Winter temperature and forest cover have shaped red deer distribution in Europe and the Ural Mountains since the Late Pleistocene

Short title: Deer distribution since Late Pleistocene

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Key words: environmental niche modelling, expansion-contraction model, forest habitat, Holocene, January temperature, Last Glacial Maximum refugia, paleoecology, radiocarbon dating, temperate climatic zone, ungulates

Abstract

Aim: The Expansion-Contraction model has been used to explain the responses of species to climatic changes. During periods of unfavorable climatic conditions, species retreat to refugia from where they may later expand. This paper focuses on the paleoecology of red deer over the past 54 ka across Europe and the Urals, to reveal patterns of change in their range and explore the role of environmental conditions in determining their distribution.

Location: Europe and western Asia to 63° E.

Taxon: Red deer (*Cervus elaphus*)

Methods: We collected 984 records of radiocarbon-dated red deer subfossils from the Late Pleistocene and the Holocene, including 93 original dates. For each deer sample we compiled climatic and biome type data for the corresponding time intervals.

Results: During the last 54 ka changes in red deer range in Europe and the Urals were asynchronous and differed between western and eastern Europe and western Asia due to different environmental conditions in those regions. The range of suitable areas for deer during the Last Glacial Maximum (LGM) was larger than previously thought and covered vast regions not only in southern but also in western and eastern Europe. Throughout the period investigated the majority of specimens inhabited forests in the temperate climatic zone. The contribution of forests in deer localities significantly decreased during the last 4 ka, due to deforestation of Europe caused by humans. Mean January temperature was the main limiting factor for species distribution. Over 90% of the samples were found in areas where mean January temperature was above -10° C.

Main conclusions: Red deer response to climatic oscillations are in agreement with the Expansion-Contraction model but in contradiction to the statement of only the southernmost LGM refugia of the species. During the last 54 ka red deer occurred mostly in forests of the temperate climatic zone.

1. Introduction

Climatic oscillations during the Pleistocene, involving alternating periods of glacial and interglacial cycles with irregular intervals of varying durations, had a major impact on demographic changes and the distribution of plant and animal species in Europe (Hewitt, 2004). Many European temperate species survived the unfavorable environmental conditions in refugial areas (Hewitt, 1999, 2004; Provan & Bennett 2008). According to the expansion-contraction model (EC), the ranges of temperate species shrank to cover Mediterranean regions, and during postglacial periods the species recolonized temperate and boreal areas (Hewitt 1999, 2000, and references therein; Sommer & Zachos 2009). However, in the case of some temperate mammals, archaeozoological evidence has revealed that they also existed during glaciations outside the Mediterranean refugia e.g. around the Carpathian Mountains

(Davison et al., 2011; Deffontaine et al., 2005; Herman et al., 2016). In addition to latitudinal changes, there were also range expansions in east-west directions, or changes in body forms, as species adapted to different environmental conditions related to climatic humidity (Matosiuk et al., 2014; Stewart, Lister, Barnes, & Dalen, 2010 and reference therein;).

The red deer (*Cervus elaphus*) is a widely distributed game species in Europe (Milner et al., 2006; Zachos and Hartl, 2011), which can survive in diverse habitats such as woodlands, moorlands, meadows, and at different altitudes, including mountains (Dolan, 1988; Geist, 1998; Heptner, Nasimovich, & Bannikov, 1961). The current distribution of red deer is assumed to be strongly influenced primarily by colonization history during the Late Pleistocene and the early Holocene (Sommer et al., 2008) and also by human activities (e.g. Carden et al., 2012; Doan et al., 2017; Fernández-Garcia et al. 2014). The red deer is also one of the most abundant large mammal species in archaeological sites dated to the Late Pleistocene across Europe (Sommer & Nadachowski, 2006). According to Geist (1998), the European red deer is a savannah-type deer with a mixed feeding strategy, but the majority of present-day red deer populations in Europe inhabit forests rather than open areas (Apollonio, Andersen, & Putman, 2010 and references therein). The EC model of species response to long-term environmental changes assumes a high degree of niche conservationism (i.e. the tendency of species to retain their niche-related ecological traits over time), especially with regards to the abiotic, climate-related dimension of a species niche (Wiens et al., 2010 and references therein).

The history of red deer may have been more complex than explained by a simplistic EC model. Studies by Sommer et al. (2008), Meiri et al. (2013) and Queiros et al. (2019) suggest that red deer could have also survived during glacial times outside southern European peninsular refugia, especially in northern areas of western Europe. Furthermore, the distribution of western (European) and eastern (Asian) genetic lineages of red deer shifted alongside climatic changes, as indicated by studies on ancient Crimean red deer populations (Doan et al., 2018; Stanković et al., 2011). After the LGM when the climate became warmer, western red deer populations expanded in Europe. The eastern lineage – a more cold-adapted open-country grazer (Geist, 1998) – disappeared from previously occupied areas (Doan et al., 2018).

In addition to natural environmental change, human wildlife management over recent centuries has affected red deer populations via selective hunting, translocations, isolation of deer in enclosures, and through the creation of barriers resulting in habitat fragmentation (Carden et al., 2012; Hartl, Zachos, & Nadlinger, 2003; Niedziałkowska, Jędrzejewska, Wójcik, & Goodman, 2012). From a biogeographic perspective, translocations and introductions may be the main factors that could have led to erroneous conclusions about postglacial recolonization routes of the red deer.

In this study, we analysed Late Pleistocene and Holocene red deer samples to investigate the complex population history of this species across Europe and the Ural Mountains since 54 ka. There are still many questions and hypotheses that need to be verified, as previous studies mainly concentrated on the southern and western parts of the continent (Meiri et al., 2013; Queiros et al., 2019; Sommer et al., 2008). During the Last Glacial Maximum (LGM), glacial extent reached its southern limit in western Europe much earlier (about 23 ka cal BP) and extended further south than in eastern Europe (Patton, Hubbard, Andreassen, Winsborrow, & Stroeven, 2016; Patton et al., 2017). Therefore, larger areas were available for boreal and temperate species in eastern Europe and western Asia than in western Europe. Using fossil records and paleobotanical data Markova, Simakova, & Puzachenko (2009) showed that during the LGM there were large areas of land with environmental conditions suitable for many boreal and temperate species including red deer in eastern and south-eastern Europe. However, until now few studies have demonstrated that eastern parts of

Europe could have played important roles as LGM refugia for temperate and boreal species (Korbut, Rusin, Neumann, & Banaszek, 2019; Niedziałkowska 2017; Sommer et al., 2009). We expect that, although the changes in distribution of red deer in Europe and the Urals during the last 50 ka years can be explained to large extent by EC model, the species survived the LGM in larger areas than previously thought. We suppose that the the potentially suitable areas for deer included not only the well-known southern refugia but also vast regions of eastern Europe and western Asia. We also put a hypothesis that although the European red deer is ecologically flexible species, it has been best adapted to temperate climate conditions and forested habitats.

