Faunal and human biogeography during the Terminal Pleistocene

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PhD Thesis Bournemouth University

May 2018

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Volume I of II

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M.V. Knul

Abstract

The evocative megafauna of the mammoth steppe, such as woolly mammoths and woolly rhinos, are part of a complex and changing faunal and environmental system. The dynamic processes leading to faunal change (including extinction) are currently not fully understood. In order to unravel these biogeographical processes, which may take decennia up to millennia, the latter part of the Pleistocene (60-10 thousand years ago) that involved large and irregular climate changes in Europe was investigated.

This project aimed to gain better understanding of the biogeographical processes of the mammals in this period. This was done by collecting published data on faunal assemblages and their respective radiocarbon dates. There are differences in the accuracy and reliability of the radiocarbon dates. To separate these, this thesis presents a standardised way of auditing radiocarbon dates to improve the comparison of studies in Palaeolithic Europe.

The changes in biogeographical ranges were studied based on the presence of mammal species throughout Europe. Species distribution modelling of current climatic niches provided a new quantifiable framework for defining the ecology of mammals in Europe today to enable the reconstruction of past environments. Based on this framework, this thesis investigated the non-analogue communities of the Late Pleistocene. The ecological niche models based on present-day distributions found that non-analogue combinations were unlikely in the past, although the data used may not reflect all climatic and biogeographic variability and so there were likely fleeting combinations of taxa not seen today.

Finally, the most famous, extinct and therefore non-analogue, taxon was investigated in detail: the Neanderthal. The climatic niche of the Neanderthal was explored with climatic niche modelling. The models confirm the Neanderthal was a temperate adapted taxon that retreated to the southwest of Europe during MIS3. Furthermore, the climatic niche model shows a tentative link where the Greenland Stadials had a negative impact on the distribution of the projected climatic niche in both climatic and geographic space.

This thesis therefore provides an integrated study with new frameworks and results on the biogeographic ranges of mammals in past environments, that are relevant for multiple disciplines such as archaeology, palaeontology, ecology and phylogeography.

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Acknowledgements

I’d like to pay tribute to my father Menno Knul and my colleague Dr. Rebecca Miller who both died during my time as a PhD candidate. I miss them.

There are not enough words to describe how thankful I am to all those who’ve guided, supported and aided me through my PhD and my life whilst writing this thesis. So here is the short version:

John: there would be no PhD without you. Thank you for your unquenchable enthusiasm for our field, your extensive guidance and training, your generous emotional and practical support, your teachings of the natural world (whether alive or fossilised), the life lessons, and all the coffees, wine evenings and double whiskeys over the past years.

Amanda Korstjens, Philippa Gillingham, my two second supervisors were brilliant. Mandy, thank you for all the behavioural insights, meticulous proofreading, the Dutch directness, en de gezelligheid. Pippa, thank you for teaching me how to analyse distribution patterns, how to climb and how to have a work-life-balance. I will make it to one of your gigs one day!

Keith Wilkinson, my beacon of sanity throughout the PhD. Your calmness was eye-opening. Thank you for giving me the chance to work on your projects and everything Armenian.

My gratitude goes out to: Paul Valdes, for providing the climate simulations. William Davies provided the archaeological data and advice. Adrian Lister and Tony Stuart, my PhD family, advised on the mammalian extinction patterns. Hans van der Plicht has taught me how to radiocarbon date my own samples in the lab and has considered all things 14C with me.

I am grateful for the discussions had on my work, field seasons and the new techniques taught by these people in no particular order: Thijs van Kolfschoten, Andre Ramcharan, Nick Ashton, Simon Parfitt, Simon Lewis, Rob Dinnis, Natascha Reynolds, Thibaud Devièse, Viviane Slon, Team Trou Al’Wesse and Team Armenia (especially Jenni!).

It was hard to leave my Dutch friends behind. Astrid, Lisa, I hope to see you more in the future. New friends were quickly made. Thank you all for being awesome! Especially: Gitte, Jenny, Hayley, Alex, Oxala, Ella, Kelly, Paul, Jackie, Katharine, and Hannah. Let’s go camping soon.

Joost, thank you for absolutely everything. Mamičko, dekuji že jsi mě držela tolika palečky a že jsi na mě myslela. Pomohlo to hodne.

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Author’s declaration

I confirm that this thesis is the result of my own work. Additional datasets and material used in this thesis have been fully referenced and acknowledged throughout.

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1 Introduction

The Late Pleistocene is the most recent period in which dramatic climate changes took place with both warming (Pleistocene-Holocene) and cooling (Last Glacial Maximum, LGM) events recorded (Lowe and Walker 2015). These large and irregular climate changes greatly influenced the distribution and genetic diversity of plants and animals (Hofreiter and Stewart 2009). Indeed, the threat posed by climate change on Late Pleistocene animals was very similar to the one posed by current climate changes on modern fauna (Lister and Stuart 2008; Proença and Pereira 2013; Ukkonen et al. 2011). However, research on how climatic change affects the ecological processes of organisms, is still at an early stage. Neo-ecology struggles to observe these long-duration ecological processes such as community assembly, migration and extinction, even in multidecadal studies (Vegas-Vilarrúbia et al. 2011).Present-day community structure largely assembled after the LGM and thus studies, such as the one presented here, should focus on longer periods of time to study the changes in such communities (Rull 2014). Studying these past processes may shed light on likely future processes regarding climate change and faunal range change (Townsend et al. 2008), which is essential since the extinction rate of terrestrial mammals is rising and may soon reach the height of a new worldwide mass extinction event (Barnosky et al. 2011; Proença and Pereira 2013).

1.1 Short background of the Late Pleistocene

1.1.1 Climate and vegetation

The Late Pleistocene is defined to start with the geomagnetic reversal called the Blake event during the Eemian interglacial (Marine Isotope Stage (MIS)5e, also known as the Ipswichian and Mikulinian and other names, based on geographic location and stratigraphy) and leads into the last glacial, the Weichselian (or Devensian and Valdaian, spanning MIS 5, 3, and 2) (Gibbard et al. 2010; Gibbard and Lewin 2016). The temporal scope of this thesis falls within the Weichselian (60,000-10,000 years ago or 60-10ka bp). The Late Pleistocene is characterised by long glacials (100,000 years) and short interglacials (15,000 years) (Lowe and Walker 2015; Pisias and Moore 1981).

The Weichselian has both warmer and colder periods of millennial and submillenial scale (see Figure 1.1). There are 17 submillenial events within the temporal scope of the thesis (60-10ka bp) called Dansgaard-Oesscher events (DO events), that comprise of cold phase Greenland stadials (GS) and warm phase Greenland interstadials (GI) (Rasmussen et al. 2014; Sanchez

Goñi and Harrison 2010). During this period, Heinrich events (HE) occurred, sometimes simultaneously with GS. Heinrich events are events where large numbers of ice bergs broke loose from ice sheets into the North Atlantic Ocean. These events are identified by ice rafted debris in stratigraphical sequences and so far six have been associated with GS, Figure 1.2 (Guillevic et al. 2014; Huntley et al. 2013; Rasmussen et al. 2014).

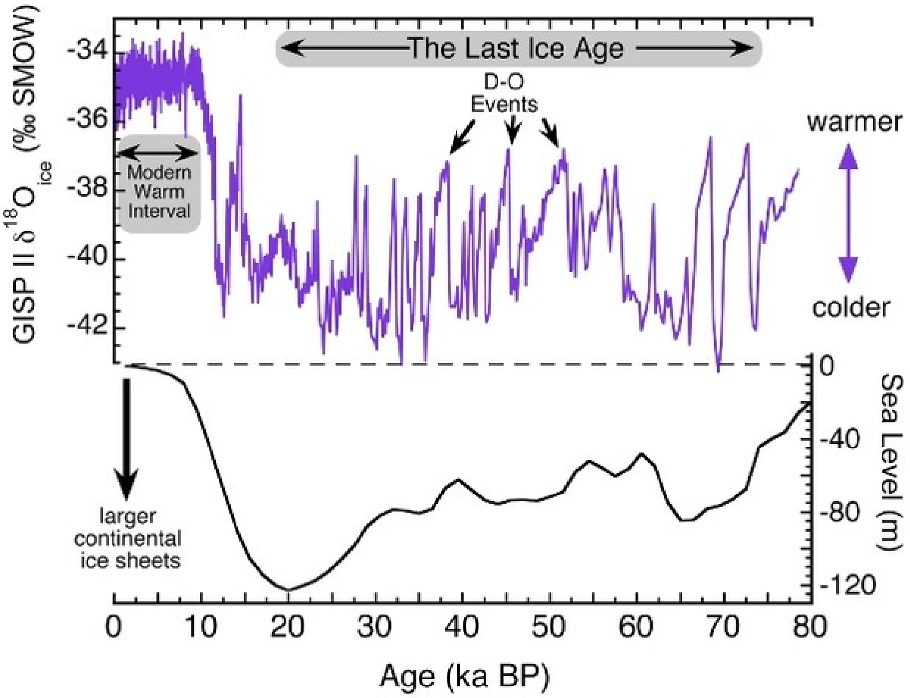

Figure 1.1 climate variability over the past 80,000 years. Top panel shows the oxygen isotope record (δ18Oice) from the Greenland Ice Sheet Project II (GISP II) ice core over the last 80,000 years (Stuiver & Grootes 2000). Colder air temperatures are indicated by more negative δ^{18}Oice values. Bottom panel shows changes in global sea level over the same time period (Waelbroeck et al. 2002), reflecting the waxing and waning of continental ice sheets during the last ice age. Figure and caption from Schmidt and Hertzberg (2011).

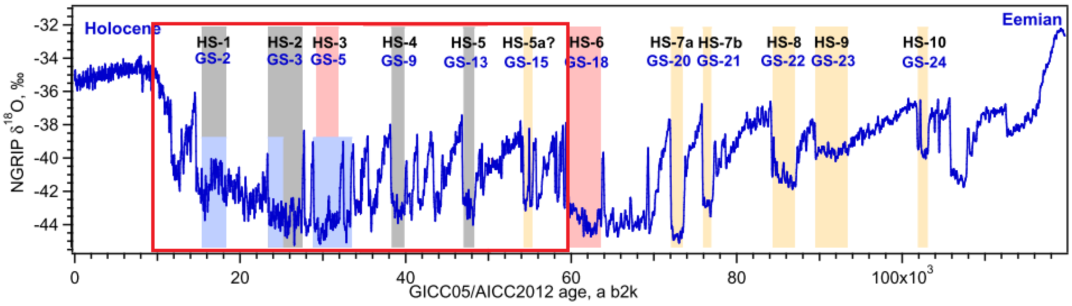

Figure 1.2 Dansgaard-Oeschger events (cold events marked as GS-) and Heinrich Stadials (HS) during the last glacial period. Blue line: NGRIP δ^{18}O, ‰. The coloured blocks are the HS. Grey: HS-1, HS-2, HS-4 and HS-5 mainly of Laurentide origin. Pink: HS-3 and HS-6 of European origin. Yellow for HS-5a and HS-7 to HS-10 minor ice rafter debris event. Blue: periods of low salinity. Red box is the temporal scope of this project. (Guillevic et al. 2014).

The high climatic variability during the Weichselian glaciation had a large impact on the environment in Europe. Large glaciers emerged on the mountain ranges and the sea-level dropped. The climatic variability created a mosaic of vegetation types throughout Europe in contrast to the banded vegetation we experience today (Roberts 2014). Three main stages within MIS3 (59-23 ka bp) have been recognised. Early MIS3 is dated from 59 to 44 ka bp and was initiated by a number of long and mild DO events (Van Andel and Davies 2003). This period was the stable warm phase of MIS3, marked by an increase in temperature and retreating ice sheets and glaciers. Middle MIS3 (44-37 ka bp) is regarded as the transitional phase, a relatively unstable period, with closely spaced relatively cold DO events, with a final mild GI-8 around 37 ka bp (Huntley and Allen 2003; Rasmussen et al. 2014). The end of MIS3 (37 – 23 ka bp) marked a cooling into MIS2. The mosaic vegetation structure of MIS3 was largely influenced by the structure and rhythm of DO events. Warm type DO events enabled the spread of pine and juniper among the grassy steppes in the south and a less pronounced spread of dwarf-shrub taxa and a weak appearance of pine, birch and juniper in the steppe-tundra north of the Alps (Huntley et al. 2013).

Recent stratigraphic research was able to place the Last Glacial Maximum (LGM) in GS3 on basis of the dust occurring in the ice cores (Hughes and Gibbard 2014). During the LGM, global ice cover reached it greatest extent, with the largest ice sheet over Scandinavia and Finland, a major centre in the Baltic region and another major centre in the Alps. The maximum extent of the Fennoscandian ice sheet in the southwest (Germany) was reached around 28 ka and in the east between 17-15 ka (Bell and Walker 2005; Clark et al. 2009). It was very dry and cold with sparse vegetation and steppe tundra to polar desert in Northern Europe (Barron et al. 2003). In Southern Europe, open grasslands prevailed with isolated pockets of forest in sheltered areas (Guthrie and Van Kolfschoten 2000).

After the LGM, Europe slowly began to warm up towards the Holocene, with an intermediate warm phase the Bølling/Allerød (GI-1 circa 14.7–12.6 ka bp). This temporarily allowed temperate vegetation to return to Europe, such as pine, oak, birch, hazel and fir (Barbaza 2011). After the Bølling/Allerød, the vegetation returned to the shrub-tundra and steppic environments of the Late Pleistocene. The early Holocene started at 11.5 ka bp with the onset of rapid warming of 15˚C over 1500 years (Bell and Walker 2005). Sea levels rose dramatically due to the vanishing of the ice sheets. The warmer and wetter conditions enabled tree species to recolonise Europe. This quick recolonization led to a chaotic period with non-analogue co-occurrences, such as the aspen – birch combination at the retreating edge of the Fennoscandian ice sheet (Roberts 2014).

1.1.2 Late Pleistocene mammals

The changes in climate and vegetation had a marked influence on the mammalian community in Europe. The predominant environment, created by the climatic variability, was lush grass steppe and tundra-steppe mosaics that were dry and received minimal snow cover - often referred to as the 'mammoth steppe' (Guthrie 1982, 2001; Markova et al. 2013; Zimov et al. 2012). The mammoth steppe stretched from mid and northwest Europe all the way across Beringia into North America. For a tundra-steppe environment, the grasses of mammoth steppe created a reasonably high productivity environment that supported the co-occurrence of the woolly mammoth, woolly rhinoceros, bison, aurochs, musk ox, horse, reindeer, saiga antelope, red deer, elk, giant deer, hyena, wolf and lion (Guthrie 1982); Figure 1.3. Apart from the extinct taxa, this combination of species cannot be found today with extant taxa, such as the Pleistocene combination of the saiga antelope, that retracted to southwest Asia, and the reindeer, that is now found in northern Palearctic (Guthrie and Van Kolfschoten 2000; Musil 1991).

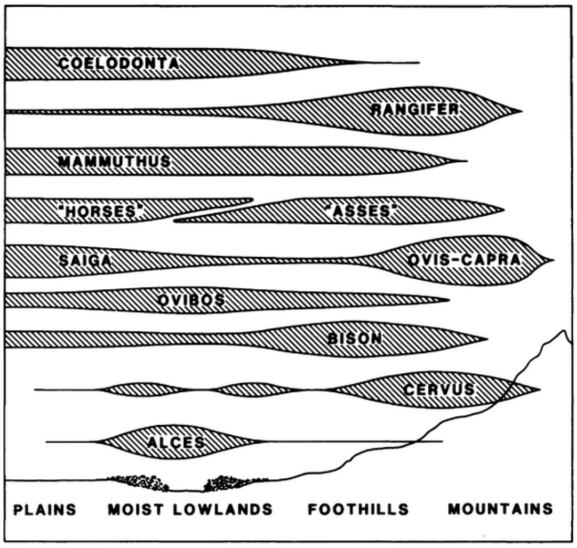

Figure 1.3 Mammalian herbivores are frequently separated by habitat preferences. The width of the illustrated bands indicates the relative abundance of the taxon at a particular habitat. (Guthrie 1982)

The so-called interglacial survivors (mammals with expanded ranges during MIS5e) had trouble coping with the open dry and cold landscape of MIS3 and retracted into more temperate refugia (Stuart 1991). For some taxa, the refugia did not meet their needs and the taxa went extinct. This was the first wave of megafaunal extinction in Europe and included the Neanderthal, Merck's rhinoceros, narrow-nosed rhinoceros, straight-tusked elephant, cave bear and spotted hyena (Stuart and Lister 2007). Roe deer, brown bear, and wild boar, also in refugia at that time, managed to survive (Randi et al. 2004; Valdiosera et al. 2007). The second wave of extinctions came with the warming towards the Holocene. Increased temperature and humidity changed the flora into the current vegetation belts with an increase of boreal and temperate forests, dismantling the vast Mammoth Steppe (Roberts 2014). The taxa retracted into various refugia, with most retreating to the north east (Siberia), but others like the saiga antelope to the southeast. Some taxa could not maintain healthy populations in these refugia, which led to the second wave of extinction which included the woolly mammoth, woolly rhinoceros, giant deer, and cave lion (Stuart and Lister 2007).

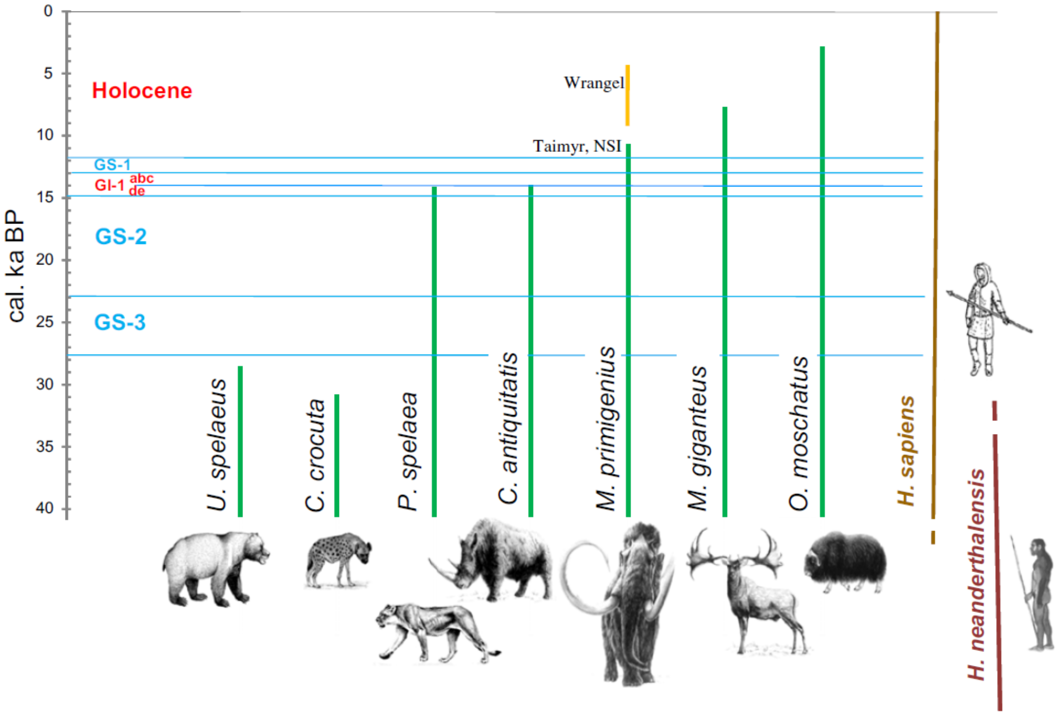

Figure 1.4 Eurasian megafaunal extinctions with the interglacial survivors and glacial survivors shown. The cold stages (GS) are indicated in blue and the warm stages (GI) are indicated in red. Picture from Stuart and Lister (2013).

Further into the Holocene the aurochs and wild horse go extinct as well (Gaunitz et al. 2018; Mona et al. 2010). Other taxa such as the bison, elk, reindeer, and arctic fox survive in their respective refugia today (Barnosky 2007; Stewart and Dalén 2008; Stewart et al. 2010). The onset of the Bølling/Allerød and the beginning of the Holocene enabled the recolonization of Europe by more temperate taxa, although the Younger Dryas caused a temporary contraction. The south-central regions of Europe were less affected by the Younger Dryas, with forested areas and fauna with wild boar, roe deer and red deer remaining (Nielsen 2013). Increasingly, techniques to look at ancient DNA (aDNA) point to the recolonization from cryptic refugia in more northern areas as well as population expansions from the east (Randi et al. 2004). The classic south-to-north expansion model has proven to be more complex, and models with potential source-and-sink regions may help identify distribution changes in mammals (Ohlemüller et al. 2012).

These broad patterns, including the sympatry of taxa in the mammoth-steppe fauna and the extinction of certain megafaunal taxa, have slowly started to emerge from decades of research (Lister and Stuart 2008). Recognition of the importance of such studies has developed because the Late Pleistocene has been regarded as an analogue for the current biological processes and geographical spread (Townsend et al. 2008). Understanding of the past responses of mammalian taxa to climate change can help model how the biota may react to future climatic changes. Furthermore, it enables us to observe biological processes that take place over longer timescales (Jackson and Erwin 2006; Stewart and Cooper 2008). Three interdisciplinary projects: PALEOFAUNA, FAUNMAP and the Stage 3 project have been the largest studies of Late Pleistocene biogeography to date, incorporating climate and vegetation change as well as the distribution of species through time and space (Graham and Lundelius 1994; Markova et al. 1995; Van Andel and Davies 2003). Stuart and Lister have done most of the single species distribution and extinction studies with direct dating programs (Lister 2004; Lister and Sher 2001; Lister and Stuart 2008; Pacher and Stuart 2009; Stuart and Lister 2007, 2011, 2012, 2014). Modern phylogeographic studies and the emergence of aDNA has enabled studies to be conducted on separate species to identify population level changes within species, expanding our knowledge on population dynamics and refugia (Brace et al. 2012; Dalén et al. 2007; Edwards et al. 2012; Fedorov and Stenseth 2001; Hofreiter et al. 2012; Jaarola and Searle 2002; Lorenzen et al. 2011; Randi et al. 1998; Santucci et al. 1998; Stiller et al. 2014; Valdiosera et al. 2007). Increased computing power enables researchers to start modelling the past distributions of species with methods like ecological niche modelling (Flojgaard et al. 2011; Nogués-Bravo 2009; Nogués-Bravo et al. 2010; Ohlemüller et al. 2012). Ecological niche modelling is a computational method that uses environmental variables to predict the taxon's distribution through time and space (Elith and Leathwick 2009). The reconstruction of the past distribution of the taxa beyond their fossil locations enables researchers to investigate the abiotic drivers in the taxon's distribution. Combined approaches of fossil analyses, ancient DNA studies and ecological niche modelling offer new perspectives on past populations (Lagerholm et al. 2017; Lorenzen et al. 2011).

The combination of new methods and an increased understanding in the individual behaviour of different taxa can now be used to investigate longstanding topics of research regarding the climatic adaptations of individual taxa (e.g. Stewart 2009), the existence of non-analogue communities (e.g. Stafford et al. 1999) and lastly the climatic niche of extinct megafauna including the Neanderthal (Banks et al. 2008). Each of these topics relies on the availability of archaeological and palaeontological data with a spatial and temporal aspect. The spatial aspect is simple: the location of where the fossil was found. However, the temporal aspect relies on the absolute dating techniques used in the past decades and the reliability of subsequent produced absolute dates for the faunal remains is variable.

1.2 Which techniques are used to date the Late Pleistocene and what are the problems?

To investigate biogeographical patterns through time, an absolute age must be connected to the faunal remains of interest to the studies. The most often used absolute dating method in the Late Pleistocene is radiocarbon dating. The method relies on the radioactive decay of carbon isotope ^{14}C to ^{14}N and has been in use since the late 1950's (Mook and Waterbolk 1985). This method can date back to 45ka bp for collagen and to 50 ka bp for other sample materials (Van der Plicht and Palstra 2014). Problems with the radiocarbon dating method are mostly caused by contamination and erroneous interpretation of the results. Contamination of the sample by younger or older carbon – when not sufficiently removed with pretreatment methods – can have a profound effect on the date determined, especially for samples of Pleistocene age (Bronk Ramsey 2008). Further problems are related to the association and context. If the sample is not contemporaneous with the rest of the archaeology or fauna, the date will be misleading and can change the interpretation of the archaeological or palaeontological pattern. Therefore, effective ways of separating the reliable dates from the unreliable dates are needed. This need has been recognised throughout the fields of archaeology and palaeontology and different methods of excluding the worst dates have been applied (Lister and Stuart 2013; Miller 2012; Verpoorte 2005). The most systematic auditing method has been proven to be good but not applicable to many published radiocarbon dates, because the required information has not been published (Graf 2009; Pettitt et al. 2003). The need for a systematic auditing method that can evaluate the published radiocarbon dates and make an assessment on their reliability, is addressed in Chapter 2 or this thesis (Seddon et al. 2014).

1.3 Palaeoenvironmental reconstructions and the climatic niche of modern mammals

Reconstructions of past environments provide context to the distribution and behaviour of taxa and especially help inform on the ways of life of past hominin populations (e.g. Gaudzinski-Windheuser and Roebroeks 2011). The Pleistocene environmental reconstructions are often multiproxy to provide the most accurate reconstruction (Huijzer and Vandenberghe 1998; López-García et al. 2012). However, a multiproxy approach is not always possible due to taphonomic constraints. In the Late Pleistocene, faunal remains are often very abundant and readily available, and they frequently provide a direct association with human behaviour (for example hunting). Environmental reconstructions are therefore often based on mammalian presences. The basic assumption is that the climatic (and further ecological) requirements of modern taxa have not changed (the uniformitarian principle (Scott 1963)) and therefore the modern tolerances can be used to infer the past climate (Reitz and Wing 1999). However, the present distribution of taxa, and thus the climatic tolerances expressed, are limited due to human pressures (Faurby and Araújo 2018). Furthermore plastic adaptations to temperature and environment, such as Bergmann's rule and observed hyenas during the Pleistocene, complicate the picture (Clauss et al. 2013; Klein and Scott 1989). There is thus a need to develop a framework which ensures that the use of modern analogues to reconstruct the past, incorporates the full range of climatic range that a taxon can tolerate (Seddon et al. 2014).

1.4 The existence of non-analogue mammalian communities during the Late Pleistocene

The mammoth steppe was an environment that does not exists today nor do the combinations of taxa that were living in it (Guthrie 1982; Lister and Sher 2001; Stewart 2009). For example, the reindeer and saiga antelope were sympatric in the past, but their ranges do not overlap present-day. However, the existence of these non-analogue communities or even non-analogue combinations of taxa have been disputed: they may have been an artefact of imprecise dating techniques and mixed stratigraphic assemblages (Coope 2006). New methods such as species distribution modelling and the increase of directly dated faunal remains together with improved precision of dating techniques warrant a new investigation of this issue. There is a need to investigate if non-analogue communities were a real phenomenon, since future environments may create similar situations, and it will also help to understand what drives the expansion and contraction of taxa through time as well as their stable realised niche (Seddon et al. 2014).

1.5 The new climatic tolerances of the Neanderthal

The Neanderthal has been discovered over two hundred years ago and slowly the paradigms on its behavioural abilities and climatic tolerances are shifting (Roebroeks and Soressi 2016). The Neanderthal has been classed as a hyper-arctic adapted hominin, exceptionally suited to deal with the glacial environments of the Middle and Late Pleistocene (Steegmann et al. 2002). However, research has gradually shown that the Neanderthal is likely to be more temperate adapted, based on physiological adaptations and faunal associations (Rae et al. 2011; Stewart 2004; Stewart et al. 2003), as well as Neanderthal exploiting Mediterranean environments (Finlayson et al. 2016; Tzedakis et al. 2007). As a result, little research has been done into the new climatic niche of the Neanderthal (Benito et al. 2017; Melchionna et al. 2018; Nicholson 2017). There is thus a need to investigate which abiotic factors drive the climatic niche of the Neanderthal and whether the climatic niche of the Neanderthal remained stable through time or shifted towards the extinction of the species (Seddon et al. 2014).

1.6 Thesis aims and objectives

This PhD thesis will address the following question:

What are the dynamics of biogeographic ranges, in response to the climatic changes during MIS3 to MIS1, of mammal species (including Neanderthals) found at archaeological and palaeontological sites?

In order to answer this question, this research aims to address the following sub-questions:

1. Which radiocarbon dates in the database are reliable so they can be used for further analysis?
2. Can modern data be used to infer biogeographic ranges for Pleistocene populations?
3. Do non-analogue mammalian faunas exist during MIS3 and MIS2?
4. What is the climatic niche of the Neanderthal and how does it develop over time?

1.6.1 Research Objectives

1. To test the hypothesis that we can pinpoint faunal and human presence more securely by using dates on materials best associated with them (relates to research question 1).
2. To test the hypothesis that uniformitarianism does not always hold for Pleistocene populations of taxa when constructing their biogeographic ranges (relates to research question 2).
3. To test the hypothesis that non-analogue communities existed and are not a result of imprecise dating methods (relates to research question 3).
4. To test the hypothesis that the Neanderthals had a temperate climatic niche and that the suitable area for the Neanderthal in Europe contracted towards its extinction (relates to research question 4).

1.6.2 Thesis structure

This thesis consists of this introduction (Chapter 1) which is followed by four research chapters, each addressing the aims and objectives set out above. Every chapter has its own introduction into the topic, methods, results and discussion section. The thesis is concluded by a discussion chapter that summarises and evaluates the findings of the individual chapters as a whole (Chapter 6).

Chapter 1: Introduction

This chapter provides context to the thesis in the form of a review of the relevant literature and provides background information to the time period studied. The gaps in knowledge are identified and research aims and objectives are presented.

Chapter 2: Improving the reliability of published radiocarbon dates

This chapter presents a comprehensive database of current information on species assemblages and their estimated dates in the Late Pleistocene. The chapter identifies the issues with the dating methods used for the Late Pleistocene and presents an auditing method that enables the researcher to select only the most reliable absolute dates. The data assembled and evaluated in this chapter form the basis for the analyses conducted in the following research chapters. This chapter addresses research question 1 and objective 1.

Chapter 3: Implications of predicted climatic niche of mammals today on palaeoenvironmental reconstructions of the Late Pleistocene

This chapter identifies the difficulties of creating an environmental reconstruction based on the presence of mammalian faunal remains. It develops a quantitative framework for researchers to use when making environmental reconstructions by using ecological niche modelling. The resultant framework and predicted distribution of modern taxa is used in Chapter 4. This chapter addresses research question 2 and objectives 1 and 2.

Chapter 4: The case for non-analogue faunas. Modelling the impact of Late Pleistocene climate change to species-specific distributions.

Chapter 4 investigates the existence of non-analogue communities by ecological niche modelling. The predicted climatic niches in Chapter 3 are projected to the past to investigate if taxa that are allopatric today could be sympatric in the past, based on their current climatic niches. This chapter addresses research question 3 and objective 3.

Chapter 5: The predicted Neanderthal stable realised niche and the contraction of its geographic range.

The presumed climatic tolerances of the Neanderthal has gone from hyper-arctic to temperate adapted (e.g. Rae et al. 2011; vs. Steegmann et al. 2002). This chapter investigates the climatic niche of the Neanderthal and how the climatic niche develops through time to the extinction of the taxon. This chapter addresses research question 4 and objective 4.

Chapter 6: Discussion

This chapter evaluates the research presented in Chapters 2-5. It discusses limitations to the research and makes recommendations for future research building on the findings of this thesis.

1.6.3 Research ethics

The Research Ethics e-module and Ethics checklist were completed and approved by Bournemouth University. Ethical considerations for this thesis were minimal since no live subjects were studied. Most data used in this thesis are open-source or gathered from publications and all are suitably referenced. The climate simulations of the BRIDGE team (used in Chapter 4 and 5) are closed data and were used with prior agreement and acknowledgement of the BRIDGE team.

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2 Improving the reliability of published radiocarbon dates

2.1 Introduction

Palaeolithic archaeology relies on absolute dating techniques to construct chronologies of human presence in Europe. Radiocarbon dating is a widely used absolute dating technique that is able to date the past 50,000 years and has been used by researchers for over 60 years (Bronk Ramsey 2008; Povinec et al. 2009). Because of the longevity of this dating method, there are differences in the accuracy and reliability of radiocarbon dates. Over the past years, the accuracy and precision of the radiocarbon dates has greatly improved following changes in sampling methods, dating techniques, and analyses (Gillespie et al. 1977; Godwin 1969; Millard 2006; Mook and Waterbolk 1985; Taylor et al. 2014; Waterbolk 1971; Zazzo and Saliège 2011). However, radiocarbon dates of varying reliability are being used due to the increased popularity of comparative chronological studies that use large databases of radiocarbon dates (Miller 2012). To separate the reliable from the unreliable radiocarbon dates, an auditing process is required to evaluate every radiocarbon date. Unfortunately, there is no consistency in the auditing process, and many researchers still create their own auditing criteria specific to their research focus (Graf 2009; Lorenzen et al. 2011; Stuart and Lister 2012). This results in scholars including radiocarbon dates that others have excluded, and in turn leads to incomparable chronologies, making it more difficult to study human presence in Europe. This study presents validation schemes to standardise the auditing process, and applies the schemes using three sites.

The present validation schemes are based on the information that is available in the published record and considers technological advances in the dating method. Each radiocarbon date is considered individually by methodological and contextual criteria, after which a verdict is given that represents the reliability of each radiocarbon date. After the initial validation, the radiocarbon dates can contribute towards research questions that are based on the contextual quality of the sample. After considering the context per sample, a final auditing verdict of poor, fair, or good is given to the radiocarbon date.

An alternative auditing method that assigns a numeric grade to every radiocarbon date is used as a comparison (Pettitt et al. 2003). This is the first published auditing method that equally separates methodological and contextual assessment of the radiocarbon dates. The user follows a multiple-choice system which results in a grade (0-30 points), with a pass rate of above 16 points. The auditing method is comprehensive, but the required information to go through the multiple-choice system is sometimes lacking in the publication of the radiocarbon date. This makes this auditing method less suited to deal with large amounts of published radiocarbon dates (Graf 2009). This auditing method is used to compare the outcomes of both methods as a way to test the method of the present study.

2.2 Materials and Methods

2.2.1 Materials

Theoretical basis: the dating method

A brief summary of the radiocarbon dating method will be provided here, more detailed information is published (Bronk Ramsey 2008; Mook and Waterbolk 1985; Taylor et al. 2014). The radiocarbon dating method is based on the occurrence of three isotopes of carbon, ^{12}C, ^{13}C and ^{14}C. Whilst ^{12}C and ^{13}C are stable and occur frequently, ^{14}C is very rare and unstable. The radioactive ^{14}C is produced in the atmosphere by the interaction with nitrogen and cosmic ray neutrons, after which it is taken up in the global carbon cycle (i.e. plants and animal) and decays back to ^{14}N. The decay rate is assumed to have a half-life of 5730 years (although the 5568 years are used due to the research history), which is used to calculate the age of the object. The dating is done by measuring the isotopic ratio of $^{14}C/^{12}C$ by either measuring the decay rate (conventional methods) or by counting the atoms directly (Accelerator Mass Spectrometry hereafter AMS). This ratio is corrected for fractionation and compared to the standard ratios, followed by calculating the radiocarbon age with the half-life value. Since the ^{14}C concentration changes in the atmosphere through time, the radiocarbon age cannot be used as an absolute age and has to be calibrated. Calibration is done with available calibration curves of OxCal and IntCal that match the radiocarbon date (and error) to the curve where the ^{14}C concentration is equal.

Problems with the radiocarbon dating method have also been discussed and many methodological and technical improvements have been made (Gillespie et al. 1977; Godwin 1969; Millard 2006; Mook and Waterbolk 1985; Taylor et al. 2014; Waterbolk 1971; Zazzo and Saliège 2011). These problems are mostly based around the nature of the samples and less on the methods and techniques used (Mook and Waterbolk 1985).

Theoretical basis: Sample materials and their problems

The ^{14}C date quality relies heavily on the state of preservation of the sample material that was dated (Van der Plicht and Palstra 2014). If the material has a good state of preservation, with little contamination by modern carbon and not preserved with preservatives or glue, it is likely a methodologically good date will be produced. How informative the date is for the archaeological or environmental narrative is highly dependent on the context of the sample. The four most used sample materials in the Palaeolithic that can be used for ^{14}C dating each have their own advantages and disadvantages for this process.

Collagen

Bone, antler, teeth, and ivory are most frequently used for dating. They provide a date on the archaeological event by association and can additionally provide information relating to the species that was dated (environmental and dietary factors via stable isotopes) and humans that left their trace on the sample (butchery marks etc). This group of materials is usually dated by their organic collagen fraction (sometimes called gelatin or protein remnants) (Brown et al. 1988).

