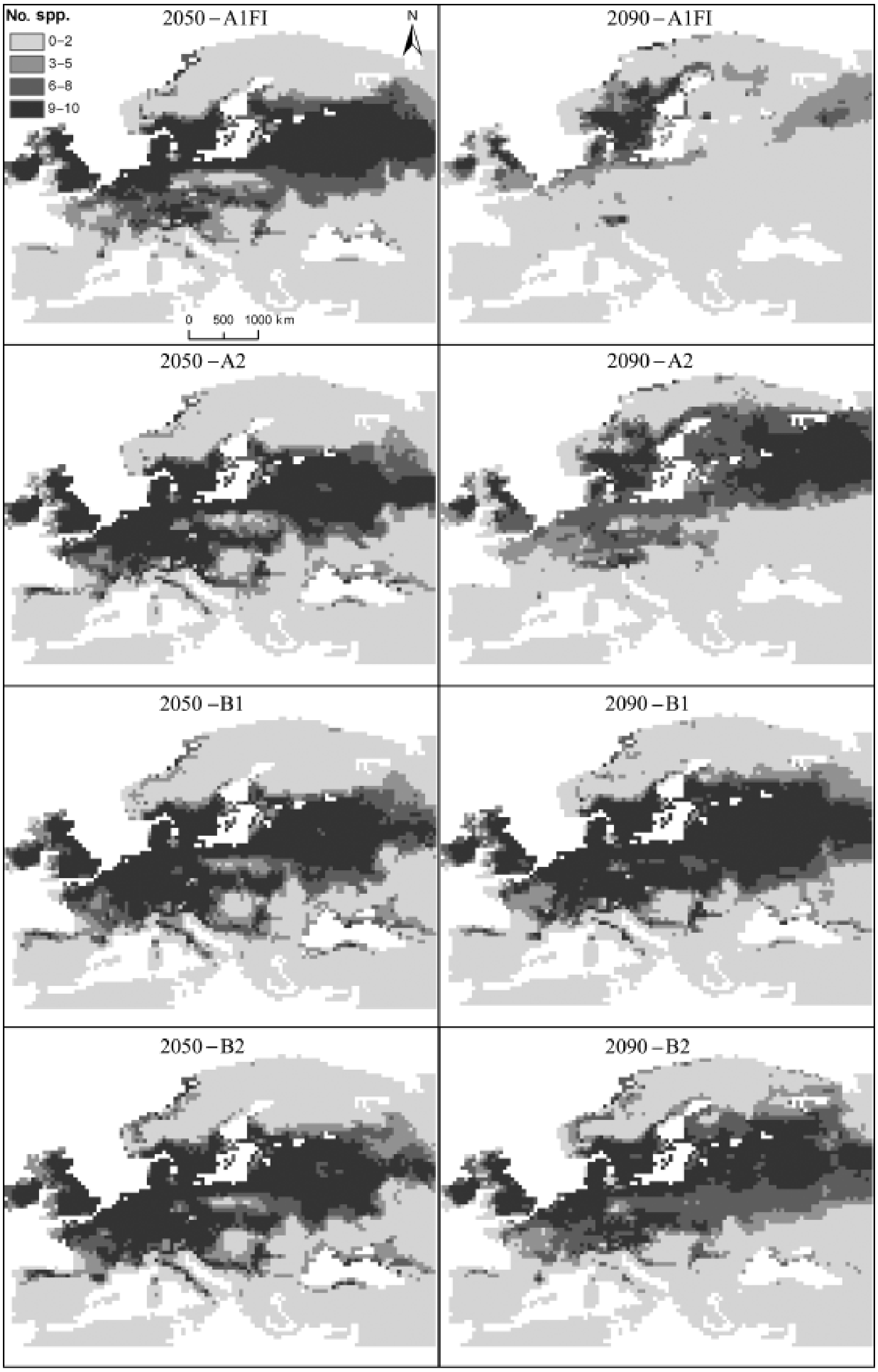

Fig. 4 Modelled potential distribution of bat diversity for the Temperate biogeographic group for two time periods (2050–2060 and 2090–2100) and four IPCC scenarios (A1FI, A2, B1 and B2). See Fig. 1 to check which bat species were included in this group.

an enclave for the remaining species in this group. Scenario B1 was very similar to B2 but with more suitable areas predicted in northern Europe. To sum up, it is likely bats in the Boreal group will face serious challenges to their survival by the end of the century whichever scenario is modelled.

