



# Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time

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## ABSTRACT

This article examines the role of the Late Pleistocene climatic changes in the disappearance of the European populations of spotted hyenas. A species distribution model was built using both current and past environmental requirements of the species. Model projections were made with climatic scenarios provided by the GENESIS 2.0 General Circulation Model (126 ka, 42 ka, 30 ka and 21 ka). Those projections indicate (1) that during the Late Pleistocene warm scenarios spotted hyenas should have been widespread in Europe, and (2) that during the last glacial maximum their potential climatically suitable geographic distribution diminished in size. The decrease in the potential climatic distribution was strictly restricted to Northern Europe. Climatic conditions in Southern Europe during the Late Pleistocene remained within the spotted hyena climatic tolerance. Hence, climate changes could have directly affected the Northern distribution of the species during the last glaciations. However, climate change alone is not sufficient to have caused the disappearance of the spotted hyena populations in Southern Europe. That is, other factors, such as prey abundance or human ecological impacts, in addition to climatic change, are needed to completely account for extinction of the European spotted hyena.

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## 1. Introduction

At the end of the Pleistocene (approximately 50–10 ka), a worldwide extinction, called the megafauna extinction, affected many of the larger species of mammals (Beck, 1996; Alroy, 1999; MacPhee et al., 2002; Forster, 2003; Barnosky et al., 2004; Louys et al., 2007). In the western Palaearctic region, more than one third of mammalian megafauna genera went extinct (Barnosky et al., 2004), and several widespread and charismatic species disappeared at that time, including *Mammuthus primigenius* (the woolly mammoth), *Homo neanderthalensis* (the Neanderthals), *Megaloceros giganteus* (the Irish Elk), *Coelodonta antiquitatis* (the woolly rhinoceros) and *Crocota crocota* (the spotted hyena) (Stuart and Lister, 2007). The Pleistocene was characterised by an unstable climate with frequent oscillations between ice ages and warmer interglacial climates (Jackson and Overpeck, 2000). The megafauna extinction coincided temporally with two major events: (1) the last

glacial period and the climatic amelioration of the beginning of the Holocene, and (2) *Homo sapiens'* expansion out of Africa (dated from 45 to 50 ka (Mellars, 2006)). Therefore, the late Pleistocene extinction is generally considered a regionally contingent event generated by the combined effect of climate changes and human impacts (Barnosky et al., 2004). In the case of Eurasia, climate change would have caused range shifts (Huntley, 1991) that, together with the increase in human populations, could have negatively and severely impacted large mammal populations (see Nogués-Bravo et al., 2008).

*C. crocota* (the spotted hyena) is one of the large mammals that became extinct in Europe at the end of the late Pleistocene. Prior to their extinction, spotted hyenas were present in Europe for at least 1 million years (García and Arsuaga, 1999; Carrión et al., 2001). Fossil remains of the species suggest that during the Pleistocene they were present all over the continent from the Iberian Peninsula to the Urals (Testu, 2006). Some authors have assigned the European spotted hyena fossil remains to a subspecies of the African spotted hyenas (*Crocota crocota spelaea*, *Crocota crocota intermedia*; see Kurtén, 1957, 1968; Werdelin and Solounias, 1991), while others consider them a distinct species (*C. spelaea*; Soergel, 1937; Musil,

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1962; Markova et al., 1995). Recently, the taxonomic status of the Pleistocene European spotted hyenas was revised using ancient DNA. That analysis confirmed the existence of genetic flow between the African and Eurasian populations during the Pleistocene (Rohland et al., 2005). Thus, similar to the situation for plants, it appears that the dominant response of mammal species during Quaternary climatic oscillations was extinction or range shift, not evolutionary change (Willis and Niklas, 2004). In this paper, we considered the European spotted hyena fossil remains as belonging to *C. crocuta* following Rohland et al. (2005). First, we estimate the climatic niche of this species from distributional data (the set of a priori favourable climatic conditions for the species) using the climatic information generated by the GENESIS 2.0 General Circulation Model (Pollard and Thompson, 1997). Second, we geographically projected this estimated niche in Europe for five temporal scenarios (126 ka, 42 ka, 30 ka, 21 ka and present) to ascertain the possible role of Pleistocene climatic changes on the potential distribution of European spotted hyenas. Climate is frequently considered a key factor in explaining the geographical distribution of species at large spatial and temporal scales (Bowyer et al., 1998; Geffen et al., 2004). Macroecological and biogeographical studies based on current data support the hypothesis that climate controls or at least strongly contributes to explaining the distributions of species (Currie, 1991), and many paleontological analyses also highlight the relevance of climate. For example, the Plio-Pleistocene crisis (Kostopoulus et al., 2007) or species replacements during the Pleistocene are usually related to climatic changes (Cardoso, 1996; Barry et al., 2002; Coard and Chamberlain, 1999; Sommer and Benecke, 2005). In this article, we address the question of whether climatic change alone was sufficient to account for the extinction of spotted hyenas in Europe. We test whether extinction of the spotted hyena in Europe was related to a decrease in climatically favourable area during the Pleistocene. Finally, we discuss methodological influences on model predictions when using paleontological data.