The preservation of collagen is variable and is highly dependent on environmental conditions. The degradation of collagen can cause a loss of available collagen for dating and may make it more prone to absorb contaminants (Brock 2013; Vincke et al. 2014). To remove any younger carbon, pretreatment methods have been steadily improving over time. The most recently developed pretreatment method is ultrafiltration, where the gelatinized collagen is filtered for high molecular weight components, since contaminants consist of lower molecular weight components (Brock 2013; Higham et al. 2008). This pretreatment step is especially suitable for the older (Pleistocene) samples, producing older dates that are in better accordance with the charcoal dates (Higham et al. 2008). However, the rigorous cleaning of collagen may result in low collagen yields, so low that the sample can’t be dated. In the case of poorly preserved bones this method is too rigorous. More research is being undertaken on what exactly the ultrafiltration step does and how the filtration procedure can be improved (Brock 2013). Some argue that the effect of other pretreatment steps (intensity and duration) has a greater influence on the eventual age of the date than the ultrafiltration does (Fülöp and Heinze 2013). Cleaning the ultrafilters might not be sufficient to remove all the contamination (Minami et al. 2013). Therefore, new filtering techniques such as nanofilters are being developed (Boudin et al. 2013a). However comparison dates on the Niederwenigen mammoth bones show that the adapted Longin method is enough to decontaminate the sample and that the extra filtration step may not be necessary (Hajdas et al. 2011). Especially when the %C and %N is within the modern range, ultrafiltration should not be necessary (Van der Plicht and Palstra 2014).

Charcoal

Charcoal had already been recognised as an excellent material for ^{14}C dating in the 1950's (Matson 1955). When organic materials are charred they retain their physical structure, but the chemical properties change enabling the material to withstand decomposition to a greater degree after burial (Braadbaart and Poole 2008; Schmidt and Noack 2000). This presumed inertness makes the material excellent to date since it is less prone to degradation and will survive in most depositional environments. However, studies have revealed that charcoal does occasionally degrade and absorb exogenous (mostly younger) carbon (Bird et al. 2014; Braadbaart and Poole 2008; Braadbaart et al. 2009; Wood et al. 2012).

In order to remove contamination by rootlets and exogenous carbon, pretreatment methods have been developed. The most common pretreatment method is ABA (acid-base-acid wash) and is used at most radiocarbon dating laboratories. Since the ABA is not always able to remove all the younger carbon from old (Pleistocene) samples, a more rigorous procedure has been developed: ABOX (acid-base-oxidation with stepped combustion) which has led to older and more accurate dates in the Oxford laboratory ORAU (Bird et al. 1999; Wood et al. 2012). However, a cross-dating study with Groningen indicates that the ABA protocol used there produces equally good dates (Haesaerts et al. 2013). As with the ultrafiltration of bone, the ABOX pretreatment can remove too much from highly degraded samples, rendering the remaining sample too small to date (Wood et al. 2012).

Shell

Shells are frequently present at archaeological sites. When dating shell, it is necessary to identify the species. Terrestrial gastropods incorporate ^{14}C-deficient (dead) carbon from the local geology into their shells when growing. This can result in a date that is up to 3000 years too old (Pigati et al. 2010). Other species are prone to absorb younger carbon into their shells when they start to degrade after burial. The composition of carbonate polymers in shell is species specific. Some will consist of 100% calcite, others of 100% aragonite, and every mixture in between. The calcite in the shells is prone to recrystallization which can lead to the incorporation of younger exogenous carbon into the shell. Recent advances in pretreatment technology have led to improved dating of the shell carbonates reducing the problems with recrystallization and secondary carbon (Douka et al. 2010). The date may also be influenced by the water the mollusc lived in or consumed if the water carries ^{14}C-deficient carbon, called the reservoir effect (Ascough et al. 2005; Rick et al. 2005). For samples influenced by a marine environment, calibration curves are available, mitigating the age offset (Reimer 2013; Stuiver et al. 1986).

Plant remains

Plant remains that have not been charred have been recognised as excellent dating materials, especially trees. Trees store atmospheric ^{14}C in annual concentric layers (tree rings). As the tree grows, it builds an archive of the amount of atmospheric ^{14}C per year. This makes very accurate dating possible, and is the origin of the calibration curve (Godwin 1969).The structure of wood (high in cellulose) makes it able to withstand harsh pretreatment methods (Mook and Waterbolk 1985). The longevity of some tree species such as oak, can produce dates that are older than when humans made use of the wood (Allen and Huebert 2014). Therefore, if possible, species identification and reconstruction from what part of the tree the piece comes from may avoid the issue. Also, a preference to use branch wood for fuel mitigates the old wood effect (Crombé et al. 2013). Recent methodological advances show that liquid scintillation spectroscopy may date wood samples down to the 50-70 kyr range when proper blanks, these are radiocarbon free materials that are prepared as the rest of the samples to detect contamination added during the process, are used (Hogg et al. 2007).

Plant macro remains such as seeds, leafs or plant fibre are also used for radiocarbon dating. Especially materials that build up annually (such as hazelnuts or annual crops) can be dated with the greatest accuracy, whilst bark may build up over multiple years (especially tree species that can reach high ages). Overall, there do not seem to be big differences in pretreatment methods or problems compared to wood (Godwin 1969). Post recovery storage can however influence the age of the macro remains because of the growth of fungi or micro-organisms in the wet samples (Wohlfarth et al. 1998).

Dating the macro remains from peat is more difficult. Roots entering the peat, decomposition followed by displacement of dissolved organic carbon and the formation of methane, can lead to younger carbon absorption in older carbon of plant remains (Godwin 1969; Nilsson et al. 2001). Dating peat bulk samples will give very wide date ranges that may be incorrect due to issues mentioned above (Van der Plicht 2012). Dating single entity remains at least removes the issue of bulking and a study by Nilsson and colleagues shows that dating *Sphagnum*, a common mire species, produces the most reliable dates (Nilsson et al. 2001).

If there are no plant macro remains present, one can date the pollen that are present in peat or sediment (Brown et al. 2006). However, if dating the pollen, one should have a time and depositional control by annual lamination in the sediment and complementary macro remains if possible. Without these controls, when the pollen samples are not pure enough, one cannot intercept false dates (Kilian et al. 2002).

2.2.2 Publication issues

It is important to evaluate the ^{14}C date (or sets of dates) to assure it represents the event in question accurately (Waterbolk 1971). It is generally agreed that critical evaluation of the ^{14}C date is necessary and different evaluation approaches have been developed (Graf 2009; Pettitt et al. 2003; Taylor et al. 2014). However, few take the record of often poorly published ^{14}C dates into account (Graf 2009). The best manner to publish radiocarbon dates is by following the conventions designed by Millard (Millard 2014). Information is often lacking in older publications, with the possibly lacking information summarised in Table 2.1. When essential information on the ^{14}C date is lacking, such as the laboratory code or the sample material, it is very difficult to begin to assess the quality of a radiocarbon date and the radiocarbon date should not be used.

Table 2.1 Problems with publication of radiocarbon dates are divided into four topics that may be missing or are incomplete in the publication. If essential information is missing from the publication, the quality of the radiocarbon date is very hard to asses.

	Labelling	**Sample**	**Context**	**Methods**
Essential	Laboratory code ^{14}C age or calibrated	Sample material Bulk sample	Redated site	Conv/AMS
Useful		Species identification Human modification Post recovery preservation	Stratigraphy Association with archaeology Reworking Relation to other ^{14}C dates	Pretreatment method Quality control measurements Year produced

The laboratory code provides information regarding the radiocarbon dating facility and in some cases if the date has been produced on an AMS (such as GrA, OxA). The following number indicates how many radiocarbon dates have been produced and the first occurrences with new pretreatment protocols is sometimes listed with the laboratory code (Higham et al. 2008). The number thus gives you some indication on when the date was produced using what methods. Radiocarbon dates should be published uncalibrated, but early literature can be confusing in this matter: sometimes omitting to mention the pure radiocarbon date and only quoting the calibrated date. Sample material and if it has been bulked or not needs to be known, for the type of material dictates the methods used and the accuracy of the date as explained above. When redating programmes have shown older ^{14}C dates to be incorrect, these should be removed from the auditing process (Higham et al. 2014).

Genus/species identification and human modification help associate the sample to the research question, such as the dating of human presence. The genus/species identification informs the researcher on the direct presence of humans, but also on potential prey (herbivores) or competition (cave bear, hyena). It is unlikely for humans to have been present at precisely the same time as cave bear, as they likely competed for cave sites (Stiller et al. 2010). The size of the SE's however may mean the presence of the carnivore and the humans cannot be teased apart (for example if they occur within 50 years apart). If cut marks underlie gnaw marks on the bone the animal was probably exploited by humans, thus dating the event of human presence.

The context of the sample is important if the researcher wants to date an event by association (such as the age of a stratigraphic layer with Aurignacian lithic artefacts). Knowledge of the site's stratigraphy, possible reworking on the site, and relation to other ^{14}C dates within the stratigraphy are needed to make a proper assessment.

Finally, methodological information on the production of the ^{14}C date will inform the quality of the sample used. See below for a detailed explanation of the quality control measures. The year the date has been produced should be published; this allows an assessment based on the standard methods that were used in that year if they are not published alongside the radiocarbon date.

There are few labs that have published their methods and cross-dating experiments such as those of Groningen and Oxford (Brock and Higham 2010; Van der Plicht et al. 2000). Because of their clear publication record and high proportion of Palaeolithic radiocarbon dates (combined form 60% of the Stage Three project database), these two labs may be considered separately during the auditing sequence, whilst grouping the other radiocarbon dating facilities.

Quality control measures

The radiocarbon laboratories disclose supplementary information, quality control measures, with the radiocarbon date that can help evaluate if the produced date is correct. The quality control measures should be published with the radiocarbon date itself (Millard 2014). The provided information is dependent on the sample material and methods used. When dealing with conventional dates on any material and mostly with dates produced after 1980, the laboratories will provide the $\delta^{13}C$. The $\delta^{13}C$ (‰) is a ratio of ^{13}C:^{12}C or less commonly ^{14}C:^{13}C and is indicative of the organism's uptake. The organism's processes may result in a higher uptake of the lighter isotope ^{12}C compared to the heavier isotope ^{13}C, this is called isotopic fractionation and differs between groups of organisms (for example shells and terrestrial mammals). Fractionation can also accidentally occur in the laboratories during sample processing (Bronk Ramsey 2008). The value $\delta^{13}C$ represents the deviation from the standard VPDB (Vienna Pee Dee Belemnite, used as a standard because it is deprived of ^{14}C) and is used by most laboratories to correct the radiocarbon age for fractionation (Bronk Ramsey 2008). It is important to check the $\delta^{13}C$ value, for if the value falls outside of the accepted range there might be something wrong with the radiocarbon age (Stuvier and Polach 1977). Table 2.2 provides an overview of the $\delta^{13}C$ values for the most common sample materials mentioned in this paper. It is also important to note if the $\delta^{13}C$ was produced by the Isotope Ratio Mass Spectrometer (IRMS) or different methods, for only the IRMS measurement may be used for dietary reconstructions or corrections for the reservoir effect (Millard 2014).

Table 2.2 Mean $\delta^{13}C$ values for the main materials mentioned in this article. The full list is available in the paper by Stuiver and Polach (Stuvier and Polach 1977).

Material	**$\delta^{13}C$ per mil relative to VPDB standard**
Grains, Seeds, Maize, Millet	-10 ± 2
Marine Organisms	-15 ± 2
Bone Collagen, Wood Cellulose	-20 ± 2
Fossil Wood, Charcoal	-24 ± 2
Peat, Humus	-27 ± 3

If the date has been produced by AMS, part of the sample may have been analysed by an IRMS that measured the %C and in case of collagen and shell also the %N. The %C indicates if the sample was in good condition with a high percentage of carbon present in the sample. If there is a high percentage of carbon, it is likely that the resulting date is correct (Bronk Ramsey 2008). The %N indicates the quality of the collagen and in the case of shell, the species. The combination of the values %C and %N in collagen, as well their ratio are good indicators of a sample's (and eventual radiocarbon age) integrity. The value for %C should range between the 30 and 40% of carbon in collagen and the value for %N should range between the 11- 16% of nitrogen content, the ratio of the two falling in between 2.9 and 3.6 (Ambrose 1990; DeNiro 1985; Kuitems et al. 2013; Van Klinken 1999). The C/N ratio has already been widely used in this way (Higham et al. 2014), however not much attention has been given to the individual %C and %N values. One can get an adequate ratio even when the %C and %N values are extremely low or skewed. It is therefore of the utmost important to not only consider the ratio, but also the individual percentages.

Dating of bone, especially older bone is difficult (especially because of the lack of a proper measurement blank; a blank contains no 14C and shows if the process has introduced contaminant carbon and it works best when the blank comes from a similar environment as the samples); therefore the maximum datable age is recently set to 45ka bp (Van der Plicht and Palstra 2014). Any bones dated older than 45 ka bp should be infinite and considered with care (Van der Plicht and Palstra 2014).

Theoretical basis: the auditing method

The auditing method is designed on the basis of published literature, incorporating the advances and drawback of techniques in radiocarbon dating. The choices in the flowchart schemes are based on the differences in techniques with the major choices coming down to Accelerator Mass Spectrometry (here after AMS) / Conventional methods and the different types of pretreatment protocols as discussed above.

Both Conventional and AMS methods are able to yield excellent results and each method has its own drawbacks. For Conventional measurements a large sample is required, which is often not available for Palaeolithic sites. This may lead to bulked samples (organic sediment or multiple pieces of bone) which are contextually less certain. AMS can date small samples (i.e. >10 mg charcoal) but the influence of contamination on such a small sample is greater. Both methods are considered in the flowcharts.

The pretreatment protocols are laboratory dependent, and thus individual laboratories are sometimes mentioned. For example the OxA (Oxford radiocarbon laboratory) ultrafiltration method for collagen samples is scored as more reliable than their ABA protocol (Bronk Ramsey et al. 2007).

The final choices are based on the quality control measurements. The $\delta^{13}C$, and in the case of collagen %C, %N and C:N, are essential to evaluate the reliability of the radiocarbon date. When the values are outside the accepted range or not published, the assessed reliability of the date weakens (Ambrose 1990; DeNiro 1985; Kuitems et al. 2013; Van Klinken 1999).

Archaeological sites

The auditing method has been applied to radiocarbon dates present in the database that has been constructed for this thesis. The database temporal scope is MIS3 and MIS2 and the geographical limit is Europe up to the Ural and Caucasus mountain ranges. The database is an amalgamation of several existing databases: Stage 3, S2AGES, INQUA database v18 and PALEOFAUNA (Gamble et al. 2005; Markova et al. 1995; Van Andel 2002; Vermeersch 2017) and literature research. The database holds information on 3396 archaeological sites, the associated identified faunal remains in 1692 sites and a total of 15308 absolute dates. Due to research history (less sites and absolute dates), Eastern Europe is underrepresented. Of the absolute dates in the database, 89 % are radiocarbon dates which have been audited by the method in this chapter. The methodological audit has identified 10.8% good dates, 22.2% fair dates, 45.9 % poor dates and a final 21.1% unusable dates. For the associated fauna tables within the database, taxonomic choices have been made that are the same as the faunal database for the Stage 3 project and described as such in the publication (Stewart et al. 2003). For example, fauna identified as bison or aurochs have been lumped to Bos/Bison because they are taxonomically hard to distinguish, and all hyenas have been assigned to *Crocuta crocuta*. For all raw taxa in the database see Appendix Chapter 2. The database is available to researchers upon collaboration.

To show the workings of the auditing method, three archaeological sites with multiple layers and radiocarbon dates have been selected as an example: Abri Pataud, Grotte des Romains and L'Arbreda.

Abri Pataud is a Palaeolithic site in southern France (Les-Eyzies-deTayac, Dordogne region). It's located in a shelter in limestone cliffs and holds 14 occupation phases that relate to the Aurignacian, Magdalenian, Gravettian and Solutrean. The archaeological horizons are separated by sterile layers that are caused by collapse of the shelter roof (Movius et al. 1984). Layer 3 and 5 from Abri Pataud have been audited using to the present method, and these layers have also been audited by the alternative auditing method. Furthermore, layer 5 has been redated by Oxford (Higham et al. 2011; Pettitt et al. 2003).

Grotte des Romains is a rockshelter in a limestone cliff above the Rhône, in the Pierre-Châtel region (southern France). Of the six layers, Magdalenian is found in layer III and less material in layer II. Unfortunately, the layer is disturbed by rock fall and mixing from the layer above (Bocquet et al. 1970; Loebell 1980). This site is used for comparison because it is assessed by Pettit et al. in their method (Pettitt et al. 2003).

The third site is L'Arbreda, situated in the Bonyoles-Besalú Basin and is the southernmost of the three Reclau Caves (northeastern Spain). It is a collapsed cave with archaeological artefacts indicating Mousterian to Epipalaeolithic human presence. The archaeological levels (B, Solutrean to I, Mousterian) are determined by piece plotting of the artefacts (Wood et al. 2014). The difference between the Mousterian and Aurignacian is clear due to the use of different raw material sources, with the Mousterian made on local quartz and quartzite and the Upper Palaeolithic tools are made on imported flint (Bischoff et al. 1989). For this study the Mousterian level I is considered.

2.3 Methods

Four auditing schemes (Figure 2.1, Figure 2.2, Figure 2.3, Figure 2.4) were designed, one for each material category, because the type of material dictates the laboratory methods used as well as the research questions the sample can be used for. The descriptions take the reader through the schemes step-by-step.

A verdict is issued per radiocarbon date on basis of their methodological aspects as well as their contextual value. The following grading system is used: *unusable*, *poor*, *fair*, and *good. Unusable* indicates that there are such methodological problems with the radiocarbon date that it should not be used for auditing and further interpretation of the data. The next level is *poor*. This indicates that there are problems with the radiocarbon date and that the researchers need be cautious when including this date into their chronology. The verdict *fair* indicates that the radiocarbon date is of reasonable quality, *good* indicates that the radiocarbon date is trustworthy and should be included in further analyses.

2.3.1 Collagen flowchart (Figure 2.1)

The radiocarbon date is *unusable* for auditing if the publication suggests that there are pretreatment problems with the sample, the sample has been bulked (a combination of multiple bones), or the bone has been dated before 1980 when the improved Longin pretreatment protocol was not yet in place (Brown et al. 1988).

If the radiocarbon date passes this stage, the next step is to determine if the date has been dated by AMS or conventional methods. If it was dated by AMS, the next step is to determine the pretreatment method: was it pretreated by Groningen with the improved Longin protocol, by ultrafiltration at any lab, by Oxford (following their ABA protocol), or was the sample treated in another lab? If there is no additional information published along that the date is an AMS date, then the verdict is *poor*. The next step regards the δ13C value. When the value has not been published or is outside of the normal range, then the verdict is *fair*. If the δ13C value is present and within range, the next step is to look at the %C, %N and C/N ratio. If these (or in the least case the C/N ratio) are adequate, then the sample is marked as *good*.

When the date is produced conventionally, the next step is to determine if it has been dated by Groningen or another laboratory. If Groningen produced the date, and the δ13C is within range, the date is marked as *good*. All other labs, regardless of the δ13C, are marked as *poor*, based on dates that have turned out to be too young in other studies (Higham et al. 2011, 2008; Stevens et al. 2009).

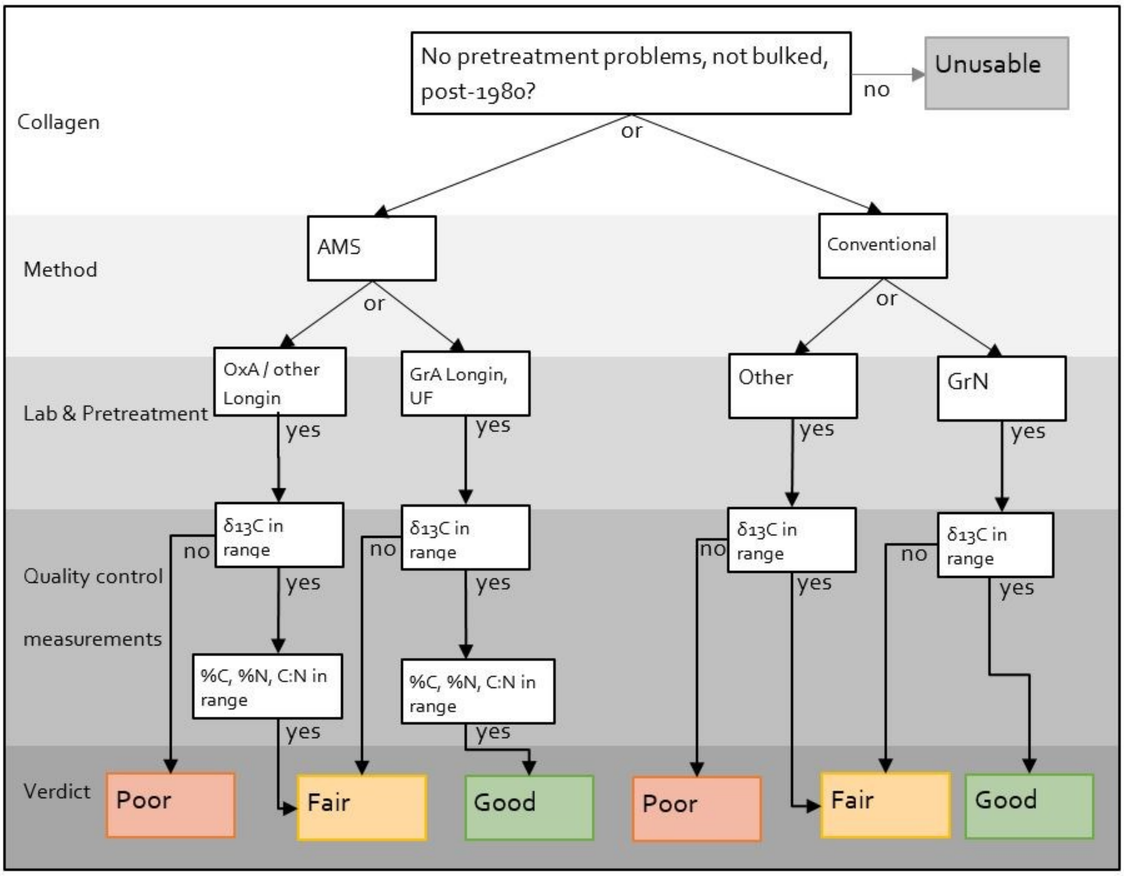

Figure 2.1 Collagen flowchart.

2.3.2 Charcoal & Wood flowchart (Figure 2.2)

The date may only be used if there were no pretreatment problems published and if the bulking of the sample (in conventional methods) has been done sensibly, for example from a single hearth feature.

For AMS dates: Groningen ABA and other lab ABox dates with a good δ13C are considered *good* dates. Groningen ABA and other lab ABox dates with a bad/not present δ13C are considered *fair*. Other labs with ABA pretreatment methods with a good δ13C value are considered *fair*. Other labs with ABA pretreatment methods with a bad δ13C value are considered *poor*.

For conventional dates: Groningen dates with within the δ13C range are *good* dates. Groningen dates with bad/not present δ13C are *fair* dates. Dates produced by other labs with a good δ13C value, the dates are *fair*. Dates produced by other labs with bad/not present δ13C are *poor*.

Charcoal and wood should both be identified to species. If the sample contains the outermost ring including the bark, that will negate the old-wood (long living trees) effect. Otherwise, this should be taken into account when using radiocarbon dates from circa the Last Glacial Maximum (when the standard errors become sufficiently small) and younger (Waterbolk 1971).

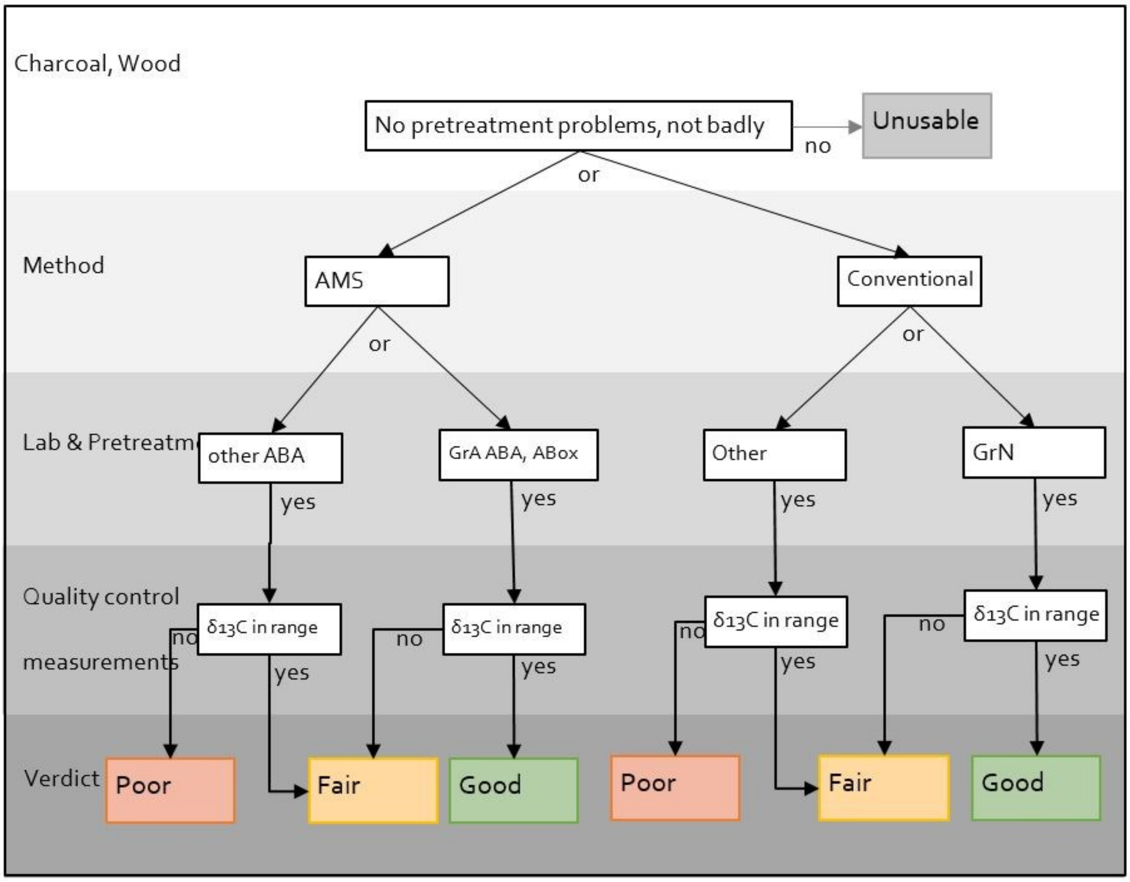

Figure 2.2 Charcoal and wood flowchart.

2.3.3 Shell carbonates flowchart (Figure 2.3)

In order to be able to audit the date further, the sample has to have been dated by AMS, identified to species, it has to be a marine specimen and the local reservoir effect needs to be known.

When the pretreatment method is unknown, the %calcite is unknown or outside of the calcite range or the δ13C is unknown or outside of the acceptable δ13C range for shell carbonates then the date is marked as *poor*. Is the pretreament CarDS and the %calcite is good, and δ13C as well, then the date is marked as *good*. If the pretreatment method was something else, but the quality control indicators of %calcite and δ13C are good, then the sample is considered to be *fair*.

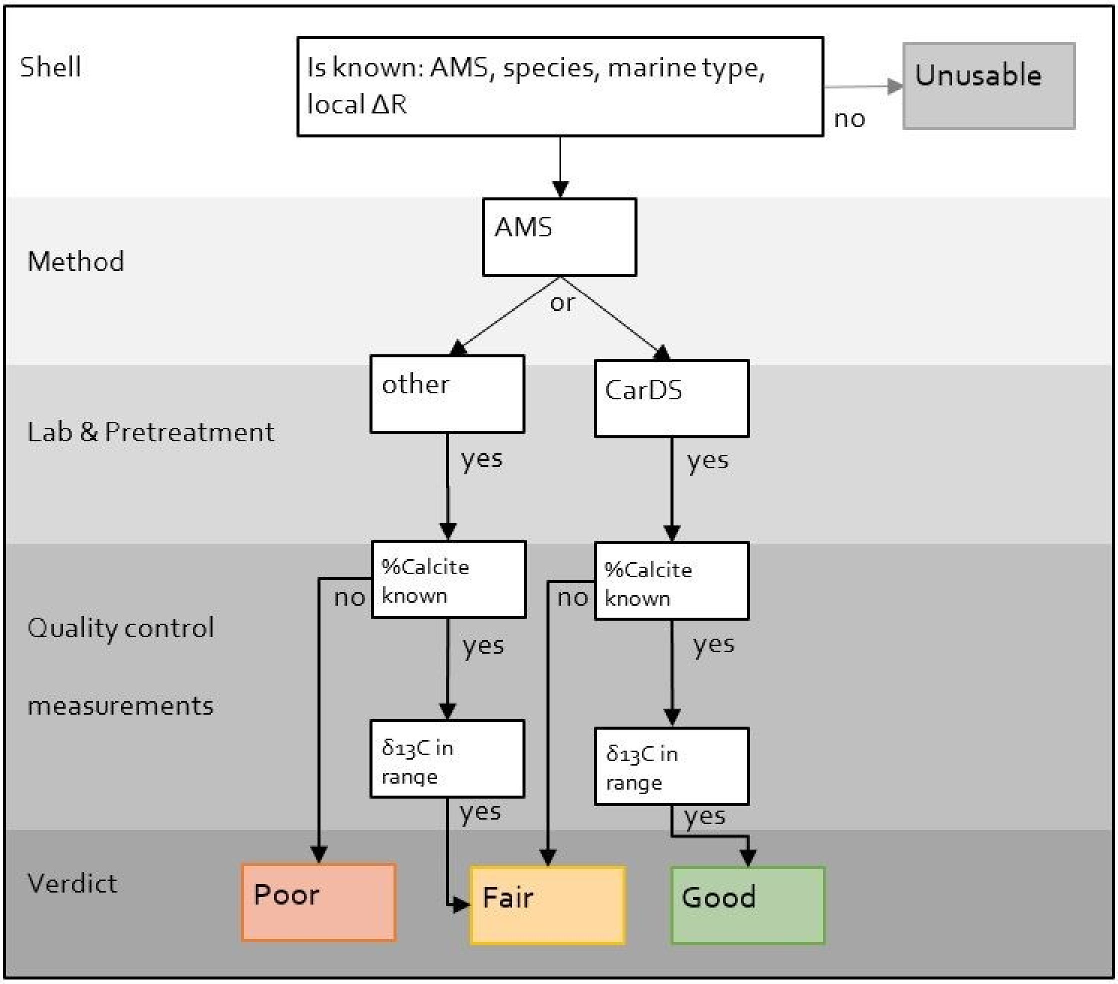

Figure 2.3 Shell carbonates flowchart

2.3.4 Context Flowchart (Figure 2.4)

After assessment of the methodological quality of the date, the interpretation of the date is reliant on the research question posed and consequently on the stratigraphy and context. There are three main research questions:

- Question 1: when humans were present (via direct dates);
- Question 2: when a faunal or floral species was present (via direct dates);
- Question 3: how old the associated archaeology/fauna is (by dating a sample within that archaeological horizon/ stratigraphic layer).

To identify human presence (Question 1) unambiguously, samples of human remains identified to genus or species, or samples with anthropogenic modifications (such as artefacts, cutmarks, or charring) are needed. The sample provides a direct date for human activity; irrespective of its stratigraphical or contextual position. To identify when a certain species was present (Question 2), a direct date on a sample identified to genus or species can be used. The stratigraphic context is of less importance. In these cases the sample itself will determine whether a genus/species is present or not at a certain time.

If one is interested in dating an event (i.e. the archaeology or presence of fauna in the stratigraphic layer or archaeological horizon/ATU, Question 3), the sample needs to come from a reliable stratigraphic context. Dating an archaeological horizon is difficult and extensive knowledge of the geology of the site is needed. If the provenance and possibility of reworking of the sample are not clear, it is much more difficult to associate it to the layer in question. Guidelines on assessing the stratigraphic integrity have been published widely (e.g. Boaretto 2009; Bowman 1990; Taylor et al. 2014).

The best samples that can be used for the Palaeolithic are those that are either human or have clear signs of human modification with a species ID and are from a good stratigraphical context, since such a sample may be used to answer all three 'levels' of research questions (Higham et al. 2011). However, since the archaeological record is patchy and such optimal samples do not occur frequently, it is down to the researcher to decide what level sample is acceptable for their research question in terms of accuracy.

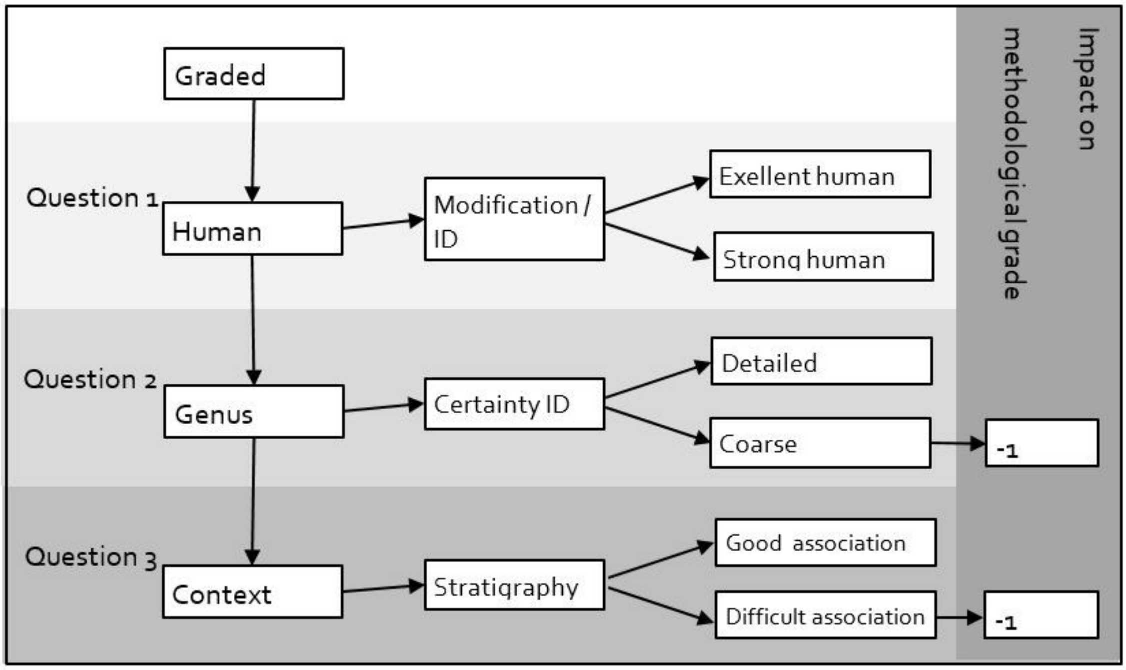

Figure 2.4 Context flowchart.

Each radiocarbon date should be evaluated with the flowchart that matches the sample material to get a value for the methodological quality of the date. It should also be placed within the research question framework of the last flowchart. If the sample is less ideally suited to use for a certain research question, reducing the methodological outcome by one grade is suggested (for example a *good* date with an uncertain context becomes *fair*). For example, if the date on a bone sample is audited as *good*, but the researcher wants to use the bone to estimate the age of the lithic artefacts and the geology of the layer is unresolved, the final audit should be brought down to *fair*. This means a good methodological date cannot be used to overcome a bad depositional context.

2.3.5 Multiple dates per layer / site

When the individual dates have been audited and the research question deals with stratigraphic association, including multiple dates over multiple layers, the researcher can proceed with Bayesian analysis in Oxcal (Bayliss 2009; Bronk Ramsey 2003). Bayesian analysis has quickly grown to be the standard way of reconstruction site chronologies within the radiocarbon age range (Bronk Ramsey 2003; Fernández-Ponce et al. 2013). The researcher can include a measurement of uncertainty for each radiocarbon date based on the assessments within the Oxcal or the researcher can test whether the dates marked fair (as opposed to good) are considered outliers by Oxcal (Bronk Ramsey 2008).

2.4 Results

The auditing method was applied to three sites and compared to the alternative auditing method, as well as to recent redating programmes. The alternative auditing method was applied to the Gravettian layer 3 lens 2a in Abri Pataud and to the Magdalenian layers (level III & IIb) in Grotte des Romains (Pettitt et al. 2003).

2.4.1 Abri Pataud

The auditing method was applied to two layers, the Gravettian layer 3 and layer 5 in Abri Pataud. Since layer 3 has not been redated, this study also included layer 5, to test how this method works on redated sites / layers (see Table 2.3). The archaeological layers at Pataud are separated by a sterile layer caused by collapse of the shelter roof (Movius et al. 1984). Within each layer there may have been reworking of artefacts due to the sloping nature of the sediments. Because the layers are separated from each other, this study works under the assumption that all samples have not been reworked from other layers. There are only five samples with human modification on them, all located in layer 5. All three scenarios were considered: dating human presence, directly dating species and dating the archaeology by association. Only layer 5 has dates that can be used to establish human presence and or date faunal species (the Oxford redates). These are faunal bones with human modifications. They were rated as *good* because all relevant information was provided in the publication, although the %C and %N are not given.