The Temperate group currently occupies the largest potential area in Europe. There were no visible differences in predicted distributions among the different scenarios until 2050–2060 (Fig. 4). In fact, we predict a trend of species richness becoming highest initially towards the north. However, by the end of the century

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the different scenarios have completely different outcomes. In scenario A1FI we expect that there will be a major reduction in the species richness of Temperate bats throughout mainland Europe. Only Scandinavia and the United Kingdom are exceptions, with an increase from present day richness, hence they could become the most important areas for this group. Scenario A2 also predicts a major disappearance of European species, although it also predicted high levels of richness in northern Europe and the Alps. Again, scenarios B1 and B2 predicted the largest areas of relatively high richness with these becoming focussed in central and northern Europe. Nevertheless, both scenarios predict the almost complete disappearance of this group from southern Europe. This is more visible in the B2 scenario. Briefly, the future of these bats seems to be highly dependent on which scenario we model. It varies between almost total extinction (in scenario A1FI) to a widespread high level of diversity being maintained in central Europe (in scenarios B1 and B2).

We would expect that bats of the Mediterranean group could be the greater beneficiaries of climate change because they are already adapted to warm conditions. Models predicted a gradual expansion to north of their current distribution and until 2050–2060 there were no major regional extinctions predicted in their current range (Fig. 5). Again, however, bats face more dramatic consequences of climate change by the end of the century. In scenario A1FI, major extinctions occur in southern Europe and a general movement of bat species richness moves northwards. Only some parts of Scandinavia, United Kingdom and northern Europe will potentially harbour high levels of diversity. Apart from scenario A1F1, only scenario A2 predicted major extinctions in the current range of Mediterranean bats, with the remaining scenarios forecasting a major expansion of this group in Europe. Overall, central and northern Europe were predicted to become highly suitable for the richness of Mediterranean bats in the future. Once more, the future of this group is dependent on which scenario is modelled. As long as the A1FI scenario is avoided, we do not expect that bat diversity in this group is at serious risk considering bioclimatic conditions only.

Predicted range shifts of the biogeographic groups

The three biogeographic groups generated very different predictions regarding their occupied area throughout the 21st century (Fig. 6). Nevertheless, scenario A1FI is clearly the worst for all biogeographic groups and for the vast majority of the 28 bat species (Table 2). By the end of the 21st century scenario A1F1 predicted major reductions in areas occupied by bats and even some extinctions. On the other hand, scenarios B1 and B2 had least impact, although the Boreal group suffered a considerable decrease in occupied area even under these conservative models. In fact, the Boreal group will probably suffer the most severe consequences from climate change. No matter which scenario is chosen, a steady decline in the area occupied by Boreal bat species is predicted throughout the 21st century, and *Myotis dasycneme* is predicted to be at risk of extinction by 2050–2060 whichever scenario is modelled (99% reduction in occupied area by the end of the 21st century; species data available as Table S2). The other three Boreal species (*Nyctalus noctula*, *Eptesicus nilssonii*, and *Vespertilio murinus*) also suffer major reductions in areas predicted to be suitable for occupation under all scenarios modelled.

The area predicted to be suitable for bats in the Temperate group varies according to the scenario used. Nevertheless, in general occupied areas may increase until 2050–2060 independently of the modelled scenario. By the end of the century model predictions differed considerably: scenarios A1FI and A2 predicted a decrease in occupied area, whereas the B1 and B2 scenarios predicted a slight increase. *Plecotus auritus* and *Barbastella barbastellus* were the Temperate species that will probably face major reductions in their occupied area (around 90% and 62% reduction under A1FI, respectively), while *Myotis mystacinus* and *Nyctalus leisleri* had the greatest predicted increase in occupied area under all scenarios except for A1FI (up to 72% and 39% increase, respectively), where all species decrease their range.

Climate change seems to have least impact upon the area predicted to be suitable for the Mediterranean group. An increase in occupied area is predicted for the majority of species except under the A1FI scenario. Moreover, occupied area is not predicted to decrease for any species under the B1 and B2 scenarios. *Myotis blythii*, *M. myotis* and *Rhinolophus euryale* will be the most affected species with a considerable decrease in occupied area in the A1FI and A2 scenarios by the end of the century (up to a decrease of 80%, 66% and 58% respectively). *M. blythii* might even face extinction in the A1FI scenario while the majority (71.4%) of the remaining species will probably suffer a reduction in their distribution. On the other hand, *N. lasiopterus*, *Hypsugo savii* and *Tadarida teniotis* had the greatest increase in the occupied area in all scenarios (up to 194%, 229% and 222% for the B2 scenario, respectively).