The aims of this study were to: (i) describe changes in red deer distribution before and after the LGM, (ii) identify potentially suitable areas for deer during the LGM in eastern Europe and the Ural Mountains, and (iii) analyse the response of red deer to changes in climate and habitat availability during the last 54 ka.These aims were addressed by collating existing geolocated radiocarbon dates from the literature and supplementing them with new measurements on previously undated red deer material. These were used to assess the climatic conditions and habitats occupied by red deer through the last 54 ka and investigate the species' ecological flexibility, alongside environmental niche modelling to assess the potential niche for red deer through time in Europe and the Urals.

2. Methods

2.1. Sampling

We obtained red deer subfossil teeth and fragments of bones from zoological and archeological collections in Europe and the Ural Mountains in agreement with the collection owners. Species identification was based on comparative macroscopic and morphometric analyses and confirmed by genetic analyses (sequencing of cytochrome b of mtDNA, see Doan et al., 2017 for details). In the next step, 93 samples were radiocarbon-dated using accelerator mass spectrometry (AMS) at the Gliwice Absolute Dating Methods Centre (GADAM, Poland).

Literature searches were performed to source additional data on red deer distribution in the Late Pleistocene and Holocene in Europe and western Asia. Records analysed in this study also derive from the Faunal Database of the Stage Three Project (https://www.esc.cam.ac.uk/research/research-groups/research-projects/stage-three-project/stage-three-project-database-downloads) and data collected by the authors of this manuscript during their earlier scientific projects. We focused specifically on records that have been radiocarbon-dated either directly or indirectly, i.e. dates derived from charcoal, humus, or bones of other animals found in the same layer as red deer fossils. Samples that were not radiocarbon-dated, were excluded from the analysis.

All radiocarbon dates were calibrated using OxCal v. 4.2 (Bronk Ramsey, 2009) and the IntCal13 calibration curve (Reimer et al., 2013). Hereafter, the ages are provided as cal BP, i.e. calibrated age in years before AD 1950, using medians of the calibrated radiocarbon dates.

2.2. Spatial and temporal analyses

The radiocarbon dataset used in this study (N = 984, including 93 new measurements, Appendix 1: Table S1) covers Europe as well as western Asia up to 63° E (Figure 1, Appendix 2: Figure S1) and extends from the Late Pleistocene (54 000 calibrated years BP – 54 ka cal BP) until modern times (0 cal BP). The largest number of records originated from the periods >34-26 ka cal BP (253 samples) and 54-34 ka cal BP (239 samples). The smallest number of samples were dated to the most recent time period (>4 - 0 ka cal BP; 98 samples) and the LGM (>26-18 ka cal BP; 99 samples). The chosen time periods reflect episodes when significant climatic and environmental changes occurred (Figure 2). The first period represents the time prior to the LGM, the second represents the pre-LGM period, when temperature started to decrease, the third spans the LGM, the fourth represents the time after the LGM, when temperature started to increase, the fifth covers the early Holocene, and the sixth period corresponds to the time period with clear signs of human-caused deforestation across Europe (Fyfe, Woodbridge, & Roberts, 2015). The approximate northern limits of red deer in different time periods were determined based on the distribution of red deer samples in the above mentioned time intervals. The present red deer range was created based on IUCN data (Lovari et al., 2018), published data on red deer distribution (Albayrak, Pamukoğlu, & Kaya 2007; GBIF.org 2020; Loggers, Thévenot, & Aulagnier, 1992; Milner et al., 2006; Niedziałkowska et al., 2011) and the Atlas of Mammals in Russia (http://rusmam.ru/atlas/map).

We tested the latitudinal shifts of the northern edge of red deer range among the studied periods with the Generalized Linear Model (GLM) using Gamma error structure. Before modelling, for each considered period, we selected the most northern localities (sample sites ≥ 0.9 quantile), which represented the northern limit of the species range. In the GLM sample site latitude was set as a continuous response variable, while the studied period (categorical variable) served as explanatory factor. The analysis was done in R ver. 3.5.2 (R Core Team, 2018).

Sea level and the shape of coast lines in each of the defined time periods were mapped based on data published by Waelbroeck et al. (2002) and applying GEBCO bathymetric model of the World's oceans (Weatherall et al., 2015). Changes inthe Baltic Sea level were mapped based on Björck (1995) for the period 13-8 ka BP and Lambeck, Purcell, Zhao, & Svensson (2010) for the period before the LGM. The extent of the Fennoscandian Ice Sheet was drawn based on the database of Hughes, Gyllencreutz, Lohne, Mangerud, & Svendsen (2016; 10-30 ka BP) and Lambeck et al. (2010; 39 ka and 49 ka BP).

2.3. Climatic and environmental analyses

Climatic (mean annual, mean January, mean July temperatures, and mean annual precipitation) and biome data were obtained from the FAMOUS database (FAst Met. Office and UK Universities Simulator) (Smith & Gregory, 2012, Appendix 1: Table S2). The FAMOUS database was downscaled to the spatial resolution of 2.5’ using the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) as a baseline (current climate data). Biome data were used in their original resolution (5.00° × 7.50°). In our analyses, we merged the biome categories from the FAMOUS database into the following categories (Appendix 1: Table S2): Tundra (Tun), Forest (coniferous, mixed, deciduous, montane – For), Sclerophyl woodland (Scl wood), Xerophytic shrub (Xer shr), Grassland and Desert (Grass Des). More details on the methods used to extract climatic and biome data are given in Appendix 3.