The age of the associated archaeology could be determined for layers 3 and 5 by using multiple dates. Layer 3 only had dates that were considered to be *poor* based on the methods and publications of the pretreatment methods. Two Groningen dates GrN-4506 and -4721 could be rated higher, however the samples have only been pretreated with acid instead of the full procedure, this signals possible problems with the sample material (fragile) and makes the removal of contaminants harder. All other dates for layer 3 and 5 were labelled as *poor*. They were produced by Oxford in their early years, and even though the redated fractions of the same samples are consistent, caution is urged over these dates, to the point of excluding them from any analysis as suggested by Higham et al. (2011). Pettitt et al. (2003) also called for caution but they marked the dates with 22 out of 30 points using their auditing method, well over the 15 point pass-rate. The Groningen dates (rated *unusable* using the method of the present study) were also passed by Pettitt et al (2003), although they again urged for a degree of caution (Pettitt et al. 2003).

Layer 5 has OxA-169 and OxA-581 audited as *poor* dates, based on the lack of information on the samples and their pretreatment. This is in agreement with Higham et al. (2011) that dates produced by Oxford prior to 1989 are unreliable. This only leaves the recent Oxford dates that were audited as *good*. Bayesian modelling of the layer 5 dates confirms their validity (Higham et al. 2011). By taking out the 4 dates from layer 3, the overall age of the layer has become older by circa 3 ka. By taking out 17 bad dates, the average age for the layer became 2.5ka older.

The outcome of the auditing scheme is daunting, excluding almost all radiocarbon dates produced before 2000. However, the redating programme of Abri Pataud (Higham et al. 2011) indicates that this is the correct approach.

Table 2.3 Abri Pataud, Layer 3 and 5. Only the dates that were audited are presented here. Radiocarbon date & SE: age BP and Standard Error. Bulk = If the sample material has been bulked. Material= the sample material that has been dated. Human mods= human modification on the sample such as cutmarks or burning indicatied by modified or artefact.Type = type of method, conventional or AMS (accelerator mass spectrometry), Pretreatment methods = type of pretreatment applied to sample with AF (ultrafiltration), ABA (acid base acid) etc. δ13C = value provided by lab, same for %C (percent carbon) and the C:N (carbon:nitrogen ratio). Year produced = when radiocarbon date was produced by the lab. Alternative auditing: auditing method Pettit et al. (2003) and their grades. Human presence, Species and Association relate to Questions 1, 2 and 3 and hold the final grade: np (not possible), Poor, Fair or Good.

Laboratory Code	Radiocarbon Date & SE	Bulk	Material	Human Mods	Conventional/ AMS	Pretreatment Method	δ13C	%C	C:N	Year produced	Alternative auditing	Human presence	Species	Association
Layer 3, recent Gravettian with microgravette points (or Perigordian IV)														
OxA-163	23180 ± 670		whole collagen extract of bone		AMS					1985	22	np	np	Poor
OxA-164	24250 ± 750		Amino acids of OxA-163		AMS					1985	22	np	np	Poor
OxA-165	24440 ± 740		Amino acids of OxA-163		AMS					1985	22	np	np	Poor
OxA-166	26100 ± 900		bone amino acids		AMS					1985	22	np	np	Poor
OxA-580	20400 ± 600		bone amino acids		AMS					1986		np	np	Poor
OxA-599	21740 ± 450		bone amino acids		AMS					1986		np	np	Poor
OxA-685	23200 ± 500		bone [whole collagen?]		AMS					1986		np	np	Poor
OxA-686	24500 ± 600		bone amino acids		AMS					1986		np	np	Poor
OxA-687	25500 ± 700		bone amino acids		AMS					1986		np	np	Poor
Layer 5, oldest Gravettian layer														
OxA-169	28400 ±1100		bone amino acids		AMS					1985		np	np	Poor
OxA-21585	28180 ±270	No	Long bone, medium-sized herbivore	artefact	AMS	AF	-19		3.1	2007		good	np	good
OxA-21586	28230 ±290	No	Radius, Fragment of distal shaft, Rangifer tarandus	modified	AMS	AF	-18.7		3.1	2007		good	good	good
OxA-21587	28150 ±290	No	Metacarpal III-IV,Fragment of proximal epiphysis and proximal shaft, Rangifer tarandus	modified	AMS	AF	-18.8		3.2	2007		good	good	good
OxA-21588	28250 ±280	No	Central þ fourth tarsal, Whole bone, Rangifer tarandus	modified	AMS	AF	-19		3.1	2007		good	good	good
OxA-581	26000 ±1000	No	bone amino acids		AMS					1986		np	np	Poor
OxA-X-2225-38	26780 ±280	No	Femur, Fragment of proximal shaft, Rangifer tarandus	modified	AMS	AF	-18.8		3.2	2011		good	good	good

2.4.2 Grotte des Romains

The two charcoal dates Ly-16 and Ly-1307 are both bulked conventional charcoal dates. The lack of necessary information in the publications makes it difficult to estimate their quality. They are marked as *poor* and use for estimating human presence is not recommended. The direct dating of species can be achieved with confidence by two AMS dates on reindeer because the δ13C values and %C are within acceptable range. The stratigraphy of Grotte des Romains is problematic. Therefore the confidence in using these dates is lower than the purely methodological assessment of the date (Bocquet et al. 1970). It is therefore not advised to use these dates for dating the archaeological layer. Pettitt et al. (2003) reveals that all the dates for level IIb were considered well above the 16-point pass rate (18-24), but caution for using these dates was advised. Ly-16 was considered an AMS date on charcoal and scored 16 by Pettitt et al. (2003), however the date was produced before the development of AMS (Combier 1977). It is thus a conventional date consisting of bulked hearth charcoal (Evin et al. 1969), which makes it a *poor* date according to the new classification system. GrA-9709 is considered a bulked sample and is scored 14 (Pettitt et al. 2003), whilst it is actually an AMS sample of a single reindeer bone (GrA database). This study agrees that the Ly-16 is of low quality, but considers GrA-9709 *good* for directly dating reindeer presence. Based on the present auditing method, both layers represent similar geological ages and may indicate transportation of younger material to the lower layer (or vice versa).

Table 2.4 Grotte des Romains, later IIb and layer III. All audited dates are shown. Radiocarbon date & SE: age BP and Standard Error. Bulk ?= If the sample material has been bulked. Material= the sample material that has been dated. Human mods= human modification on the sample such as cutmarks or burning indicatied by modified or artefact.Type = type of method, conventional or AMS (accelerator mass spectrometry), Pretreatment methods = type of pretreatment applied to sample with AF (ultrafiltration), ABA (acid base acid) etc. δ13C = value provided by lab, same for %C (percent carbon) and the C:N (carbon:nitrogen ratio). Year produced = when radiocarbon date was produced by the lab. Alternative auditing: auditing method Pettit et al. (2003) and their grades. Human presence, Species and Association relate to Questions 1, 2 and 3 and hold the final grade: np (not possible), Poor, Fair or Good.

Laboratory Code	Radiocarbon Date & SE	Bulked	Material	Human Mods	Type	Pretreatment Method	δ13C	%C	C:N	Year produced	Alter-native audit	Q1: Human presence	Q2: Species	Q3: Association
Layer IIb, Magdalenian														
GrA-9710 (Lyon-643)	12830± 60		Bone, Rangifer tarandus		AMS	AAA	-19.4	46.2		1998	24	np	good	fair
Ly-1307	10280 ±630	yes	Charcoal		Conv					1978	24	Poor	np	Poor
Layer III, Magdalenian VI														
Ly-16	14380± 380	yes	Charcoal		Conv					1969	16?	Poor	np	Poor
GrA-9709 (Lyon-642)	12690± 60		Bone, Rangifer tarandus		AMS	AAA	-19.9	44		1998	14?	np	good	fair

2.4.3 L'Arbreda

The present auditing method shows that human presence can be indicated by the dates produced during 1980-1990, however, they are marked as *poor* on basis of the lack of information provided in the publication. The new dates by Oxford are well published and have human modification on the material (longitudinal fractures / charcoal through burning) (Wood et al. 2014). Both the charcoal and bone dates from Oxford have been found to be *good* measurements for the direct dating of species presence. The layer association in this site is slightly more problematic, even though the stratigraphy has been argued to be secure two intrusive elements were identified on basis of young radiocarbon ages (Higham et al. 2014; Wood et al. 2014). Therefore, dates that are methodologically *good* may not be useful to date the archaeological layer by association. Great caution should be taken with the *poor* dates, based both on methodology and stratigraphy (not yet piece plotted with total station). The redating of the site indicates that the old dates do not agree with the new dates (the old dates produce older 14C ages). The charcoal dates may represent an older event than the bones, more dates on charcoal are therefore necessary (Wood et al. 2014). This is also signalled by the fair status of the auditing method (good has been lowered to fair because of the stratigraphic mixing). The auditing method appears to hold ground with this redated site and how it compares the old dates to the new dates in a less straightforward stratigraphy.

Table 2.5 L'Arbreda layer I. All available dates are audited and shown here. Radiocarbon date & SE: age BP and Standard Error. Bulk = If the sample material has been bulked. Material= the sample material that has been dated. Human mods= human modification on the sample such as cutmarks or burning indicated by modified or artefact. Type = type of method, conventional or AMS (accelerator mass spectrometry), Pretreatment methods = type of pretreatment applied to sample with AF (ultrafiltration), ABA (acid base acid) etc. δ13C = value provided by lab, same for %C (percent carbon) and the C:N (carbon:nitrogen ratio). Year produced = when radiocarbon date was produced by the lab. Alternative auditing: auditing method Pettit et al. (2003) and their grades. Human presence, Species and Association relate to Questions 1, 2 and 3 and hold the final grade : np (not possible), Poor, Fair or Good..

Laboratory Code	Radiocarbon Date & SE	Material	Human Mods	Type	Pretreatment Method	δ13C	%C	C:N	Year produced	Human presence	Species	Association
Layer I, Mousterian												
OxA-3731	44560 ±2400	bone		AMS	ABA	-18.1	42.9		1992	Np	Np	Fair
AA-3776	39400 ±1400	charcoal		AMS	ABA				1989	Poor	Np	unusable
AA-3777	34100 ±750	charcoal		AMS	ABA				1989	Poor	Np	unusable
AA-3778	41400 ±1600	charcoal		AMS	ABA				1989	Poor	Np	unusable
OxA-19994	38350 ± 400	Charcoal Pinus sylvestris		AMS	ABOX	-24.5	39.6		2009	Good	Good	Fair
OxA-21662	37300 ±800	Bone, Cervus elaphus	yes	AMS	AF	-20.0	42.4 (%N 4.4)	3.2	2008	Good	Good	Fair
OxA-21702	44400 ±1900	Bone, Cervus elaphus	yes	AMS	AF	-19.5	46.1 (%N 5.8)	3.3	2008	Good	Good	Fair
OxA-21663	32100 ±450	Bone, Cervus elaphus	yes	AMS	AF	-19.4	45.6 (%N 3.1)	3.2	2008	Good	Good	unusable
OxA-21703 (duplicate OxA-21663)	32300 ±450	Bone, Cervus elaphus		AMS	AF	-19.6	47.1 (%N 4.7)	3.3	2008	np	Good	unusable
OxA-21704	39200 ±1000	Bone, Cervus elaphus	yes	AMS	AF	-19.4	47 (%N 6.2)	3.3	2008	Good	Good	Fair

2.5 Discussion

The interpretation of the archaeology is largely dependent on the dating evidence and resultant chronology (e.g. Becerra-Valdivia et al. 2017). Auditing methods help increase the accuracy of the dating evidence to create a reliable chronology. As seen in the results, validation schemes of this study excludes more radiocarbon dates than the comparative scheme of Pettitt et al. (2003). The age ranges of the respective layers have increased in age compared to the comparative scheme. This is more in-line with the re-dating evidence. The older age-range for the archaeology changes the interpretation of archaeological layers slightly and can be of great importance for understanding archaeological transitions, such as the Châtelperronian and other transitional industries(Davies et al. 2015; Talamo et al. 2012). However, the context of the radiocarbon dates is of crucial importance for relating an age to an industry, unless it can be directly dated such as Split Based Points from the Aurignacian (Szmidt et al. 2010).

Constructing chronologies with a spatial aspect, especially to understand the expansion or contraction of a phenomenon, whether that is the decline of the woolly mammoth or the spread of the Magdalenian, can greatly benefit from an auditing scheme, as established by both Pettitt and colleagues, and Graf (Graf 2009; Pettitt et al. 2003). The impact for archaeological interpretation of large chronological studies by removing the worse dates from the analyses is demonstrated by Higham et al. (2014). This study shows that the disappearance of the Neanderthal is set back thousands of years compared to previous research, by selecting the more reliable radiocarbon dates (Higham et al. 2014). This has implications for the duration of overlap between the Neanderthals and anatomically modern humans as well as the duration and attribution of transitional industries.

Not all methodological, and especially contextual issues, will be picked up by the auditing method constructed by the present study. This is mostly due to the information provided in the publications. The incorporation of other independent absolute dating techniques and/or chronological markers may help to refine the existing age models (Davies et al. 2015; Kehl et al. 2018; Quiles et al. 2016). However, sometimes problems do not come to light until more research has been done on a particular context by new radiocarbon dates or geological research informing on depositing or taphonomy. For example, new radiocarbon dates question the contemporaneity between a Streletskian point (considered to indicate early modern human presence in Russia) and the rest of the lithic material from Kostienki 11 layer III (Dinnis et al. 2018).

Large freely available databases of archaeological sites and radiocarbon dates (Vermeersch 2017) are a wonderful resource to conduct large chronological studies. The INQUA database is widely used and updated regularly with new data. It is used throughout archaeology, palaeoecology and biogeography as a resource. However, the data is treated differently by each study with most studies being aware that there are problems with the radiocarbon dates. The most common approach in biogeography is to only use the AMS dates and from those only the ones with an SE that is 10% or less of the mean (e.g. Melchionna et al. 2018). This creates a false precision and does not consider redated samples, the context nor association issues. This can lead to vastly different interpretations of the same data in different studies. It would therefore be useful to include a measure of quality (the results of the present auditing method or similar) into the database, or at least incorporate all the published methodological variables (Millard 2014) with the radiocarbon dates into the database.

Finally, the radiocarbon dating method keeps improving technologically and methodologically. For example, new radiocarbon laboratories are being constructed with the availability of smaller AMS machines and the purchasing of new-technology AMS machines in older laboratories. (Crann et al. 2017; Olsen et al. 2017; Szidat et al. 2014). New methods for pretreatment (Dumoulin et al. 2017), new compound-specific dating techniques (Boudin et al. 2013b; Devièse et al. 2018; Fernandes et al. 2017; Marom et al. 2012; Nalawade-Chawan et al. 2014), new screening techniques for collagen preservation pre-pretreatment (Harvey et al. 2016; Vincke et al. 2014), faster dating of wood (Sookdeo et al. 2017), the use of very small samples (<200µg), and the importance of reducing contamination when using this technique (Fewlass et al. 2018) for extracting DNA and 14C from the same sample within one procedure (Korlević et al. 2018). New methods are also being developed for materials previously impossible to date such as pollen (Brown et al. 2006), cremated bones (Van Strydonck 2016), and phytoliths (Asscher et al. 2017). However, these new techniques and methods are not yet widely and commercially available and will come with their own set of problems. When these techniques break through commercially (so they can be used by Palaeolithic archaeologists), the auditing method should be adjusted to accommodate for these changes. Furthermore, frequent research of the literature is necessary to keep informed about laboratory corrections and quality assessment (McIntyre et al. 2016; Meadows et al. 2015). Overall, the future for radiocarbon dating seems to be more precise and accurate than ever and combined with redating archaeological sites, it might make the previously published radiocarbon dates obsolete(Van Strydonck 2017). Although the arms race where 'the improved method is better than the older ones and thus they should not be used' and the question of context will always remain sticking points.

2.6 Conclusion

The presented auditing method provides researchers, dealing with large datasets of published radiocarbon dates, with the means to select the most reliable radiocarbon dates based on methodology and context. Using this auditing method will improve the certainty with which archaeological or palaeontological interpretations are made. When used over multiple studies on similar subjects, it will create comparable chronologies which in turn improve the interpretation of large spatiotemporal patterns. Therefore, this method is used to assess the radiocarbon dates used for the following chapters in this thesis.

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3 Implications of predicted climatic niche of mammals on palaeoenvironmental reconstructions of the Late Pleistocene

3.1 Introduction

The Late Pleistocene (60-10 kya) is a period with extensive climatic change with associated large environmental changes. Archaeological sites dating to this period can be used to reconstruct the environment to provide context to the distribution and behaviour of Neanderthal and Anatomically Modern Humans. The environment can be reconstructed using different proxies, such as geomorphological, lithological to biological evidence (Lowe and Walker 2015). One of the more readily available proxies, that also informs about human behaviour, is the study of mammalian faunal remains found at sites associated with human activity. Environmental reconstructions for the archaeological sites are often based on the presence of certain mammalian taxa (Currant and Jacobi 2001; Kahlke et al. 2011; Stewart et al. 2003a, 2003b). Species associations with environment and climatic conditions in the present are used as an environmental indicator for past conditions (Hernández Fernández 2006). It is common practice to assign the different species to wider environmental categories such as temperate, catholic, open, or forested (Discamps et al. 2011; Graham 1997; Stewart 2009).

The environmental categories to which species are assigned are often based on previous publications and the original assignment and reasoning becomes hard to trace (Álvarez-Lao 2014; Graham 1976). This may lead to confusion when species become an indicator for two contradicting environments. In addition, present-day distribution of species is not always fully representative of the potential distribution of a species and the full range of climatic conditions it can occur in naturally. In some cases, human encroachment limits species' distributions while in other cases human-facilitated introductions and breeding may expand a species' natural climatic niche. For example, red deer (*Cervus elaphus*) is not easy to assign to a specific environment under current conditions, ranging from Spain to the arctic circle in Norway and into continental Europe (IUCN 2017). In zooarchaeological studies, the red deer is classed as being indicative of a temperate environment for one study and as a species that is not indicative of any specific landscape for the other study (eg. Álvarez-Lao 2014; vs. Álvarez-Lao and Méndez 2016). A similar contradiction exists for the common vole (*Microtus arvalis)* which is either classed as temperate or cold (Cyrek et al. 2010; vs. Discamps et al. 2011). Therefore, there is a need within Palaeolithic archaeology and palaeoecology to confirm whether the long-held classifications match the possible climatic tolerances and geographical distributions of species in the present. This can be done via species distribution modelling

(SDM), whereby the species' current distribution is used to model a potential geographic extent based on modern associated climatic conditions (Elith and Leathwick 2009). This is a commonly applied technique within the fields of ecology, conservation and increasingly also in palaeoecology, that enables the researcher to predict the impact of climate on the species distribution, for the present, past and future (Nogués-Bravo 2009; Pitt et al. 2016; Zimmermann et al. 2010).

This chapter aims to model the potential climatic niche of extant species commonly found on Late Pleistocene archaeological sites, to ensure that the past environmental reconstructions can be based on the full potential tolerances and distribution of species. Furthermore, this chapter will provide new climatic categories based on the outcomes of the models, improving the transparency of characterisation of the fauna found at archaeological sites.

3.2 Methods

3.2.1 Distribution data of the taxa

The taxa selected for the models are the currently extant terrestrial mammal taxa living in, and native, to Europe (Mitchell-Jones et al. 1999), which are also present in the archaeozoological database collated for this thesis (Chapter 2). Because zooarcheologically, it can be difficult to distinguish certain taxa from each other, some are only identified to genus level. Of difficult to distinguish taxa, the whole genus is run as a model as well (for example *Lepus* sp.). Therefore, genus and taxon will be referred to as taxa throughout the text. The taxa selected can be found in Table 3.2 to Table 3.6.

Distribution data for the selected taxa is drawn from two sources: IUCN Red List of Threatened Species (here after Red List) and the Global Biodiversity Information Facility (GBIF). The Red List shows the currently known distribution of wild taxa within their native range. It does not include semi-managed fauna, such as the managed reindeer herds of the Sami people. The distribution is shown as one or multiple polygons, covering the entire range (IUCN 2017). The GBIF data consists of individual observations paired with geographic (coordinates) information and is available as point data (Beck et al. 2014). The observations in GBIF are both within and outside of the native range of the taxon (Chapman and Speers 2005). Combining the two datasets provides us the widest possible climatic diversity within a taxa's range, incorporating both the full extent of the native range (not always well represented in GBIF, but good in Red List) and where the taxa have been introduced and established in other areas (available in GBIF but not in the Red List).

The GBIF point data were downloaded per genus from the GBIF website (GBIF 2015). Studies have shown that the GBIF point data are not always correctly georeferenced or taxonomically correctly identified (Beck et al. 2013, 2014; Hjarding et al. 2015; Yesson et al. 2007). The data were therefore cleaned to extract only the relevant and reliable point data. The cleaning included the removal of records that were museum specimens, lived in captivity (such as zoos), had incorrect species names, double entries, and those where the coordinates were clearly incorrect (such as in the ocean). The Red List data was downloaded as polygons per taxon. No cleaning was required.

The presence-only data is, as stated above, a combination of GBIF and Red List data. The two sources do not provide the same type of data (polygon and point data). The two sources were combined in ArcGIS 10.4.1. The RedList data are polygons Extent of Occurrence (EOO). An EOO for the GBIF data was not sufficient, for the large gaps between points created unrealistic ranges (covering oceans and mountain ranges). Therefore, the GBIF data was buffered to 20km to mimic an approximate range of individual mammals. The resulting polygons were merged with the Red List polygons and random points (using a standard polygon partitioning algorithm in ArcGIS, 1000 random points for a range larger than an average country, 500 for the approximate size of a country -estimated at 100.000 km2-, and 100 for a localised area) were created within the full range. These random points were then imported into MaxEnt as the taxa presence data.

3.2.2 Assumptions

Using the Red List and GBIF data requires accepting several assumptions because of the nature of the data. The Red List data consists of convex hull polygons that stretch over terrain where the animal may not be present (such as mountain ranges), with some regions of absence removed after expert assessment. This has proven problematic for regional risk assessments and the polygons are expertly refined to make them work for regional conservation efforts (Gardenfors et al. 2001). However, such a refinement of the Red List data was not feasible for this study, nor necessary seeing the difference in scale (continental vs regional), and thus the assumption with the Red List data is that the ranges are as accurate as necessary for this study and the taxa occupies the drawn range fully.

The GBIF data consists of observations of individuals of the taxa. The assumption made here is that the data in the GBIF database used in this analysis are correctly taxonomically identified and georeferenced. The second assumption is that the observations reflect the full climatic range of the taxa well enough – even though it is known that the observations are linked to where humans are most likely to venture and observations are limited in difficult-to-reach areas and for taxa that are less easy to detect.

3.2.3 Climatic data

Climate maps are provided by Bristol Research Initiative for the Dynamic Global Environment (BRIDGE). The maps are constructed using the HadCM3 (Hadley Centre Coupled Model, 3rd version) which is a general circulation model (GCM), where the atmospheric and oceanic inputs are coupled(AOCGM) (Gordon et al. 2000; Pope et al. 2000). The global model has a spatial resolution of 2.5° x 3.75° (latitude by longitude) which equates to 417 x 278 km at the equator and to 295 x 278km at 45° latitude (Gordon et al. 2000). The climate simulation is given for time ranges of present day (2015) and then 1000 year slices for the 10-24ka period, and 2000 year slices for the 26-60ka period. The following climate variables were used here: mean annual precipitation, mean annual temperature at 2m above ground, mean annual snow cover, mean annual difference in precipitation of the wettest-driest month and the difference in mean annual temperature between the warmest and coldest month are used (Gordon et al. 2000). The maps were cut to the continents of Europe, Asia, Africa, Australasia, North and South America and only the terrestrial data were used for the faunal modelling.

3.2.4 Species Distribution Modelling

Maximum entropy species distribution modelling was carried out in MaxEnt (Phillips et al. 2009). MaxEnt works with presence-only data which is appropriate because the data in the zooarchaeological and palaeontological field is also only indicative of presence(Phillips et al. 2006). MaxEnt uses the presence points within a study area (assumes that the taxon is able to survive within its climatic tolerances and geographical environment) and takes the average value of the variables provided for a set of random training data (subset of presence points). These averages are then compared to the known locations and given variables. The model assumes a uniform distribution, but through machine learning, it moves away from the uniform distribution based on the constraints provided by the known locations and their values for the variables. Based on these constraints MaxEnt then creates the geographic distribution of the climatic niche. This can then be projected to other areas or time periods (Phillips et al. 2006, 2004).

Five predictor variables of the climate models were chosen (Precipitation, Snow cover, Temperate at 2m, Warmest/coldest month and Wettest/Driest month) based on ecological relevance (Thuiller et al. 2004). A correlation test was performed to only use the least correlated variables. Correlations among variables were tested using by running a correlation test in R3.4.2 and RStudio with libraries DISMO, RGDAL and CORRPLOT. Precipitation, Temperature and Snow Cover are the least correlated (Rho<0.7; Table 3.1). The MaxEnt modelling was thus carried out with these three predictor variables only.

Table 3.1 Correlation matrix (Spearman's Rho) of the climatic variables available for the climate models.

Variables	precipitation	snow cover	temperature	warmest/coldest	wettest/driest
precipitation	1	-0.05369	0.428258	-0.569	0.752954
snow cover	-0.05369	1	-0.28255	0.007766	-0.11886
temperature	0.428258	-0.28255	1	-0.81406	0.515188
warmest/coldest	-0.569	0.007766	-0.81406	1	-0.58131
wettest/driest	0.752954	-0.11886	0.515188	-0.58131	1

The modelling was conducted on a random seed (where a different training set is selected every run). The regularization multiplier was set to 2.5 to prevent overfitting. Replicates were set to 10 with crossvalidated runs. This means it has 20% test data and 80% training data and runs each model ten times with different selections and creates a mean over those 10 times. The threshold rule for environmental suitability were set to Equal training sensitivity and specificity (Liu et al. 2005) and the Maximum training sensitivity plus specificity logistic threshold was used to determine the threshold for the binary maps per taxon (Freeman and Moisen 2008; Liu et al. 2013). The results presented in this chapter are averages of the models and are only presented when the measure of performance, the AUC is valid, i.e. over 0.7 (Swets 1988).

3.2.5 Defining climatic categories

The MaxEnt results provide climatic niche information per taxon and were explored using the responses of the taxon to changes in temperature, precipitation and snow cover. Here, climate classifications for taxa were fitted according to the Köppen-Geiger Climate Classification system (Kottek et al. 2006) because it is one of the most used climate classification systems. The KG climate system is divided into five main groups (warm, arid, temperate, cold, and arctic) that are subdivided into subgroups based on precipitation and temperature fluctuations (Kottek et al. 2006). Only the five main groups are used since these groups are most-often used when describing a climatic association with a species. Furthermore, the comparison of with the KG map has been limited to Europe because of the scope of the thesis and that most Pleistocene climatic associations made by palaeontologists/zooarchaeologists are based on research and the climate in Europe. The taxon's distribution model output could not be directly compared to the Köppen-Geiger (KG) Climate Classification system because the same climatic variables were not used for the MaxEnt models as were used for the construction of the KG system (Kottek et al. 2006). To resolve this, the modelled probability distribution plots of the taxa were imported into ArcGIS 10.3. From the distribution plot, one polygon was calculated on the basis of the threshold value. The polygon was laid over the KG map and the polygon area overlapping with each KG climate class was calculated as percentages of the full range, so that different taxa could be compared to each other.

The climatic categories assigned to taxa were based on the percentage land cover of the climate groups in the KG system. Taxa were given the category 'catholic' when they were widespread over the different climate categories, which has been defined as a minimum of 20% area cover for three groups. When the taxa were not that widespread, the climate categories were assigned. Each taxon was given a 'main category' and a 'sub-category' based on at least 66.7% of its polygon's categorisation. If 66.7% of the taxon's polygon fell within one category, that category was used to label the taxon. If the two top categories added up to 66.7% or more, the taxon was given two categorisations, with the top category mentioned first. For example, the wildcat has 21.8% of its climatic niche in the warm climate category, 47.2% in the arid category, 21% in the temperate category, 7.2% in the cold category and 1% in the arctic category. Three climate categories have over 20% of the taxon climatic niche and thus the taxon is classed as catholic. The collared lemming has 0.7% of its total area in the arid category, 0.1% in the temperate category, 59.5% in the cold category and 34.4% in the arctic category. Since no three climate categories have a coverage of 20% each, the combination of two largest categories gain the 66.7% boundary, this results in the main category being mentioned first 'cold - arctic' for the final climate category of the collared lemming.

3.2.6 Anthropogenically influenced geographic ranges

The current geographic ranges of animals are partly shaped by human interference in several ways: habitat loss by human encroachment (agriculture, deforestation, climate change etc.), diminishing number of individuals per population by exploitation (hunting), management of animals (semi-domesticated herds), introduction to new areas and translocation (mixing of populations from the same taxon) (Ducatez and Shine 2017). Some taxa have been introduced to new areas (or re-introduced) and these populations are sometimes managed (e.g. the horse and reindeer); this can result in the taxon adapting to the new habitat. For these taxa (fallow deer, rabbit, wild boar, horse and reindeer) the current native range, (that is created by the Red List, hereafter RL range), was modelled as well as the introduced or managed range (based on both Red list and GBIF data, hereafter GBIF+RL range). The implications of the taxon's climatic tolerance and relevance to the past will be discussed in the results.

3.3 Results

The results of the modelling of the geographic ranges of the taxa are organised according to the climate category assigned to the taxon (Table 3.2, Table 3.3, Table 3.4, Table 3.5, Table 3.6). The modelled distribution maps as well as the response curves to each environmental variable are listed per taxon in Appendix Chapter 3. A total of 74 models were made (all models had an AUC over 0.7 except for *Vulpes vulpes and Vulpes* sp. that has an AUC of 0.68). All models have an adequate representation of the taxons' climatic niche.

3.3.1 Climate category: Cold

The analyses show that 23 taxa can be classified as showing a cold distribution (Table 3.2). The distribution is highly influenced by mean annual temperature, followed by mean annual precipitation. Mean annual snow cover is important for the distribution of narrow-headed vole (*Microtus gregalis)*, elk (*Alces alces)*, mountain hare (*Lepus timidus*) and otter (*Lutra lutra*). Reindeer (*Rangifer tarandus*) has been modelled twice because it is a managed taxon. The difference between the ranges based on the two modelling approaches is small, with the GBIF&RL range extending further south than the RL range. The modelled distribution of the otter is very broad and encompasses most of Europe except for the far south and southeast.

Table 3.2 Summary of results of the MaxEnt modelling for taxa that were given the category Cold. AUC = the AUC value (Area under ROC curve) on model performance. Temperature = the relative contribution (%) of the annual mean temperature. Precipitation = the relative contribution (%) of the annual mean precipitation. Snow cover = the relative contribution (%) of the annual mean snow cover. Threshold= is the maximum sensitivity and specificity threshold used to produce the binary range. No value= the areas in % where the range did not overlap with the KG climate system. Arid/Warm/Temperate/Cold and Arctic refers to the % area in % of the modelled taxon's range polygon that overlapped with the correspondingly labelled Köppen-Geiger classification. Category= the resultant category assigned to the taxon's climatic niche.

Taxon	**AUC**	**temperature**	**precipitation**	**snow cover**	**Threshold**	**No value**	**Warm**	**Arid**	**Temperate**	**Cold**	**Arctic**	**Category**
Alces alces	0.84	89.1	5.9	5	0.32	2.7		6.3	1.0	79.1	10.9	Cold
Arvicola amphibius	0.83	92.2	7	0.9	0.40	1.8		19.2	5.0	71.7	2.3	Cold
Arvicola sp.	0.81	91.7	7.5	0.8	0.40	1.9		18.8	5.4	70.5	3.5	Cold
Bison bison	0.86	62.8	37.2	0	0.21	2.7	0.0	15.7	11.5	68.1	1.9	Cold
Bison sp.	0.88	77.4	22.6	0	0.32	1.9		11.5	2.3	82.2	2.0	Cold
Capra siberica	0.93	76.9	23.1	0	0.15	1.4		21.3	0.4	75.6	1.2	Cold
Castor fiber	0.90	76.3	23.7	0	0.20	2.4		12.7	7.9	75.5	1.6	Cold
Dama pygargus	0.86	96.7	2.8	0.5	0.35	1.9		17.0	0.7	77.9	2.5	Cold
Gulo gulo	0.85	91.9	8.1	0	0.30	3.8		3.3	0.4	72.8	19.8	Cold
Lemmus lemmus	0.91	88.7	11	0.3	0.17	4.1		1.9	0.5	71.4	22.1	Cold
Lepus timidus	0.83	87.6	7.6	4.8	0.31	2.8		6.8	0.3	76.5	13.6	Cold
Lutra lutra	0.74	88	9	3	0.43	2.5	0.0	13.1	11.4	68.2	4.7	Cold
Lynx lynx	0.81	93.4	3.8	2.9	0.39	2.4		7.1	0.4	79.0	11.1	Cold
Microtus agrestis	0.85	78.1	21.8	0	0.34	2.3		9.6	5.2	79.9	3.0	Cold
Microtus gregalis	0.90	78.2	14.8	7	0.44	2.9		14.0	0.1	66.7	16.4	Cold
Microtus oeconomus	0.84	90.2	8.9	0.9	0.33	2.6		5.4	0.3	78.5	13.1	Cold
Myodes glareolus	0.88	72.2	27.8	0	0.30	2.5		13.2	9.5	73.3	1.6	Cold
Ochotona sp.	0.89	94	5.8	0.2	0.24	2.3		16.2	2.5	76.5	2.5	Cold
Rangifer tarandus RL	0.87	93.9	6.1	0	0.29	4.1		2.5	0.2	70.4	22.8	Cold
Rangifer tarandus GBIF+RL	0.86	92.6	7.4	0	0.29	3.8		2.8	0.4	72.6	20.5	Cold
Sorex araneus	0.84	83.3	16.3	0	0.32	2.1		12.3	3.8	79.0	2.8	Cold
Talpa europea	0.91	73.5	26.5	0	0.32	2.2		15.1	11.3	70.5	0.9	Cold
Ursus arctos	0.84	90.3	9.6	0.1	0.32	3.1		5.3	0.8	76.7	14.1	Cold

3.3.2 Climate category: Cold-arctic

Six taxa have been classed as cold – arctic (Table 3.3). Among these are the arctic fox (*Vulpes lagopus)* and the arctic hare (*Lepus arcticus)*. Hare (*Lepus* sp.) has been classed as cold-arctic, but could be considered to be in the category cold, seeing as it is just below the cut-off point (66.7%). The wolf, even though it occurs in west and central Europe, is modelled to preferentially occupy north eastern Europe.

3.3.3 Climate category: Cold-arid

Most taxa that are classed as cold-arid are modelled to have a wide distribution throughout Europe (Table 3.3). For example, the yellow-necked field mouse (*Apodemus flavicollis*), striped field mouse (*Apodemus agrarius*), badger (*Meles meles*), common vole (*Microtus arvalis*) and the red fox (*Vulpes vulpes*) are likely to occur in most of Europe except the far south and the far north/north east. However, distribution of the steppe pika (*Ochotona pusilla*) and the corsac fox (*Vulpes corsac*) are modelled to occur in the north-east of Europe.

3.3.4 Climate category: Cold-temperate

Eleven taxa are classed within the cold-temperate category (Table 3.3). The distribution of these mammals extends less far north compared to the other cold-categories. Roe deer (*Capreolus capreolus*) is often used as an indicator taxon for a temperate and forested environment (Currant and Jacobi 2001). The models show that the taxon is projected into much colder terrain as well.

Table 3.3 Summary of results of the MaxEnt modelling for taxa that were given the category Cold-arctic, cold-arid and cold-temperate. AUC = the AUC value (Area under ROC curve) on model performance. Temperature = the relative contribution (%) of the annual mean temperature. Precipitation = the relative contribution (%) of the annual mean precipitation. Snow cover = the relative contribution (%) of the annual mean snow cover. Threshold= is the maximum sensitivity and specificity threshold used to produce the binary range. No value= the areas in % where the range did not overlap with the KG climate system. Arid/Warm/Temperate/Cold and Arctic refers to the % area in % of the modelled taxon's range polygon that overlapped with the correspondingly labelled Köppen-Geiger classification. Category= the resultant category assigned to the taxon's climatic niche.