## 2. Materials and methods

### 2.1. Spotted hyena data

Spotted hyenas show high morphological plasticity (Klein and Scott, 1989; Mills and Hofer, 1998). The magnitude or morphological differences among extant populations (Mills and Hofer, 1998; Reynolds, 2007) and across Pleistocene periods is similar (Dockner, 2006). In addition, analysis of DNA from extant populations and from Pleistocene samples (i.e., ancient DNA) indicate that European and African spotted hyenas are the same species (Rohland et al., 2005). Hence, following Rohland et al. (2005) we treat the extinct European populations and the extant African populations as different populations of the same species. Location data on the current occurrence of *C. crocuta* in Africa came from different sources, including the “IUCN Hyena Status Survey and Conservation Action Plan” (Mills and Hofer, 1998) and the African National Parks fauna lists, which collectively constitute 655 presence records (Fig. 1a). European Pleistocene fossil sites were chosen from a database that comprises published records of the species during the Late Pleistocene in Eurasia (see Varela et al., 2009). We used two criteria for including location data for the Pleistocene. First, fossil localities had to be adequately dated (radiocarbon dates were calibrated into calendar years using the CalPal 2005 SFCP application including 95% confidence intervals). Second, these fossil localities with adequate dating and GENESIS 2.0 scenarios had to overlap (a temporal error of  $\pm 3$  ky was arbitrarily stipulated following Nogués-Bravo et al. (2008) and Banks et al. (2008a)). After applying these two criteria, more than 400 spotted hyena

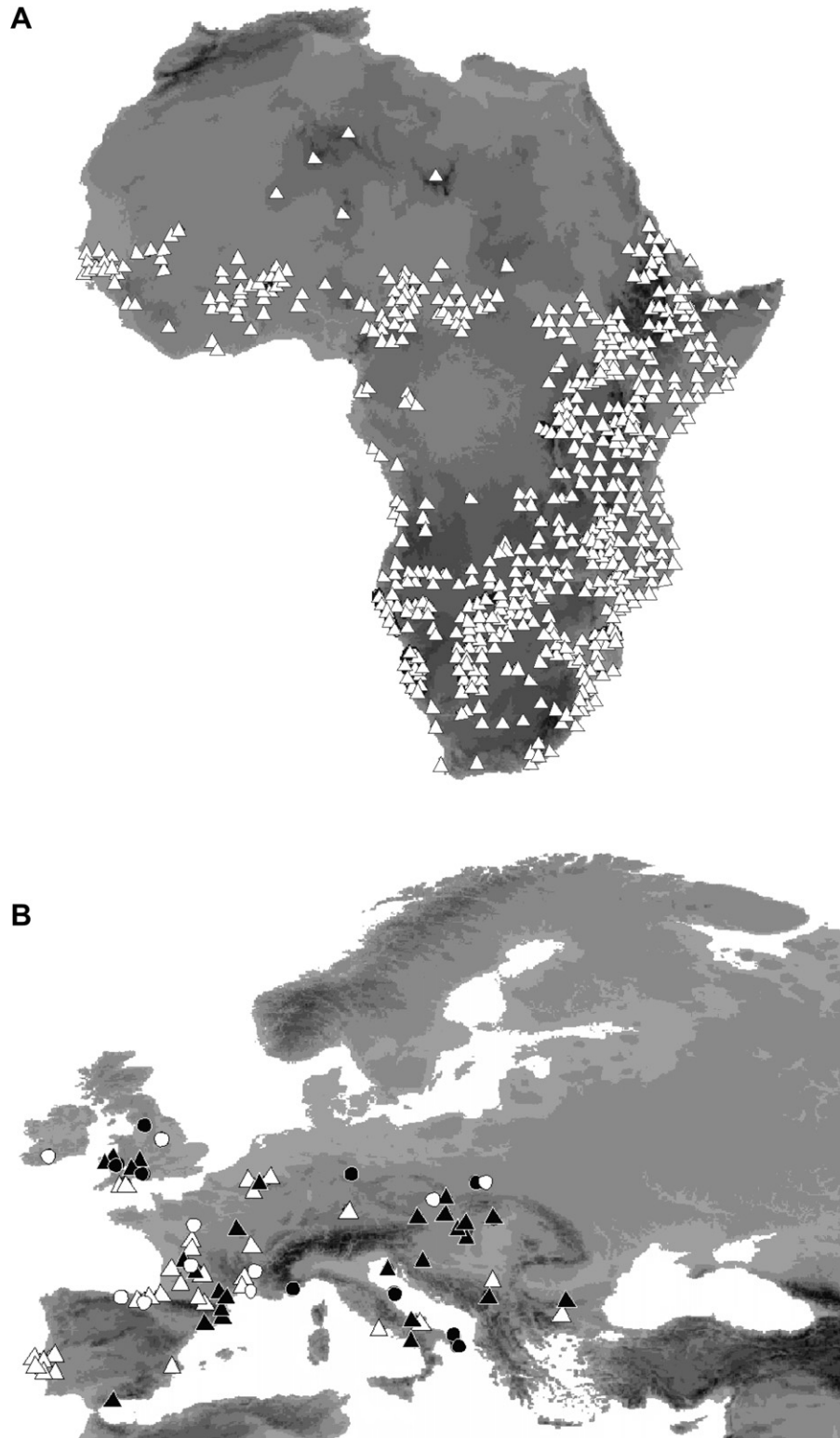
fossil sites were discarded. The number of selected locations was as follows: 9 points for the 126 ka scenario, 33 points for the 42 ka scenario, 27 points for the 30 ka scenario and 10 fossil sites for the 21 ka scenario (Fig. 1b). See Varela et al. (2009) for more information on the sources used.