Additional information on the relative abundance of different land cover types throughout the Holocene (for the period 11-0 ka BP) was obtained from a pollen-inferred land cover change database (after Fyfe et al., 2015, Appendix 1: Table S3). This database contains pan-European land cover classification for the last 11 ka years at 200-year temporal resolution and was created by applying the pseudobiomization (PBM) method (Fyfe et al. 2010) to almost 1000 fossil pollen records from across Europe. Land cover types were extracted around the red deer data points, similarly to the approach taken to extract climatic data, using ArcGIS 10.3.1 software (ESRI 2015, Appendix 3). To determine the potential distribution of red deer in the six time periods, we created environmental niche models using Maxent software (Phillips, Anderson, & Schapire, 2006) using deer records as occurrence data and mean January temperature as an environmental variable (for more details concerning the modelling approach see Appendix 3). All statistical analyses were performed in STATISTICA 7.1. (StatSoft, 2005).

3. Results

3.1. Changes in red deer distribution since the Late Pleistocene

In general, the range of red deer shrank during the colder periods (54-18 ka cal BP) and expanded after the LGM (18-0 ka cal BP), when the climate became warmer (Figures 2, S1 and 3). The changes in the northern limits of deer occurrence (statistically significant in most cases; Table S4) were in agreement with the predictions of the EC model.

However, the scale of these changes was different in western and eastern parts of the continent (Figures 2 and S1). For the earliest studied time period (54-34 ka cal BP), the northernmost deer records were found above 60° N latitude in the Urals and above 52° N in western Europe (present-day Ireland). Between 54 and 26 ka cal BP the red deer disappeared from their northern areas moving about 200 km in a southerly direction (on average about 14 km ka^{-1}) in western Europe (distance measured along longitude 0° WE) and 950 km (on average about 68 km ka^{-1}) in western Asia (along longitude 60° E) (Figures 2 and S1). Before and during the LGM (> 34-18 ka cal BP) red deer became extinct in large areas of Europe and the species' range shifted 750-800 km (on average about 100 km ka^{-1}) further to the south in western Europe, but remained stable in the eastern part of the continent and the Urals. During the LGM (>26-18 ka cal BP) the species range was at its minimum covering areas up to about 44° N latitude in present-day France and Italy, 48° N latitude in Moldova, 55° N in the Urals (Figures 2 and S1).

After the LGM, red deer started to recolonize the European continent in a northerly direction (Figures 2, 3, S1, Appendix 2: Table S4). However, the recolonization was notably faster in the western than in the eastern part of the continent. Red deer started to expand from the south-west towards the north and north-east. Between the end of the LGM and 11 ka BP the range edge moved 1500 km northward (measured along the longitude 0°E, on average 200 km ka^{-1}) and 1800 km north-east (on average 240 km ka^{-1}, measured along a line from 0°WE, 50°N to 20°E, 60°N) in western Europe. In the eastern part of the continent and the Urals, the range expansion of deer (measured longitudinally between 30°E and 60°E and along lines from 30^{o}E, 50^{o}N to 50^{o}E, 60^{o}N and from 40^{o}E, 50^{o}N to 60^{o}E, 60^{o}N) was smaller (0-250 km; rate 0-33 km ka^{-1}). After the LGM red deer rapidly surpassed the northern limits from the pre-LGM period (54-26 ka cal BP, comp. Figures 2 (upper and middle panels), 3, S1 and Table S4).

In the Holocene (between 11-2 ka cal BP, prior to human translocations of red deer), the range of red deer continued to shift significantly (Figures 2,3, S1, Table S4) in a northerly direction. The edge of species occurrence moved from 350 km to 1450 km (rate 64-264 km ka^{-1}) to the north (measured along 40^{o}E and 0^{o}WE respectively) and 400-2000 km (rate 73-364 km ka^{-1}) to the north-east (measured from 20^{o}E, 50^{o}N to 40^{o}E, 60^{o}N and from 40^{o}E, 50^{o}N to 60^{o}E, 60^{o}N, respectively). In both Europe and the Urals red deer crossed 60^{o}N (Figures 2 and S.1). In comparison to the contemporary red deer range, the range recorded around 2 ka cal BP extended much further to the east, north-east and south (comp. Figures 1, 2 and S1). Around 400 cal BP red deer still occurred in the Urals (Table S1). The present-day eastern border of the continuous red deer distribution ends in the west of the European part of Russia (Figures 1, S1).

3.2. Climatic conditions in red deer sample locations

We compared climatic variables in the red deer record site locations for the six time periods. Mean annual and mean July temperatures were significantly different among the studied periods, especially between the Late Pleistocene and the Holocene periods (Figures 4 and S.2). Median annual temperatures varied between 7.8 and 9.5^{o}C and those of July temperatures between 14.4 and 18.2^{o}C. Annual temperature in the earlier periods (54 - 26 ka) was lower than in more recent times, especially when compared with the period prior to 11-0 ka (Figure S2). Median July temperature in deer sample locations decreased from > 54-34 ka reaching a minimum at the LGM, and then increased until the present (Figure 3, upper panel). However, we found no statistical differences in the mean January temperatures among the study periods (Figure 4, upper panel). Median January temperatures were between -1° and 1°C in all six time periods (Figure 4, upper panel). As many as 67% of all deer records were found in locations with mean January temperature between -5 and 5°C (Figure 4, lower panel) and more than 90% of samples occurred in locations where mean January temperature range was above -10°C (Figure 4, lower panel).

Annual precipitation in deer sample locations varied through time (Figure S2). During the LGM and postglacial periods (>18-11 ka BP) it was significantly higher than in earlier periods (54-34 ka BP) and the Holocene (Figure S2). Median annual precipitation was highest during the LGM (720 mm) and lowest in the period 54 - 34 ka BP (about 600 mm) and the Holocene (Figure S2).

3.3. Habitat niche of red deer in Europe

The biome type identified around each of the dated deer records are presented in Figure S1. The majority of all samples (57%) were located in forests of different types (coniferous, mixed and deciduous) (Figures 4 lower panel, S1 and S3). The second biome most frequently occupied by red deer was sclerophyllous woodland (29% of samples) in southern and western Europe. Less than 10% of samples were found in other categories of biomes such as tundra, xerophytic shrub, grassland or desert (Figures 4 lower panel, S2 and S3). The combination of different biomes, to which the samples were assigned, varied among time periods (Figure S3). The share of forest was lowest (about 35%) in the pre-LGM period (>34-26 ka cal BP) and highest in the Holocene (77% to 84%). The pre-LGM and postglacial (>18-11 ka cal BP) samples were slightly more often assigned to sclerophyll woodland than to forest.