Taxon	AUC	temperature	precipitation	snow cover	Threshold	No value	Warm	Arid	Temperate	Cold	Arctic	Category
Canis lupus	0.72	82.8	16.9	0.3	0.42	3.1		16.1	0.6	66.3	13.9	Cold - arctic
Dicrostonyx sp.	0.91	94.2	5.8	0	0.29	5.4		0.7	0.1	59.5	34.4	Cold - arctic
Lepus arcticus	0.91	96.8	1.7	1.4	0.24	5.0		0.6	0.1	53.4	40.9	Cold - arctic
Lepus sp.	0.78	93.2	4.4	2.4	0.37	3.1		13.5	2.6	65.7	15.2	Cold - arctic
Ovibos moschatus	0.94	86.4	11.1	2.6	0.19	5.3		0.2		47.9	46.6	Cold - arctic
Vulpes lagopus	0.88	98.1	1	0.9	0.27	4.3		1.5	0.2	59.4	34.6	Cold - arctic
Apodemus agrarius	0.87	95.3	4.7	0	0.29	2.5	0.1	23.1	16.5	56.8	1.0	Cold - arid
Apodemus flavicollis	0.92	82.2	17.8	0	0.25	3.0		19.6	18.0	58.5	0.8	Cold - arid
Capra sp.	0.85	75.9	24.1	0	0.28	2.0	0.0	34.5	10.2	52.6	0.8	Cold - arid
Lepus europaeus	0.89	95.2	4.8	0	0.34	1.8		29.5	10.6	57.6	0.4	Cold - arid
Meles meles	0.90	87.4	12.6	0	0.27	2.4	0.0	24.4	15.9	56.9	0.5	Cold - arid
Microtus arvalis	0.90	96.1	3.9	0	0.34	2.1		26.3	10.0	60.7	0.9	Cold - arid
Ochotona pusilla	0.98	76.5	23.5	0	0.09	0.6		37.3	0.5	61.5	0.1	Cold - arid
Vulpes corsac	0.94	64.1	35.9	0	0.16	0.8		35.9	1.6	61.6	0.2	Cold - arid
Vulpes sp.	0.68	87.3	11.5	1.2	0.41	3.2		18.4	3.1	60.6	14.7	Cold - arid
Vulpes vulpes	0.68	75	17	8	0.43	2.6		20.1	5.7	63.1	8.5	Cold - arid
Apodemus sp.	0.85	99.1	0.9	0	0.29	2.4	0.1	26.1	16.4	54.0	0.9	Cold - arid
Apodemus alpicola	0.99	54.2	45.8	0	0.31	6.5		10.3	31.3	49.1	2.8	Cold - temperate
Apodemus sylvaticus	0.98	80	20	0	0.16	3.3	0.1	23.8	31.0	41.1	0.7	Cold - temperate
Arvicola schermann	0.98	69	31	0	0.09	3.7		11.8	37.9	45.2	1.3	Cold - temperate
Capra ibex	0.99	55.8	44.2	0	0.20	5.9		11.0	30.1	50.6	2.4	Cold - temperate
Capra pyrenaica	0.98	85.3	14.7	0	0.32	3.4	0.0	28.1	40.3	27.7	0.6	Cold - temperate
Capreolus capreolus	0.90	77.6	22.4	0	0.23	2.7		15.6	15.0	65.7	1.0	Cold - temperate
Cervus elaphus	0.93	78	22	0	0.21	3.3	0.0	19.5	21.5	54.4	1.3	Cold - temperate
Eliomys quercinus	0.92	75.7	24.3	0	0.23	2.9	0.0	17.9	20.5	57.7	1.0	Cold - temperate
Rupicapra rupicapra	0.97	68.4	31.6	0	0.17	3.5		16.8	33.5	45.2	1.0	Cold - temperate
Rupicapra sp.	0.97	72.2	27.8	0	0.20	3.9	0.0	15.2	35.4	44.3	1.2	Cold - temperate
Spermophilus citellus	0.98	86.2	13.8	0	0.24	3.3		19.4	33.1	43.5	0.7	Cold - temperate

3.3.5 Climate Category: Temperate-arid, Temperate-cold and Warm-arid

The only taxa classed as temperate-arid (Table 3.4) is the European rabbit for its RL range, the GBIF+RL range range is catholic (Table 3.6). The spotted hyena (*Crocuta crocuta)* is the only taxon that is classed as warm-arid with warm as the main group. Based on the current distribution of the spotted hyena, the modelled range lies outside of Europe (Appendix Chapter 3).

Table 3.4 Summary of results of the MaxEnt modelling for taxa that were given the category temperate and warm. AUC = the AUC value (Area under ROC curve) on model performance. Temperature = the relative contribution (%) of the annual mean temperature. Precipitation = the relative contribution (%) of the annual mean precipitation. Snow cover = the relative contribution (%) of the annual mean snow cover. Threshold= is the maximum sensitivity and specificity threshold used to produce the binary range. No value= the areas in % where the range did not overlap with the KG climate system. Arid/Warm/Temperate/Cold and Arctic refers to the % area in % of the modelled taxon's range polygon that overlapped with the correspondingly labelled Köppen-Geiger classification. Category= the resultant category assigned to the taxon's climatic niche.

Taxon	**AUC**	**temperature**	**precipitation**	**snow cover**	**Threshold**	**No value**	**Warm**	**Arid**	**Temperate**	**Cold**	**Arctic**	**Category**
Oryctolagus RL	0.98	86.8	13.2	0	0.17	3.5	0.0	32.3	45.9	17.8	0.5	Temperate - arid
Crocuta crocuta	0.89	89.3	10.7	0	0.33	3.0	53.4	24.7	18.8		0.1	Warm - arid

3.3.6 Climate category: Arid

Four taxa are classed as arid (Table 3.5). The potential distribution of the Asian wild ass (*Equus hemionus*) is modelled to the far southeast of Europe and the eastern part of Iberia. Striped hyaena is projected to the very south of Europe, the Greek and Italian islands. The mouflon (*Ovis orientalis*) has a more widespread modelled distribution, stretching from southern to south eastern Europe and northern coast of west to central Europe. The saiga (*Saiga tatarica*) has a modelled distribution that is very similar to the Asian wild ass.

3.3.7 Climate category: Arid-cold

European bison (*Bison bonasus*), Caucasian tur (*Capra caucasica*) and the horse (*Equus sp.*) are all classed as Arid-cold (Table 3.5). The modelled distribution of the European bison (currently only present in Poland) is mostly located in Central Europe and branches out to southern Scandinavia and the United Kingdom. The Caucasian tur has a modelled distribution of south-eastern Europe and some localised patches in Spain, Italy, The Netherlands and the UK. The horse (*Equus ferus*) and its RL range (Table 3.5, Figure 3.1) is modelled to occur in the eastern most corner of Europe. The GBIF+RL range is much broader and classes the wild horse as catholic (Table 3.6).

3.3.8 Climate category: Arid-temperate

The golden jackall (*Canis aureus*) and the Iberian lynx (*Lynx pardinus*) have been classed as arid-temperate (Table 3.5), both occupying a range limited to southern Europe.

Table 3.5 Summary of results of the MaxEnt modelling for taxa that were given the category arid. AUC = the AUC value (Area under ROC curve) on model performance. Temperature = the relative contribution (%) of the annual mean temperature. Precipitation = the relative contribution (%) of the annual mean precipitation. Snow cover = the relative contribution (%) of the annual mean snow cover. Threshold= is the maximum sensitivity and specificity threshold used to produce the binary range. No value= the areas in % where the range did not overlap with the KG climate system Arid/Warm/Temperate/Cold and Arctic refers to the % area in % of the modelled taxon's range polygon that overlapped with the correspondingly labelled Köppen-Geiger classification. Category= the resultant category assigned to the taxon's climatic niche.

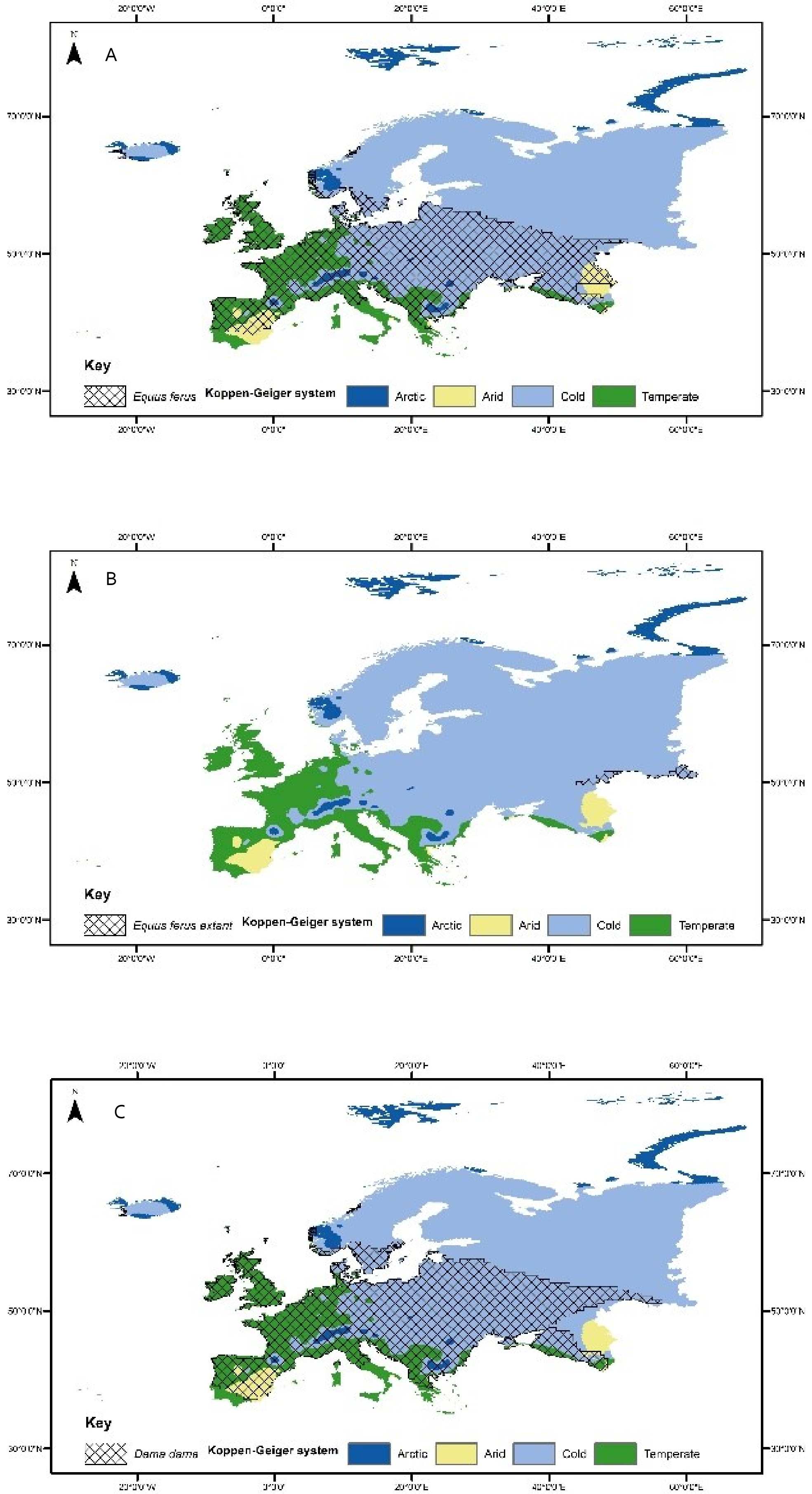
Taxon	**AUC**	**temperature**	**precipitation**	**snow cover**	**Threshold**	**No value**	**Warm**	**Arid**	**Temperate**	**Cold**	**Arctic**	**Category**
Equus hemionus	0.96	54.8	45.2	0	0.24	0.2		79.1	0.8	19.9		Arid
Hyaena hyaena	0.91	71	29	0	0.20	2.7	20.6	69.3	7.5			Arid
Ovis orientalis	0.94	68.8	31.2	0	0.18	1.8	0.0	75.3	12.6	10.2	0.1	Arid
Saiga tatarica	0.99	54.6	45.4	0	0.03	0.2		79.1	0.8	20.0		Arid
Bison bonasus	0.97	97	3	0	0.55	1.2		47.8	8.2	42.5	0.2	Arid - cold
Capra caucasica	0.98	98.7	1.3	0	0.62	1.2		53.9	18.5	26.0	0.4	Arid - cold
Equus ferus RL	0.97	57.2	42.8	0	0.52			66.1		33.9		Arid - cold
Sus scrofa GBIF+RL	0.77	98.1	1.9	0	0.43	2.5	0.1	34.9	19.8	42.0	0.6	Arid - cold
Canis aureus	0.86	71.3	28.7	0	0.21	2.7	16.9	59.0	17.0	4.2	0.1	Arid-temperate
Lynx pardinus	0.95	87.3	12.7	0	0.59	2.0	0.0	65.0	18.5	14.4	0.2	Arid-temperate

3.3.9 Climate category: Catholic

The catholic taxa (Table 3.6) are modelled to have a very wide distribution over Europe and are not predicted in the far northeast of Europe. The GBIF+RL range of wild horses (such as in the Oostvaardersplassen in the Netherlands, *Equus ferus* in Table 3.6 and Figure 3.1, indicates most of Europe to be suitable. The horse has gained a large temperate component to the range compared to the RL distribution (Table 3.5). Within Europe, there is no difference in distribution between the wild boar's GBIF+RL range and the RL range. Outside of Europe, there is a 0.2% difference between the RL and RL+GBIF range, which means that the RL range is classed as arid-cold, whilst the RL+GBIF range is catholic. The wild cat (*Felis sylvestris*) is modelled to occupy most of Europe, although avoiding the Alps and the Tatra mountains. The modelled distribution of the leopard (*Panthera pardus*) is restricted to Southwestern France, Iberia, Italy the Balkans and Greece. Based on the modelled distribution and percentages per area, the assigned category for the leopard could almost be arid-warm. It is noteworthy that the European rabbit (*Oryctolagus cuniculus*) has a different modelled range (temperate-arid) for the RL range compared to the GBIF+RL range (catholic). The rabbit was introduced to north-western Europe by the Romans and again during the Middle Ages, and more recently to all continents (except Antarctica) (Mitchell-Jones et al. 1999).

Table 3.6 Summary of results of the MaxEnt modelling for taxa that were given the category catholic. AUC = the AUC value (Area under ROC curve) on model performance. Temperature = the relative contribution (%) of the annual mean temperature. Precipitation = the relative contribution (%) of the annual mean precipitation. Snow cover = the relative contribution (%) of the annual mean snow cover. Threshold= is the maximum sensitivity and specificity threshold used to produce the binary range. No value= the areas in % where the range did not overlap with the KG climate system. Arid/Warm/Temperate/Cold and Arctic refers to the % area in % of the modelled taxon's range polygon that overlapped with the correspondingly labelled Köppen-Geiger classification. Category= the resultant category assigned to the taxon's climatic niche.

Taxon	**AUC**	**temperature**	**precipitation**	**snow cover**	**Threshold**	**No value**	**Warm**	**Arid**	**Temperate**	**Cold**	**Arctic**	**Category**
Dama dama GBIF+RL	0.95	83	17	0	0.20	3.1		22.2	24.1	49.8	0.8	Catholic
Dama dama RL	0.97	80.8	19.2	0	0.42	3.4	0.0	31.2	37.2	27.7	0.5	Catholic
Equus ferus GBIF+RL	0.94	94.9	5.1	0	0.36	3.1		29.7	24.0	42.2	1.0	Catholic
Felis sylvestris	0.76	90.4	90.6	0	0.39	2.6	21.8	47.2	21.0	7.2	1.0	Catholic
Sus scrofa RL	0.77	98.6	1.4	0	0.43	2.7	0.1	35.8	21.4	39.4	0.7	Catholic
Panthera pardus	0.77	95.3	4.7	0	0.43	3.0	30.6	42.6	21.6	2.1	0.1	Catholic
Chionomys nivalis	0.95	91.3	9.7	0	0.44	3.2		21.7	33.4	40.8	0.8	Catholic
Oryctolagus GBIF+RL	0.96	81.9	18.1	0	0.18	3.1	0.0	24.5	30.2	41.5	0.7	Catholic
Arvicola sapidus	0.98	80	20	0	0.06	3.3	0.1	20.6	47.1	28.5	0.6	Catholic
Rupicapra pyrenaica	0.98	76.9	23.1	0	0.43	3.2	0.0	22.8	42.2	31.2	0.6	Catholic



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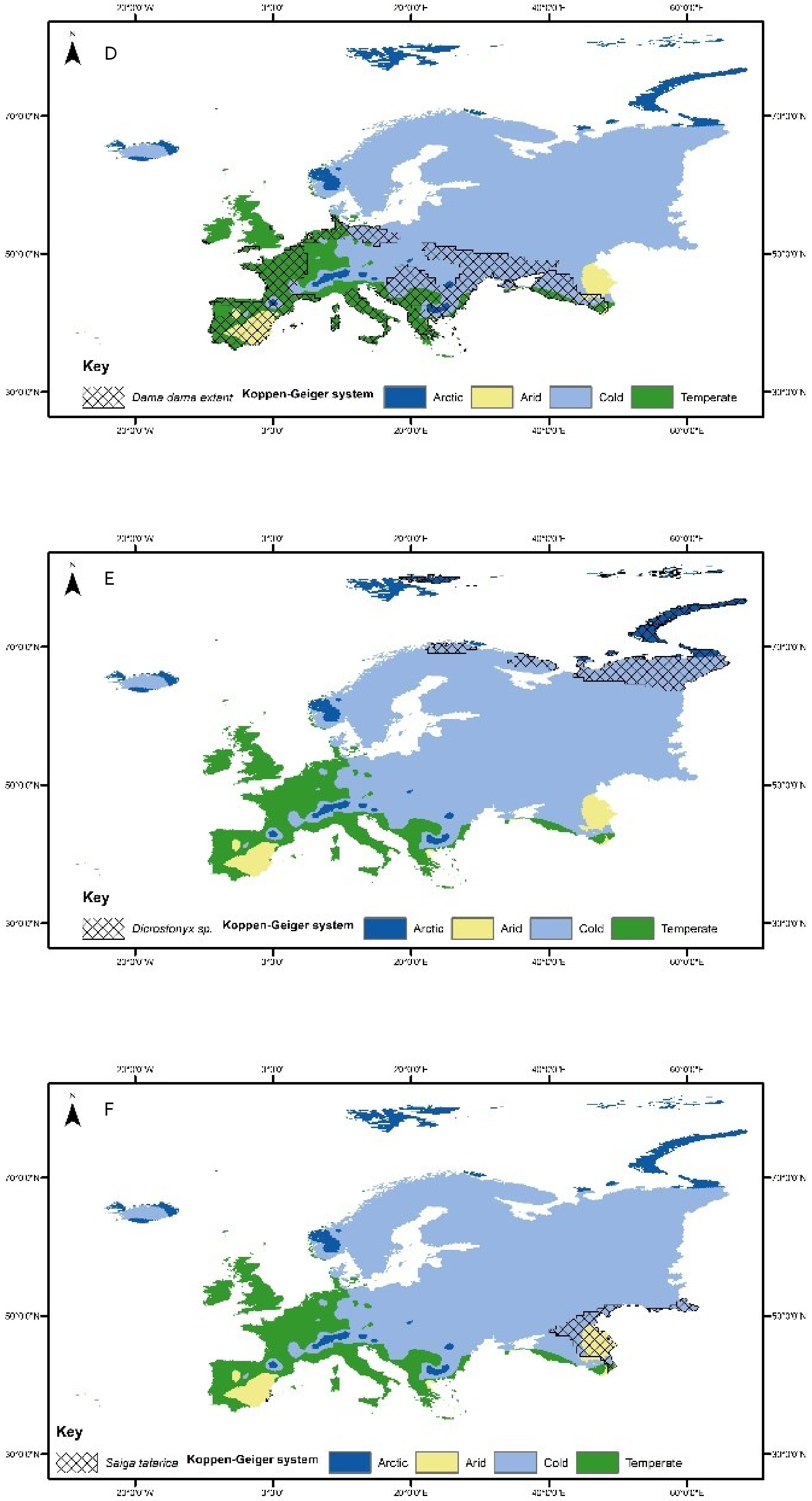

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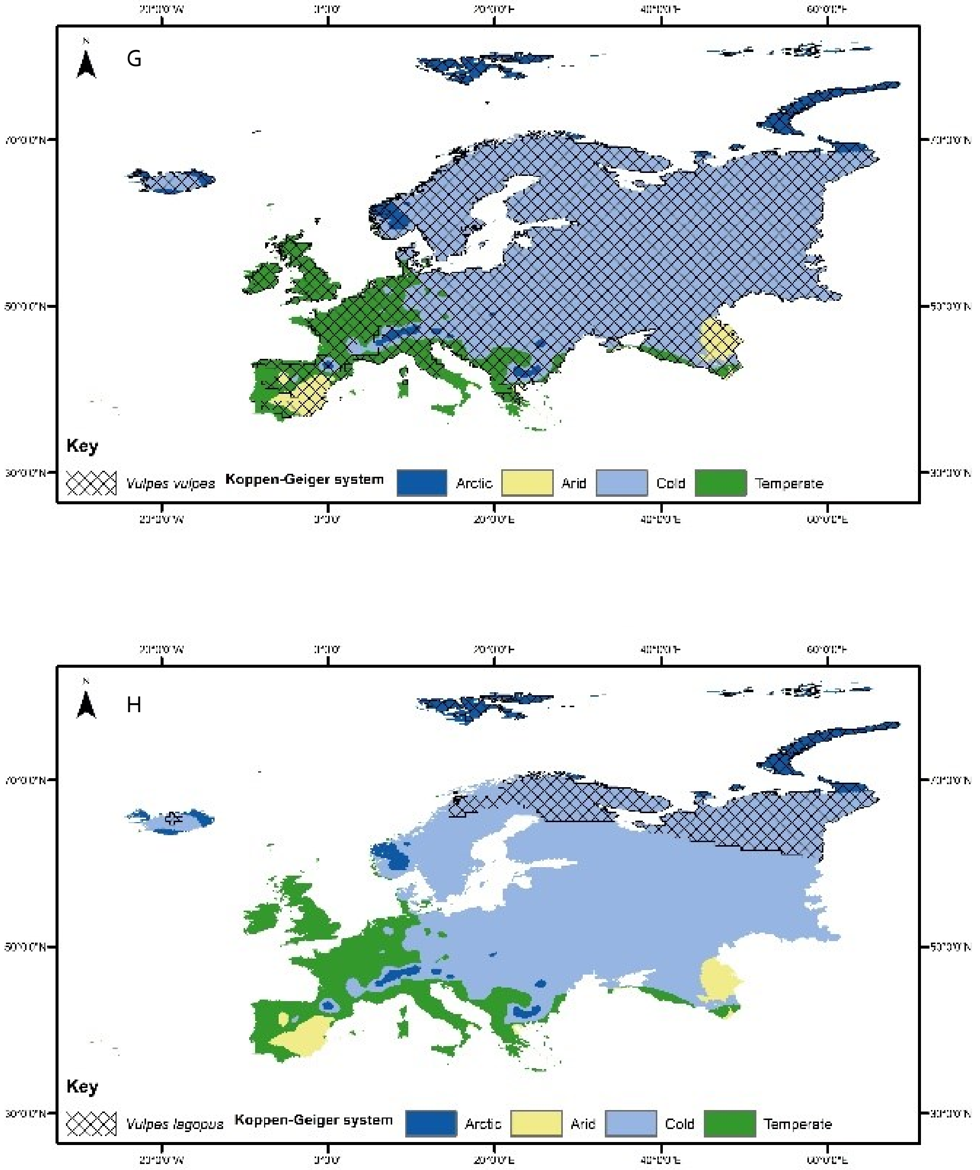

Figure 3.1 Maps of the modelled climatic niche in Europe (hatched) against the KG-climate system. A. Equus ferus RL+GBIF range. B. Equus ferus RL range. C. Dama dama RL+GBIF. D. Dama dama RL range. E. Dicrostonyx sp. F. Saiga tatarica. G. Vulpes vulpes. H. Vulpes lagopus. KG-climate system: Blue=Arctic, Yellow=Arid, light blue=Cold, Green= Temperate.

3.4 Discussion

The obtained climatic categories for the modelled taxa distributions provide a new quantitative framework for palaeoecologists and zooarchaeologists for the reconstruction of past environments with large and small mammals. The climate categories are broad categories that provide the main climatic indication as frequently used in the literature, such as 'cold-adapted fauna' (Sommer et al. 2014; Yurtsev 2001). These terms have been established through a long research history and are often not well defined or based on the perceived ecological association of mammals in past environments (e.g. Currant and Jacobi 2001). Some have formalised these descriptions via models where groups of mammals were assigned to a regional complex (Puzachenko and Markova 2015) or via statistical methods (discriminant analysis) to class individual taxa into climate zones (Hernández Fernández 2001; Hernández Fernández and Peláez-Campomanes 2003). Here the presented results are compared with the categories provided by other researchers (Table 3.8 to

Table 3.14).

Many publications refer to the (vegetational) habitat of the taxon rather than climatic indicators (for example taiga instead of cold). Therefore a comparison is made between the Köppen-Geiger categories and the biomes of the terrestrial ecoregions of the world (Olson et al. 2001). The comparison was made in a similar way as was done for the climate categories, where the KG map is overlain over the biomes and then the percentages of each variable per area were calculated (Appendix Chapter 3). A summarising table indicates the different biomes each climate category encompasses (Table 3.7). For example, the European beaver is classed in the literature as occurring in taiga and deciduous forests, this fits best with the climatic category cold (Table 3.7). Deciduous forests are often associated with temperate climate, but they also occur in cold climates (Table 3.7).

The assigned climate categories in this study broadly correspond to those in the literature, especially the taxa that are classed as arid and cold-arctic. For example, all research categorises reindeer as a cold to arctic adapted taxon and the saiga antelope as an arid taxon. Discrepancies occur in taxa that are in the cold to temperate categories, as well as the catholic taxa. For example, the bioclimatic models of Hernández Fernández and colleagues place 12 taxa in temperate (to temperate-cold) categories whilst they are classed as cold (to cold-arctic) in this research (Table 3.8) (Hernández Fernández 2001; Hernández Fernández and Peláez-Campomanes 2003). This discrepancy is likely due to the use of a different climate classification system (Walter 1977) and by focussing their data on Europe rather than worldwide. Which means that they consider areas as temperate compared to the rest of

European climates, but on a global scale, those areas are relatively cold. Furthermore, the research of Hernández Fernández and colleagues did not take anthropogenic range change of mammals into account. Other studies, such as those conducted by Markova and colleagues are often regional studies focussing on eastern Europe and the east Palaearctic (Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015). This creates a bias that taxa are categorised in climates that are more continental and of higher latitudes (i.e. colder) and are thus missing part of their climatic niche in the assessment.

Indicator taxa that are said to signal a temperate environment in the literature were mostly modelled as either more catholic or cold adapted here. For example, the wild boar (*Sus scrofa*) is often mentioned as a typical indicator for a temperate environment in the Pleistocene (Sommer and Nadachowski 2006). However, the wild boar is indicated as a more catholic taxon ranging from deciduous forests to steppe environments (Table 3.13). The fallow deer (*Dama dama),* considered to be an indicator for a temperate to warm environment, is categorised as catholic (Álvarez-Lao and Méndez 2016; Stewart et al. 2003b). The RL range of the fallow deer is more restricted to the south and coastal climates, and one could argue for a more restricted category. However, even with the more conservative model, the fallow deer was still projected into a cold climatic niche here. Some small mammal taxa, such as the bank vole (*Myodes glareolus,* previously known as *Clethrionomys glareolus),* are classed as temperate by the literature when they are modelled as cold and their climatic niche extends into northern Europe (Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016). These discrepancies are likely caused by regional studies, the use of Pleistocene occurrences to determine the climatic niche (presence of a taxon during a glacial or interglacial (Currant and Jacobi 2001)) or by using the association with other taxa that have a well-defined climatic niche (such as the association of red deer with roe deer, making red deer a temperate taxon).

Table 3.7 Comparison KG system to the Biomes of the terrestrial ecoregions of the world.

Köppen-Geiger categories	Biomes
Warm	Tropical and Subtropical Moist Broadleaf Forests
	Tropical and subtropical grasslands, savannas, and shrublands
Arid	Deserts and Xeric Shrublands
	Tropical and subtropical grasslands, savannas, and shrublands
Temperate	Temperate Broadleaf and Mixed Forests
	Tropical and Subtropical Moist Broadleaf Forests
	Tropical and subtropical grasslands, savannas, and shrublands
Cold	Boreal Forests/Taiga
	Temperate Broadleaf and Mixed Forests
	Tundra
Arctic	Rock and Ice
	Tundra

Table 3.8 Comparison of framework to previous publications. Table with taxa categorised as cold.

Taxon	**(Stewart et al. 2003b, 2003a)**	**(Musil 1985)**	**(Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015)**	**(Kahlke 1999, 2013)**	**(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)**	**(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)**	**(Cyrek et al. 2010)**	**(Hernández Fernández 2001)**	**Category this study**
Alces alces	Catholic	Subarctic forest including taiga/ arctic steppe	Cold, forests, deep snow cover	forests			Open and marshy areas, forest	Cold-temperate	Cold
Arvicola amphibius						primarily temperate	marshy grounds and terrain containing watercourses and bodies of water	Cold-temperate, Arid-temperate, typical-temperate, winter rain/summer drought	Cold
***Arvicola* sp.**									Cold
Bison bison								Cold temperate to warm temperate	Cold
***Bison* sp.**		The arctic steppe, the loess steppe, the steppe		Northern regions	(bison priscus) Steppic, periglacial. 2016: catholic	Ecologically plastic, open environments. Can occur in woodland and forest.			Cold
Capra siberica									Cold
Castor fiber		Subarctic forest including taiga/ the mild zone forest, meadows, water	Most abundant in taiga/mixed forests, deciduous forests, true steppe					All types of temperate and Winter rain / summer drought	Cold
Dama pygargus									Cold

Gulo gulo	cold	Tundra	Periglacial forest-steppes, steppes	Taiga and tundra	cold			Arctic, cold-temperate, typical temperate	Cold
Lemmus lemmus	cold	Tundra	Cold-arctic. Tundra, forest-tundra				cold climate, open and marshy areas		Cold
Lepus timidus		Tundra/ The arctic steppe, the loess steppe, the steppe	forest areas together with widely distributed open tundra–steppe				cold climate		Cold
Lutra lutra	Catholic	the mild zone forest, meadows, water	Forests and steppe, not in tundra						Cold
Lynx lynx	Catholic	Subarctic forest including taiga/ the mild zone forest, meadows, water	Forests with thick undergrowth. Not arctic. Taiga and deciduous forests, wooded steppes.				deciduous and mixed forests		Cold

Table 3.9 Comparison to literature. Table of taxa categorised as cold (continued from table above).

Taxon	**(Stewart et al. 2003b)**	**(Musil 1985)**	**(Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015)**	**(Kahlke 1999, 2013)**	**(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)**	**(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)**	**(Cyrek et al. 2010)**	**(Hernández Fernández 2001)**	**Category this study**
Microtus agrestis						primarily temperate	Open and marshy areas, border open areas - diversified forest		Cold
Microtus gregalis						Cold climate, tundra	cold climate conditions on dry open terrain	Arctic, Cold-temperate, Arid-temperate	Cold

Microtus oeconomus						cold-climate	marshy grounds and terrain containing watercourses and bodies of water		Cold
Myodes glareolus			forest areas together with widely distributed open tundra–steppe			temperate	deciduous and mixed forests	Cold-temperate, Arid-temperate, typical temperate, Winter rain/summer drought	Cold
***Ochotona* sp.**		The arctic steppe, the loess steppe, the steppe	steppe				cold climate		Cold
Rangifer tarandus	Cold	Tundra/ Subarctic forest including taiga/ The arctic steppe, the loess steppe, the steppe	Tundra, taiga, eurobiotic species arctic tundra to savanna-like ecosystems in southern Russia. Just no forests.	Tundra, Arctic	Cold & open	Highly plastic species, glaciers, tundra/barren ground, taiga woodland, subalpine and forested mountainous regions. Adapted to extreme cold and wind.	cold climate	Cold-temperate, arctic	Cold
Sorex araneus			forest areas together with widely distributed open tundra–steppe						Cold
Talpa europea			forest areas together with widely						Cold

			distributed open tundra–steppe						
Ursus arctos	Catholic	Subarctic forest including taiga/ the mild zone forest, meadows, water						Cold-temperate, arid-temperate, typical temperate, winter rain summer drought	Cold

Table 3.10 Comparison of framework to previous publications. Table with taxa categorised as cold-arctic and cold-arid.

Taxon	(Stewart et al. 2003b)	(Musil 1985)	A K Markova 1995; Anastasia K. Markova et al. 2010)	(Kahlke 1999)	(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)	(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)	(Cyrek et al. 2010)	(Hernández Fernández 2001)	Category this study
Canis lupus		Subarctic forest including taiga/ the mild zone forest, meadows, water		Holarctic (catholic)				Equal distribution all climate zones except Equatorial	Cold - arctic
***Dicrostonyx* sp.**		Tundra	Cold to arctic, steppes, forest-tundra			Arid, Cold climate, tundra	cold climate conditions on dry open terrain		Cold - arctic
Lepus arcticus									Cold - arctic
***Lepus* sp.**									Cold - arctic
Ovibos moschatus	cold	Tundra/ The arctic steppe, the loess steppe, the steppe	Subarctic, thin snow cover	Arctic tundra	Cold & open				Cold - arctic
Vulpes lagopus	cold	Tundra/ The arctic steppe, the loess	Arctic, tundra (periglacial open landscapes)	Arctic, tundra, taiga (in winter)	cold			Cold temperate (boreal) and arctic	Cold - arctic

		steppe, the steppe							
Apodemus agrarius									Cold - arid
Apodemus flavicollis									Cold - arid
***Capra* sp.**			Steppe						Cold - arid
Lepus europaeus									Cold - arid
Meles meles									Cold - arid
Microtus arvalis						primarily temperate	cold climate conditions on dry open terrain		Cold - arid
Ochotona pusilla			forest areas together with widely distributed open tundra–steppe				cold climate conditions on dry open terrain		Cold - arid
Vulpes corsac			Steppes, deserts, arid						Cold - arid
***Vulpes* sp.**									Cold - arid
Vulpes vulpes		the mild zone forest, meadows, water						Arid, Warm-temp, Temp, Arid-temp, Cold-temp, arctic	Cold - arid
***Apodemus* sp.**									Cold - arid

Table 3.11 Comparison of framework to previous publications. Table with taxa categorised as cold-temperate.

Taxon	**(Stewart et al. 2003b)**	**(Musil 1985)**	**A K Markova 1995; Anastasia K. Markova et al. 2010)**	**(Kahlke 1999)**	**(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)**	**(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)**	**(Cyrek et al. 2010)**	**(Hernández Fernández 2001)**	**Category this study**
Apodemus alpicola									Cold - temperate

Apodemus sylvaticus						temperate shrubland and woodland environments			Cold - temperate
Arvicola schermann									Cold - temperate
Capra ibex							cold climate conditions on dry open terrain		Cold - temperate
Capra pyrenaica					Alpine, rocky				Cold - temperate
Capreolus capreolus	Catholic	the mild zone forest, meadows, water	Forested into steppe zone, thermophilic.		Forested	Ecologically plastic. Mainly forest (coniferous/deciduous) adapted.	deciduous and mixed forests		Cold - temperate
Cervus elaphus		Subarctic forest including taiga/ the mild zone forest, meadows, water	Ecologically plastic, preferred forest-steppes, true steppe		Temperate 2016: catholic	Great ecological plasticity. Can tolerate steppe environments, but not tundra.			Cold - temperate
Eliomys quercinus						temperate			Cold - temperate
Rupicapra rupicapra					Rocky				Cold - temperate
Rupicapra sp.									Cold - temperate
Spermophilus citellus			forest areas together with widely distributed open tundra–steppe			cold-climate		Widespread, all zones except Equatorial and Warm-temperate	Cold - temperate

Table 3.12 Comparison of framework to previous publications. Table with taxa categorised as temperate-arid, temperate-cold and warm-arid.

Taxon	(Stewart et al. 2003b)	(Musil 1985)	(Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015)	R.-D. Kahlke, 1999; Ralf-Dietrich Kahlke,	(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)	(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)	(Cyrek et al. 2010)	(Hernández Fernández 2001)	Category this study
Oryctolagus RL									Temperate - arid
Crocuta crocuta	Catholic		Elevated but not cold, true steppe						Warm – arid

Table 3.13 Comparison of framework to previous publications. Table with taxa categorised as arid.

Taxon	(Stewart et al. 2003b)	(Musil 1985)	(Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015)	R.-D. Kahlke, 1999; Ralf-Dietrich Kahlke,	(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)	(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)	(Cyrek et al. 2010)	(Hernández Fernández 2001)	Category this study
Equus hemionus		The arctic steppe, the loess steppe, the steppe	Deserts, semideserts, steppes, low precipitation, low snow cover.	Desert, semidesert, steppe					Arid
Hyaena hyaena									Arid
Ovis orientalis			Steppe						Arid
Saiga tatarica	cold	The arctic steppe, the loess steppe, the steppe	Arid, steppe/ semi-desert	Steppes, semiarid, Cold	Cold & open				Arid
Bison bonasus			Broadleaf deciduous and wooded steppes	Northern Europe,					Arid - cold

Capra caucasica							cold climate conditions on dry open terrain		Arid - cold
***Equus ferus* RL**		The arctic steppe, the loess steppe, the steppe/	Cold, Steppic, low snow fall	Forested steppes, steppes, semidesert	Herbaceous open		cold climate conditions on dry open terrain		Arid - cold
Sus scrofa		the mild zone forest, meadows, water	Cold, forested-steppe around wet biotopes		Forested		Forest		Arid - cold
Canis aureus									Arid- temperate
Lynx pardinus	Warm								Arid- temperate

Table 3.14 Comparison of framework to previous publications. Table with species categorised as catholic.