### 2.2. Climatic data

The climatic conditions at each location were estimated using variables from the General Circulation Model (GCM) GENESIS 2.0. GENESIS 2.0 combines an atmospheric model derived from the NCAR CCM1, a surface model, multilayer models of soil, snow and sea-ice, a slab mixed layer ocean model, and vegetation models (Thompson and Pollard, 1995a, b; Pollard and Thompson, 1997; Cosgrove et al., 2002). There are other climatic simulations restricted to Europe (Banks et al., 2008a, b), but GENESIS 2.0 GCM was used because it has different simulations for the global climate of the late Pleistocene, including the last interglacial (126 ka). The GENESIS 2 model has been widely used in paleoclimate studies (e.g. Levis et al., 1999; Doherty et al., 2000; Barron and Pollard, 2002). When simulating past climates it performs in the middle of a range of a paleoclimate models (Kohfeld and Harrison, 2000), and it reproduces past climates reasonably well (Harrison et al., 1998; Harrison and Prentice, 2003). Five different scenarios were used: a simulation for a warm climatic event, dated 126 ka, which corresponds to the Marine Isotope Stage 5 (MIS 5); two different scenarios for the MIS 3, dated 42 ka and 30 ka, representing two different periods of cold and dry conditions (Geraga et al., 2005); the last glacial maximum scenario, dated 21 ka, corresponding to an extremely cold period during which the northern ice sheet reached middle Europe (MIS 2) (Bowen, 1995), and a climatic simulation of the present climate. The present-day GCM simulation was used to estimate the current climatic conditions in Africa that correspond with where the species is found. Carbon dioxide levels were specified at 200 ppm for MIS 2 and MIS 3, within the range of what was found in the Byrd and Vostok ice cores (Raynaud et al., 1993). For MIS 5, 345 ppm was used (Vavrus, 2001), somewhat higher than the top Vostok value of 300 ppm. For MIS 2, we used ICE-4 G paleotopography (Peltier, 1994). For MIS 3, ice sheet and topographic boundary conditions were the same as those detailed in Barron and Pollard (2002). The Last Interglacial reconstruction uses prescribed vegetation, and MIS3 and MIS 2 simulations use the BIOME4 vegetation model. Simulated paleoclimates in Eurasia show reasonable agreement with paleoclimates inferred from pollen and plant macrofossils (Batra, 2003; Kaspar et al., 2005). All climatic information was available at a resolution of  $2^\circ \times 2^\circ$  grid cells. Downscaling methodologies were discarded. As different vegetation or ice-core geographic distribution may modify the atmosphere circulation at global and local scales (Gornitz, 1995) and the atmospheric circulation of the Pleistocene scenarios could be different from the current one (Bowen, 1995), we prefer not to use current local atmospheric circulation anomalies to downscale the coarse output of the past GCM simulations.

### 2.3. Species distribution modelling

The set of environmental conditions associated with those localities in which the species may have a positive intrinsic growth rate constitutes a partial representation of the fundamental niche (Soberón, 2007). But the fundamental niche can only be completely determined by experimental or physiological studies (Kearney, 2006). Hence, the environmental conditions associated with the occupied area (the geographic distribution of the species) would be a subset of those constituting the fundamental niche due to the effects of biotic interactions or dispersal limitations, as well as the



**Fig. 1.** (a) Current presence records of the spotted hyena, and (b) location of the Pleistocene presence sites included in the analysis, dated from 126,000 yr BP (black circles), 42,000 yr BP (black triangles), 30,000 yr BP (white triangles) and 21,000 yr BP (white circles).

available environmental space (Jackson and Overpeck, 2000). Thus, if we aim to generate an appropriate geographical representation of the species' niche using distribution data, we must use simple techniques and the most complete set of data (see Peterson et al., 2007; Jiménez-Valverde and Lobo, 2008). We use a simple climatic envelope (Busby, 1986) to estimate the potential climatic

distribution of the species in the different temporal scenarios, basing our model in the climatic requirements of a multitemporal presence data set. The climatic envelope model represents the minimal rectilinear envelope for the sampled multidimensional climatic requirements of the species, according to the available distributional information for the different Pleistocene periods and