Based on more detailed data on forest cover in Europe during the Holocene (Fyfe et al., 2015) derived from fossil pollen data, we identified that mean forest cover ± SE (standard error) was 62% ± 0.8 (range 37-80) in locations of red deer records before 4 ka BP (11-4 ka

BP) and 46 % ± 1.5 (range 27-71) after 4 ka BP (4-0 ka BP). These differences in forest cover between the two periods were statistically significant (Mann-Whitney test, U = 2299, $p < 0.0001$).

All environmental niche models (Figure S4) generally had good predictive ability with AUC values (explained in Appendix 3) for training data between 0.8 and 0.9 (the lowest AUC=0.809 for 0-4 ka BP and the highest AUC=0.896 for 18-26 ka BP). The results of modelling showed that during the LGM the most suitable conditions for red deer occurred in western and southern Europe, in areas surrounding the Black See and in Asia Minor. The model for the most recent time period (4-0 ka BP) corresponds very well with the contemporary geographic range of European red deer (comp. Figure 1 and the last panel in Figure S4). The only outliers consistently located in the unsuitable modelled habitat were deer specimens found in easternmost Europe and the Urals (Figure S4).

4. Discussion

4.1. Contraction and expansion of deer range

During the last 54 ka the range of red deer has shifted according to the EC model, which reveals range contraction during colder period and expansion during warmer episodes (Sommer et al., 2008; Meiri et al., 2013). However, the scale of red deer range oscillations were different in western Europe in comparison with eastern Europe and western Asia. This pattern is still evident when uncertainty in the distribution of red deer in eastern parts of Europe due to lower sample coverage (less material available) in that region is taken into account.

During the oldest time period investigated (between 54 ka BP and 34 ka BP), the northern boundary of the red deer range was located more northwards in the eastern part of the continent than in western regions. Although, just before and during the LGM, a much greater loss of red deer range occurred in western Europe, where the southern extent of the ice sheet about 23 ka cal BP crossed 50° N latitude. In the eastern part, the ice sheet extended from 53° N in eastern Poland to 75° N to the north of the Urals (Patton et al., 2017) and it reached its southern limit much later than in central and western Europe (Patton et al., 2016).

The northernmost remains of red deer dated to the LGM were found in Moldova (48° N latitude) and in western Asia (up to 55° N in the Urals), but not further than 44° N in western Europe. This indicates that large previously unrecognized refugial areas of red deer existed in eastern Europe. Markova et al. (2009) also identified that during the LGM large areas provided suitable habitats for many mammal species in this region. However, analyses of ancient DNA (aDNA) of red deer from eastern Europe and western Asia, dated to the LGM, are necessary to answer questions concerning phylogenetic assignment of those animals and their contribution to the contemporary deer populations.

Radiocarbon dated subfossil remains (Sommer et al., 2008; this study), genetic data from red deer and a climatic suitability model for this species indicated that during the LGM the species also occurred in south-western and western regions of France and possibly even in southern Ireland (Meiri et al., 2013; Queiros et al., 2019). After the LGM, red deer started to recolonize western Europe rather fast, which may be due to the fact that prior to17.8 ka BP deglaciation was more rapid in the western margins of the ice sheet than in its central and eastern parts (Patton et al., 2017). Furthermore, sea level was much lower, so in the early Holocene more land was available to terrestrial animals in western and northern Europe than is available today. This recolonization process is evident in the contemporary distribution of mtDNA lineages of red deer: the majority of individuals inhabiting western, northern and central parts of Europe belong to the western mtDNA clade (called haplogroup A, Niedziałkowska et al. 2011; Skog et al., 2009). During the Holocene, red deer extended their range to almost the whole of western and central Europe (excluding the very most northern parts).

Red deer in eastern Europe underwent rather different process. In the mid-Holocene a clear disjunction is apparent in their eastern range (comp. Figures 2 and S1). Firstly in the lower and middle Volga River region, where the most recent deer remains were dated (by archaeological context) to 5 ka BP (P. Kosintsev, pers. communication). By 1.5 ka BP red deer disappeared from the Ufa region, west of the southern Ural Mountains (Sungatov & Levchenko, 2014). It was only in the Urals and Western Siberia that red deer survived until the 18th − mid 19th century (Kirikov, 1959). The most likely causes for such a large-scale extinction of red deer from its eastern most range during the Holocene were changes in climate (towards more continental) and habitats (aridization) (Bolikhovskaya & Kasimov, 2010; Khokhlova, Morgunova, Khokhlov, & Golyeva, 2019). Furthermore, the contemporary eastern border of the European red deer range, stretching from the Baltic States to the Caucasus Mountains, runs parallel to the isoline of mean January temperature between -10^{o} and -15^{o}C (see e.g. DWD, 2019), which is consistent with the 50-ka-long climatic limits (mean January temperature below -10°C) of red deer found in this study.

The results of our study confirmed our hypothesis that the species survived the LGM not only in the well-known southern European refugia, but also in more northern areas of western and eastern Europe and in the Urals. The environmental niche modelling was to a large extent in agreement with these results, yet the model indicated that the environmental conditions in the easternmost Europe and in the Urals, where several red deer samples were found, were unsuitable for the species. This apparent discrepancy can be explained by the fact that in the easternmost Europe two major lineages of deer, the western (European) and the eastern (wapiti *C. el. canadensis*), co-occurred in the past (Doan et al., 2018; Meiri, et al. 2018). Results of an ancient DNA study performed by Doan (2017) showed that 11 out of 15 red deer samples analysed in our paper belonged to the wapiti mtDNA lineage. According to Geist (1998) the eastern red deer has been better adapted to cold and dry climate than the western lineage. This was also supported by the study of Stepanova (2010), who indicated that the wapiti deer occurred in Yakutia (Eastern Siberia), where mean January temperature was -36.8°C. The EC model for the more cold-tolerant eastern red deer would probably be different than the model for the western red deer, however, a more detailed study is needed to recognize the pattern of occurrence of wapiti in the Late Pleistocene and Holocene.