Taxon	**(Stewart et al. 2003b)**	**(Musil 1985)**	**(Markova 1995; Markova et al. 2010; Puzachenko and Markova 2015)**	**R.-D. Kahlke, 1999; Ralf-Dietrich Kahlke,**	**(Álvarez-Lao 2014; Álvarez-Lao and García 2011; Álvarez-Lao and Méndez 2016)**	**(Discamps et al. 2011; Discamps and Royer 2017; Royer et al. 2016)**	**(Cyrek et al. 2010; Socha 2014)**	**(Hernández Fernández 2001)**	**Category this study**
Dama dama	Warm	the mild zone forest, meadows, water			Forested	Adapted to open environments, steppe, prairie. Reduced snow fall.			Catholic
***Dama dama* RL**	Warm	the mild zone forest, meadows, water			Forested	Adapted to open environments, steppe, prairie. Reduced snow fall.			Catholic
Equus ferus							cold climate conditions on dry open terrain		Catholic
Felis sylvestris	Catholic	the mild zone forest, meadows, water	All forest types and wooded steppes				forest		Catholic
***Sus scrofa* RL**		the mild zone forest, meadows, water	Cold, forested-steppe around wet biotopes		Forested		Forest		Arid-cold
Panthera pardus	Catholic?								Catholic

Chionomys nivalis			forest areas together with widely distributed open tundra–steppe			rupicolous species; middle and high latitudes of the Pyrenees Mountains			Catholic
***Oryctolagus* introduced**		the mild zone forest, meadows, water							Catholic
Arvicola sapidus						temperate climate			Catholic
Rupicapra pyrenaica					alpine				Catholic

Taxa that have an extremely reduced range, such as the saiga antelope (*Saiga tatarica*) and the spotted hyaena (*Crocuta crocuta*), can be more difficult to model. Both taxa are extirpated from Europe and their present-day range does not reflect their past distribution (historic range). The historic range during the 17th -18th century, of the saiga has been reconstructed and the distribution of the saiga has been modelled in MaxEnt (Jurestovsky and Andrew Joyner 2017). By using the historic range, the modelled present-day range comes into central Europe. The reconstruction of a historic range can thus greatly influence the modelled distribution of a taxon whose present-day distribution is severely reduced by human encroachment. Unfortunately, no threshold of the historic range is provided on the likelihood of occurrence and thus it is hard to estimate if the saiga would indeed be likely to spread as far back as the Czech Republic. No historic range is available for the spotted hyeana, because the retreat into Africa occurred before the Last Glacial Maximum (Stuart and Lister 2014). A previous distribution model for the spotted hyaena simulated a similar present-day distribution for the taxon in Europe as the current study (Varela et al. 2009). The spotted hyaena was present throughout Europe during the Late Pleistocene through large climatic changes. The hyaena was present during MIS3 a period that was generally cooler than present-day, before it extirpated. Therefore, it seems to suggest the loss of one or several populations with a more cold-tolerant climatic niche than the present-day populations (Stewart 2009; Stewart et al. 2003a; Stuart and Lister 2014; Varela et al. 2009). The climate categories provided for the species in this study, to aid environmental reconstruction in the past, are thus a conservative estimate of the potential range of the taxon.

Even with the conservative estimate, many taxa had a modelled climatic niche that encompasses two-thirds of Europe (eg. wild boar, red fox, voles and mice, beaver, otter, red deer etc.) and only became distinctly associated with certain climate categories (i.e. more arid or colder) in Asia. Mammals are endothermic and thus maintain constant body temperature, making them less dependent on environmental temperature. This enables mammals to use a wider array of habitats (Stoddart 2012). Mammals can thus occupy a wider climatic niche than beetles for instance (often used in climatic envelopes for past environmental distributions). Furthermore, the European continent is mostly ameliorated by the coastal climate caused by the warmth of the Atlantic Meridional Overturning Circulation (AMOC, also known as the oceanic conveyor belt), making the climatic transitions less pronounced for western Europe during the interglacials (Bohm et al. 2015). A more distinct climatic distribution between species in Europe may be observed during glacials, when the climatic amelioration has subsided because the AMOC has stopped delivering warm water to Europe and climatic differences within Europe became more extreme.

The climatic niche modelled for the mammals has been created to give a realistic estimate of where and in which climate zones these taxa can occur. The spatial resolution of the climatic variables are coarse, because the model used climatic data that is available for hindcasting the climatic niche at a 2000 year interval. Much more fine-grained variables (such as Bioclim) are available for the present day, Mid-Holocene and the LGM and could improve the precision of the study (Fick and Hijmans 2017). Furthermore, the climatic niche may be transformed into a biogeographic range when other biotic and abiotic variables (such as vegetation) are incorporated into the model, making the species distribution more accurate and precise. However, these variables are not available for the same intervals and extent as the climatic maps used for this thesis. A further improvement to the models would be the use of actual presence data of the mammals with minimal bias rather than generated random points and absence data. This would greatly enhance the certainty of the model (Elith and Leathwick 2009).

3.5 Conclusion

This research provides a quantitative framework to infer the climatic niche of mammals in Europe to aid with environmental reconstructions of Pleistocene archaeological and palaeontological sites. The framework is built by running species distribution models (MaxEnt) for over 60 European mammals, providing each taxon with a broad and realistic climate category. Comparison to existing literature shows that the model is broadly in agreement with the consensus. However, the climatic categories are often broader than the climate classes in the literature as this is the only model that uses the modelled climatic niche (and incorporates a wider geographic distribution encapsulating a wider climatic tolerance) to provide the taxon’s climate category.

The models are intended for use in the Pleistocene period, where future research in projecting the models to the past to predict species presence as well as training the models with archaeological data to optimise them, will provide new ways to explore and analyse the past. The created niche models are used in the next chapter to explore the existence of non-analogue fauna.

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4 The case for non-analogue faunas. Modelling the impact of Late Pleistocene climate change to species-specific distributions.

4.1 Introduction

Did taxa that do not occur together today occur together in the past? Or are the combinations of the faunal remains of these taxa a result of stratigraphically mixed faunal assemblages? This is the essence of the non-analogue faunal communities' discussion (for review see Stewart (2009)). Non-analogue faunas are defined as faunal communities that consist of multiple taxa with biogeographic ranges that do not overlap today (allopatric), but were found together in the past (sympatric) (Graham 1985). These combinations of species could have existed due to the individual response of taxa to climate change, where specific climatic conditions allowed taxa to become sympatric (Gleason 1926; Kullman 1998; Stewart 2009). Two main non-analogue mammalian community combinations have been identified: the combination of temperate taxa with cold or arid taxa (Stafford et al. 1999) and the combination of cold with steppic taxa (Guthrie 1982; Kahlke 2013). The most well-known combination of steppic and cold taxa is the *Mammuthus-Coelodonta* fauna or the mammoth steppe fauna that occupied the mosaic habitat called the steppe-tundra or mammoth steppe (Guthrie 1982; Kahlke 2013). This mosaic habitat governed the Late Pleistocene Eurasian environment but disappeared at the start of the Holocene, which would have led to the disappearance of the non-analogue communities (Guthrie 1984, 2001; Lister and Sher 2001; Lister et al. 2005; Stewart 2007).

Whether the appearance of non-analogue taxa was real or an artefact of stratigraphic mixing of faunal assemblages is not fully resolved (Stewart 2009). The stratigraphic mixing of faunal assemblages means that taxa living in different environments and different times have become a single faunal fossil assemblage at an archaeological or palaeontological site, due to taphonomic movement of the sediment. Another variant of this is the slow accumulation of sediment creating a palimpsest; stretching over multiple climate changes, and thus the faunal composition within a layer shows a combination of different environments and taxa. The argument for mixed assemblages is the most serious challenge to the existence of non-analogues and was used to explain a non-analogue beetle assemblage at Earith, where there were elements indicative of both temperate and arctic climates (Coope 2000).

It is possible to test if non-analogue faunal assemblages are a result of stratigraphic mixing by radiocarbon dating individual specimens from the taxa that signify the different (current) environments. Non-analogue faunas that indicate more steppic vs. boreal environments have been tested for their contemporaneous occurrence by AMS radiocarbon dating specimens of (among others) *Spermophillus suslicus* and *Lemmus sibiricus* from the same stratigraphic layer (Stafford et al. 1999). The radiocarbon dates are in agreement on 2σ, approximately 200 years for these dates, and thus the data confirm geological contemporaneity of the species (Stafford et al. 1999). However, this study does not incorporate the calibration of radiocarbon dates and the radiocarbon dating plateaus. Furthermore, this analysis does not consider alterations to the modern natural range of taxa due to human activity (Ducatez and Shine 2017). Range alterations are especially common for the larger mammals and research has shown that using contracted ranges results in a bias in climate change forecasts (Faurby and Araújo 2018). This also applies to hindcasting and the most anthropogenically affected extant mammals are also the most iconic taxa for the non-analogue mammalian faunal assemblages (such as reindeer and saiga antelope). And finally, the study by Stafford et al. (1999) does not include the full potential past range of the involved taxa, showing where these species may have been sympatric and where not. Reconstructing the full past range is important, because populations that are extinct now may have had wider climatic tolerances than extant populations and thus occupied a larger range (Stewart 2009). These populations with wider climatic tolerances may have been the ones that were in the non-analogue associations.

The present study therefore attempts to reconstruct what the modern ranges would be like without human activity and uses these ranges to hindcast distributions into past environments (60 ka to 10 ka). Using niche models has been proven a successful approach for smaller scale models in Britain (Polly and Eronen 2011).The modelled past ranges can then be compared to each other to infer where the species may have been sympatric (and thus non-analogous). These models are compared where possible with directly dated taxa locations. Finally, the models are trained with the directly dated occurrences, so that extinct populations are accounted for. These final models provide the past range of the species modelled at 2000-year intervals and shows which taxa were non-analogous and under which climatic conditions.

4.2 Methods

4.2.1 Selection of non-analogous taxa

Classic non-analogous species discussed in the literature were selected for analysis (Table 4.1). These taxa were divided into three categories based on their environmental associations as stated in the literature: temperate, cold, and arid. Some taxa may have been assigned a different climatic category in Chapter 3, therefore the categories used here are based on their distribution as modelled in Chapter 3. The taxa assigned to a category in the literature are listed in Table 4.1.

*Table 4.1 Taxa that are part of the non-analogous faunas described in the literature listed per climatic category (cold, arid, temperate). Taxa with a * were not modelled in this, nor the previous, chapter because these taxa are not present or very rare in the database constructed for this thesis. Taxa in brackets are extinct.*

Cold	**Arid**	**Temperate**
Dicrostonyx sp. (Stafford et al. 1999)	* *Lagurus lagurus* (Stafford et al. 1999)	*Ursus arctos* (Hewitt 2000)
* *Lemmus sibericus* (Stafford et al. 1999)	* *Spermophilus suslicus* (Stafford et al. 1999)	*Cervus elaphus* (Magniez and Boulbes 2014)
Microtus gregalis (Stafford et al. 1999)	* *Cricetulus migratorius* (Stafford et al. 1999)	*Capreolus capreolus* (Markova 1995)
[*Coelodonta antiquitatis* (Kahlke 2013)]	*Saiga sp.* RL range (Kahlke 2013)	*Sus scrofa* (Magniez 2014)
Vulpes lagopus (Kahlke 2013)	[*Equus sp.* (Kahlke 2013)]	*Apodemus sp.* (Hewitt 1999)
[*Mammuthus primigenius* (Kahlke 2013)]	*Ochotona pusilla* (Fiore et al. 2004)	*Sorex araneus* (Lisá et al. 2018)
Rangifer tarandus (Kahlke 2013)		*Arvicola terrestris* (Hewitt 2000)
Ovibos moschatus (Kahlke 2013)		
Bison sp. (Kahlke 2013)		

Additional non-analogous extant taxa were selected based on the modelled ranges in Chapter 3. For *Saiga tatarica*, *Ursus arctos*, *Lynx lynx* and *Canis lupus* the historic ranges were modelled as well (because their current ranges have contracted greatly under recent human influence), according to the 17th (saiga) and 15th century historic ranges (Singh et al. 2010; Wolf and Ripple 2017). The taxa were divided into three groups: southern, northern and eastern groups, based on the modelled ranges. Pan-European taxa have not been selected. These groups correspond with the classic description of cold, temperate and arid taxa that have modelled ranges that currently do not overlap with each other to any great extent, their exact percentage overlap is presented in Table 4.3, Table 4.4 and Table 4.5.

Table 4.2 Taxa that do not have a pan-European range on the basis of the distribution models of Chapter 3.

Northern group	**Eastern group**	**Southern group**
Lepus timidus	*Capra caucasica*	*Arvicola scherman*
Lynx lynx (historic range)	*Equus hemoinus*	*Bison bonasus*
Alces alces	*Saiga tatarica* (historic range)	*Apodemus alpicola*
Lepus arcticus	*Ovis orientalis*	*Capra ibex*
Gulo gulo	*Lynx pardinus*	*Canis aureus*
Microtus oeconomus	*Ochotona* sp.	*Capra pyrenaica*
Capra siberica		*Panthera pardus*
Dama pygargus		*Arvicola sapidus*
Canis lupus (historic range)		*Rupicapra pyrenaica*
Lemmus lemmus		*Felis sylvestris*
		Spermophillus citellus
		Chionomys nivalis
		Dama dama
		Apodemus sylvaticus
		Ursus arctos (historic range)

The ranges of extinct taxa (*Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp.), were modelled on past climatic timeframes. The timeframe with the most radiocarbon dates and the best geographical spread of each of these taxa was selected as the basis for the subsequent models. The radiocarbon dates are part of the archaeozoological database collected for this thesis (Chapter 2). Following the protocol in Chapter 2, only dates classed as good and fair were used as data points. From these presence points, a convex hull polygon was drawn and subsequently random points (following the same methods as in Chapter 3) were created within this. The random points ensured the maximum distribution of the species; otherwise the models would underestimate the climatic niche. The radiocarbon dates were calibrated with OxCal 4.3 to a 95.4% confidence interval with the calibration curve IntCal13 (Bronk Ramsey 1995; Reimer 2013).

4.2.2 Climate data and MaxEnt models

The climatic niches of taxa were modelled in MaxEnt (Phillips et al. 2009), following the same methods as in Chapter 3. The hindcasting was done on the same climatic variables (mean annual precipitation, mean annual temperate and mean annual snow cover) for every 1000 years starting at 10ka and going back to 22ka, after which the hindcasting was done on the same climatic variables at an interval of 2000 years going back to 60ka (Gordon et al. 2000; Pope et al. 2000).

The 1000- and 2000-year time frames often hold one or multiple distinct climate fluctuations (Greenland Interstadials and Greenland Stadials). For example, the 32-34 ka time frame has GI

5.2, GS 6 and GI 6 within its period. Both GI's have a duration of circa 400 years where the climate warmed up slowly and cooled down very quickly (Rasmussen et al. 2014). However, the available climatic maps are a snapshot of one year from within the 1000 or 2000 year time period and thus do not encapsulate all the climatic changes that occurred during each interval.

Polygons of the probable distribution were created based on the *Maximum training sensitivity plus specificity logistic threshold* in ArcMap 10.3. These polygons were then analysed for percent overlap for the different taxa per timeframe.

4.2.3 Comparing climatic niche models to radiocarbon dates

The climatic niche models were compared to the zooarchaeological/palaeontological faunal remains of directly radiocarbon dated taxa and associated taxa assembled in Chapter 2. The radiocarbon dates have been calibrated in Oxcal with the IntCal13 curve. The radiocarbon dates were considered to be part of a time frame (either 1000 or 2000 years) when 1σ (or 68.2%) of the calibrated age range fell within the time frame. This means that there is a 13.6% chance date may have been part of the younger or older period (to 2σ, or 95,4% certainty). Each radiocarbon date was only used once. If the 1σ age range does not fall within the time frame brackets, it was not used.

Model improvement was only undertaken for reindeer. If the model agreed with the distribution of radiocarbon dated specimens of the taxa over the different timeframes, the hindcasted models were considered accurate (the models for the southern taxa were considered accurate, all others were not). If there were directly dated individuals that fall outside of the modelled range, the model needs improving, this was thus done for reindeer. The individuals falling outside of the range (when directly dated and with a good to fair classification) are assumed to be correct and may be part of an extinct population with a wider climatic niche. To improve the model, a convex hull polygon was created with the most reliable radiocarbon dates. Random points were created in this polygon following the methods in Chapter 3. The random points were then used as additional training data, whilst the locations of the radiocarbon dated individuals were used as test data.

4.3 Results

All models have a good fit with an AUC over 0.7. The AUC values are presented in Chapter 3 for the extant taxa, The AUC values for the extinct taxa are presented in Appendix Chapter 4. The models and the locations of the radiocarbon dated faunal remains of two representative taxa per group are presented in the Appendix.

Figure 4.1 and Figure 4.2 show the modelled present-day climatic distribution of the taxa from Table 4.1, the taxa that are ascribed to a certain climate group in the literature. Two taxa from the arid group overlap with the cold group. This implies that pikas (*Ochotona sp.* & *Ochotona pusilla*) cannot be considered non-analogue because they could live in sympatry today with the cold group. Seven temperate taxa have ranges that extend northwards, showing that part of their climatic ranges overlap with cold and arid taxa. The 'classic' temperate taxa cannot be classed as non-analogue in the past since they are able to occur (partly) in sympatry today with the cold and arid taxa. The 'classic' temperate taxa have been used in further analyses to see if they remain sympatric in the past.

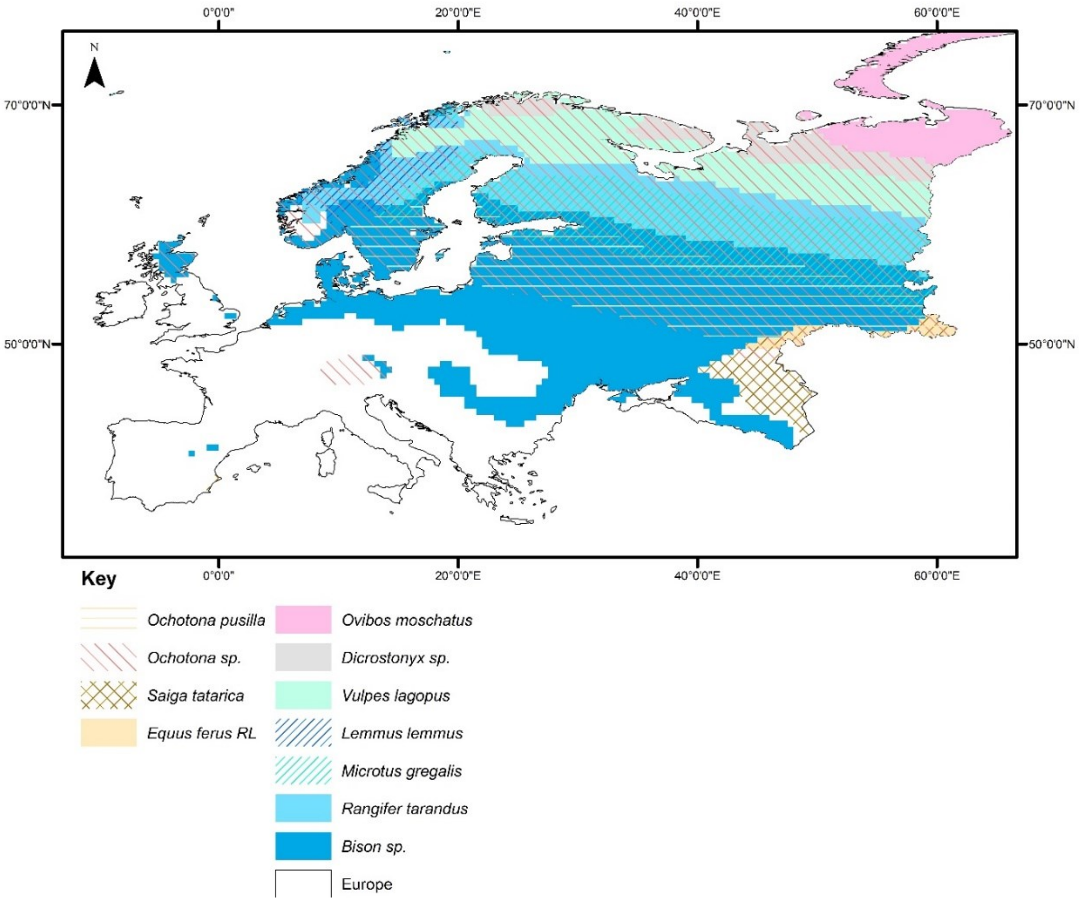

Figure 4.1 Present-day predicted distribution of taxa divided into the arid (yellow tones) and cold group (blue and pink tones).

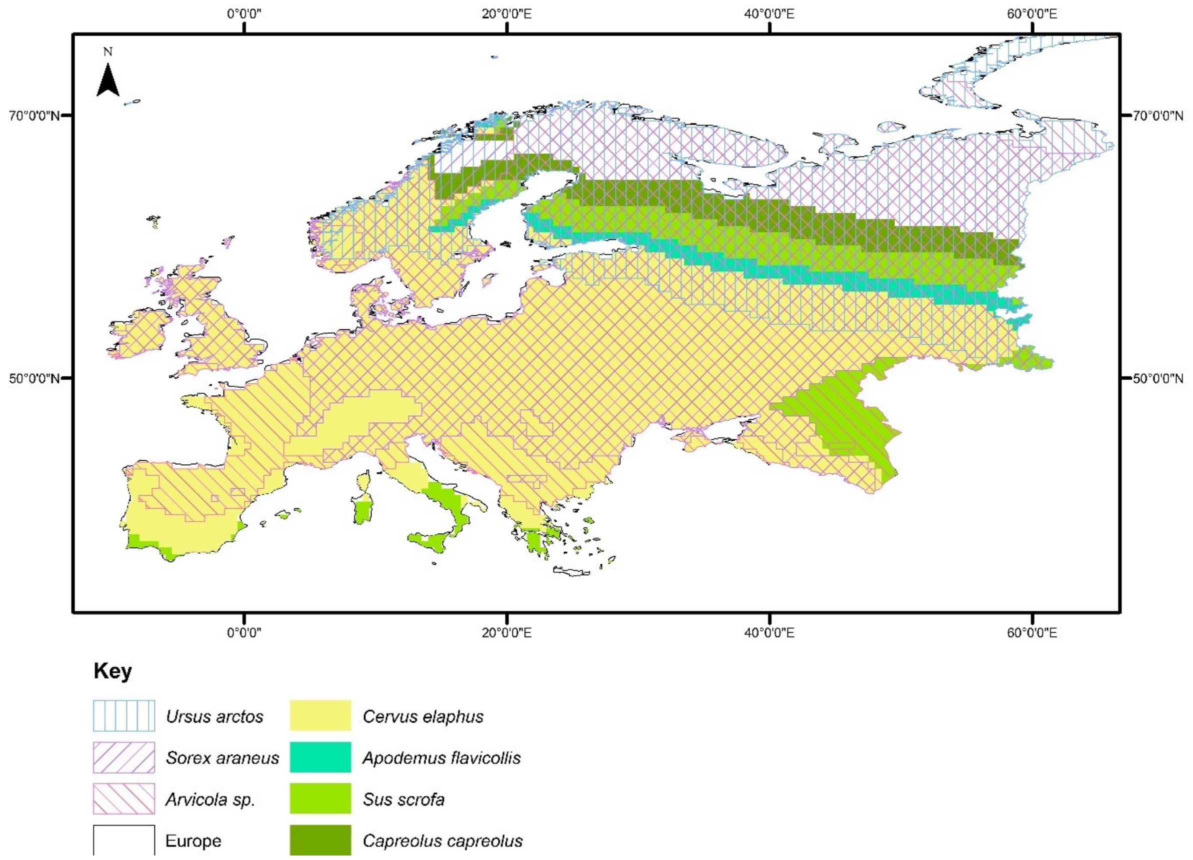

Figure 4.2 Present-day predicted distribution of taxa that fall in the temperate group.

Table 4.3 Percent overlap of the ranges between the cold and arid group. Only Ochotona pusilla and Ochotona sp. (from the arid group) overlap with taxa from the cold group.

Taxa	***Ochotona pusilla***	***Ochotona* sp.**
Dicrostonyx sp.	0.0	11.2
Vulpes lagopus	0.0	28.5
Lemmus lemmus	0.0	9.2
Microtus gregalis	26.1	36.5
Rangifer tarandus	0.0	9.6
Bison sp.	73.9	4.9

The additional taxa from Table 4.2 are shown in the maps below (Figure 4.3, Figure 4.4, Figure 4.5). The present-day models were analysed for their percentage overlap of all individual taxa from one group with the taxa from other groups (i.e. the cold group was compared the arid and temperate group; Table 4.3, Table 4.4, Table 4.5). Part of the climatic range of these taxa is thus sympatric with taxa from another group (southern, northern or eastern). Since no taxon overlaps with all taxa from another group, all taxa had their past distribution modelled.

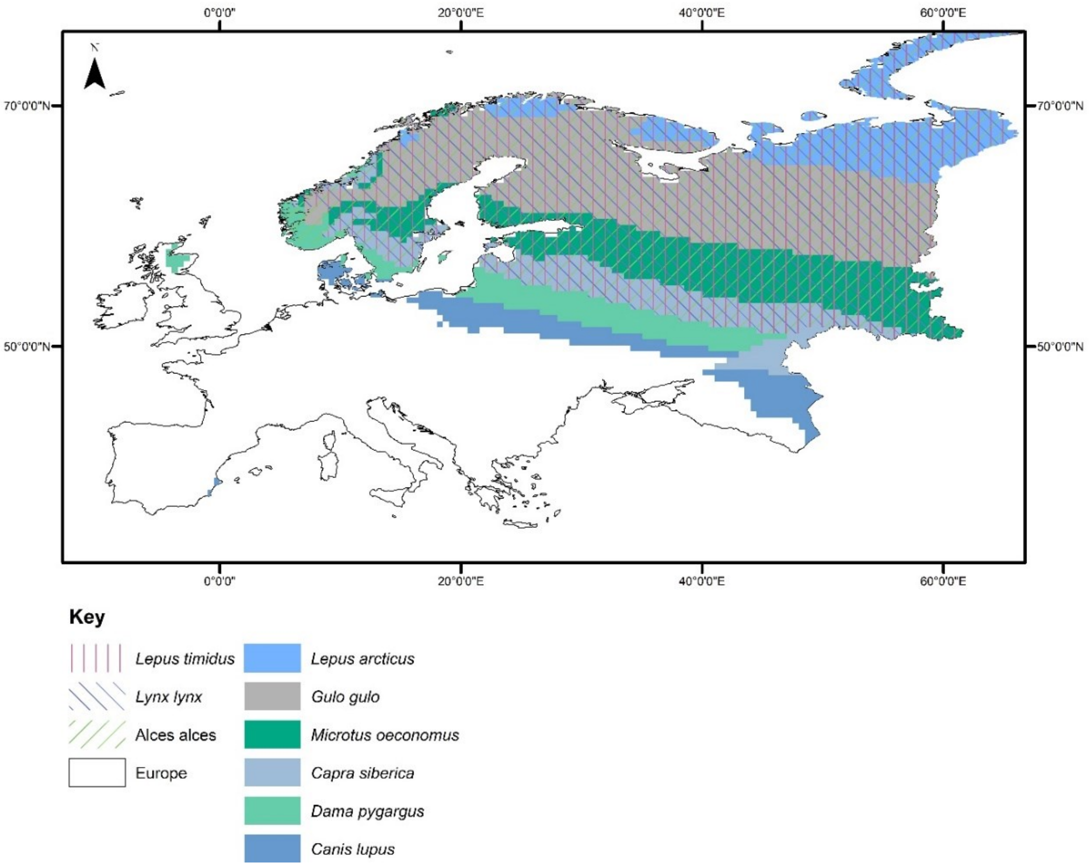

Figure 4.3 Predicted distribution for the extra taxa of the northern group.

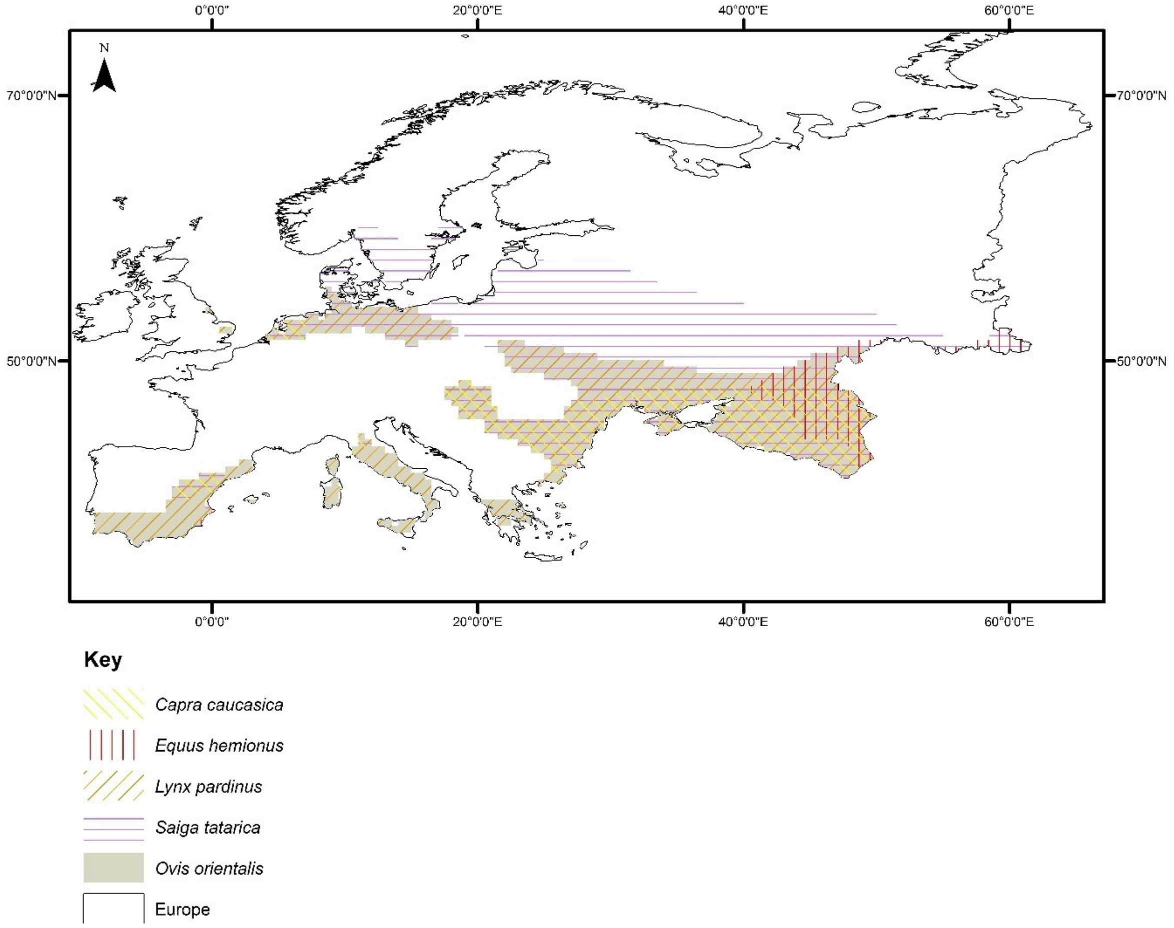

Figure 4.4 Predicted distribution of eastern extra. Saiga is modelled based on its historic range.

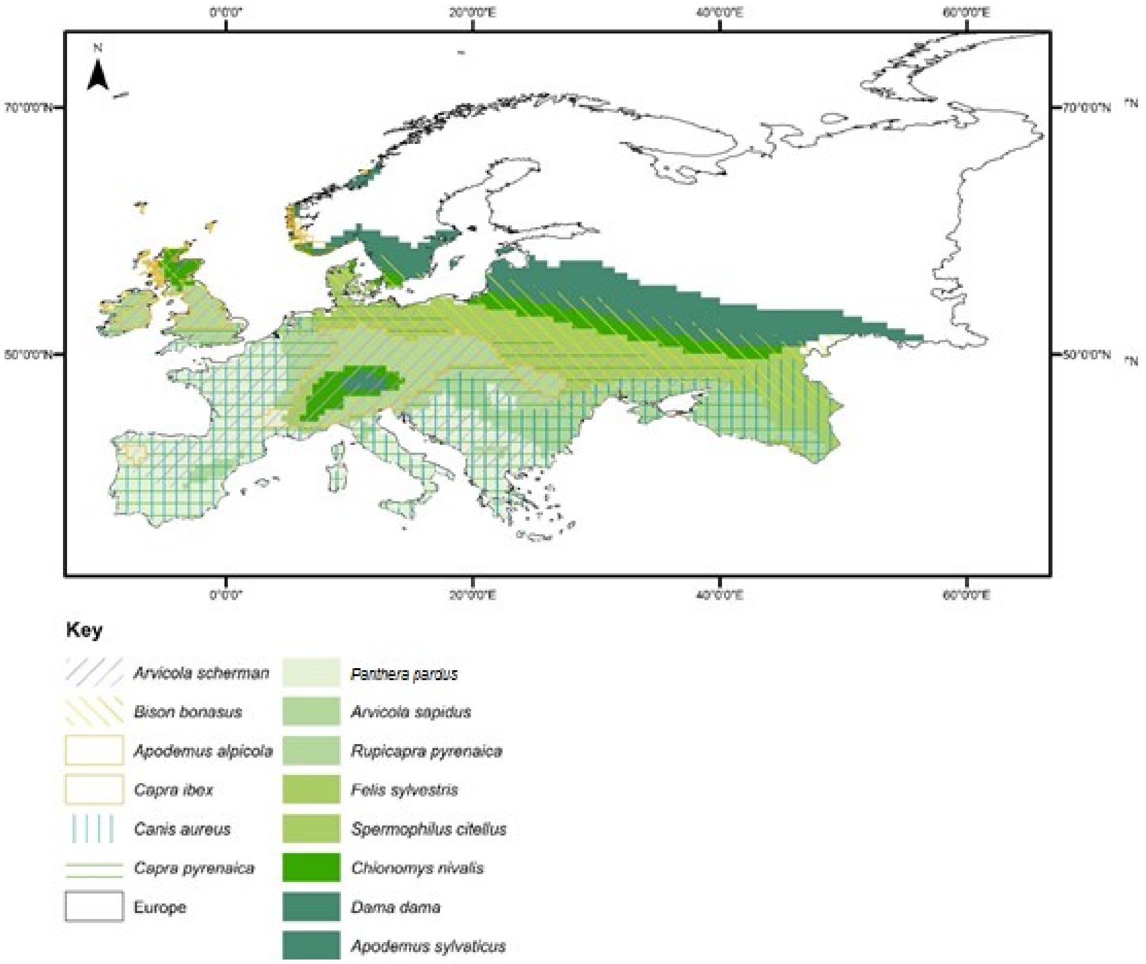

Figure 4.5 Predicted distribution of extra taxa for the temperate group. Taxa with the same colour in the key have the same distribution.

Table 4.4 Percent overlap of northern vs southern of all taxa based on present-day modelled distributions. The darker green indicates a higher % overlap.

Taxa	Southern distribution					
Northern distribution	*Arvicola scherman*	*Bison bonasus*	*Apodemus alpicola*	*Canis aureus*	*Dama dama*	*Apodemus sylvaticus*
Lepus timidus		0.1			96.9	100.0
Alces alces	0.1		56.7		3.1	
Capra siberica		10.3				
Dama pygargus	3.1	44.8	43.3			
Canis lupus		44.8		18.8		
Bison sp.	96.9			81.2		

Table 4.5 Percent overlap of southern vs eastern of all taxa based on present-day modelled distributions, saiga is based on the historic range. The darker green indicates a higher % overlap.

Taxa	Southern distribution					
Eastern distribution	*Arvicola scherman*	*Bison bonasus*	*Apodemus alpicola*	*Canis aureus*	*Dama dama*	*Apodemus sylvaticus*
Capra caucasica	25.0	11.4		62.8		
Equus hemionus		10.2		1.2		
Lynx pardinus	58.5			36.0		
Saiga tatarica		78.5			96.6	
Ochotona sp.	16.5		100.0		3.4	100.0

Table 4.6 Percent overlap of eastern vs northern taxa based on present-day modelled distributions, saiga is based on the historic range. The darker green indicates a higher % overlap.

Taxa	Northern distribution					
Eastern distribution	*Lepus timidus*	*Alces alces*	*Capra siberica*	*Dama pygargus*	*Canis lupus*	*Bison* sp.
Capra caucasica					33.5	48.8
Equus hemionus	0.8		100.0		2.0	
Lynx pardinus						46.9
Saiga tatarica	12.7			92.9	64.5	
Ochotona pusilla	16.7					
Ochotona sp.	69.7	100.0		7.1		4.3

4.3.1 Percentage overlap of taxa through time

The climatic niches of individual taxa of the three groups (northern, southern and eastern) throughout time have been compared to each other, and the percentage overlap has been calculated. Summary graphs (Figure 4.6, Figure 4.7, Figure 4.8) present the percentage overlap with the taxa from different groups (taxa from the northern group compared to southern and eastern taxa and the southern taxa compared to the eastern taxa) that did overlap at points in time. Taxa not listed in the graphs did not have any overlap. The data on which these graphs have been drawn are presented in the Appendix Chapter 4.