the present (Guisan and Zimmermann, 2000; Beaumont et al., 2005). Thus, binary presence-absence maps were created based on the multidimensional envelope that includes the range of climatic conditions in which the species was observed. We also built a continuous geographic representation, using the Mahalanobis distance (Farber and Kadmon, 2003) as a measure of climatic favourability. This measure differs from the Euclidean distance in that it takes into account the dependence among variables and is scale-invariant (i.e., the variables have the same weight independently of their variance). To emphasise the role of environmental limits (Huston, 2002) as well as to avoid the effect of bias in current and past fossil distribution data, we used amplitude ( $(\text{maximum} - \text{minimum})/2 + \text{minimum}$ ) to calculate the central point of the  $n$ -dimensional climatic values for all past and present known presence cells. Thus, optimum climatic niche conditions would be equidistant from the extremes of the climatic values present in all known Pleistocene and current localities. This method avoids the bias generated by the use of central tendency measures (mean, mode or median) when estimated on a biased set of data (in this case, there are over 10 times more distributional localities of the spotted hyena in present climatic conditions than there are for all considered past times).

Niche climatic envelopes also depend on the type and number of predictor variables used in their estimation (Beaumont et al., 2005). Due to this, a necessary first step should be the selection of the predictor variables with a higher likelihood of being relevant to the distribution of species. We used ecological-niche factor analysis (ENFA) to identify the major climatic requirements of the spotted hyena (Hirzel et al., 2002; Basille et al., 2008; Calenge and Basille, 2008; Calenge et al., 2008). This exploratory analysis (see Hirzel et al., 2002 for a detailed explanation of the method) allows the identification of those variables that explain both marginality (the difference between the conditions inhabited by the species and the regional average conditions) and the specialisation of the species (i.e., the tolerance of the species to the climatic gradient in the study area). Five separate ENFA analyses were carried out: four in Europe for past time simulations and one in Africa using present-day climatic simulations. Those variables with factor loadings  $>0.33$  for the marginality or specialisation axes in any one of the ENFA analyses were selected. In total, seven climatic variables from the complete set of GENESIS variables were retained and used in modelling procedures: actual evapotranspiration, annual precipitation, maximum monthly precipitation, minimum monthly precipitation, annual mean temperature, mean temperature of the warmest month, and mean temperature of the coldest month.

### 3. Results

Spotted hyenas inhabit a wide range of annual precipitation and mean temperature conditions, although Pleistocene European localities appeared to have lower temperatures and, to a lesser extent, lower precipitation than current African localities (Fig. 2). Presence data for Europe during the warm/wet conditions of the Pleistocene 126 ka scenario had different climatic conditions than those from the cold/dry conditions of the last glaciation.

The geographical projections of the climatic niche derived from all fossil and current data indicated that *C. crocuta* had suitable climatic conditions in Europe during the last 126 ka (Fig. 3). The potential climatic distribution of the species covered Europe in the last interglacial age (Fig. 3a), when the climatic conditions were similar to current ones. Model predictions suggested geographic range was reduced by 8% for the MIS3 for both the 42 ka and 30 ka simulations and by more than 30% for the last glacial maximum (Fig. 3d). The present-day simulation (Fig. 3e) predicted an increase in the potential climatic distribution of the species similar to the

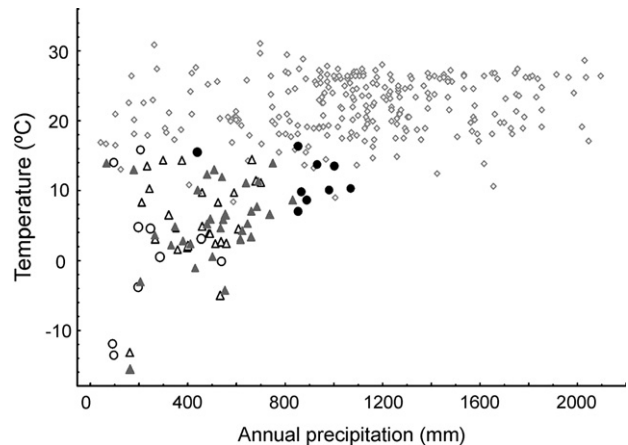


Fig. 2. Mean temperature and precipitation of the spotted hyena presence sites for the different temporal data sets: 126 ka (black circles), 42 ka (grey triangles), 30 ka (white triangles), 21 ka (white circles) and present (grey rhomboids).