4.2. Ecological niche of red deer during the last 54 ka years

According to the Köppen-Geiger climate classification (e.g. Peel, Finlayson, & McMahon, 2007), since the Late Pleistocene red deer have occurred mainly in the temperate and partly also in the cold climate zones. The reconstructed measures of precipitation, annual and July temperatures in red deer sampling sites strongly varied among the studied periods, especially between the Late Pleistocene and the Holocene, thus testifying to high tolerance of red deer to those climatic variables. The truly limiting factor for the species was mean January temperature, the only climatic index which was generally stable in all time periods investigated and throughout the highly variable deer range. The majority of red deer samples (92%) were found in areas where mean January temperature was not lower than -10°C. The optimal winter temperature (indicated by the largest proportion of red deer samples found) was between 0 and 5°C, which means that the temperate zone was most suitable for red deer for at least the last 54 ka. Also, the study by Borowik, Cornulier, & Jędrzejewska (2013) showed that mean January temperature is one of the most important factors limiting contemporary red deer abundance in Poland.

The majority of the analysed red deer samples were found in sites where mean July temperature was above 10°C. The isotherm 10°C of the warmest month is an indicator for the treeline extent (Tuhkanen, 1993), which is consistent with the results of biome analyses in our study. The majority of deer records occurred in places where different types of forest were modelled in a given period. This is also consistent with the habitat preferences of contemporary red deer, which is a forest-dwelling species (Borowik et al,. 2013; Heptner et al., 1961). Although red deer are able to exist in open areas, e.g. in the Scottish Highlands (Perez-Espona et al., 2008), in most of its European range the species inhabits forests (Apollonio et. al., 2010) and its abundance positively correlates with forest cover (Borowik et al., 2013; Wawrzyniak et al., 2010;). Forest played an important role in enhancing gene flow among populations of this species in the lowlands of north-east Poland (Niedziałkowska, Fontaine, & Jędrzejewska, 2012).

Biome types inhabited by red deer in some periods studied (e.g. sclerophyllous woodland before and after the LGM) were probably connected with the availability of different biomes during those times, as determined by temperature and precipitation. Generally, the representation of forest biomes was much higher in deer sites dated to the Holocene than in those from the Late Pleistocene. Interestingly, among deer samples dated to the Late Pleistocene, the largest proportion of records were found in forests during the LGM, when red deer range was restricted to the warmest parts of Europe and western Asia. In the Holocene, forest cover represented at deer sites significantly declined after 4 ka BP, which reflects the human-induced deforestation of Europe (Fyfe et al., 2015).

The results of our study showed that during the last 54 ka the range of European red deer was restricted mainly to the temperate climatic zone with -10^{o}C January temperature as the limiting factor. Forests were the preferred habitats of deer. Within the context of large-scale and long-term changes in climate and habitat availability, the European red deer tracked the environmental characteristics to which it has been well adapted.

5. Conclusions

During the last 54 ka, the range of red deer in Europe and the Ural Mountains changed in response to climate oscillations, generally decreasing in cooler periods and expanding in warmer periods to a large extent in agreement with the EC model. However, these processes were asynchronous and differed in western and central regions when compared to eastern parts of Europe and the Ural Mountains. In all analysed time periods the results of environmental niche modelling were in concordance with the distribution of radiocarbon dated red deer samples in most of Europe, except its easternmost parts and the Urals, where more cold-tolerant subspecies of *C. elaphus* – wapiti deer - had occurred. In the LGM, the range of red deer was more extensive than previously thought and included large areas north and east of the southern European peninsulas. A major limiting factor for European red deer distribution was mean January temperature (below -10°C). Throughout the entire study period, the majority of deer records were found in forests. The temperate climate zone with mean January temperature between -5°C and 0°C, and forests as the dominating vegetation type, has been the optimal habitat for European red deer throughout the last 54 thousand years. The results of this study will be valuable in modeling changes in the spatial distribution of deer in relation to present and future climate changes.

Data availability statement

Data used in the analyses are provided in the Supporting Information.

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Figures

Figure 1. Spatial distribution of radiocarbon-dated red deer (*Cervus elaphus*) samples from the Late Pleistocene and Holocene covering Europe and the Urals. Mercator projection.

Figure 2. Changes in the northern limits of red deer (*Cervus elaphus*) ranges in the given time intervals before and during the Last Glacial Maximum (upper panel) and during and after the LGM (middle panel) in Europe and the Urals. The extent of the ice sheet for given time periods (ka BP). Lower panel: Antarctic (data from the Vostok ice core) temperature oscillations in the study period (source: FAMOUS database; Smith and Gregory 2012). See Figure S1 for maps of deer records in each time period. Maps in Mercator projection.

Figure 3. Mean (+/- SE) latitudes of the most northern red deer (*Cervus elaphus*) study sites (localities ≥ 0.9 quantile) reflects the contraction (before the LGM) and expansion (after the LGM) of red deer range. N from 6 to 10 localities. Time periods as in Figure 2. See Table 4 for the statistics.

Figure 4. Upper panel: Mean January (left) and mean July (right) temperatures for the red deer (*Cervus elaphus*) sample locations across Europe and the Urals in the six periods investigated. Significant differences among time periods are marked by horizontal lines with asterisks: ***p < 0.001, **** p < 0.0001 (Kruskal-Wallis test). N from 98 to 255 deer samples. Lower panel, left: Numbers and percentages of red deer samples (N = 984) in relation to reconstructed mean January temperature and the radiocarbon date of each deer sample in Europe and the Urals; Lower panel, right: Percentages of red deer records in different reconstructed biomes in Europe and the Urals, which have been assigned to each sample location and radiocarbon date (N = 984 samples).

Biosketch:

Magdalena Niedziałkowska is a scientist at the Mammal Research Institute, Polish Academy of Sciences in Białowieża, Poland. Her interests concern the population ecology, genetic diversity and phylogenetics of mammals (ungulates, large carnivores and rodents) at regional and continental scales, and factors which affect them, such as landscape structure, and the history and origin of populations. M.N., K.D., K.S., B.J., P.M. and A.S. conceived the ideas and applied for the financial support; M.N., K.D., K.S., M.S., B.R., U. Sch., P.K., D.M., M.Ch., D.K., E.R., U.S., M.A., N.M., V.V.T., P.H., A.B., K.T., U.D., O.K., J.W.,T.O., G.L., and A.A. collected the red deer samples; M.N., K.D. and U. Sch. gathered the red deer records, N.P., S.P. and M.S. radiocarbon-dated the samples. R.F. and J.W. produced the land cover reconstruction from fossil pollen datasets, M.G. extracted the environmental data, performed the GIS analyses and prepared the maps, M.N., K.D. and B.J. analysed the data, M.N., B.J. and M.G. wrote the paper. All authors contributed to data interpretation and revisions to the manuscript.