How much of the current range will still be occupied in the future projections, varies considerably according to scenario (Fig. 7). During initial stages, the proportion

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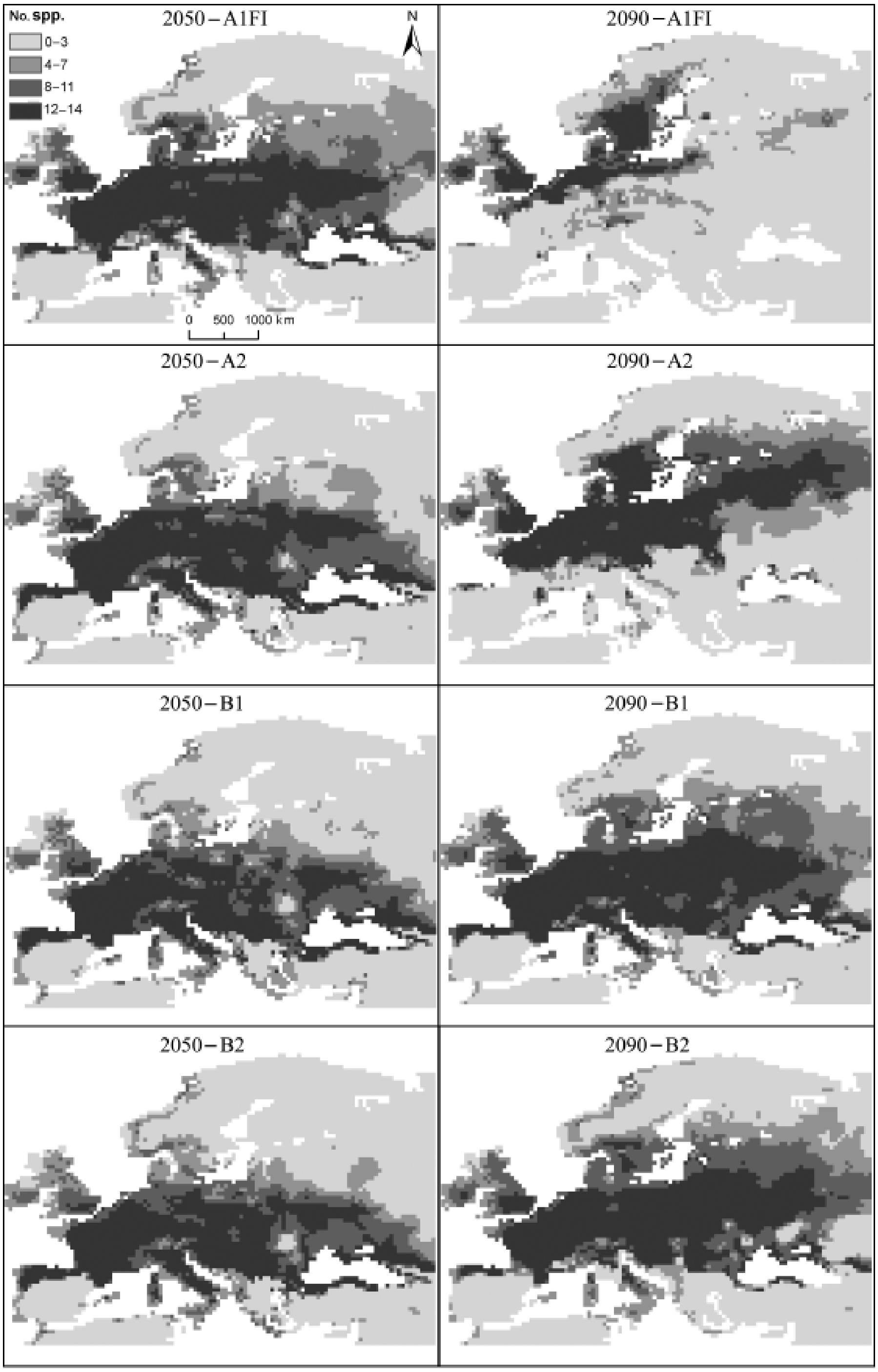

Fig. 5 Modelled potential distribution of bat diversity for the Mediterranean biogeographic group for two time periods (2050–2060 and 2090–2100) and four IPCC scenarios (A1FI, A2, B1 and B2). See Fig. 1 to check which bat species were included in this group.

of lost area in the current range is similar for all biogeographic groups for all projections (Table 3) with no major reductions for the majority of the species. However, for the last two modelled periods the overlapped area between current and future predicted distributions decreases the most for the Boreal group whereupon it suffers major reductions resulting in the probable disappearance from its current range whichever scenario is modelled. Regarding the Temperate and Mediterranean groups, there is no significant difference among them between the rate at which they contract from their current range (Table 3), with a more