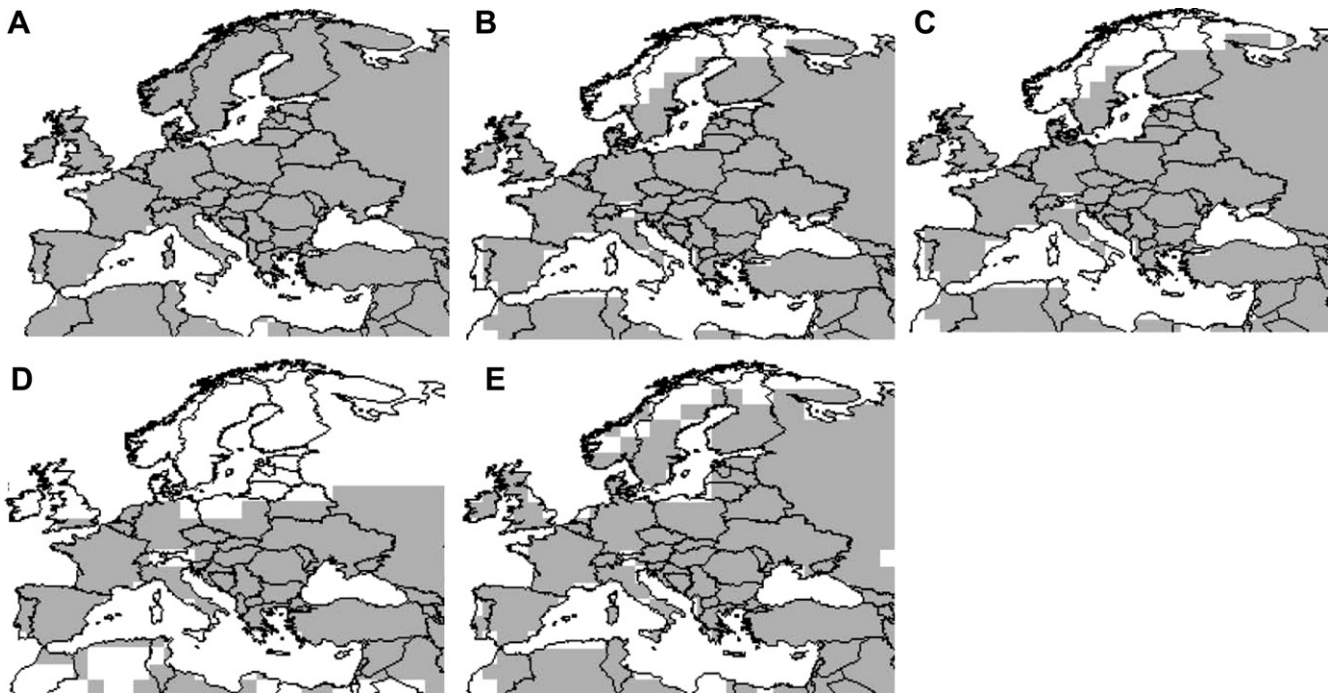
MIS3 estimates, although the species went extinct during the Pleistocene-Holocene transition (Carrion et al., 2001).

Continuous Mahalanobis predictions indicated that *C. crocuta* had suitable climatic conditions in Europe during all of the Late Pleistocene. Most of European territory is located at short distances from the estimated central climatic niche conditions (Fig. 4), although these distances differed significantly among periods, both in the case of all European cells (Kruskal-Wallis test:  $H = 2755.64$ ,  $p < 0.0001$ ,  $df = 4$ ,  $N = 4427$ ) and in the case of cells with *C. crocuta* presences ( $H = 77.25$ ,  $p < 0.0001$ ,  $df = 4$ ,  $N = 338$ ). Thus, although the climatic suitability distances of the spotted hyena presences during the last glaciation overlap with the estimated values in all other periods (Fig. 4), our analyses suggested a significant decrease in the area with very favourable conditions. Interestingly, Africa generally harboured more unstable and less suitable average climatic conditions than Europe in all periods. Furthermore, during the last glaciation, the geographical separation between the favourable areas in Africa and Europe increased substantially (Fig. 4).

### 4. Discussion

The geographical representations of the climatic envelope model indicate that the European extinction of the spotted hyena populations could not be related directly to the Pleistocene climatic changes. Our results suggest that the extreme cold conditions prevailing during the Last Glacial Maximum (LGM) would have diminished the extent of the climatically suitable European territory, but even under this apparently extreme climatic scenario, a high proportion of southern and central Europe would remain habitable for *C. crocuta*. Other evidence also supports the view that climate was probably not the most crucial and decisive factor in explaining the extinction of *C. crocuta* in Europe. First, many cold periods occurred during the Pleistocene (Allen et al., 1999) and they did not cause extinction in Europe. Considerable fossil evidence demonstrates that the spotted hyena was present in Europe during Pleistocene glacial conditions. During these time the spotted hyena, coexisted with species such as the woolly rhinoceros and the woolly mammoth (Werdelin and Solounias, 1991; Testu, 2006). Furthermore, our results show that the distances from the estimated climate optimum are even higher on the continent in which *C. crocuta* still survives (Africa) than in Europe during the last 126,000 years.

Late Pleistocene climatic changes could not be linked directly to the final extinction of the spotted hyena. European Pleistocene