In Figure 4.6, the overlap is fairly minimal and mainly occurs with *Ochotona sp.* The taxa *Apodemus agrarius*, *Apodemus flavicollis* and *Sorex araneus* always overlap for a minimum of 25% of their respective ranges with *Ochotona sp.* Occasional overlap occurs with *Ochotona pusilla*, the overlap occurs at different periods with different taxa. *Apodemus flavicollis* overlaps fully with *Ochotona pusilla* during 16ka, 22-26ka and 30-38. *Bison bonasus* and *Arvicola scherman* both overlap during 36ka with *Ochotona pusilla. Bison bonasus* and *Felis sylvestris* have a variable overlap with *Saiga tatarica* throughout the Pleistocene, hovering around the 50%. Finally, *Felis sylvestris'*s whole range overlaps with that of *Lynx pardinus.*

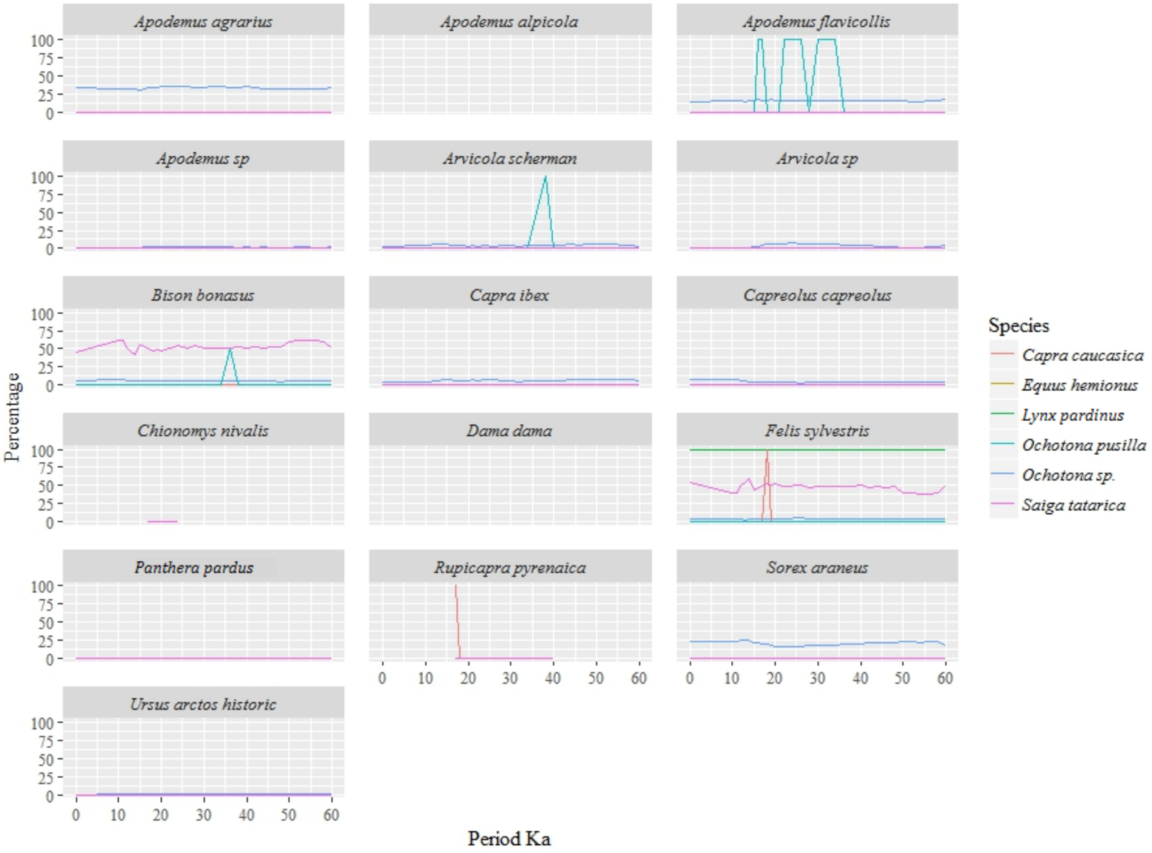

Figure 4.6 Percentage overlap of the modelled ranges of southern taxa (titled graphs) with the modelled ranges of eastern taxa (legend) over the entire time span (0, 10-60 ka).

The percentage overlap between the northern taxa and eastern taxa (Figure 4.7) is minimal as well. *Bison sp.* overlaps periodically with *Ochotona pusilla* with a dip during the LGM and at 36ka. There is a constant small overlap of *Canis lupus (*both models based on the extant and historic range) with *Equus hemionus*. The historic range of *Canis lupus* overlaps party but continuously with S*aiga tatarica* and *Lynx pardinus* as well. There is also a short period of high overlap during 18ka between the modelled historic ranges of *Canis lupus* and *Capra caucasica. Dama pygargus* overlaps with *Saiga tatarica* for around 50% of its range throughout time. *Lynx lynx* has a 75% overlap with *Ochotona sp.* and a small spike of overlap with *Ochotona pusilla* at 36ka.

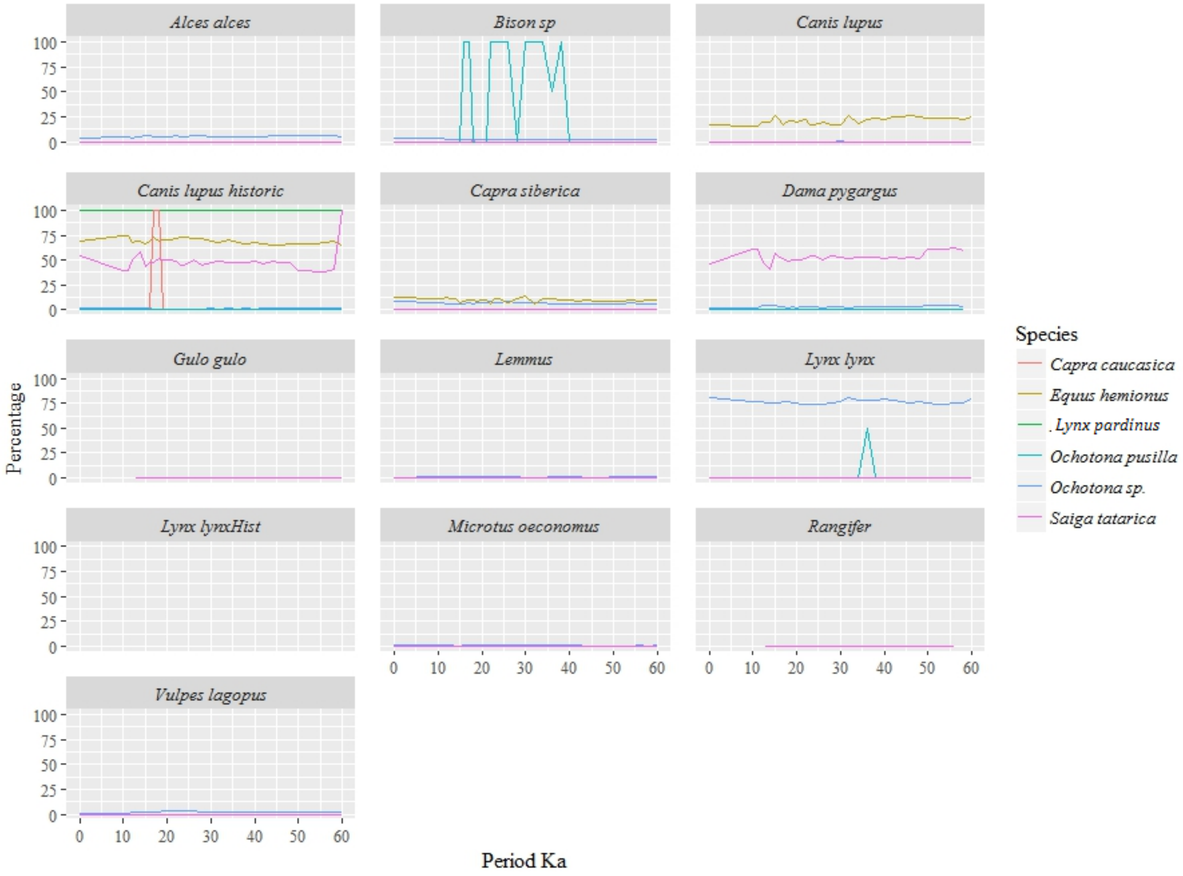

Figure 4.7 Percentage overlap of the northern taxa (titled graphs) with the eastern taxa (legend) over the entire time span (0, 10-60 ka). The projected historic and modern ranges for lynx and wolf are shown.

The northern taxa and southern taxa have the most percentage overlap with each other (Figure 4.8). Most notable are the overlap of *Apodemus sp.* with *Canis lupus (*historic range) and *Dama pygargus*. Even though both taxa overlap, their overlap seems to behave in opposite directions during the climatic fluctuations i.e. the overlap lessens during 20-40 ka between *Canis lupus* and *Apodemus* sp. whilst it increases for the same period for *Dama pygargus*. The lynx (*Lynx lynx*) overlaps to a large degree with most southern taxa for the whole period modelled here.

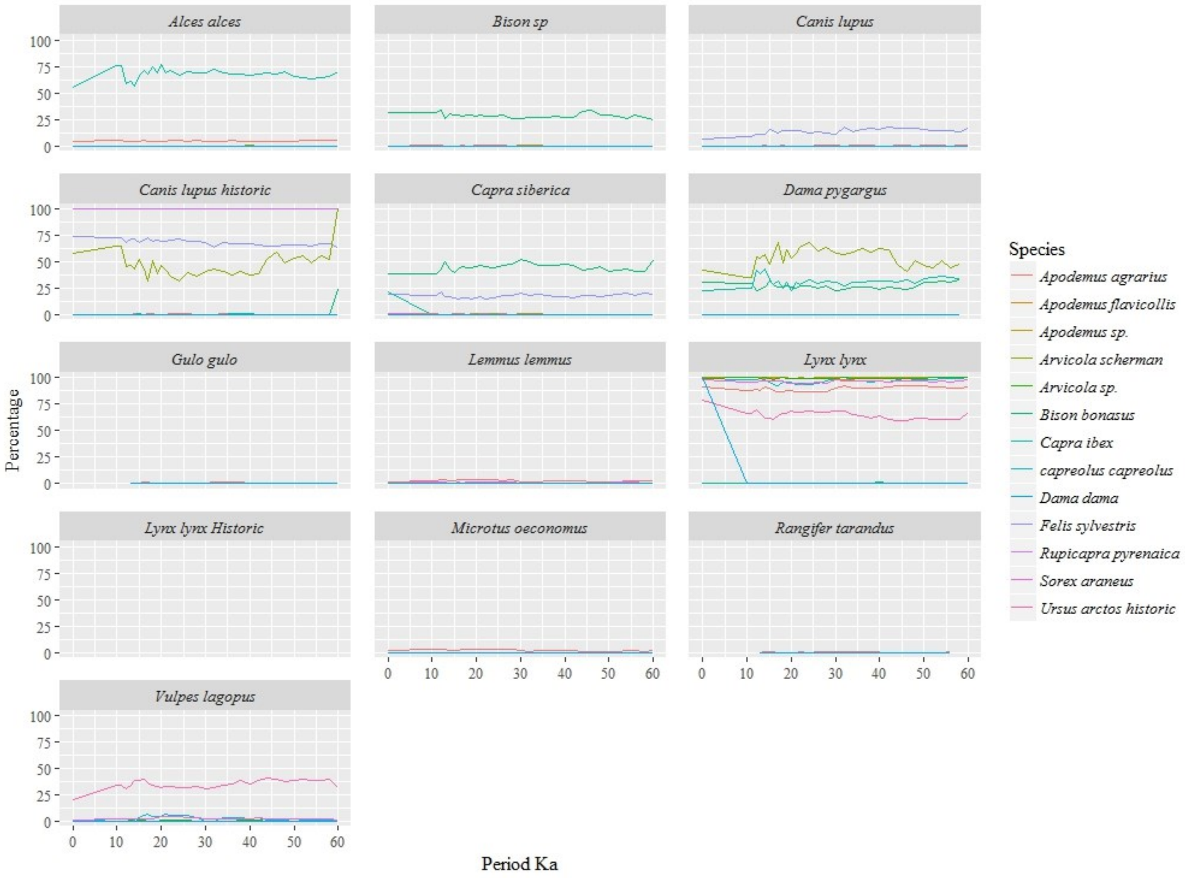

Figure 4.8 Percentage overlap of the northern taxa (titled graphs) with the southern taxa (legend) over the entire time span (0, 10-60 ka).

Based on the percentage overlap analyses, few taxa from the three groups overlap. The taxa that tend to overlap are mostly taxa with very large climatic ranges (such as *Canis lupus*). There is no temporal signal visible, where a different combination of taxa occurs during different climatic regimes (i.e. the non-analogue combinations).

4.3.2 Models of the extinct taxa

The extinct taxa horse, woolly mammoth, woolly rhino, cave bear, cave lion and cave hyaena were modelled based on the time slice with the most remains of each taxon with radiocarbon dates. This indicates that the taxon was not yet in decline and it is assumed that this represents the widest distribution of the taxon. Each taxon was modelled separately, and the resultant models can be found in Appendix for Chapter 4 and are discussed below.

Horse (Equus sp.)

The Pleistocene horse is officially extinct, there are no wild living descendants (Gaunitz et al. 2018). The time frame of ka16 was selected based on 13 locations with direct radiocarbon date occurrences. The model then predicted the distributions of the horse throughout all other time frames. The predicted range seems to be restricted compared to the faunal remains, where the predicted range does not stretch northeast nor southwest enough during almost all time frames to match archaeological reality.

Woolly mammoth (Mammuthus primigenius)

The woolly mammoth went extinct circa 12ka in western/central Europe (Lister and Stuart 2008; Markova et al. 2013). The predicted models (made on convex hull of radiocarbon dates at 28ka) show a gradual displacement to northern Europe where after 13 ka, the range does not change much. The greatest retreat occurs between 16 and 13 ka. The predicted climatic niches fit reasonably well with the radiocarbon dated faunal remains up to 17ka. After that, the mammoth is archaeologically found outside of the predicted range. And finally, the climatic niche of the mammoth is predicted to exist in northern present-day Europe. The persistence of the niche beyond species survival has been previously attributed to human impact (Nogués-Bravo et al. 2008). However more research is needed for this.

Woolly rhino (Coelodonta antiquitatis)

The woolly rhino went extinct at the onset of the Allerød (13.9ka) in Europe (Lister and Stuart 2013). Comparison with radiocarbon dated faunal remains show an agreement until 16ka. Between 16 and 13 ka, there are sites where the woolly rhino was present outside of the predicted climatic range. The woolly rhino is predicted to still have suitable climate in northern Europe.

Cave bear (Ursus spelaeus)

The models of the cave bear (modelled on the 30ka timeframe with random points) generally correspond well with the direct radiocarbon dated faunal remains throughout the different timeframes. However, the range is not predicted as far northeast as some associated faunal remains are situated. The predicted range is at its smallest around the time the cave bear went extinct (25ka uncal), however it still covers most of middle and southern Europe. The cave bear is predicted have suitable climatic conditions throughout the LGM to present-day. The modelled present-day range has contracted to the northeast of Europe. This is not in line with archaeological reality.

Cave lion (Panthera leo spelaea)

The cave lion became extinct from Europe before the onset of the Holocene, around 14ka (Stuart and Lister 2007). The predicted models seem to match up reasonably well with the faunal remains, with only few data points found slightly outside the predicted range. There is a geographic displacement towards the northeast of the predicted range from 15ka onwards.

However, the niche does not contract much and is predicted to continue existing into present-day in northern Europe. The timing of the north-east contraction does correspond with the disappearance of the cave lion.

Spotted hyaena (Crocuta crocuta)

The spotted hyaena models correspond well to the directly dated faunal remains of the taxon (modelled to the convex hull of 32ka). The models show a westward contraction to 30ka, after which the hyaena becomes extinct in Europe (Stuart and Lister 2014). The models do not show a severe range contraction and the climatic niche continues to exist throughout the LGM until 16ka. From 16ka to present-day the predicted range fragments and shifts north-eastwards. The predicted survival of the climatic niche into present-day does not correspond with the disappearance of the spotted hyaena from Europe.

4.3.3 Comparison of climatic niche models to radiocarbon dates

The results of the overlap analysis shows limited overlap of the three groups. This suggests that there were no non-analogue associations in the Late Pleistocene. To test this, the models were compared to the location of taxa with direct radiocarbon dates, as well as associated fauna. The comparison of the models with the archaeological evidence allows for an evaluation of the climatic niche models. The maps of all taxa through time can be found in Appendix Chapter 4, where the modelled range, direct radiocarbon dates (split per quality indicator) and associated taxa are displayed on a map of Europe per time frame.

The climatic niche models of the southern taxa correspond to the direct radiocarbon dates the best – meaning that the range overlaps with the location and timeframe where the taxon was found. The model does not seem to correspond well with the most northern margins of the range, where (mostly) associated dates are found.

The northern and eastern groups of taxa compare poorly to the models, where the models predict the taxa to be more northern and eastern throughout all the timeframes, whilst the archaeology indicates the taxa occurred in southwestern Europe for most of the time. The poor fit between the models and the archaeology needed closer examination. Two main hypotheses were tested:

- The modern distribution does not encapsulate the full potential distribution of past populations. Some past populations may have had a different climatic niche. Including the past distribution of these potentially differently adapted populations in the model could account for this difference.
- The climate models used do not encapsulate the past climatic variability of Europe. This may lead to an underestimated prediction of the climatic range of the taxa. The use of more variables or different climate models of higher spatial and temporal resolution might resolve this.

4.3.4 Alternative models for reindeer

To investigate the causes for the poor fit of the models with the archaeology, the taxon with most radiocarbon dates was chosen (reindeer, *Rangifer tarandus*). Reindeer is part of the northern group and the first model (hereafter Model 1) showed a persistent north-easterly distribution, whilst the archaeology (both direct and associated dates) indicates a more southern distribution (down to the Pyrenees). Furthermore, the reindeer has genetically distinct populations, of which one is extinct (Bjørnstad et al. 2012). It therefore also ecologically makes a good candidate to use for the alternative models. Several models have been run to investigate the discrepancies.

Model 2

The first option was to improve the existing Model 1. For this, Model 2 was created using the time frame with most good and fair radiocarbon dates, which is 16ka. The modelled range of Model 1 for this time frame was used, random points (500) were created within the modelled range, with the locations of the direct radiocarbon dates as test data, and the model was re-run with the same parameters. Using the test data, which are known presences, increases the certainty and range of the model.

Improving the model in this way, would include modern and past populations. The modern populations may not express the full climatic potential that the ancestors of the taxon were capable of. Therefore, by including the archaeological locations at 16ka, the model might present a better fit to the past archaeological distributions at the other time frames.

Appendix Chapter 4 shows the results of Reindeer Model 2. The models have changed the climatic ranges of the reindeer through time but not enough to fit the archaeological data. The Reindeer Model 2 corresponds poorly to the archaeological reality.

Model 3

To investigate if the 16ka timeframe could predict the climatic niche of reindeer in other timeframes and present-day, Model 3 was made. A convex hull polygon was drawn around the archaeological distribution of direct dates (classed good and fair) and 100 random points were generated within this, which were used as the training data for the model. The locations of the direct dates were used as test data. The model was then projected to all other available time slices and to present-day.

Results are shown in Appendix Chapter 4 for Model 3. The model does predict the presence of reindeer in the past better (older than 16ka) but not the younger time frames (15ka and younger). The predicted present-day distribution has a larger spatial extent than in reality, but it does model the contraction to north-eastern Europe well.

Running the model with the past populations should ensure a better fit to the past archaeological distributions. This is only partly the case with Model 3. Therefore, the investigation continued into the climatic maps. Maybe the climate maps used did not encapsulate enough variability on the continent.

Model 4:

To test the potential problem regarding climatic variability, Model 4 was run using the same two main means to determine species distribution (mean annual temperature and mean annual precipitation) as in the former models but used a different climate simulation. Whilst climatic simulations available for this period are all consistent with each other, minimal differences in environmental conditions do occur (Lorenzen et al. 2011). Instead of the BRIDGE climate simulations used above, the BIOCLIM 1.4 for present-day, and the MIROC-ESM simulation for LGM (22ka) were used (downloaded from bioclim.org). The climate simulations were downloaded at 2,5 minutes resolution. The same presence data for training the model was used as in Models 1 and 2. The parameters were kept the same.

Model 4 was run to see if the MIROC-ESM climate simulations showed a better fit to the archaeological distribution and the predicted distribution of the reindeer (Appendix Chapter 4). This model has a very narrow prediction of the reindeer distribution, that does not match the archaeological distribution.

Because a different climate simulation was used, the variables (mean temperature and mean precipitation) may not have been expressed in the same way as the Bridge simulations. Therefore, the effects of the different variables should be investigated with all available Bioclim variables.

Model 5:

Model 5 was run to account for a difference between the BRIDGE and Bioclim climate simulations and to see if other variables are more important for the distribution of reindeer. The initial three variables used above were chosen to prevent model-overfitting. When using many variables compared to the amount of presence data, it may lead to a unrealistic distribution of the taxon (Lorenzen et al. 2011). However, since an adequate amount random points have been made, the chances of overfitting are slim. A correlation matrix was run in ArcGIS on all Bioclim variables and those with a correlation coefficient of <0.7 were selected for the models (see Appendix Chapter 4). The model was run following the same settings as for Model 4.

Results (Appendix Chapter 4) have moved the distribution for reindeer southward during the LGM. However, the distribution is limited to a narrow, unrealistic strip, indicating that this model does not reflect a realistic distribution in the past either.

Model 6:

Model 6 was run using the BRIDGE climate simulations to include all variables used in Model 5 (that were run on the Bioclim variables) at ka00 and ka22, so that the two models could be directly compared. The variables used in Bioclim were recalculated in BRIDGE and then the correlation model was run (Appendix Chapter 4). The resultant variables were used for the model, following the same setting as previous models.

This model (Appendix Chapter 4) predicts a wider distribution than Model 5. It extends more westwards and southwards than Model 1 (the original), however, it still does not compare to the archaeological reality.

4.3.5 Summary of the results

The overlap analysis shows that very few taxa between the northern, eastern and southern groups overlap. There is no temporal pattern discernible (for example cooler time periods may have been expected to show an increase of overlap with northern fauna). The overlap analysis thus shows that based on present-day distributions and present-day climatic niches, the predictions for the past climatic niches exclude the existence for non-analogue associations. Simply put, there was no such thing as non-analogue faunas according to the models.

Furthermore, a comparison was made of the models to the direct (and associated) radiocarbon dates of the different taxa. The comparison showed that the models of the taxa in the northern and eastern groups had a poor fit to archaeological reality (the taxa never got as far south or west in the models as compared to the archaeology). The models of the southern group did fit reasonably well with the archaeological record, showing that the taxa in the southern group had not changed their ranges much throughout time, likely displaying a stable realised niche. However, the poor fit of the northern and eastern taxa to the archaeology could be explained by two hypotheses: past populations could have had a wider climatic niche than present-day populations or the climatic variability was not captured by the models and thus the distribution was not correct.

Extra models to test the hypotheses were run. This included expanding the modern climatic niche with that of past populations at 16 ka, only using the past populations of 16ka to predict other time frames, using different climate simulations and using more and different climatic variables. However, all options showed a continued poor match to the archaeology. This indicates it is a complicated problem that may have multiple explanations, which are addressed below.

4.4 Discussion

The original models and the additional models for reindeer (Model 2- Model 6) all demonstrate an unrealistic predicted past distribution for the northern and eastern taxa, based on the known presences of archaeological evidence. There are several explanations for the discrepancies between the models and the archaeology.

4.4.1 Radiocarbon dated faunal remains

The first explanation is that the faunal remains of the taxa have not been dated precisely enough (each radiocarbon date has a large uncertainty, even at 1σ) and therefore one radiocarbon date can stretch over periods with severe climate change (Greenland stadials and interstadials). The individual and taxon may not have been able to tolerate the different climatic regimes and were only present in one or other extreme.

Furthermore, the taxa have been split into 1000-year and 2000-year time frames to be able to compare the archaeology to the climatic niche models. The archaeological distribution is therefore a combination of different individuals being present at different times during 1000 or 2000 years. It therefore shows a combined presence of individuals through time and space. This may not reflect reality, where the distribution of the taxa may not have covered the entire range visualised during the entirety of each time period.

Finally, the distribution and climatic tolerances of taxa may have been underestimated due to a lack of archaeological sites throughout Europe. Most sites are cave sites and are situated in mountainous regions and the highest number of sites are situated in Southern France. This is partly due to a historic research interest into Southern France and possibly due to less resources being available to researchers in Eastern Europe (Roebroeks and Soressi 2016). Furthermore, few open-air sites have been found and therefore, there is a shortage of archaeological sites on the Central European Plain. The uneven spread of archaeological sites throughout Europe may skew the distribution of the taxa and their associated past climatic niche.

The biases in the archaeological record are likely to have a great influence on the modelling of extinct taxa such as the woolly mammoth, woolly rhino, horse etcetera (Maxwell et al. 2018). A combination of a better spread of archaeological sites and more precise dating of the specimens would improve the models, although it is hard to see the first issue being resolved while the second requires significant expenditure.

4.4.2 Climate simulations

The climate simulations provided by BRIDGE are already at relatively fine time frames, but they do not encapsulate all the climatic variability in between the chosen dates. Table 4.7 shows the Greenland Stadials and Greenland Interstadials per time frame, and the variability that occurs between two timeframes. The presence points (radiocarbon dates) that occur within these time frames, may therefore be part of a colder (GS) or warmer (GI) phase. Most time frames are made during a Greenland Stadial and Greenland Interstadials seem to be underrepresented. As a result, the species distribution models do not show the shrinking and expanding of the potential ranges fully. Additionally, some taxa may not have been able to re-expand into their former range when climatic fluctuations have been too severe and frequent before the next time frame.

Table 4.7 Climatic variability present and missed in the BRIDGE climate simulations.

Time frame in ka	Greenland interstadial/stadial at time frame	Missed variability
10	Holocene	
11	Holocene	
12	GS-1	11.4ka event
13	GI-1a	
14	GI1-d	GI-1 b, c1, c2, c3
15-22	GS-2	
24-26	GS-3	GI-2.1, GS-2.2, GI-2.2
28	GS-4	GI-3
30	GS-5.1	GI-4
32	GS-5.2	GI-5.1
34	GS-7	GI-5.2, GI-6
36	GS-8	GI-7 a, b, c
38	GI-8c	GI-8 a, b
40	GI-9	GS-9
42	GS-11	GS10, GI-10
44	GS12	GI-11
46	GI-12c	GI-12 a, b
48	GS-13	
50	GI-14a	GI-13 a, b, c, GS14
52	GI-14c	GI-14 a, b
54	GI-14e	
56	GS-16.1	GS-15.1, GI-15.1, GS-15.2, GI-15.2
58	GS16.2	GI-16.1 a, b, c
60	GS18	GI 16.2, GS-17.1, GI-17.1a, b, c, GS 17.2, GI-17.2

The climate simulations of the past may not reflect the real past climate well enough for this type of modelling. Climate simulations are constructed and tested on proxy data. Climate simulations of the current climate deviate from the measured current climate (Flato et al. 2013). The proxy data used to test the climate simulations of past predictions have a wider margin of error in them than the modern data, and this makes the models less precise (Dincauze 2000). This in turn means that variables could be under- or overestimated for past palaeoclimate simulations, and therefore underestimate non-analogue climate situations. This problem was found for previous climate simulations for the Stage Three project, where the simulated cooling of northern Europe did not agree with the faunal and floral evidence (Alfano et al. 2003; Stewart et al. 2003).

Other factors may also be driving species distribution rather than just the climatic variables. Different predictors, as suggested by Stewart (Stewart et al. 2003), such as vegetation, net primary productivity, human activity or steep topography may have had more of an influence on species distribution than climate variables. The mammoth steppe may have been self-sustaining the non-analogue communities and non-analogue climate to some extent (Guthrie 2001). The large grazers would produce enough nitrogen to sustain highly productive grasslands, in turn lowering permafrost (lowering the albedo) and creating clear skies (reducing the greenhouse effect) which amplified the climatic fluctuations (Guthrie 2001; Zimov et al. 2012). These biotic factors are not incorporated into the climate simulations and therefore they may not reflect the past accurately. The combination of a dynamic vegetation model and palaeoclimate simulations allowed for a better match with the archaeobotanical record and agreed with the increased climatic fluctuations maintaining the mosaic steppe landscape (Huntley et al. 2013).

4.4.3 MaxEnt Modelling

The maximum entropy modelling technique does not consider competition with other taxa nor the differences in dispersal success and speed. The models therefore overestimate the distribution of taxa in the Pleistocene, because there is no mechanism to account for reduced or increased dispersals (due competition or dispersal ability). These mechanisms have been shown to have a large effect on predictions of the distribution of taxa during future climate change (Urban et al. 2012).

Furthermore, the MaxEnt models assume a stable fundamental niche, however the models are run on the observed realised niche (observations of where a taxon is present) (Merow et al. 2013). Non-analogue climates are therefore not considered as part of the fundamental niche (even though the taxon would be able to tolerate them), and the models can therefore not predict the species presence in it. This has been observed for tree taxa where the past distributions (22-15ka) were used to model present-day distributions (Veloz et al. 2012). In this study, taxa with stable realised niches have adequate predictions that matched with current distributions, whilst taxa that did not have stable realised niches and shifted in geographic location, were shown to have poor predictions compared to present-day distributions. For example, oak (*Quercus*) had a stable realised niche and the predicted range match with the current distribution of oak, whilst ash (*Fraxinus*) had an unstable realised niche which meant that the past distribution could not be used as a model for the present-day distribution, because ash now occupies a different climatic niche (Veloz et al. 2012). In another study, distribution modelling on tree taxa going further back in time than the Holocene has been found to be erroneous (Roberts and Hamann 2012), attributed to the lack of niche conservationism of the taxa together with the occurrence of non-analogue climates. This issue has also been observed here in the models for the mammals, demonstrated with the extinct taxa as well as the Model 3 for reindeer, where past presences were unable to predict present-day presences adequately. The incorporation of past populations in reindeer Model 2 did not alleviate the problem. This lead to the conclusion that reindeer have a larger climatic fundamental niche than can be detected in the archaeological and present-day distributions. It is therefore difficult to estimate what the full climatic niche capabilities are, and we therefore cannot adequately predict what non-analogue climates the taxon can tolerate (Fitzpatrick and Hargrove 2009).

4.4.4 Biogeography

Apart from technological matters (imprecise dating, climatic simulations and limitations of modelling technology), biogeographical responses of taxa to climatic changes occurs individualistically through time and space (Rowe et al. 2014; Stewart 2008, 2009). Not only do the taxa respond to the same variables in different ways, they also respond to different individual climatic variables and this may be of greater influence on the taxon's range. Models 5 and 6 of the reindeer distribution were run on multiple variables to test if this would provide more realistic distributions. Even though the predicted distributions changed radically with the inclusion/exclusion of variables, they did not produce a more realistic distribution.

The presence of northern or eastern taxa in southwestern Europe may also be due to the migration capabilities of the taxa. Some taxa show a greater daily mobility or seasonal migration mobility than taxa from the southern group of mammals, for example reindeer and saiga. Both these taxa undertake long distance migrations (Forbes and Kumpula 2009; Singh et al. 2010). Their dispersal ability may therefore be great, and the taxa may be able to traverse into southern Europe during short climatic excursions (such as the sub-phases of a GI or GS). It is not only the highly migratory taxa that have made it into southwestern Europe, taxa with a high daily mobility (arctic fox) and taxa that reproduce quickly (collared and Norway lemmings) were also present in Europe beyond their predicted ranges, which may have an equally high dispersal ability through different mechanisms (Tarroux et al. 2010). These short dispersals may be species specific and are impossible to separate with current dating methods. It has for example been suggested that the synchronous presence of *Mammuthus primigenius* and *M. trogontherii* at Hot Springs, a site in the United States, indicates short term (maybe even seasonal) contemporaneity or replacement (Kahlke 2013).

The southern group appears to have had a more stable geographic distribution throughout time (both in the archaeological record and in the distribution models), whilst the northern and eastern taxonomic groups demonstrated local extirpations and complete extinctions. For example, population extinctions have been shown with ancient DNA for the collared lemming, where population turnovers occurred during periods of large climatic changes (Brace et al. 2012). There were multiple migrations into western Europe from the east, with the last collared lemming population still being extant in Siberia and extirpated in Belgium. The overturning of populations suggests range contractions (local extinctions) rather than habitat tracking, which would have kept the ancient populations alive. This has also been shows for Pleistocene arctic fox and Norway lemming (Dalén et al. 2007; Lagerholm et al. 2014). As discussed above, the existence of these extinct populations with potentially different climatic tolerances to their extant populations, may be an indication that the current distribution of the taxon is an unstable realised climatic niche. The unstable realized niche can therefore help to explain the non-analogue associations because older populations would be able to occur in different climatic regimes, mixing with populations of other taxa with similar unstable realised niches (Polly and Eronen 2011). This in turn may explain any discrepancies between climate and species distributions encountered in the present analysis.

Populations of the woodmouse (*Apodemus sylvaticus*) and Northern watervole (*Arvicola amphibius)* may have been able to survive in northern refugia during the LGM and dispersed from these locations into the Holocene (Brace et al. 2016; Herman et al. 2016). The genetic survival of different populations in Europe suggests the presence of northern refugia, it also indicates a more stable geographic distribution of the southern group of taxa. Survival in cryptic refugia, whether those are northern refugia (for more thermophilous taxa) or southern refugia (for more cryophylous taxa), is argued to be possible for taxa that are habitat-generalist (Bhagwat and Willis 2008; Stewart and Lister 2001). Survival in refugia could enable the non-analogue combinations of taxa, because the taxa lingering in refugium overlap with those that have expanded their range in accordance with climatic changes.

The combination of fast dispersal of populations of one taxon and the lingering behind of another taxon may also help to explain the non-analogue combinations of taxa. Survival in cryptic refugia would have aided a fast dispersal after a climatically unfavourable episode (Snell and Cowling 2015). This is illustrated by Reid's Paradox that postulates that based on pollen records tree taxa spread faster after the Last Glacial than would be possible based on life history calculations (Clark et al. 1998). The presence of northern refugia mitigates the paradox and enables a fast expansion as shown by several studies (Moore et al. 2015; Tausch et al. 2017). The prolonged continuation of populations on the brink of extinction is sometimes referred to as extinction lag, Dead Clade Walking or extinction debt (Dullinger et al. 2013; Jablonski 2001). This phenomenon is now frequently observed with habitat loss and climate change of endangered taxa. The combination of lingering nearly-extinct populations and the fast dispersal of others could also help explain the non-analogue associations.

4.4.5 What do the models teach us about the non-analogue fauna?

This study set out to unravel if taxa were sympatric in the past that are allopatric today or whether this was an artefact of mixed faunal assemblages. The non-analogous combinations are considered to be faunas in equilibrium that existed due to non-analogous climate (Stewart 2009). The predictions of the models produced here did not meet the radiocarbon dated faunal evidence for the cold and arid taxa but were more reliable for the southern taxa.

The overlap analysis showed that, based on present-day distributions, we would not expect non-analogous faunas in the past. This is a different outcome than previous research that dealt with greater time depth in Britain, where non-analogous associations were confirmed by the models (Polly and Eronen 2011). However, both the models created in this chapter and of the research by Polly and Eronen show that there is simply little overlap in the predicted range of most taxa. However, past populations could have had a different climatic niche and it would have been those populations of different taxa that had lived in sympatry (Stewart 2009). The present study has tested for the effect of a different climatic niche in past populations (reindeer Model 2 and 3) as suggested for future research by Polly and Eronen (2011) and the issue has not been resolved. Therefore, this may indicate that there may not have been a big difference in the climatic niche of the past populations compared to present-day populations, at least for reindeer. This in turn may suggest that the non-analogue associations may not be fully explained by the differently adapted past populations.

The detection of non-analogue associations may therefore have been an artefact of the lack of precision. There is time averaging in the stratigraphy (mixing or palimpsests), imprecise dating methods especially in 60-20ka period where the 2σ often spans more than a thousand years, and the climatic simulations do not pick up all the climatic variability that occurred during the studied period. These imprecisions demonstrate that it is complicated to truly understand the nature of non-analogues.

However, it can be concluded that the non-analogue associations (if not an artefact of imprecision) would have been short-lived occurrences. There is no continued, prolonged sympatry of the taxa and therefore is seems that there were long-lived non-analogue communities were typically short-lived. The rapidly changing climate would cause a mobile mosaic of environments and taxa, each responding to the changes individualistically. This could have occasionally lead to the partial overlap of ranges of different taxa, as one is hanging on in a disappearing habitat for it while another taxon is moving into a newly emerging habitat.