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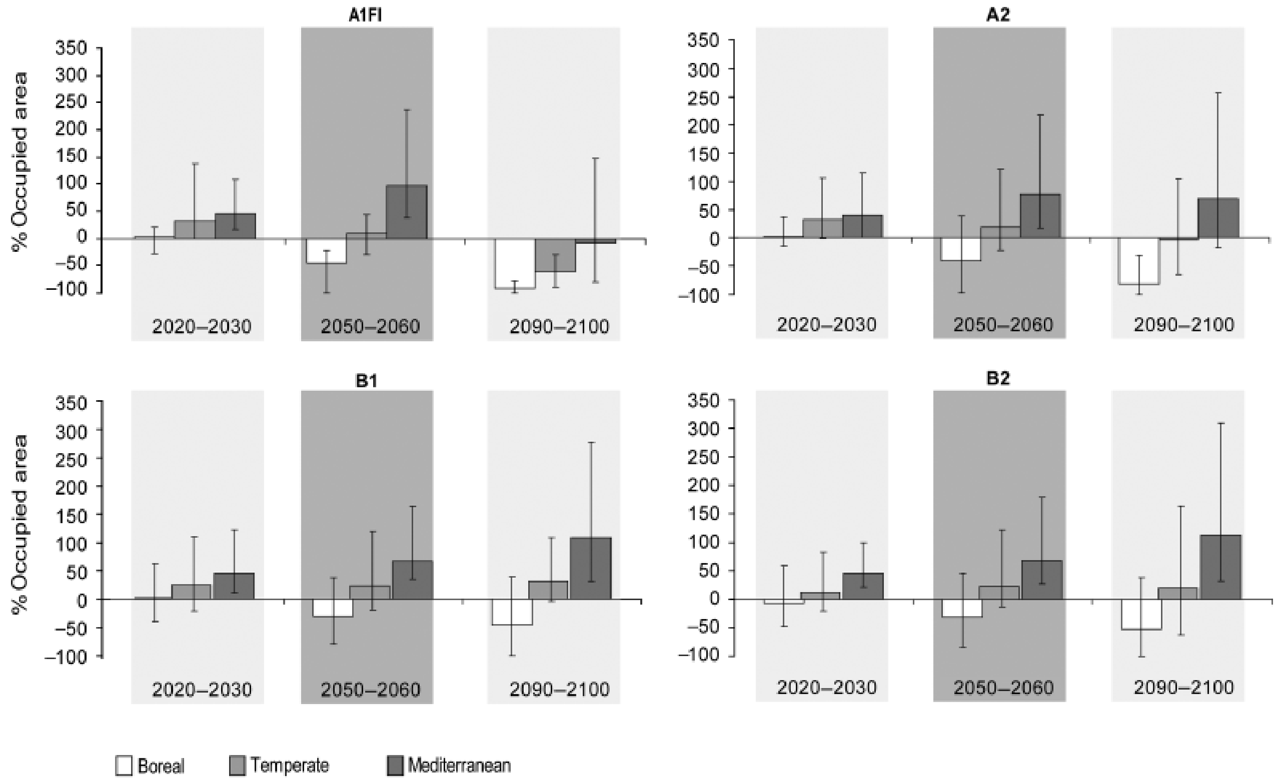

Fig. 6 Average variation of occupied area throughout the 21st century in relation to area currently occupied by each biogeographic group. The vertical bar indicates maximum and minimum values registered for a bat species within each group.

Table 2 Percentage of contracting and expanding bat species in Europe among the different biogeographic groups and modelled projections for all future scenarios

		Boreal		Temperate		Mediterranean	
Scenario	Decade	Contracting	Expanding	Contracting	Expanding	Contracting	Expanding
A1FI	2020	25	75	10	90	0	100
	2050	100	0	40	60	0	100
	2090	100	0	100	0	71.4	28.6
A2	2020	50	50	10	90	0	100
	2050	100	0	20	80	0	100
	2090	100	0	60	40	14.2	85.8
B1	2020	25	75	10	90	0	100
	2050	100	0	20	80	0	100
	2090	100	0	20	80	0	100
B2	2020	50	50	30	70	0	100
	2050	100	0	30	70	0	100
	2090	100	0	30	70	0	100

accentuated decline between 2050 and 2100. Once more the scenario A1FI is clearly the worst with major regional extinctions predicted, while the B1 and B2 scenarios predict that these groups will still occupy about half of their present range.