Supporting Information

Appendix 1. Data used in the analyses.

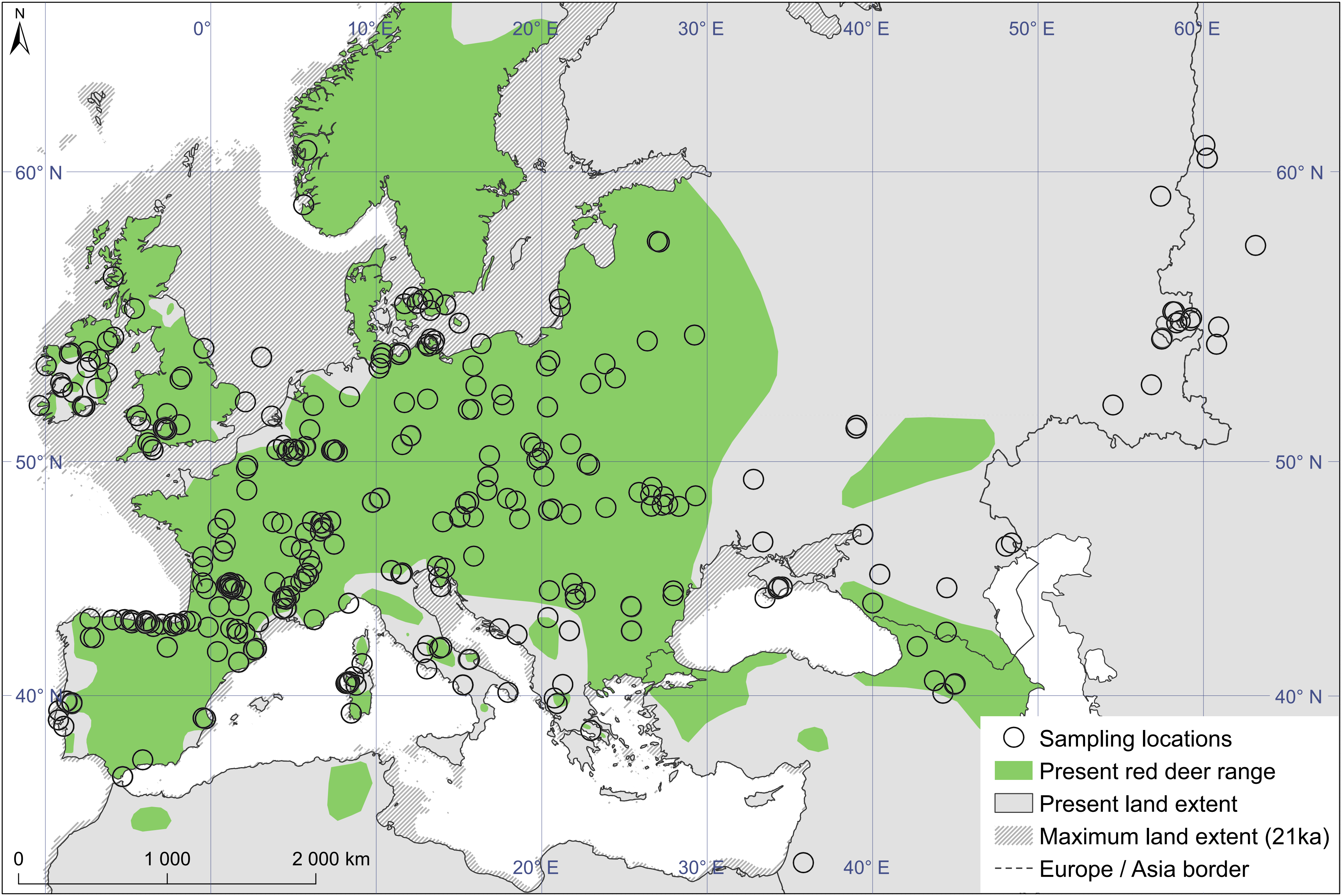
Table S1. A list of red deer records used in this study.

Table S2. Climatic and biome data determined for each of the red deer records used in this study.

Table S3. Land cover data extracted for each of the Holocene red deer records' locations using European pollen-inferred land cover change data (after Fyfe et al., 2015).

Appendix 2. Spatial distribution of red deer records and results of spatial and environmental analyses in the six studied time periods. Maps in Mercator projection.