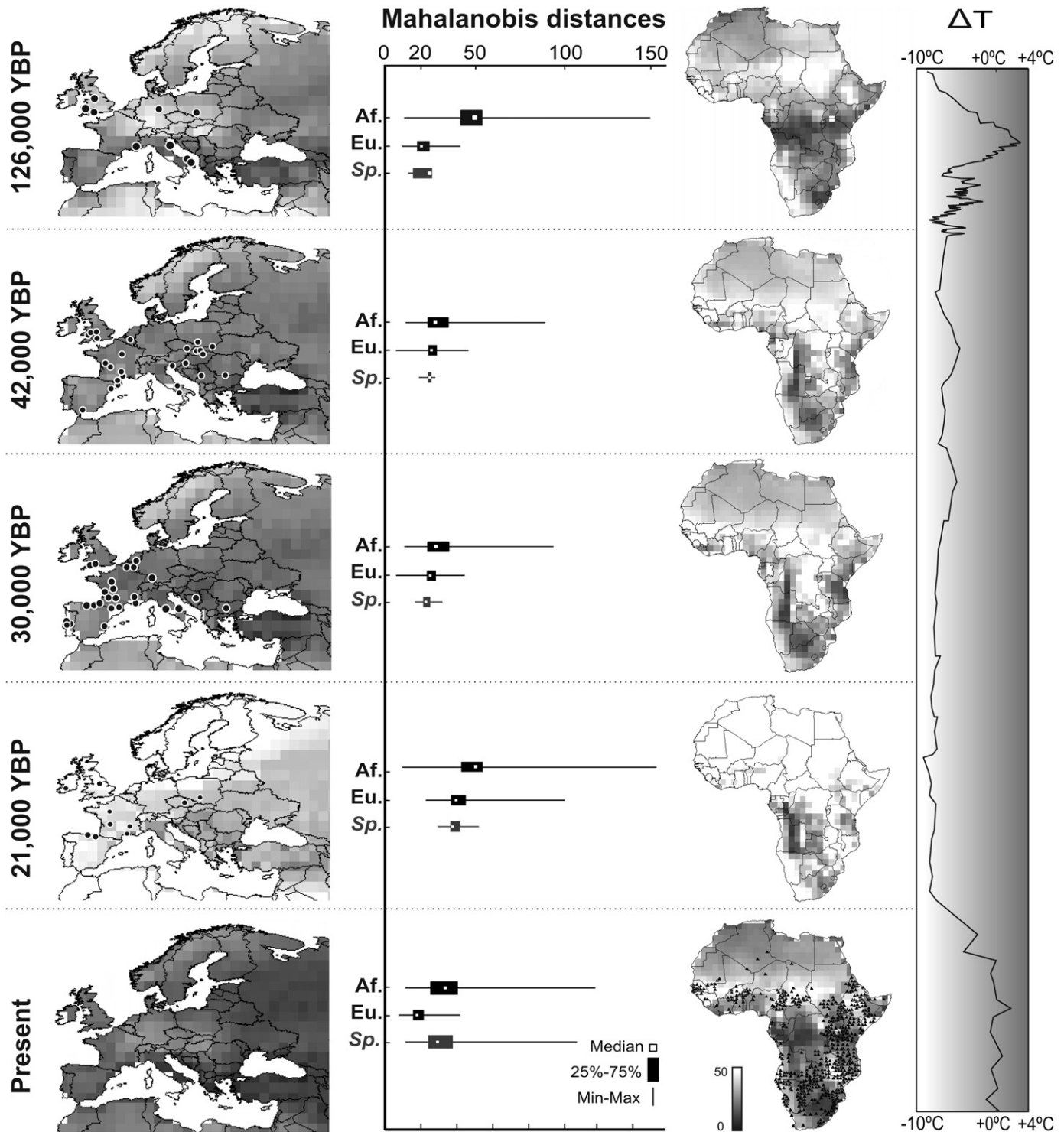
**Fig. 3.** The projection of the entire climatic envelope model for the different temporal scenarios considered: a (126 ka), b (42 ka), c (30 ka), d (21 ka) and e (present). Only during the Last Glacial Maximum (d) did the predicted distribution of *Crocuta crocuta* species appear to be climatically restricted to southern and central Europe.

fossil records of *C. crocuta* are characterised by their location near the cold extreme of the full temperature range. Thus, assuming that our methodological procedure correctly approximated the climatic optimum of the species, our results also suggest that most of the southern European territory possessed low suitability values during the LGM. More importantly, the existence of wide areas with low suitability values separated the climatically favourable areas of Africa and Europe. However, the relevance of the climatic variables highly depends on our methodological procedures. In particular, the selection of the climatic optimum is a key step in this process that may greatly affect the results. For example, in the case of the woolly mammoth, this optimum was estimated using a central tendency measure over the entire set of available climatic data, and the results suggested that climate was the main factor driving both the extinction and the decrease in distribution (Nogués-Bravo et al., 2008).

According to our results, during the LGM the spotted hyena could have suffered climatic stress and fragmentation of their potential distributional area in both Europe and Africa, although the consequences of these possible range contractions may have been different in each continent. If the complete geographic range and the probability of recolonization diminished during this cold period, other factors, such as the number of available prey or the competitive interaction with humans could have acted synergistically to precipitate the Holocene extinction of European spotted hyenas. In addition, the plant fossil records of the Palaeartic indicate that there were several short-term vegetation changes, supposedly linked to sharp climatic shifts that affected the general glacial cycles (Li et al., 2006; Wagner et al., 2009). These short-term climatic waves could have played an important role in the disappearance of the European spotted hyena populations.