Overall, by the end of the century there are major extinctions predicted in southern Europe with some areas loosing up to 25 species whichever scenario is modelled (Fig. 8). On the other hand, areas in northern Europe, British islands and Scandinavia have a potential to increase their species richness up to 24 species. Regarding differences among scenarios, once again the A scenarios have more species loss than B scenarios, especially in southern European peninsulas.

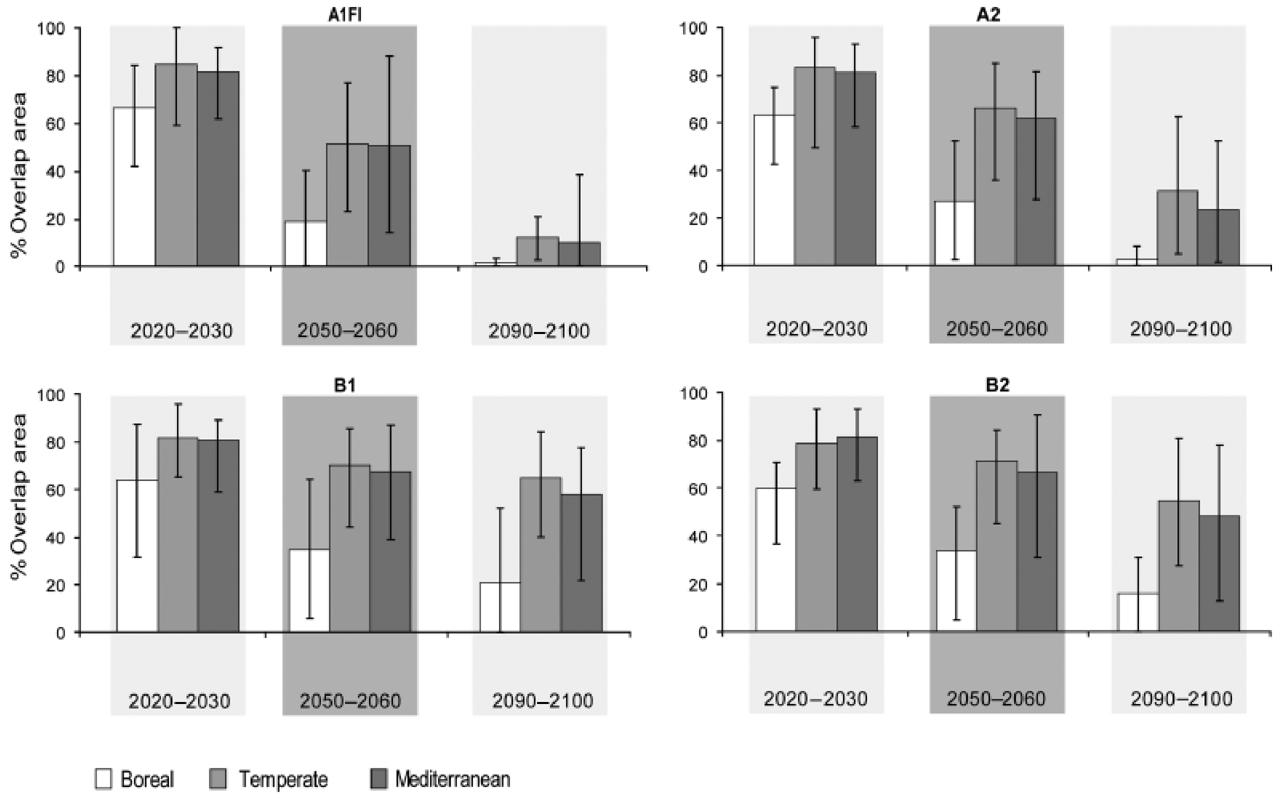

Fig. 7 Proportion of overlap area between projected models and the current potential distribution. The vertical bar indicates maximum and minimum values registered for a bat species within each group.

Discussion

Our analysis indicated that European bats may face a serious threat with predicted climate change for the 21st century due to a rapid potential movement of their populations towards the north, a decline in their occupied area and a reduction in or disappearance from their current range. Moreover, the magnitude of that impact differs considerably for different biogeographic groups of bats. Of special concern are northern latitude species where climate change could eliminate suitable climatic conditions whichever future scenario is modelled. As for Temperate and Mediterranean bat species, their future seems to be more dependent on the modelled scenario. The A scenarios of a more economically driven world resulted in the biggest losses for bat species richness whereas, as expected, the more environmentally friendly B scenarios predicted fewer losses. Nevertheless, whichever scenario is modelled there will be a reduction in bat species richness when compared with the current situation.