Appendix 3. Methods of spatial analyses.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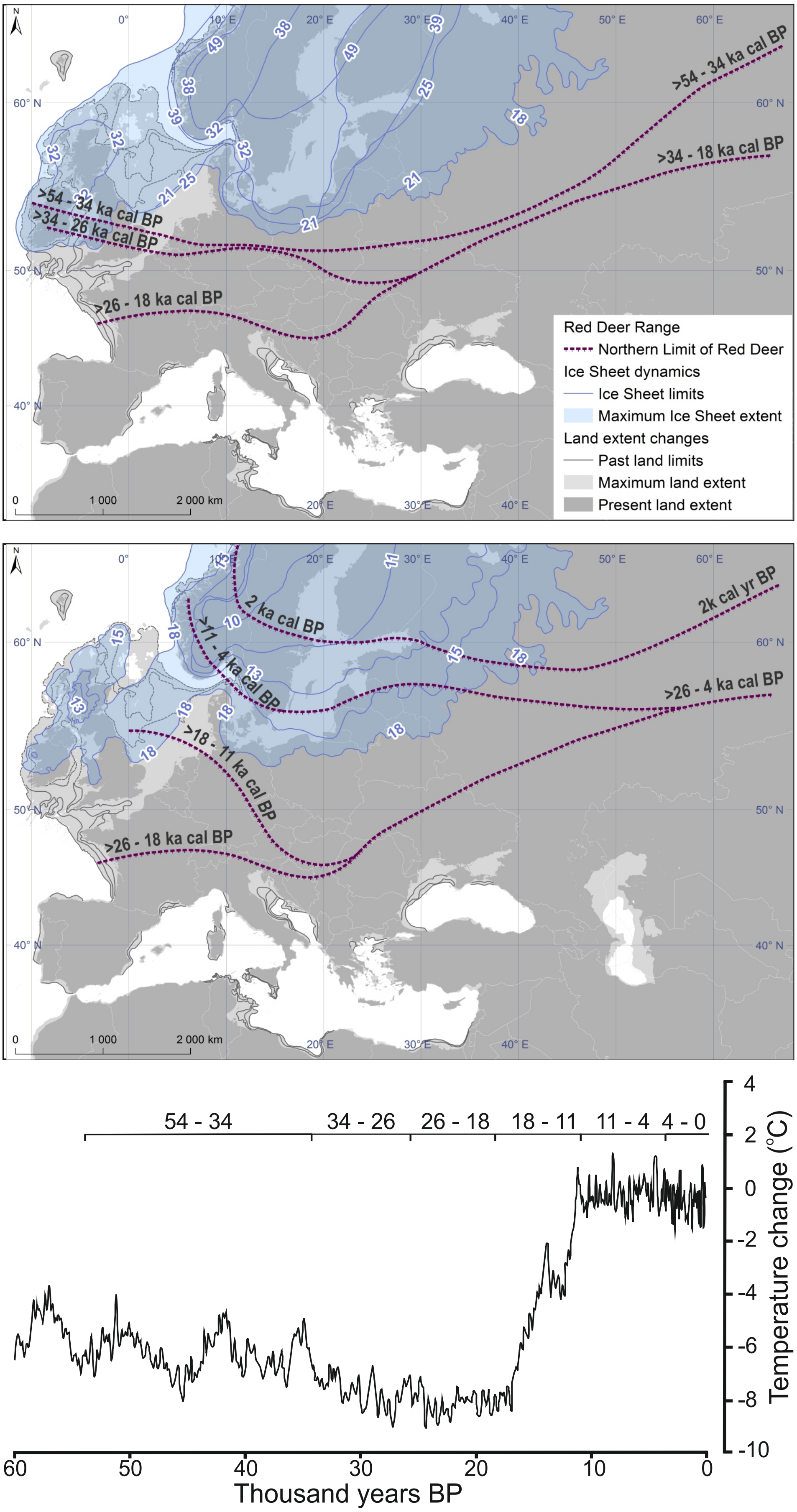
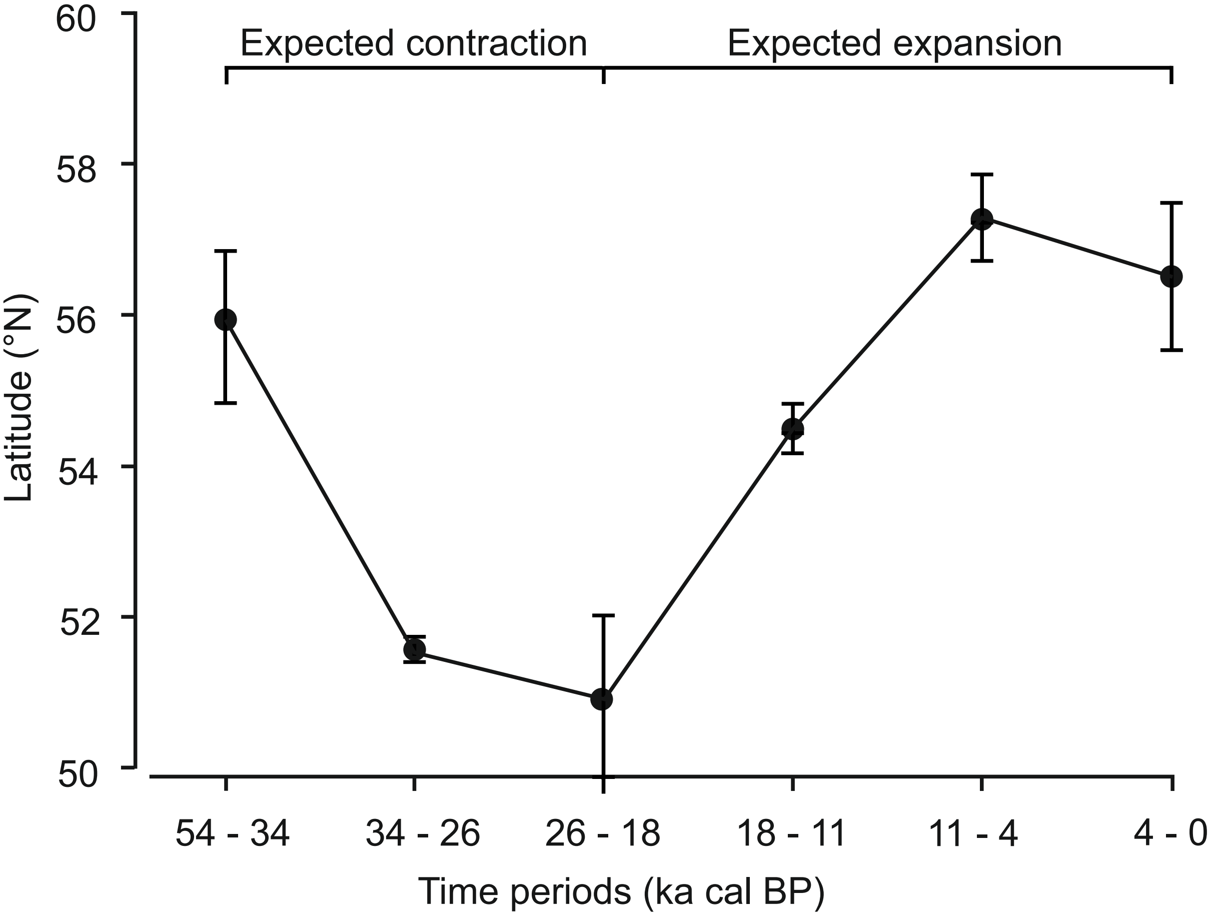
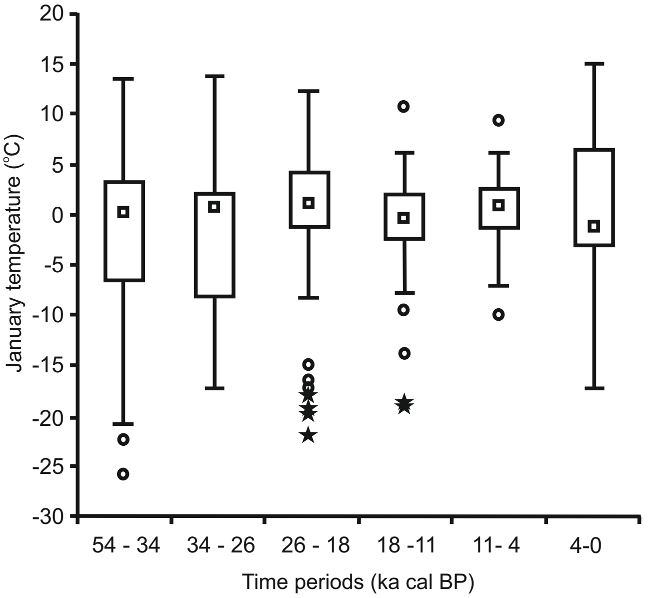
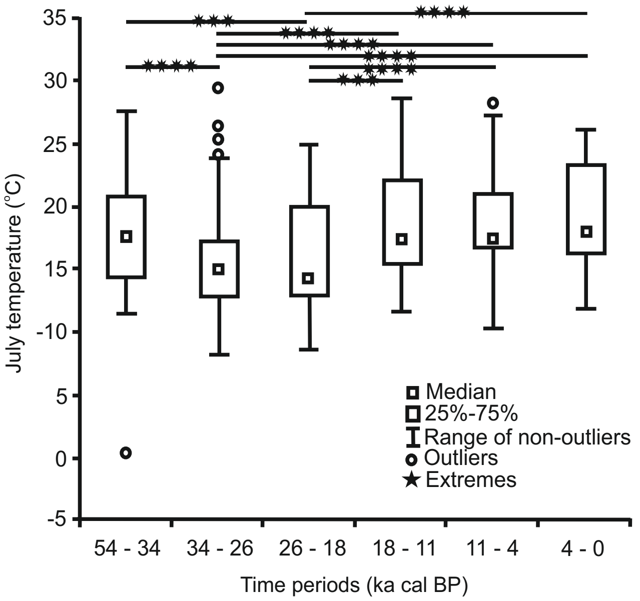
Sampling locations
Present red deer range
Present land extent
Maximum land extent (21ka)
Europe / Asia border