Finally, models demonstrate a more stable realised niche of the taxa in the southern group. The models agree better with the archaeological locations and the distribution of the climatic niche in Europe changes with the cooling and warming of the climate.

4.5 Conclusion

Neither the archaeological evidence nor the distribution models have been able to confirm or contradict the presence of non-analogue communities with certainty. This does not only illustrate the difficulty of reconstructing the past, it also illustrates the biogeographic complexities of community ecology and the partly understood climatic tolerances of individual taxa. Based on the biogeographic capabilities of the different taxa as well as the abrupt climatic changes, the sympatry of non-analogue taxa is very likely during phases of climatic instability which would have caused a mosaic of vegetative habitats (Lister and Sher 2001). However, the co-occurrence of non-analogue taxa may have been fleeting and may not have constituted functional long-lived ecological communities.

To better investigate non-analogue combinations of taxa in the past a combined approach including more precise and secure dating of faunal specimens, the creation of continuous climate simulations going through the past abrupt climatic changes and the creation of species distribution models encompassing dispersal and competition factors are needed. This would allow for both the creation of more accurate models and better testing of the models, which in turn could lead to a better understanding of the past and future sympatric distributions of currently allopatric taxa.

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5 The predicted Neanderthal stable realised niche and the contraction of its geographic range.

5.1 Introduction

The Neanderthal lived in Europe during the changing climatic conditions present there throughout time, i.e. experiencing a number of glacial-interglacial cycles (Arsuagà et al. 2014). The classic Neanderthal developed around 120ka and it is thought the taxon thrived in Europe during Late Pleistocene (Roebroeks and Soressi 2016). Global extinction of the Neanderthal has been dated to 41-39 ka and is associated with a south-westward contraction of its range (Higham et al. 2014). The rise and demise of the Neanderthal is a widely debated topic and the explanations for the extinction are mostly based on the capabilities and tolerances of the Neanderthals (Hockett and Haws 2005; Hortolà and Martínez-Navarro 2013; Hublin and Roebroeks 2009; Pettitt 1999; Sullivan et al. 2017). The paradigm of the hyper-arctic, hyper-carnivorous Neanderthal that exclusively hunts large game and thrives in cool northern Europe is slowly changing to a more temperate adapted hominin with a broader dietary palette (e.g. Stewart 2005 vs. Weaver 2003). The temperate adaptation also suggests that the Neanderthal did not thrive in glacial periods as opposed to the interglacial and interstadial periods of the Late Pleistocene. Little research has focussed on the Neanderthal during an interglacial and the research suggests did not do well in inland Europe due to its forested nature and instead preferred the coastal regions (Benito et al. 2017; Gaudzinski-Windheuser and Roebroeks 2011). Furthermore, most research on the climatic niche of the Neanderthal has focused on the final period before its demise and the possible interaction with anatomically modern human (Banks et al. 2008; Barton et al. 2011; López-García et al. 2015; Melchionna et al. 2018; Stewart 2004). This study, therefore, aims to investigate the climatic niche of the Neanderthal during its climatic optimum (expected to be at 120ka or MIS5e) and to study the contraction of its range during MIS3.

The previous chapter (Chapter 4) has shown that species distribution modelling comes with many caveats. Despite these difficulties, the field of palaeodistribution modelling is growing (Svenning et al. 2011). This includes niche models for hominin species, especially the spread of modern humans and the demise of Neanderthals (Banks et al. 2008, 2009, 2011, 2013; Beeton et al. 2014; Benito et al. 2017; Burke et al. 2017, 2018; Giampoudakis et al. 2017; Melchionna et al. 2018; Nicholson 2017). The difficulties with the models are amplified when it comes to studying hominins because their cultural inventions (for example tools or clothing) may enable hominins to persist in areas beyond their physical climatic niche limitations (Brown et al. 2017; Roebroeks et al. 2011). Furthermore, often the limitations of the models created on different climatic simulations, abiotic variables or presence data (archaeological sites) are not explored (Nogués-Bravo 2009). Finally, only a few studies test the assumption of uniformitarianism: that the realised (or fundamental) niche did not change through time if there were no physical or behavioural changes to the hominin. Therefore, this study aims to explore the limitations of the ecological niche modelling and choose the most appropriate model to assess the pattern and process of the Neanderthal niche.

This study thus investigates the realised niche of the Neanderthal (*Homo neanderthalensis*). This study will investigate the climatic niche of the classic Neanderthal and the contraction of its range towards (and beyond) the Neanderthal’s demise. This study investigates multiple climatic models, variables and training data to explore how these different models create different climatic niches for the Neanderthal. This study will then select the model that performs best in accordance with archaeological reality and use it to explore the potential realised niche of the Neanderthal in Europe.

5.2 Methods

The climatic niche of the Neanderthal was reconstructed using species distribution models with the software MaxEnt (Merow et al. 2013; Phillips et al. 2009). The same settings and methods were applied as in Chapter 3 and Chapter 4. Several models were made with different abiotic variables and training data to assess the sensitivity of the models to changes in the input variables and choose the best performing one based on validation against the archaeological record. Since the Neanderthal went extinct during MIS3 it is unlikely the entire (fundamental) climatic niche was occupied, therefore the climatic range at 120ka (MIS5e) was used to investigate the climatic niche of the Neanderthal as well as MIS3 data. The climatic niche of the Neanderthal MIS5e has been modelled in previous studies (Benito et al. 2017; Nicholson 2017).

5.2.1 Selection of archaeological locations

For MIS5e (120ka), the archaeological locations from the study by Benito *et al.* (2017) was used as training data for the models of the present study. The extent of these archaeological sites (the European continent plus Georgia, Lebanon, Syria, turkey, Armenia, Azerbaijan, Iraq, Israel, Jordan and the Palestinian territory) were used as the geographic extent for the present study. Archaeological locations used for training data for MIS3 came from two additional sources. The timeframe of 50-54ka was selected for Early MIS3 because this period has a relatively stable and warm climate. Archaeological locations were selected from the database constructed for this project (see Chapter 2) in which Neanderthal occupation has been dated by ESR, OSL or TL methods and with their mean age in the 50-54ka bracket. Finally, two time frames towards the disappearance of the Neanderthals were selected from Higham et al. (2014) at the date 44ka (incorporating sites which had at least part of the 1σ with the 2000 year time frame of 45-43ka) and 42ka (including sites falling in the 41-43ka period). The 52ka time frame has less precise dates, but more locations and is hypothesised to represent a stable (i.e. not in decline) Neanderthal population. The 44ka and 42ka time frames hold more precisely dated archaeological locations – the very last in Europe. However, since the Neanderthal is going extinct, it may not represent the full climatic niche of the taxon.

5.2.2 Selection of climatic simulations and variables

It is considered good practice to select different climate simulations if available to the researcher (Nogués-Bravo 2009). The present study used two climatic simulations at 120ka, BRIDGE and WorldClim (Otto-Bliesner et al. 2006; Valdes et al. 2017). The models were run on both simulations to see if there were substantial differences. The 2000-year time frames for MIS3 were modelled by the BRIDGE group.

All 19 bioclim variables were used from the WorldClim data, (recalculated for the BRIDGE climatic simulations, Table 5.1) as well as extra variables generated by the BRIDGE climate simulation (annual mean Wind Chill, Köppen-Geiger climate groups, Net Primary Productivity, Growing Degree Days at 5°C and Growing Degree Days at 0°C). Finally elevation, slope and aspect were calculated after the Global Multi-resolution Terrain Elevation Data 2010 (Danielson and Gesch 2011) and resampled to the WorldClim and BRIDGE raster resolutions in ArcMap 10.4. Correlation matrices were created to select variables with correlation coefficient <0.7, to prevent overfitting of the models. The correlation matrices are the Appendix Chapter 5. To assess whether different variables have a large impact on the prediction of the climatic niche of the Neanderthals, several models were run. The different MaxEnt models and the selected variables are shown in Table 5.2.

Table 5.1 Overview of the BioClim variables used and the BRIDGE variables that are similar (or have been recalculated).

Variable name	Bioclimatic variable	BRIDGE variable used
Bio01	Annual Mean Temperature	Surface temperature - annual mean
Bio02	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Mean of (Maximum absolute monthly temperature per month - Minimum absolute monthly temperature per month)
Bio03	Isothermality (BIO2/BIO7) (* 100)	Isothermality (BIO2/BIO7) (* 100)
Bio04	Temperature Seasonality (standard deviation *100)	Warmest-coldest season temp diff -annual mean
Bio05	Max Temperature of Warmest Month	Monthly absolute maximum monthly temperature - July
Bio06	Min Temperature of Coldest Month	Monthly absolute minimum monthly temperature-January
Bio07	Temperature Annual Range (BIO5-BIO6)	Warmest-Coldest month temp diff
Bio08	Mean Temperature of Wettest Quarter	Surface air temp -DJF seasonal mean
Bio09	Mean Temperature of Driest Quarter	Surface air temp -JJA seasonal mean
Bio10	Mean Temperature of Warmest Quarter	Surface air temp -DJF seasonal mean
Bio11	Mean Temperature of Coldest Quarter	Surface air temp -JJA seasonal mean
Bio12	Annual Precipitation	Annual precipitation - annual mean
Bio13	Precipitation of Wettest Month	Wettest month mean precipitation annual mean
Bio14	Precipitation of Driest Month	Driest month mean precipitation annual mean
Bio15	Precipitation Seasonality (Coefficient of Variation)	Precipitation seasonality index - annual mean
Bio16	Precipitation of Wettest Quarter	Precipitation -JJA seasonal mean
Bio17	Precipitation of Driest Quarter	Precipitation -DJF seasonal mean
Bio18	Precipitation of Warmest Quarter	Precipitation -JJA seasonal mean
Bio19	Precipitation of Coldest Quarter	Precipitation -DJF seasonal mean

Table 5.2 Models and their respective variables used to run the models.

Model	Climate simulation	Selected variables
Model 1	BRIDGE 120ka, 60-38ka	Bio01,5,7,8,9,15
Model 2	WorldClim 120ka	Bio02,3,7,8,9,10, 15, 16,17,18
Model 3	WorldClim120 ka	Bio01,5,7,8,9,15
Model 4	WorldClim 120ka	Bio02, 4, 5, 8,9,10, 15,16, 18,19, aspect, slope, elevation
Model 5	BRIDGE 120ka	Bio03, 7,8,9,12, 15, aspect, slope and elevation
Model 6	BRIDGE 120ka	Bio03, 7, 16, 17, elevation, aspect, slope, albedo, Köppen-Geiger climate system, NPP and GDD5

Variables for model 1 were selected on the BRIDGE climatic simulations of 120ka and projected to the other timeframes. Model 2 was run to compare model 1 to different climatic simulations (WorldClim), with variables based on the correlation matrix made on the WorldClim climate simulations. Model 3 was run with the same climatic variables as model 1 but using WorldClim climate simulations. Model 4 was run on WorldClim simulations with the inclusion of elevation, slope, and aspect to see if that would make a difference to the climatic niche predictions. Model 5 had the same premise, but then executed with the BRIDGE climatic simulations. And finally, model 6 was run which included the extra variables available to BRIDGE. Variables for each model were selected based on new correlation matrices run for each model, except model 3 (Appendix Chapter 5).

5.2.3 Models based on different training data

Archaeological locations have been selected for 120ka, 52 ka, 44ka, and 42 ka as described above. However, it may be argued that the archaeological locations underrepresent the actual distribution of the Neanderthal. Therefore, two extra options were explored. The first was made by drawing a buffer around the location of each site of 150 km in diameter (ArcGIS 10.4). This is based on the furthest transport of raw material by Neanderthals and suggests the size of the home range of a Neanderthal group and thus that there may be more archaeological sites in the vicinity of the archaeological location that have not been preserved or discovered (Spinapolice 2012). One hundred random points were drawn in the combined buffers. The increase of presences was thought to prevent overfitting of the climatic variables (Lorenzen et al. 2011).

A second way of artificially increasing the amount of archaeological locations was done by drawing a convex hull around the outermost distribution of the archaeological locations and then filling the polygon with 100 random points. This would counteract the problem of sampling and preservation bias in places in between the occurrences. It is also likely to increase or possibly even overpredict the climatic niche of the Neanderthal, because more surface is covered by the polygon where the Neanderthal may or may not have been able to survive. This method (extent of occurrence) is standard practice in ecology (Burgman and Fox 2003).

To test the difference between the different training data sets, models were run with every single input option (resulting in 12 models: model1 and model 7-17). For every time frame, the three training datasets (archaeological locations, random points based on buffer and random points based on convex hull) were used to run the Bridge models (variables of model 1).

5.2.4 Method of assessment on models with differing training data

The 12 resulting models were assessed on the pattern of range contraction through time and on the fit with archaeological locations. The number of archaeological locations of the respective time frame that were not covered by the climatic niche polygon created by MaxEnt was calculated. Furthermore, the value of mean annual temperature (main driver of the distributions in the models) was extracted to the archaeological locations for each time frame. The average difference in temperature of the locations outside of the climatic range and the mean of the climatic range was also calculated. The combination of percentage mismatch and the larger temperature difference helped in the assessment of model performance. The lowest percent mismatch (and secondary lower temperature difference) between the model and the archaeological sites for the four time frames was chosen as the best model.

5.2.5 Methods for Neanderthal niche exploration

To explore the niche of the Neanderthal a comparison was made between the climatic signal of the archaeological locations, the chosen model, the estimated fundamental niche, and the background climate of Europe.

The climatic signal of the archaeological locations was extracted from the rasters of the variables to the geographic location of the archaeological site in the respective time frame. The fundamental niche of the Neanderthal, which may provide a better estimate of the Neanderthal niche and can be used to study changes in the realised niche, was created by compiling a composite of the niche models. This is considered good practice (Nogués-Bravo 2009). The time frames of the climatic niche models that used the archaeological locations to model the respective time frame (model 1 at 120ka, model 7 at 42ka, model 8 at 44ka and model 9 at 52ka) were used to extract the climate variables and then combined to create the full climatic tolerance (approximation of the fundamental niche). The climate variables were extracted via the tool Sample in ArcMap 10.4. The climatic values for the chosen model (model 15) were also extracted for all modelled time frames (120ka, 60-36ka) via the tool Sample. And finally, the European-wide climatic data for all time frames (used as background and for comparison) was extracted via Sample. The four climatic niches (archaeological locations, fundamental niche, model15 and Europe) were compared to each other by time frame and per climatic variable (Bio01, Bio5, Bio7, Bio8, Bio9, and Bio015) via ANOVA's and followed by post-hoc paired T-Tests, paired by model 15 vs. Europe.

The climatic niche of model15 was further analysed by calculating the mean and standard deviation of all time slices to investigate the climatic breadth and distribution of the niche over time for the climatic variable Bio01 (the main driver of the climatic niche). A normal distribution is assumed. A linear model (i.e. ordinary least-squares regression model) was fitted with Bio01 as the dependent variable, and age (ka), group (Europe or model15), and their interaction as predictors. If the interaction between age and group was significant, it indicated that the association between age and Bio01 differed per model. A simple slope analysis was run to see what the association between age and bio01 was for each group separately. In other words, the simple slope analysis looked at how the mean annual temperature changed over time for Europe and model15 separately.

5.3 Results

All models had a satisfactory AUC (area under curve) >0.7, see Table 5.3. Summaries of the models are presented in Appendix Chapter 5. Models 1 and 5 have provided identical climatic niche predictions and so have models 2,3, and 4. The climatic niche predicted by WorldClim is slightly wider and incorporates more of the cooler areas. This may provide a better prediction for the climatic niche of the Neanderthal towards the cooler end of MIS3. However, climatic simulations in WorldClim for these timeframes are not currently available. The inclusion of the extra variables does not alter the predictions in many cases. Model 6 shows a marginally wider prediction towards the northeast. The choice is therefore made to continue with the variables from model 1. This also makes it easier to compare to previous chapters.

Table 5.3 Summary of model performance. _loc= model run on archaeological locations, _buf= model run on random points created within buffered zone, _mbg= model run on random points within minimum bounding geometry (convex hull). (FN)= these models were used to construct the fundamental niche. AUC = area under curve. Threshold= threshold based on maximum training sensitivity plus specificity logistic threshold provided in MaxEnt.

Model	**AUC**	**Threshold**
1 (Ka120_loc), (FN)	0.866	0.41
2	0.824	0.29
3	0.820	0.39
4	0.830	0.29
5	0.854	0.42
6	0.874	0.35
7 (ka42_loc), (FN)	0.891	0.40
8 (ka44_loc), (FN)	0.884	0.47
9 (Ka52_loc), (FN)	0.835	0.29
10 (Ka120_buf)	0.891	0.32
11 (Ka52_buf)	0.850	0.37
12 (Ka44_buf)	0.936	0.26
13 (Ka42_buf)	0.92	0.34
14 (Ka120_mbg)	0.887	0.36
15 (Ka52_mbg)	0.808	0.36
16 (Ka44_mbg)	0.942	0.29
17 (Ka42_mbg)	0.891	0.29

The models 1 and 7-17 were created with the different options for training data.

Table 5.4 and Figure 5-1provides an overview of model performance. Each model is described below, and a final model was chosen as the best performing one.

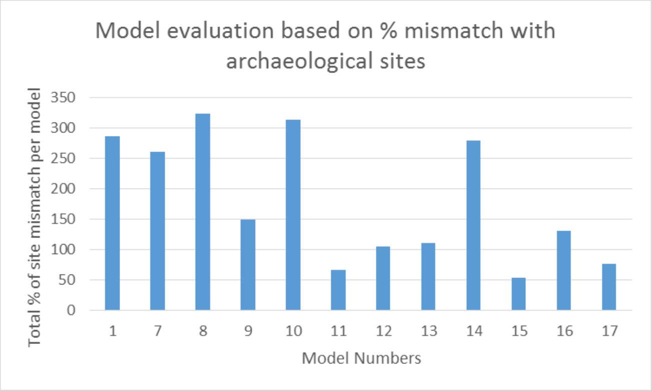

Figure 5-1 Graph shows the combined percent mismatch of all periods together for a single model. It clearly shows that model 15 has the least overall mismatch with the archaeological sites.

Table 5.4 Overview of assessment of all models. Model = model number. Time frame = time frame run within model, (base) indicates the timeframe where the training data was used. Total locations= total available archaeological locations for time frame. Locations out of range = number of locations that fell outside of predicted climatic niche. % mismatch = percentage of locations that fall outside of the climatic niche, a higher percentage indicates a worse fit with the archaeological locations. Min/Mix/Mean/SD temp model are the descriptive statistics for annual mean temperature within each climatic niche. Mean temp loc out of niche= average of mean annual temperature of location that fall outside of the climatic niche. Mean temp difference= is the difference in temperature between the mean temperature of the model and the mean temp loc out of niche.

Model	Time frame	Total locations	Locations out of range	% mismatch	Min temp model	Max temp model	Mean temp model	SD temp Model	Mean temp loc out of niche	Mean Temp Difference
1	120 (base)	33	6	18.2	7.4	23.5	12.3	2.8	7.3	5.0
1	52	34	27	79.4	7.5	20.2	12.0	2.9	7.1	4.9
1	44	9	8	88.9	11.2	19.8	14.3	1.6	7.6	6.7
1	42	13	13	100.0	8.1	15.4	12.2	2.0	6.9	5.2
7	120	33	6	18.2	6.6	23.5	12.2	2.8	7.3	4.9
7	52	34	22	64.7	7.4	20.2	11.7	2.9	6.7	5.0
7	44	9	7	77.8	9.4	19.8	14.1	1.7	6.8	7.3
7	42 (base)	13	13	100.0	7.8	15.4	11.6	2.4	6.9	4.7
8	120	33	11	33.3	7.9	23.5	12.5	2.9	9.8	2.6
8	52	34	31	91.2	8.5	16.6	13.3	2.5	7.6	5.7
8	44 (base)	9	9	100.0	11.4	16.1	14.5	1.7	8.5	6.1
8	42	13	13	100.0	10.8	15.4	12.8	1.9	6.9	5.9
9	120	33	3	9.1	6.1	23.5	12.2	3.2	4.3	7.9
9	52 (base)	34	18	52.9	6.4	20.2	10.6	2.6	6.3	4.2
9	44	9	3	33.3	7.0	19.8	11.1	2.9	5.3	5.8
9	42	13	7	53.8	5.8	19.2	10.2	3.4	4.8	5.4
10	120 (base)	33	11	33.3	7.9	23.5	12.0	2.7	11.4	0.7
10	52	34	31	91.2	8.8	16.6	12.9	2.4	7.5	5.3
10	44	9	8	88.9	9.8	16.1	13.8	1.8	7.6	8.4
10	42	13	13	100.0	0.0	0.0	0.0	0.0	6.9	-6.9
11	120	33	8	24.2	0.9	19.6	9.5	3.4	11.1	-1.6
11	52 (base)	34	8	23.5	0.7	16.4	7.1	2.9	6.5	0.6
11	44	9	1	11.1	0.7	16.1	6.3	3.1	15.5	-9.1
11	42	13	1	7.7	-1.2	15.4	5.7	3.1	13.8	-8.1
12	120	33	7	21.2	-1.3	23.2	9.8	3.7	12.1	-2.2
12	52	34	17	50.0	0.1	15.8	7.6	2.9	7.3	0.3
12	44 (base)	9	1	11.1	0.5	15.6	7.0	3.0	12.9	-5.9
12	42	13	3	23.1	-1.0	14.5	5.7	3.0	10.7	-5.1
13	120	33	8	24.2	-2.2	19.2	9.4	4.0	12.6	-3.2
13	52	34	18	52.9	0.0	15.8	7.5	2.9	7.6	-0.1
13	44	9	1	11.1	0.5	15.6	6.6	2.9	12.9	-6.3
13	42 (base)	13	3	23.1	-1.0	13.1	4.9	2.8	10.7	-5.8
14	120 (base)	33	9	27.3	7.8	23.1	11.6	2.1	12.0	-0.4
14	52	34	28	82.4	6.7	15.8	10.1	2.3	7.9	2.3
14	44	9	7	77.8	7.0	15.6	11.9	2.7	7.6	4.3
14	42	13	12	92.3	6.1	7.8	6.9	0.5	6.9	0.0
15	120	33	3	9.1	1.8	23.5	10.1	3.8	4.3	5.8
15	52 (base)	34	10	29.4	0.7	17.0	7.6	3.4	6.9	0.7
15	44	9	0	0.0	1.4	17.1	7.7	3.5		
15	42	13	2	15.4	1.3	15.6	6.9	2.9	1.0	5.9
16	120	33	11	33.3	4.6	23.3	11.3	2.5	12.4	-1.1
16	52	34	19	55.9	1.2	15.8	7.9	2.7	7.2	0.6
16	44 (base)	9	1	11.1	1.5	15.6	7.3	2.8	12.9	-5.6
16	42	13	4	30.8	0.0	14.5	5.7	3.0	9.7	-4.0
17	120	33	7	21.2	-3.3	19.2	8.2	4.3	12.1	-3.9
17	52	34	10	29.4	0.0	15.8	6.7	2.7	10.2	-3.5
17	44	9	1	11.1	-0.4	15.6	6.2	2.8	12.9	-6.7
17	42 (base)	13	2	15.4	-1.7	14.5	5.1	2.9	12.7	-7.7

Model 1 (based on 120ka, Figure 5.1-A): Predicted climatic niche at 120ka matches most archaeological locations. Climatic niche excludes the Alps and the northeast of Europe. Severe contraction of climatic niche during MIS3 (52,44 and 42ka) towards south and southwest. This contraction does not match the archaeological locations of the respective timeframes.

Model 9 (based on 52ka, Figure 5.1-B): Wider predicted climatic niche at 120ka, stretching further into north-eastern Europe and is influenced less by mountain ranges such as the Alps. A reduction of the climatic range towards the southwest of Europe is predicted throughout MIS3, though less severe than for model 1. The models do not match the full distribution of archaeological locations (especially to the east).

Model 8 (based on 44ka, Figure 5.1-C): Smallest prediction of 120ka climatic niche, with a reduced extension into north-eastern Europe. Still a good match to archaeological locations. This model predicts the most severe range reduction throughout MIS3, with very few places predicted as climatically suitable for Neanderthals. Does not reflect the archaeological locations.

Model 7 (based on 42ka, Figure 5.1-D): Predictions of 120ka and the reduction of climatic niche during MIS 3 are similar to model 1. The predictions of this model do not fit to the MIS3 locations.

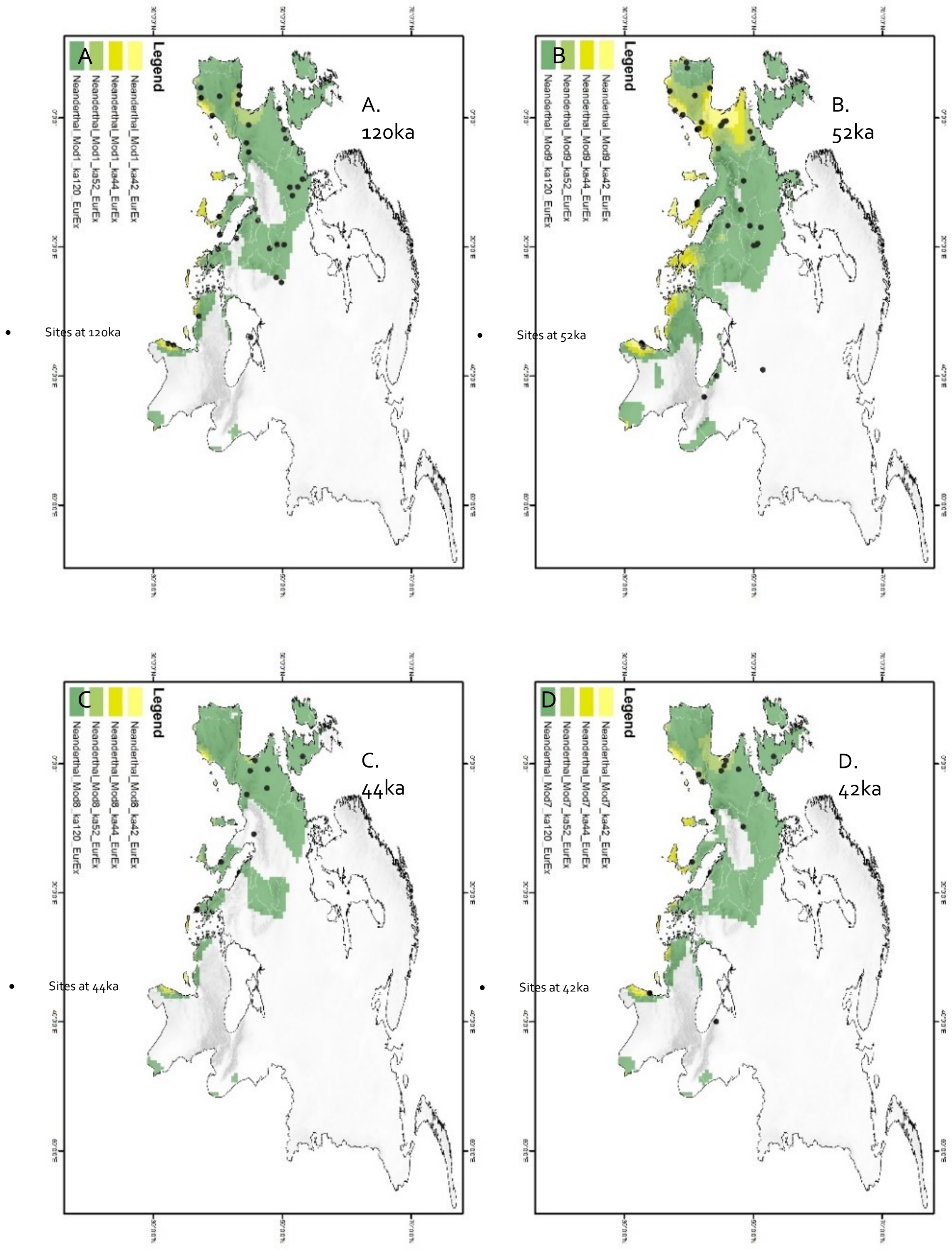

Figure 5-2 Predictive models based on location data, presented as black dots. A= Model 1 based on 120ka, B= Model 9 based on 52ka, C= Model 8 based on 44ka and D=Model 7 based on 42ka. The four predicted time frames are presented per model as described in each legend. There is always an overlap between the suitable areas in later timeframes with the earlier timeframes, meaning that those areas where overlap by younger time frames is shown was also suitable in the older timeframes.

Model 10 (based on 120 ka buffer, Figure 5.2-A): This model predicts the range at 120 ka to extend reasonably far north and northeast. The Alps are climatically unsuitable, as is most of Britain. This model shows the most severe climatic niche reduction during MIS 3, where Neanderthals are supposed to be restricted to south-eastern Europe.

Model 11 (based on 52ka buffer, Figure 5.2-B): Shows the furthest extent north and northeast of the models in this group for 120ka. Overall, the climatic niche contraction in south-westerly direction is still present, although on a less dramatic scale during MIS3. The model fits all ranges except the site Mezmaiskaya in the east.

Model 12 (based on 44ka buffer, Figure 5.2-C): This model extends the climatic niche at 120ka far to the north into the middle of present-day Norway and Sweden. The retreat of the climatic niche during MIS3 is more west-wardly and does not contract as far south into Iberia as the other models do. It matches very well with the archaeological locations at the 44ka and 42ka time frames.

Model 13 (based on 42ka buffer, Figure 5.2-D): This model extends slightly further north than Model 12 for 120ka. However, it does not extend as far eastwards. The contraction in the climatic niche to the south and west of Europe during MIS3 is a bit more restricted in the eastern side of the model compared to Model 12. It does not agree with the archaeological locations to the east for the 44ka and 42ka time frames.

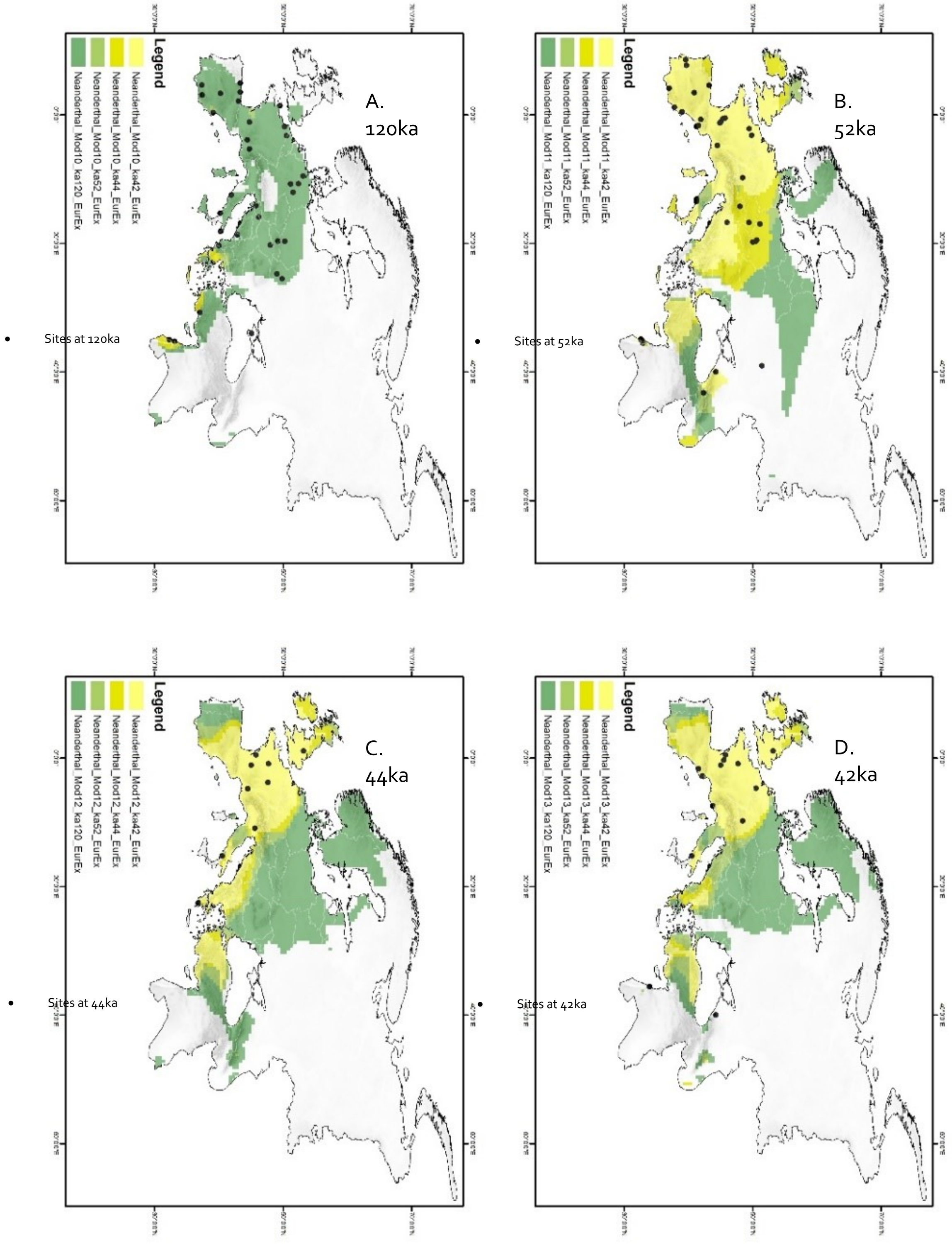

Figure 5-3 Predictive models based on buffer + random points. A= Model 10 based on 120ka, B= Model 11 based on 52ka, C= Model 12 based on 44ka and D=Model 13 based on 42ka. The four predicted time frames are presented per model as described in each legend. There is always an overlap between the suitable areas in later timeframes with the earlier timeframes, meaning that those areas where overlap by younger time frames is shown was also suitable in the older timeframes.

Model 14 (Based on 120ka, convex hull, Figure 5.3-A): The climatic niche is predicted to mainland Europe, and limited to the far west, east and northern Europe. It does not match with the archaeological location in the east. The predicted ranges for the MIS3 are severely reduced to mid-France, Greece, and Turkey. These climatic niches do not reflect the archaeological locations of the respective time frames.

Model 15 (Based on 52ka, convex hull, Figure 5.3-B): This model predicts the furthest range to the northeast of all models for 120ka. The climatic niche matches with the archaeological sites. The climatic niche contracts southwards, rather than south-westwards. It matches the archaeological locations of all MIS3 time frames well.

Model 16 (Based on 44ka, convex hull, Figure 5.3-C): This model predicts the 120ka climatic niche to a more conservative geographical range, not reaching far north or east and does not reach to southwestern Iberia. It does match well with the archaeological locations. The model shows the contraction of the climatic niche to the west for MIS3 but does not change much during the different time frames within MIS3. It does not match with the southern and eastern most archaeological locations.

Model 17 (Based on 42ka, convex hull, Figure 5.3-D): The climatic range for 120ka is predicted very far east and northwards, but not to western Iberia. The climatic niche contracts for MIS3 towards western/central Europe. The archaeological distribution does not match for the southern (Iberia, Israel) and far eastern (Russia) archaeological locations.