One of the most important outcomes of this study is the relevance of classifying species according to their biogeographic patterns. Several important climate change studies generated predictions with respect to taxonomic groups (e.g. Thomas *et al*., 2004; Araújo *et al*., 2006). We stress that it is important to take into consideration the biogeographic patterns of the species since these also reflect ecological characteristics and limitations of taxa (Cox & Moore, 2005). By considering biogeography, we reduce variability in our predictions and can more clearly determine which ecological factors are priorities for biodiversity conservation. If we had considered all bat species in a single model we would generate highly variable predictions and would not detect specific problems linked to groups associated with colder climates and northern latitudes that have lower diversity within the taxon. Such is the case of the Boreal group in the current study which is the most affected group although the one with the lowest species richness.

Our classification of the 28 bats species in three large biogeographic groups is largely in agreement with results obtained using distribution data (Horáček *et al*., 2000). Consequently, there was considerably little variability in the importance of climatic variables limiting distribution within the Boreal and Mediterranean groups. Energy, which is associated with temperature parameters in climate studies (Araújo *et al*., 2006), could be limiting the distribution of Boreal bats as suggested

Table 3 Mann–Whitney *U*-tests used to test for pairwise differences on the proportion of overlapped area among the three different biogeographic groups

Period	Boreal	Mediterranean
2020–2030		
A1FI		
Boreal		ns
Temperate	*	ns
A2		
Boreal		*
Temperate	*	ns
B1		
Boreal		ns
Temperate	ns	ns
B2		
Boreal		*
Temperate	ns	ns
2050–2060		
A1FI		
Boreal		*
Temperate	*	ns
A2		
Boreal		*
Temperate	*	ns
B1		
Boreal		*
Temperate	ns	ns
B2		
Boreal		*
Temperate	*	ns
2090–2100		
A1FI		
Boreal		*
Temperate	*	ns
A2		
Boreal		*
Temperate	*	ns
B1		
Boreal		*
Temperate	*	ns
B2		
Boreal		*
Temperate	*	ns

*$P<0.05$; ns $P>0.05$.

by Speakman *et al*. (2000). Whereas, water (relative humidity and monthly precipitation) was one of the most relevant ecological factors affecting distribution of the Mediterranean group (Russo & Jones, 2003; Rebelo & Rainho, 2009). The Temperate group had the greatest variability regarding which climatic factors were more relevant, probably reflecting the widespread distribution of this group. Moreover, the conjugation of these climatic variables, in particular temperature, has been acknowledged to exert a strong influence on European bat species richness patterns (Ulrich *et al*., 2007) hence supporting our selection of climatic variables as ecological predictors for bat distribution.

The rate and magnitude of potential shifts in distribution due to climate change poses probably one of the most dramatic challenges to a species' survival prospects (Root *et al*., 2003). Many species have little or no overlap between their current and predicted range. Such species could face enhanced extinction risk, especially those near-endemic in Europe or those with limited climatic tolerance (Huntley *et al*., 2008). In more severe cases, some species may be unable to find suitable habitats or climatic conditions to survive, since each species' ability to colonize new areas could be severely limited by their potential niche characteristics. Current studies suggest that effective species niches are conservative over time (Martínez-Meyer *et al*., 2004), meaning that when environmental conditions change dramatically outside of the ecological conditions to which populations are currently adapted, there is either migration towards new areas with suitable conditions or extinction is probable (Thomas *et al*., 2004; Hijmans & Graham, 2006). Thomas *et al*. (2004) indicated that an alarming number of species may lose a part of their range and consequently become extinct. This is of special concern for polar or boreal species where we predict a general decline in their range with climate change (Parmesan & Yohe, 2003). Additionally, these population movements may create isolated populations in their former range. The resolution of our models does not allow us to detect eventual isolated populations at a local scale, like mountain tops or valleys. Nevertheless at a broader scale, for the Boreal group in the B scenarios we expect that populations may subsist in the Alps and in some areas of Scandinavia and Scotland, although population connectivity among these regions would be difficult. For the Temperate and Mediterranean groups, only in the A1FI could some isolated populations potentially appear, especially in the Alps.