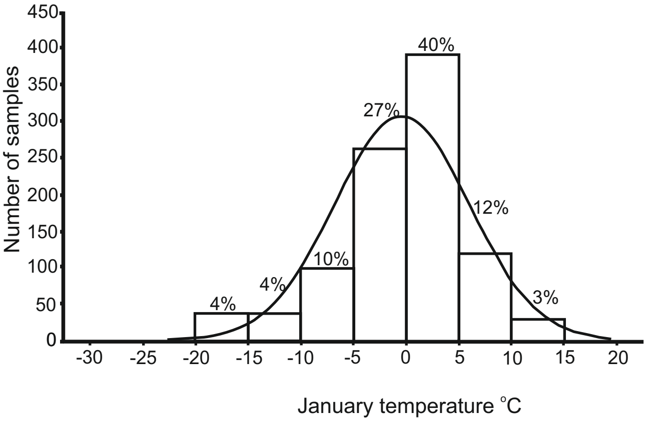


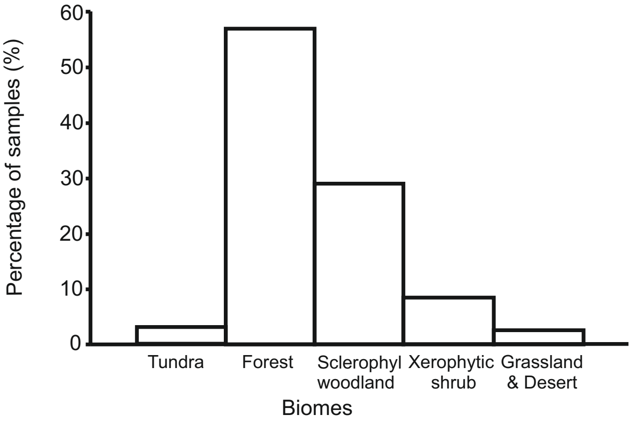
>54 - 34 ka cal BP
>34 - 18 ka cal BP
>34 - 26 ka cal BP
>26 - 18 ka cal BP
Red Deer Range
Northern Limit of Red Deer
Ice Sheet dynamics
Ice Sheet limits
Maximum Ice Sheet extent
Land extent changes
Past land limits
Maximum land extent
Present land extent
0
1 000
2 000 km
0°
10° E
20° E
30° E
40° E
50° E
60° E
60° N
50° N
40° N
2 ka cal BP
2k cal yr BP
>11 - 4 ka cal BP
>26 - 4 ka cal BP
>18 - 11 ka cal BP
>26 - 18 ka cal BP
54 - 34
34 - 26
26 - 18
18 - 11
11 - 4
4 - 0
Temperature change (°C)
4
2
0
-2
-4
-6
-8
-10
60
50
40
30
20
10
0
Thousand years BP


60
58
56
54
52
50
Latitude (°N)
Expected contraction
Expected expansion
54 - 34
34 - 26
26 - 18
18 - 11
11 - 4
4 - 0
Time periods (ka cal BP)


January temperature (°C)
20
15
10
5
0
-5
-10
-15
-20
-25
-30
54 - 34
34 - 26
26 - 18
18 -11
11- 4
4-0
Time periods (ka cal BP)


July temperature (°C)
35
30
25
20
15
-10
5
0
-5
****
***
****
****
****
****
****
***
Median
25%-75%
Range of non-outliers
Outliers
Extremes
54 - 34
34 - 26
26 - 18
18 - 11
11 - 4
4 - 0
Time periods (ka cal BP)


Number of samples
450
400
350
300
250
200
150
100
50
0
4%
4%
10%
27%
40%
12%
3%
-30
-25
-20
-15
-10
-5
0
5
10
15
20
January temperature °C


Percentage of samples (%)
60
50
40
30
20
10
0
Tundra
Forest
Sclerophyl woodland
Xerophytic shrub
Grassland & Desert
Biomes