Three aspects of our methodology could have substantially influenced our results and hence our biological interpretations. They are: (i) the temporal and spatial extent of the data used, (ii) the selection of the relevant climatic variables and (iii) the previously mentioned estimation of the species climatic optimum.

Some studies on Quaternary mammalian faunas relate species changes to the glacial/interglacial cycles and assume that there were cold-adapted and warm-adapted species. In these analyses, cold-adapted species expand their ranges during glacial periods, while warm-adapted species migrate or disappear (Martínez-Meyer et al., 2004). The spotted hyena is considered to be a warm-adapted species because it is currently living in Africa, and consequently, LGM climatic conditions have been interpreted to be a threat for the species (Jacobi et al., 2006). However, we think that the general framework of classifying organisms as warm or cold adapted based on their current realised climatic niche is an oversimplification of the potential climatic requirements. In addition, this assumption could lead to incorrect conclusions about the biological response to the environmental changes. As with other European mammals (Stewart et al., 2003), the past and present geographic distribution of the spotted hyena reflects different parts of their potential climatic niche. In our opinion, the species niche should be determined using both past and present species occurrences because the estimated climatic niche depends critically on the temporal and geographic scope of the data that are analyzed (Varela et al., 2009). It can be inaccurate to estimate the complete potentially suitable climatic requirements of a species using only a single temporal or spatial scenario. Each partially realised distribution does not cover the entire potential climatic tolerance of the species. Therefore, only when the most complete set of distribution data (from more than one different temporal scenario) is used will we best estimate the climatic niche of the species. This apparently simple factor has profound consequences for the discussion on the comparative roles of niche stability factors and niche evolution factors (Holt, 1996). Using distributional information of species, some authors suggest the existence of niche stability because climatic data on species presence sites remain unaltered (Martínez-Meyer et al., 2004; Martínez-Meyer and Peterson, 2006; Peterson and Nyári, 2008; Pearman et al., 2008a). In contrast, niche shift is frequently assumed when climate conditions derived from data coming from different periods or



**Fig. 4.** Mahalanobis distance maps representing the climatic distance of each  $2^\circ \times 2^\circ$  European and African grid cell from the central point ( $[(\text{maximum} - \text{minimum})/2 + \text{minimum}]$ ) of the  $n$ -dimensional climatic values considering all past and present known presence cells of *C. crocuta* for the five different temporal scenarios considered. The grey scale goes from the minimum distance (black), which indicates suitable conditions for the spotted hyena, to the 90th percentile of the data set (white), which indicates extremely unfavourable climatic conditions for the species (Mahalanobis distance = 50). The middle graph represents the dispersion of the Mahalanobis distances. Median, 25%–75% quartiles (black bars) and minimum–maximum values (lines) were plotted both for all of the African (Af) and European (Eu) grid cells, as well as for those grid cells in which *C. crocuta* fossil or current presence data were available (Sp). A temperature curve is also provided (modified from Petit et al., 1999).

regions do not coincide (Broennimann et al., 2007; Fitzpatrick et al., 2007; Urban et al., 2007; Pearman et al., 2008b; Steiner et al., 2008). The climatic conditions prevailing in presence localities cannot provide a reliable picture of the species niche due to the contingent effect of some factors preventing the colonisation of climatically

favourable areas. Thus, we advocate the use of as much distributional data as possible. We also suggest caution when deriving niche measures from distribution data, mainly when these data do not completely cover the temporal and spatial spectrum of conditions inhabited by the species.

Other important technical decisions that can greatly change the conclusions of these kind of studies are the selection of explanatory variables and the method used to determine the most probable location of the species optimum. Niche modelling results are highly dependent on the quantity and type of variables used (Beaumont et al., 2005). A large number of variables result in more restricted potential distributions and niche estimations. Thus, we recommend the use of an exploratory analysis, such as ENFA, to identify a minimum set of relevant variables that explain to the greatest extent possible the climatic tolerance and marginality of species (Basille et al., 2008; Calenge and Basille, 2008; Calenge et al., 2008). On the other hand, the correct estimation of the environmental niche is hindered by the frequent biases and scarceness of distributional information (Hortal et al., 2008). In the case of paleontological data, these biases are not only generated by the uneven distribution of the collection effort, but also by the patchiness of the locations of places capable of producing fossils. Although the estimation of the environmental limits may be affected by these biases, they may principally influence the calculation of the climatic optimum. That is, central tendency measures, such as mean, mode or median, might yield optimum values close to the climatic conditions prevailing in the most surveyed locations or in those where the occurrence of fossils is more frequent. To minimize this effect, we suggest that the calculation of continuous suitability measures, such as those provided by the use of the Mahalanobis distance, be based on an optimum derived from the amplitude of the climatic values for all presence data. As these central climatic niche conditions would be located in an equidistant position from the observed climatic extremes, such a procedure assumes that the distribution of climatic values is symmetrical (that is unskewed).