Matching phenology with future climatic conditions will also constitute one of the main pressures for bat populations, especially for example if temperature-driven gestation times become out of synchrony with food abundance (Sanz *et al*., 2003; Thomas *et al*., 2004). There are some indications that climate change is already affecting bats in Europe. For example, the Mediterranean species *Pipistrellus kuhlii* has expanded its range northwards in the past 15 years presumably in response to increased temperatures (Sachanowicz *et al*., 2006), while parturition in *Myotis myotis* has occurred up to 6 months before the usual birth period in southern Spain (Ibáñez, 1997). If changes in phenology and ecology are

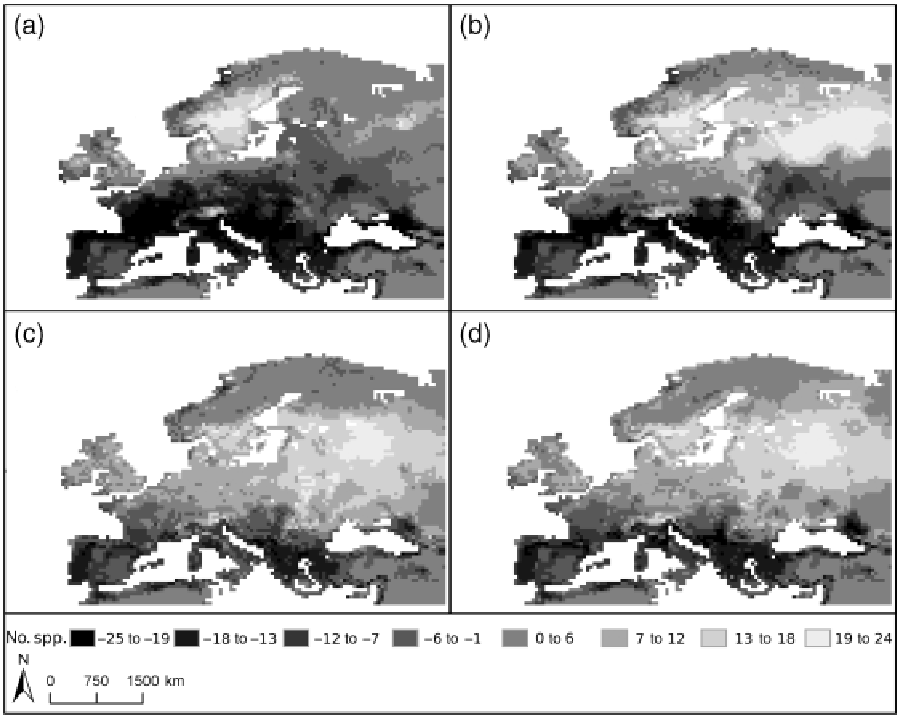

Fig. 8 Difference between present species richness and projections for 2090–2100 for scenarios (a) A1FI, (b) A2, (c) B1 and (d) B2.

already being detected when the world has only warmed by an average of 0.6 °C, many more far-reaching effects will probably occur in response to levels predicted by the IPCC (Root *et al.*, 2003). In addition, landscape changes may lead to yet greater species loss. In fact, habitat loss or alteration is currently recognized as one of the major causes of the extinction of species (Moreira & Russo, 2007). This situation could become more severe when interacting with climate change. For example, Jetz *et al.* (2007) argued that between 400 and 900 of the world's bird species will have 50% of their current range transformed into a different habitat by 2050. Bats may be more flexible than other mammals because flight may facilitate relocation as a response to climate change (Scheel *et al.*, 1996). However, the availability of roosts is one of the most limiting resources for bats (Rodrigues *et al.*, 2003; Russo *et al.*, 2004) and in combination with the needs for specific foraging habitats (Russo & Jones, 2003; Rainho, 2007), roost loss may pose an additional threat to bat survival. This may be of special concern for tree-dwelling bats since the rate of climate change may be too fast to allow the development of mature forests in the new climatically suitable areas in the north. It is not expected that large areas of mature broadleaf forest, the main habitat for the existence of tree roosts in Europe (Lewis, 1995; Russo *et al.*, 2004), could develop in northern Europe until the end of the century (McLachlan *et al.*, 2005). Besides the disappearance of suitable roosts, climate change could modify the microclimatic condition within roosts, which could affect crucial phases of bat's life cycle such as breeding and hibernation. The thermal conditions of roosts have a strong influence on bats' survival, because metabolic rate, evaporative water loss and gestation time are adversely affected when temperatures lay outside optimum conditions (Racey *et al.*, 1987; Webb *et al.*, 1995).

Bioclimatic models provide the first approximations of the potential magnitude of the effects of climate change on species distributions (Pearson & Dawson, 2003), having been used to successfully predict the potential distribution of species under both current and past conditions (Hijmans & Graham, 2006). Moreover, MAXENT also produces robust estimates of potential range shifts with climate change (Hijmans & Graham, 2006). Overall, these predictions should be considered conservative, meaning that some omission errors could exist (the species may exist in areas classified as unsuitable) but commission errors are unlikely (the species does not occur in areas predicted as suitable). This derives from the characteristics of MAXENT: using pseudo-absences in the calculations implies that predictions are prone to overfit presence data, hence this technique is likely to reflect the natural distribution or the realized niche of taxa (Zaniewski *et al.*, 2002).

Several authors have already verified that there is a great variability among projections from different future scenarios (Thuiller, 2004; Araújo *et al.*, 2006). As

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such, according to IPCC (2001) recommendations, a range of different scenarios should be used when assessing the impacts of climate change. In spite of the variability of the scenarios we have analysed, in all of them we observed a trend for species richness to shift northwards. This in agreement with other studies on other taxa that also predict a displacement of species richness towards areas that are nowadays cooler (Parmesan & Yohe, 2003; Araújo *et al*., 2006; Huntley *et al*., 2008). Several studies have predicted an increase on potential suitable area for temperate or warmer climate species due to a warming in the cooler northern ranges. However, the majority of those works rarely extend their predictions beyond 2050 (e.g. Thomas *et al*., 2004; Araújo *et al*., 2006; Jetz *et al*., 2007). Our results have also shown an increase in occupied area for most of the Temperate and Mediterranean bats over that time period. Only by the end of the century was there a clear decline for almost all bats in the more economically driven scenarios that, not surprisingly, result in the greatest changes to present climate. However, we should also take into account an eventual invasion of species from warmer climates, for example north African species. Indeed, some of those species may already exist in the southern regions of the Iberian Peninsula (Ibañez *et al*., 2006). On the other hand, it can be argued that European bat species have suffered major and rapid climatic changes in the past. In fact, during the Eemian interglacial (130k–115k years BP) or even in the Atlantic phase of the Holocene (7.5k–5k years BP) temperatures were higher up to ca. 2 °C than present conditions (Kaspar *et al*., 2005). Moreover, the fossil record suggests that the distribution of several bat species did not suffer major changes despite the occurrence of warmer conditions during the Middle and Late Holocene (Postawa, 2004). What clearly differs from the climate change future scenarios is the magnitude of temperature change. In our work, we also showed that few changes are expected in bat distribution until mid-21st century, when temperature rises reach similar values of the Eemian and Atlantic phase of the Holocene. It is when predicted temperature rises to much higher values (up to ca. 6 °C) than those acknowledged for the aforementioned periods, that we predict that bat populations will suffer a pressure not comparable with what existed over the last interglacial climates.

As species change their geographic distribution, European protected areas will face new challenges. As some of these species succeed in colonizing new areas, also new ecological relationships will be forged that can change interactions and fundamental ecosystem processes in unpredictable ways (Walther *et al*., 2002), thus it is highly probable that several ecosystems will become disrupted (Root *et al*., 2003). Protected areas could have their relevance even more enhanced by providing a continuous source of offspring to eventually colonize more favourable areas (Huntley *et al*., 2008).

Therefore, the predicted contractions/expansions in the distribution will put more pressure on the survival of the European bats. As such, we may expect that the current conservation status of several species will suffer changes, especially for the Boreal and Temperate bats that will probably become of greater conservation concern. In fact, considering bioclimatic conditions alone, we expect that only for a few Mediterranean species will populations expand irrespective of the scenario modelled. Overall, we predict that the number of threatened bat species will increase until the end of the current century, even without taking into account the consequences of changes in species interactions and ecosystems. Only with the implementation of climate change mitigation measures together with effective habitat management may we avoid the outcomes predicted by more detrimental future scenarios. By reacting proactively we may perhaps better manage the new conservation challenges for this century.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Composite map combining two sPCA axis using three climatic variables (see Results). Areas represented in red were associated with warmer climates while blue areas represented colder climates. The map identified three general bioclimatic regions in Europe: the Boreal, in blue and dark colours, including Scandinavia, the Alps/Carpathians, the Pyrenees and part of Scotland; the Temperate Humid Zone located in central and eastern Europe, most of the U.K and small areas in northern Iberian Peninsula and in Turkey; and the Mediterranean area, mainly represent by red colours, and located in southern Europe.

Table S1. Principal Component matrix for the selected climatic variables.

Table S2. Variation of occupied area throughout the 21^{st} century in relation to area currently occupied by each species. See Fig. 1 for species abbreviations. Horizontal lines separate each biogeographic group.

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