Apart from the previously described methodological questions, a few other caveats should be mentioned with respect to the interpretation of our results. In recent African spotted hyena populations, two separate clades with limited geographic overlap near the equator are recognised. These two clades are probably a consequence of colonisation from Pleistocene glacial refugees (Rohland et al., 2005). In contrast, analysis of ancient DNA analysis indicates that European fossil records from the Pleistocene and current African populations could be part of the same species (Nagel et al., 2004; Rohland et al., 2005). In addition, the high morphological plasticity detected by Klein and Scott (1989) and Mills and Hofer (1998), might reflect their capacity to inhabit a wide range of climatic conditions. Plasticity is an inherent property of species, and changes in phenotype through space and time should

be expected (Holt, 2003; Shai and Tamar, 2003; Kurtén, 1973; Smith et al., 1995, 1998). In this paper, we assumed that both present and ancient morphological or genetic variability did not substantially affect their potential response of *C. crocuta* to climatic conditions.

When estimating the factors that determine a species distribution, the variables should be measured at the scale they interact with the target species. To do this, a species' home range could be used as an indicator of the ideal spatial resolution of the climatic variables used to build the model. Spotted hyena territories can reach 1000 km<sup>2</sup>, and the mean distance away hyenas will go outside or their territory in search of prey their territory is 40 km, although that distance can be as large as 80 km (Mills and Hofer, 1998). Therefore, the maximum species geographic home range may cover around 10,000 km<sup>2</sup>. However, the available climatic scenarios for the Pleistocene have a coarse resolution, and we had to use a 2° × 2° degree grid cell to build the model (Pollard and Thompson, 1997). Furthermore, the areas of these cells vary with the latitude. The northern species presence cells are 28,300 km<sup>2</sup> while those cells located near the equator are 39,500 km<sup>2</sup>. These rough calculations indicate that the grid cells for climate modelling could be two, three or even four times larger than the spotted hyena home range. Species distribution models based on low-resolution variables tend to predict larger areas than those constructed using high-resolution grid cells (Seo et al., 2009). Therefore, because there were no high-resolution world climatic scenarios available for the Pleistocene, this was the most accurate approach we could take to estimate the range size and shift of the spotted hyena during the Pleistocene.

Finally, the potential distribution that we estimated covers the northern areas of Eurasia both for the 126 ka warm scenario and 42 ka or 30 ka cold events of the MIS3. This result is interesting, because all the spotted hyena European fossil sites were located south of 55°N (Markova et al., 1995) (Fig. 5). This pattern could be explained by a geographic bias in the data sample or because the model is missing some relevant non-climatic factor(s) related to the dispersal/survival capabilities of the species in northern latitudes. Because there are many fossil sites located in northern latitudes without *C. crocuta* remains (Fig. 5), we believe that a taphonomic bias is highly improbable. We recommend that future niche modelling studies include other non-climatic factors to explain the species' lack of ability to colonize northern Europe. One non-climatic factor that warrants further analysis is prey diversity and abundance during the Pleistocene because prey diversity and abundance is apparently fundamental to explaining the current distribution of large carnivores (Hayward et al., 2007). Another factor that should be included is the possibility of direct competition between humans and European spotted hyenas, both in their trophic preferences and in their shelter requirements. Similarly, as spotted hyenas use caves to den, we hypothesise that the absence of karstic systems in northern Europe could have been a species-specific ethological factor that constrained the northern distribution of this species during the Pleistocene. These hypotheses will be deeply discussed in future papers.

## 5. Conclusions

First, our analysis indicates that past climatic changes could have isolated Late Pleistocene *C. crocuta* populations in two different areas: Africa and Europe. The model suggests that the extinction of the European spotted hyena and the prevalence of the African populations cannot be explained solely as a function of climate. Consequently, future research should explore the importance of factors, such as human impacts or herbivore abundance, to test whether these factors may help explain the disappearance of the spotted hyenas from Europe. Second, our model predicts that

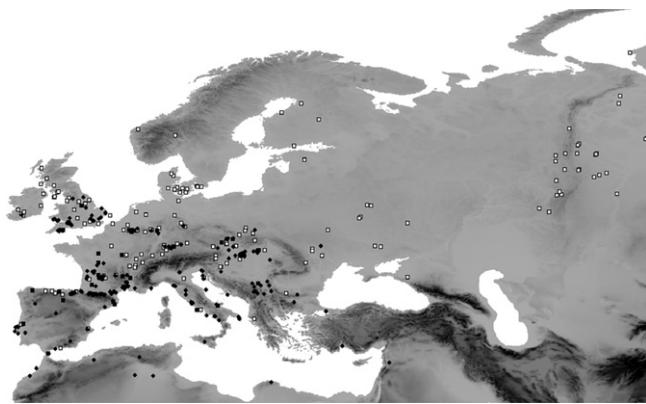


Fig. 5. General picture of the location of Pleistocene fossil sites for *C. crocuta*. There is a geographic pattern in the spotted hyena fossil record, and although there are Pleistocene fossil sites located in northern Europe (white), spotted hyena fossil remains have been recorded only in the South (black).

the spotted hyena European distribution should cover Northern Europe during the warm periods of the Late Pleistocene. The absence of *C. crocuta* fossil records from these areas could be related to the limited number of Northern European interglacial fossil sites. New fossil records in this zone would give further opportunities for model evaluation.

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