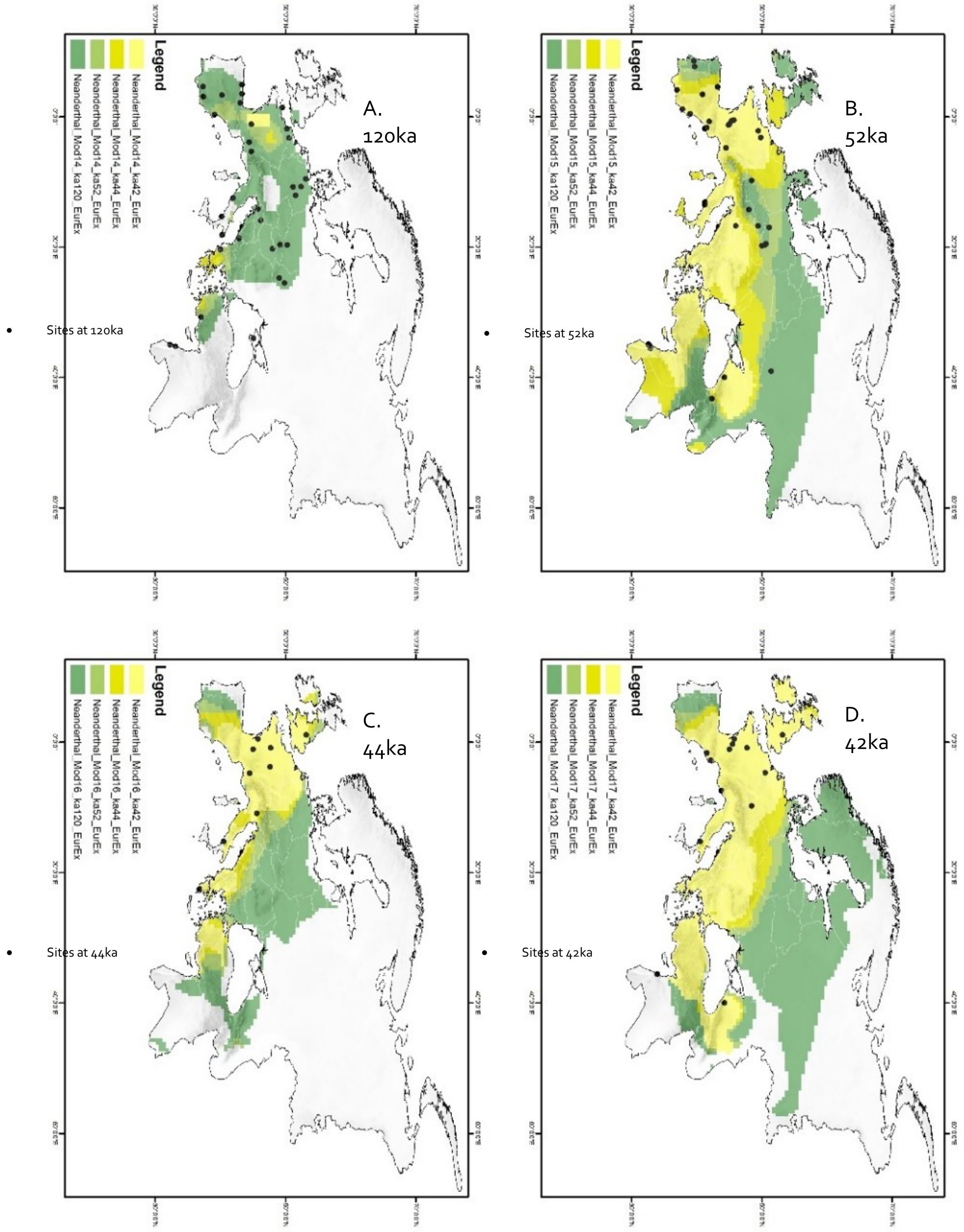

Figure 5-4 Figures based on convex hull + random points based on archaeological locations, presented as black dots. A= Model 14 based on 120ka, B= Model 15 based on 52ka, C= Model 16 based on 44ka and D=Model 17 based on 42ka. The four predicted time frames are presented per model as described in each legend. There is always an overlap between the suitable areas in later timeframes with the earlier timeframes, meaning that those areas where overlap by younger time frames is shown was also suitable in the older timeframes.

5.3.1 Which models perform best?

The three groups based on the different types of input data (archaeological locations, random points based on buffers and random points based on a convex hull) simulated from four different time zones, all display a marked range contraction between MIS5e (120ka) and MIS 3 (60-38ka modelled, 65,44 and 42ka shown above). The contraction of the range is generally the largest for the models that have been based on 120ka training data and the contraction is the least for models that were based on 52ka training data. The ranges increase with the increased spread of training data, which is to be expected because the increase of artificial points will include the new climatic environments as well as possibly change the clustering of sites into more marginal areas. As expected and explained in the methods, the created random points with the buffer method (to overcome too little training data points, overfitting climatic data) and the random points created with the convex hull (to overcome sample bias such as preservation) have increased the climatic niche of the Neanderthal considerably.

The model performance was evaluated based on the fit with the archaeological record and whether the pattern of range contraction fits with the pattern in contraction of archaeological locations. The first group (based on archaeological locations, models 1 and 7-9) match the archaeological distribution of MIS5e well, but the contraction is too severe and does not reflect the archaeological record. Therefore, the lesser contraction towards the Pyrenees is selected as the preferred model (model 9) from this group. The second group (based on the buffer, models 10-13) shows a wide variety in the predictions. Model 11 (based on the 52ka distribution) is selected as the best fitting model, because it fits the best to all archaeological periods and still displays the climatic range change between 44 to 42ka, with a contraction southward. The third group (based on the convex hull (models 14-17) has the widest climatic niches of all models, which is expected based on the input data. The preferred model for this group is again at 52 ka (model 15). It shows the southward range contraction and extends furthest east which is in line with the archaeological locations.

Out of all models, the 52ka training data has produced the best fit to both the 120ka and MIS3 time slices with the archaeological locations. Of the three best models from each group (model 9, 11 and 15) model 15 shows the best fit to the archaeological locations (this model has least archaeological locations outside of the predicted climatic niches) and demonstrates the process of contraction the best (contracting from western Iberia, as well as southwards). It seems to represent the widest climatic niche for Neanderthals. The models with 120ka and 44/42ka training data seem to predict a much narrower suitable climatic niche. The restriction of these models is so severe and over such an extended time period (30.000 years) which do not agree with the archaeological record, that it seems implausible. Therefore, the subsequent analyses have been done on model 15.

5.3.2 Exploration of the Neanderthal niche

The climatic niche of the Neanderthal in the chosen model, Model 15, is 77% driven by the variable Bio01 (annual mean temperature). An overview of the variable importance and response curves of the different variables is provided in Appendix Chapter 5. The Neanderthal climatic niche is explored below for all used variables:

BIO01 = Annual Mean Temperature - 77% contribution
BIO5 = Max Temperature of Warmest Month - 6.4% contribution
BIO7 = Temperature Annual Range (BIO5-BIO6) - 2% contribution
BIO8 = Mean Temperature of Wettest Quarter (winter) - 6.9% contribution
BIO9 = Mean Temperature of Driest Quarter (summer) - 2.2% contribution
BIO015 = Precipitation Seasonality (Coefficient of Variation) - 5.5% contribution

The niche is explored by comparing the climatic values of the archaeological locations to the fundamental niche, model 15 and the background climate of Europe at four time frames. Density plots (figures below) illustrate the different niches. The development of the Neanderthal niche is analysed by looking at the changes in the model 15 climatic niches through time and space.

5.3.3 Variable Bio01: Mean annual temperature

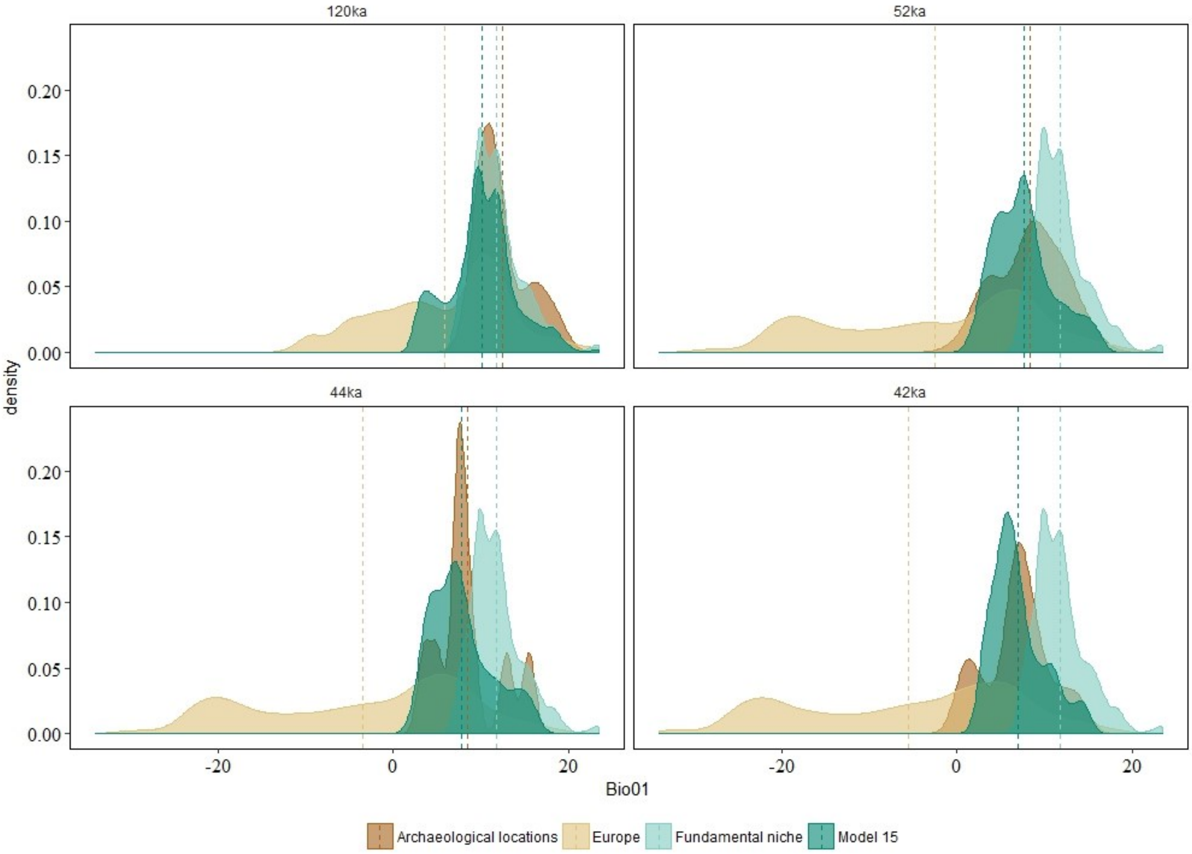

Figure 5-5 Kernel densities of Bio01 (mean annual temperature in °C) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.5 Mean annual temperatures (Bio01) during 120ka

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	12.39	2.84	-		
Model 15	10.10	3.80	.03	-	
Fundamental niche	11.79	2.88	.57	<.001	-
Europe	5.80	7.41	<.001	<.001	<.001
52ka					
Archaeological locations	8.36	3.75	-		
Model 15	7.64	3.41	.65	-	
Fundamental niche	11.79	2.88	.03	< .001	-
Europe	-2.54	11.36	< .001	< .001	< .001
44ka					
Archaeological locations	8.46	3.70	-		
Model 15	7.80	3.50	.84	-	
Fundamental niche	11.79	2.88	.29	< .001	-
Europe	-3.54	11.79	< .001	< .001	< .001
42ka					
Archaeological locations	6.93	3.73	-		
Model 15	6.99	3.01	.98	-	
Fundamental niche	11.79	2.88	.08	< .001	-
Europe	-5.56	12.29	< .001	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences 120ka: *F*(3,12394) = 756.60, *p* < .001. Omnibus test of mean differences 52ka: *F*(3,10804) = 1663.00, *p* < .001. Omnibus test of mean differences 44ka: *F*(3,10418) = 1706.00, *p* < .001. Omnibus test of mean differences 42ka: *F*(3,9751) = 1781.00, *p* < .001. Numbers in the cells indicate p-values of pairwise comparisons.

The density plot (Figure 5-5) shows in all three models (archaeological locations, fundamental niche, and model 15) that the Neanderthal niche is situated on the warmer end of the distribution of average temperatures available for Europe. During 120ka, there are significant differences in predicted mean annual temperature between archaeological locations and model 15, and between model 15 and fundamental niche (Table 5.5).

Even though model15 has the best match with archaeological locations, this shows that other variables may be of more importance to the distribution during MIS5e than mean annual temperature. However, during MIS3 the archaeological locations and model 15 move away into cooler areas compared to the fundamental niche. All groups are significantly different from the European mean during all time frames (Table 5.5). During all time frames there is a significant difference between model 15 and the fundamental niche. Finally, at 52ka there is a significant difference between the archaeological locations and fundamental niche. Overall, model15 agrees better with the archaeological locations than the fundamental niche. There seems to be a threshold of 0^{0}C that none of the models cross. This may indicate that the Neanderthal avoided areas that were year-round below 0^{0}C or areas with severe winters.

5.3.4 Variable Bio05: Maximum temperature of warmest month

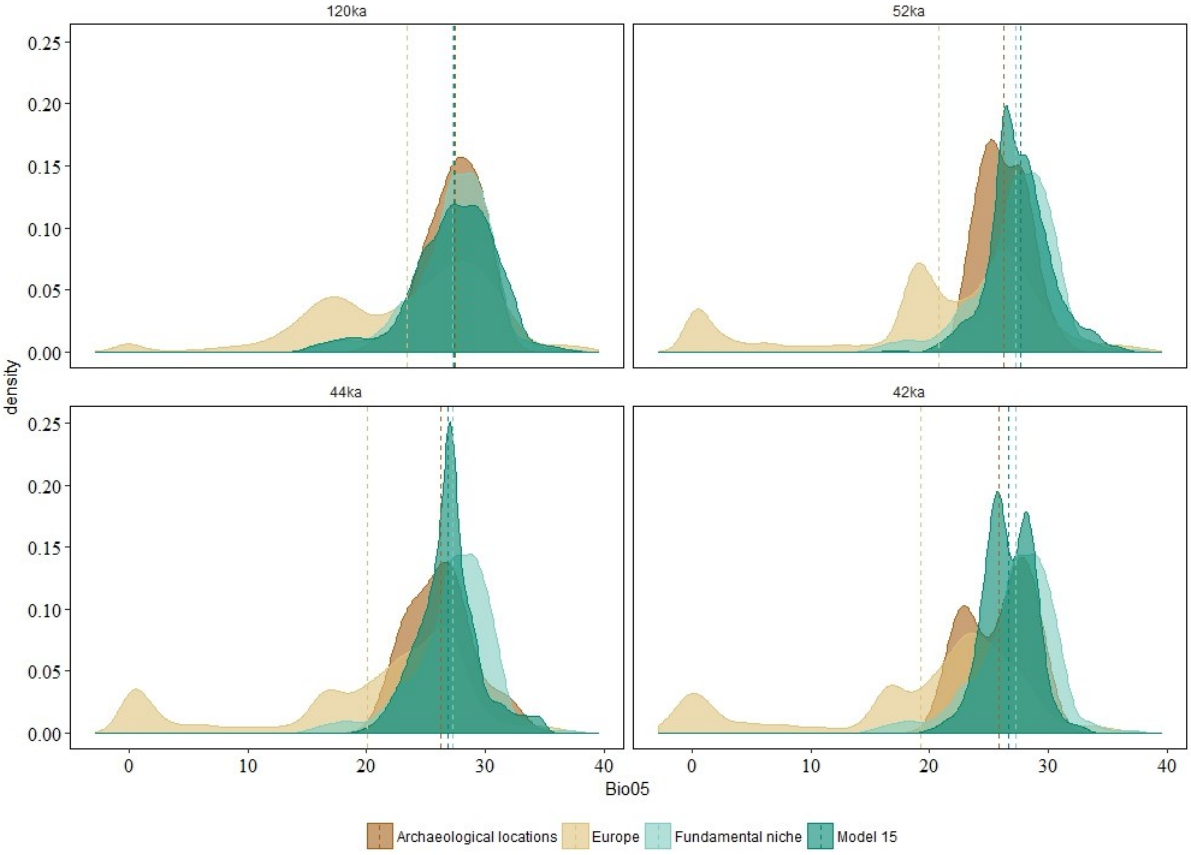

Figure 5-6 Kernel densities of Bio05 (Max Temperature of Warmest Month in ºC) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.6 Maximum temperature of warmest month (Bio05)

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	27.42	2.30	-		
Model 15	27.36	3.57	.95	-	
Fundamental niche	27.26	3.33	.87	.50	-
Europe	23.41	7.11	< .001	< .001	< .001
52ka					
Archaeological locations	26.23	1.96	-		
Model 15	27.61	2.60	.27	-	
Fundamental niche	27.26	3.33	.41	.10	-
Europe	20.82	9.01	< .001	< .001	< .001
44ka					
Archaeological locations	26.25	2.69	-		
Model 15	26.86	2.57	.80	-	
Fundamental niche	27.26	3.33	.68	.08	-
Europe	20.08	8.99	.01	< .001	< .001
42ka					
Archaeological locations	25.88	2.62	-		
Model 15	26.69	2.07	.70	-	
Fundamental niche	27.26	3.33	.52	.04	-
Europe	19.21	9.20	.002	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences 120ka: $F(3,12204) = 491.10$, $p < .001$. Omnibus test of mean differences 52ka: $F(3,10614) = 735.20$, $p < .001$. Omnibus test of mean differences 44ka: $F(3,10228) = 735.10$, $p < .001$. Omnibus test of mean differences 42ka: $F(3,9561) = 766.00$, $p < .001$. Numbers in the cells indicate p-values of pairwise comparisons.

The different models appear to be in better agreement for Bio05, maximum temperature of the warmest month, throughout time (Figure 5-6, Table 5.6). Only minimal separation between the niches is visible through time, increased towards 42ka. The only statistically significant difference is at 42ka between the fundamental niche and model 15. The mean of all models show a slight cooling towards 42ka. All models at all time frames are significantly different from Europe (the background model showing the maximum temperature for the warmest month available for the entire study area) (Table 5.6).

5.3.5 Variable Bio07: Temperature annual range

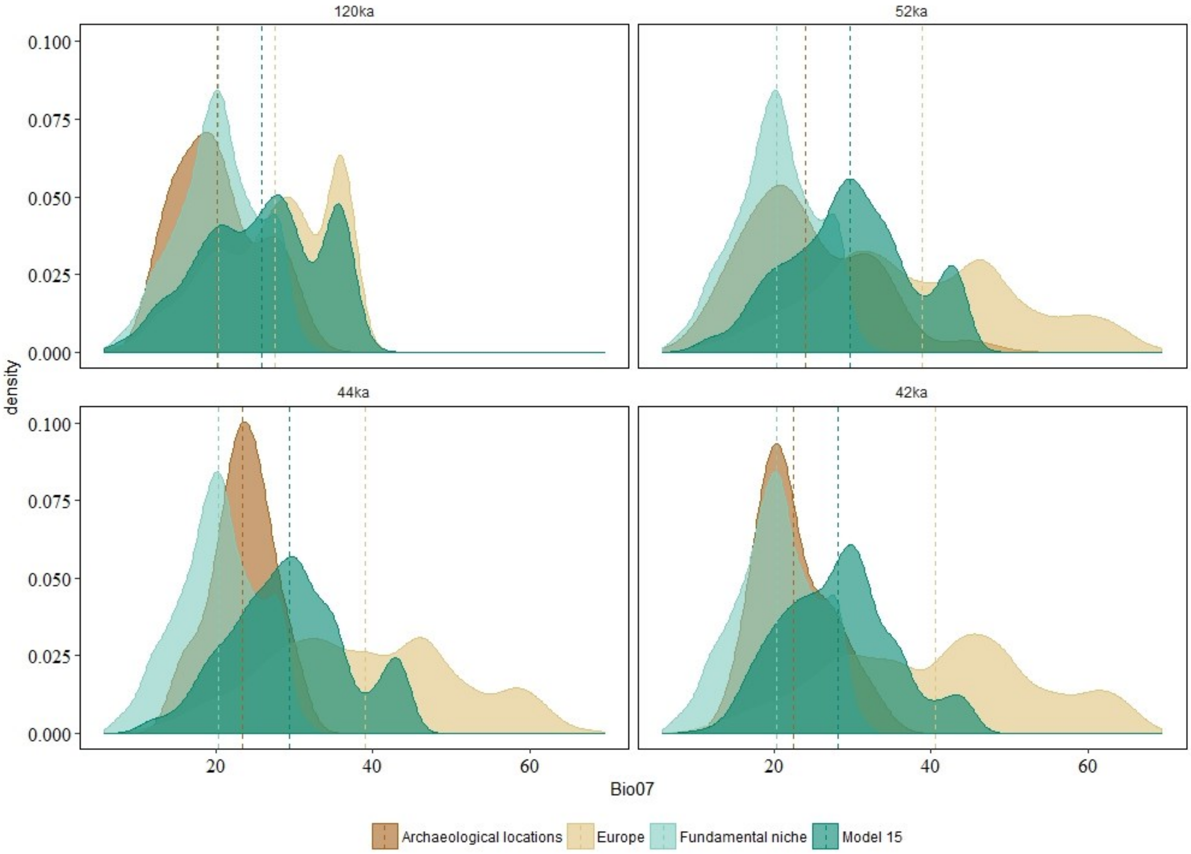

Figure 5-7 Kernel densities of Bio07 (Temperature Annual Range (BIO5-BIO6) in ºC) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.7 Temperature annual range (Bio07)

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	20.27	5.23	-		
Model 15	25.92	7.51	< .001	-	
Fundamental niche	20.30	5.11	.98	< .001	-
Europe	27.58	7.43	< .001	< .001	< .001
52ka					
Archaeological locations	23.98	7.51	-		
Model 15	29.75	7.79	.002	-	
Fundamental niche	20.30	5.11	.47	< .001	-
Europe	38.92	12.56	< .001	< .001	< .001
44ka					
Archaeological locations	23.34	3.96	-		
Model 15	29.33	7.48	.08	-	
Fundamental niche	20.30	5.11	.37	< .001	-
Europe	38.95	11.99	< .001	< .001	< .001
42ka					
Archaeological locations	22.49	4.50	-		
Model 15	28.19	7.08	.06	-	
Fundamental niche	20.30	5.11	.48	< .001	-
Europe	40.53	12.99	< .001	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences 120ka: $F(3,12228) = 548.70$, $p < .001$. Omnibus test of mean differences 52ka: $F(3,10614) = 1736.00$, $p < .001$. Omnibus test of mean differences 44ka: $F(3,10228) = 1868.00$, $p < .001$. Omnibus test of mean differences: $F(3,9561) = 1896.00$, $p < .001$. Numbers in the cells indicate p-values of pairwise comparisons.

Based on the spread of the annual temperature range (Bio07) in the density plots (Figure 5-7, Table 5.7), it looks like the fundamental niche has the least wide annual temperature range, followed by the archaeological locations and Model 15 showing the widest temperature range. This observation is statistically supported with a significant difference between the fundamental niche and model 15 in all time frames. There are also significant differences between the archaeological locations and model15 at 120ka and 52ka. All models at all time frames are statistically different from Europe (Table 5.7).

5.3.6 Variable Bio08: Mean temperature of wettest quarter (winter)

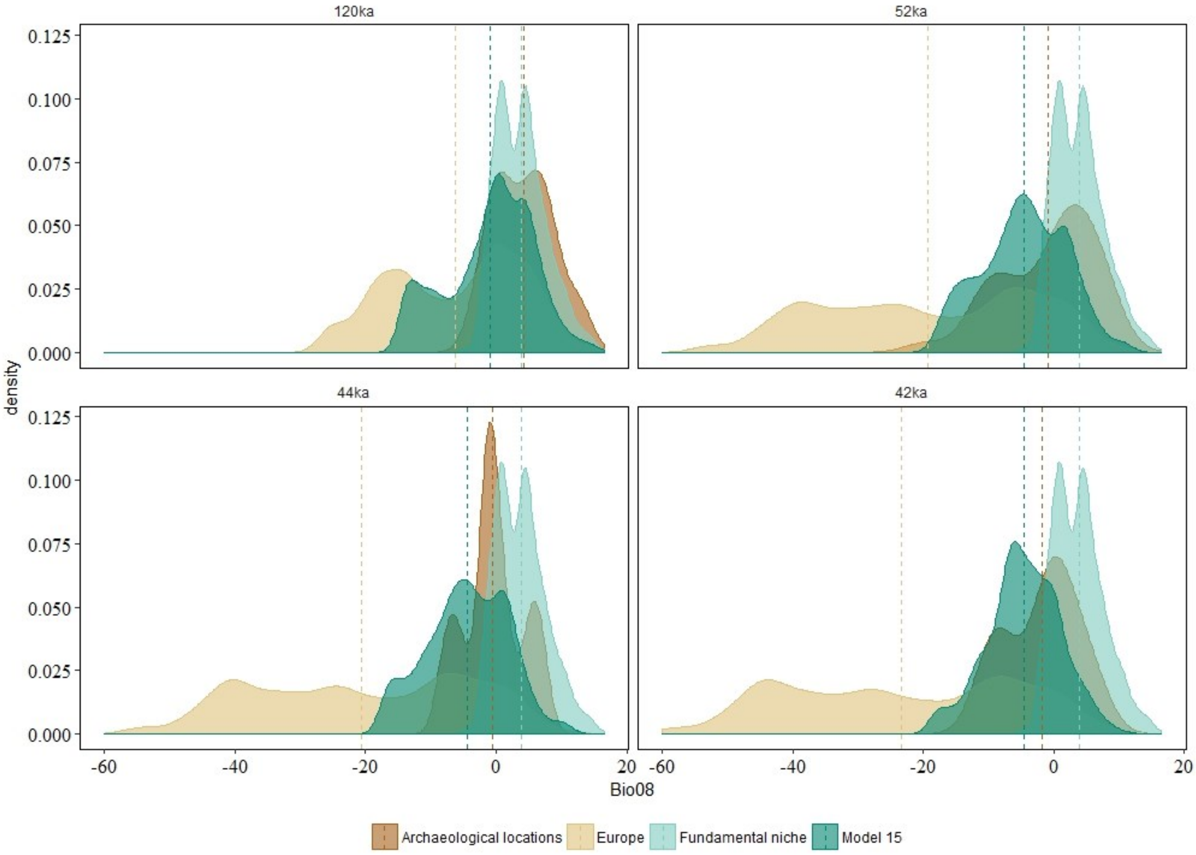

Figure 5-8 Kernel densities of Bio08 (Mean Temperature of Wettest Quarter (winter) in ºC) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.8 Mean temperature of wettest quarter (Bio08)

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	4.29	4.48	-		
Model 15	-.84	6.65	< .001	-	
Fundamental niche	3.86	3.79	.77	< .001	-
Europe	-6.26	10.00	< .001	< .001	< .001
52ka					
Archaeological locations	-.90	7.09	-		
Model 15	-4.52	6.44	.10	-	
Fundamental niche	3.86	3.79	.03	< .001	-
Europe	-19.36	15.98	< .001	< .001	< .001
44ka					
Archaeological locations	-.46	4.58	-		
Model 15	-4.35	6.18	.37	-	
Fundamental niche	3.86	3.79	.32	< .001	-
Europe	-20.60	16.24	< .001	< .001	< .001
42ka					
Archaeological locations	-1.80	5.38	-		
Model 15	-4.81	5.56	.48	-	
Fundamental niche	3.86	3.79	.15	< .001	-
Europe	-23.38	17.19	< .001	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences: $F(3,12204) = 899.90$, $p < .001$. Omnibus test of mean differences 52ka: $F(3,10614) = 2033.00$, $p < .001$. Omnibus test of mean differences 44ka: $F(3,10228) = 2130.00$, $p < .001$. Omnibus test of mean differences 42ka: $F(3,9561) = 2187.00$, $p < .001$. Numbers in the cells indicate p-values of pairwise comparisons.

Model 15, as shown in the density plot (Figure 5-8), has consistently the coldest mean in winter/wettest month of all niches throughout time. There are always significant differences between the warmer fundamental niche and cooler model 15 throughout the time frames (Table 5.8). During 52ka there is a significant difference between the archaeological locations and the fundamental niche. Most of the time, the archaeological locations are in the middle between the fundamental and model 15 niches. All models at all time frames are statistically different from Europe (Table 5.8).

5.3.7 Variable Bio09: Mean temperature of driest quarter (summer)

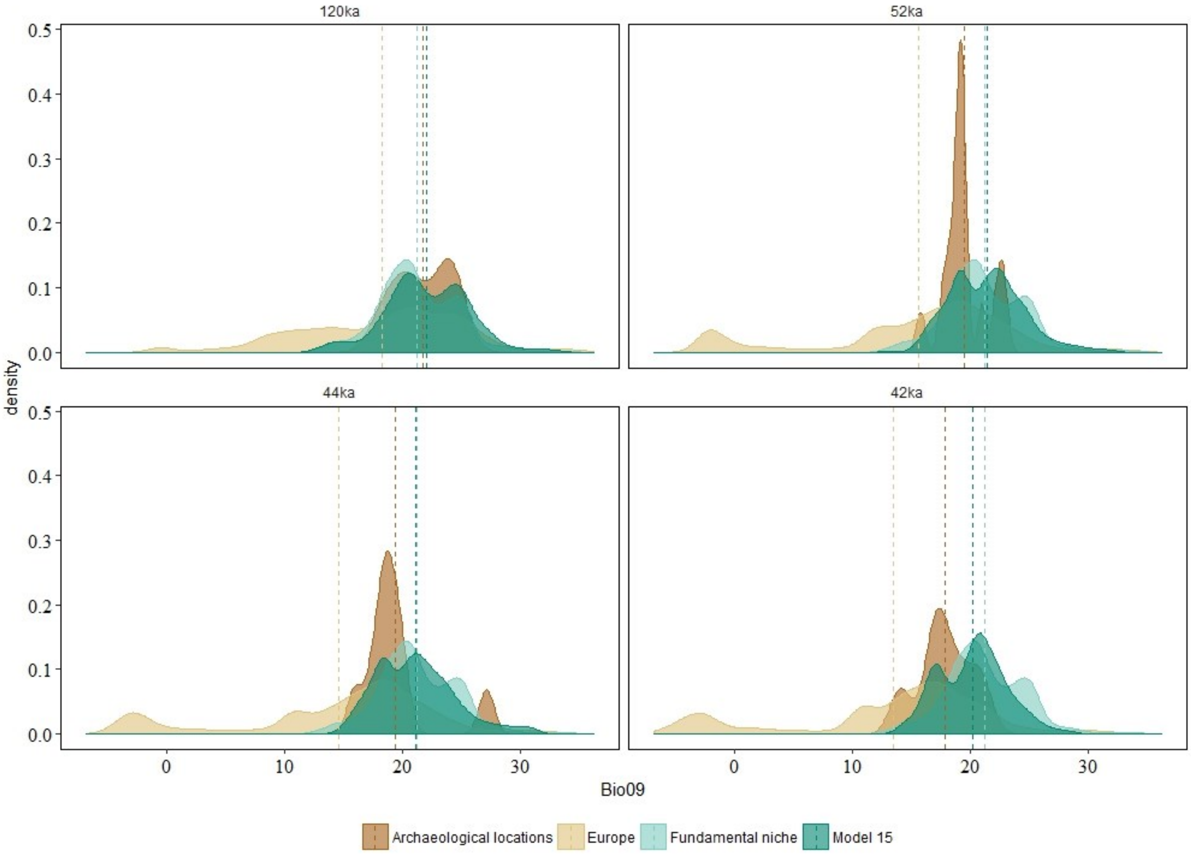

Figure 5-9 Kernel densities of Bio09 (Mean Temperature of Driest Quarter (summer) ºC) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.9 Mean temperature of driest quarter (Bio09)

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	21.75	2.33	-		
Model 15	22.08	3.53	.74	-	
Fundamental niche	21.25	3.30	.61	< .001	-
Europe	18.27	6.85	.004	< .001	< .001
52ka					
Archaeological locations	19.50	1.83	-		
Model 15	21.42	3.12	.10	-	
Fundamental niche	21.25	3.30	.13	.39	-
Europe	15.62	8.17	.007	< .001	< .001
44ka					
Archaeological locations	19.40	3.14	-		
Model 15	21.12	3.31	.45	-	
Fundamental niche	21.25	3.30	.42	.54	-
Europe	14.59	8.37	.04	< .001	< .001
42ka					
Archaeological locations	17.86	2.25	-		
Model 15	20.20	2.84	.23	-	
Fundamental niche	21.25	3.30	.08	< .001	-
Europe	13.50	8.42	.03	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences 120ka: $F(3,12228) = 434.50$, $p < .001$. Omnibus test of mean differences 52ka: $F(3,10614) = 645.40$, $p < .001$. Omnibus test of mean differences 44ka: $F(3,10228) = 752.30$, $p < .001$. Omnibus test of mean differences 42ka: $F(3,9561) = 794.20$, $p < .001$. Numbers in the cells indicate p-values of pairwise comparisons.

For variable Bio09, summer temperatures (and driest quarter) visually agree broadly between the three models; although some significant intervals between the fundamental niche and Model 15 (Figure 5-9). The mean summer temperature does decline towards MIS3 for the archaeological locations and model15 (Table 5.9). Where model15 was usually on the cooler side, it is this time on the warmer side together with the fundamental niche compared to the actual archaeological locations during 52ka, 44ka, and 42ka.

5.3.8 Variable Bio015: Precipitation seasonality

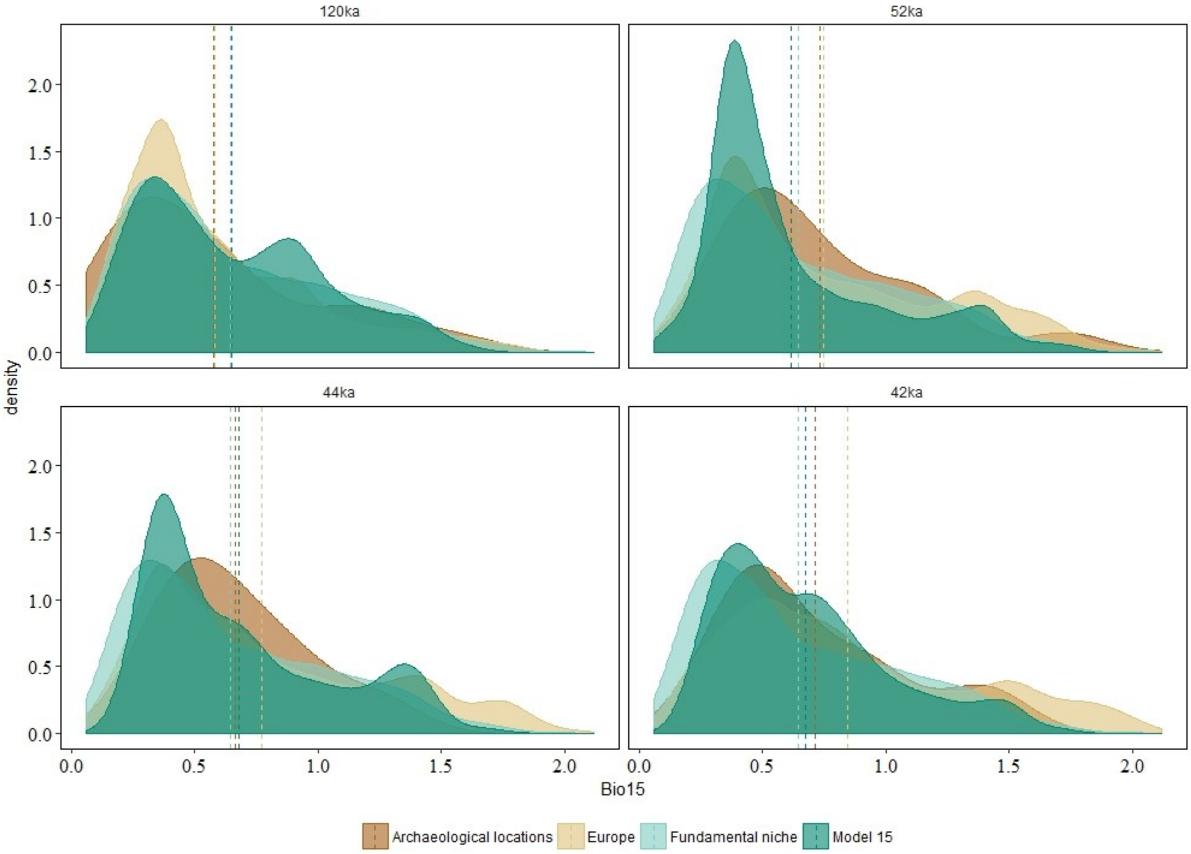

Figure 5-10 Kernel densities of Bio015 (Precipitation Seasonality (Coefficient of Variation)) of archaeological locations (brown), Europe (beige), fundamental niche (aquamarine) and model 15 (teal). The dashed line indicates the mean for each distribution. The higher density can be used as an estimate for suitability.

Table 5.10 Precipitation seasonality (Bio015)

Model	M	SD	Archaeological locations	Model 15	Fundamental niche
120ka					
Archaeological locations	.58	.41	-		
Model 15	.65	.36	.29	-	
Fundamental niche	.64	.39	.32	.70	-
Europe	.58	.37	.94	< .001	< .001
52ka					
Archaeological locations	.73	.38	-		
Model 15	.62	.36	.12	-	
Fundamental niche	.64	.39	.24	.29	-
Europe	.75	.45	.81	< .001	< .001
44ka					
Archaeological locations	.66	.29	-		
Model 15	.68	.37	.92	-	
Fundamental niche	.64	.39	.89	.009	-
Europe	.77	.47	.46	< .001	< .001
42ka					
Archaeological locations	.71	.37	-		
Model 15	.68	.34	.76	-	
Fundamental niche	.64	.39	.57	.05	-
Europe	.84	.49	.30	< .001	< .001

Note: Omnibus test (ANOVA) of mean differences 120ka: $F(3,12394) = 31.37$, $p < .001$. Omnibus test of mean differences 52ka: $F(3,10804) = 71.36$, $p < .001$. Omnibus test of mean differences 44ka: $F(3,10418) = 55.28$, $p < .001$. Omnibus test of mean differences 42ka: $F(3,9751) = 127.90$, $p < .001$. Numbers in the cells indicate p-values of pairwise comparisons.

There is good visual agreement and little change between the models and timeframes (Figure 5-10). This is mostly supported by the statistical analyses, where only 44ka holds a statistical difference between the archaeological locations and fundamental niche (Table 5.10). Precipitation and the changes in precipitation seem to have less influence on the changes in climatic niche of the Neanderthal.

5.3.9 Fundamental niche

For most the variables the calculated fundamental niche has a narrower range of values than the archaeological sites. The fundamental niche is mostly located on the warmer and drier side of the distribution of the archaeological locations. This shows that the compilation of models based directly on the archaeological locations of different timeframes does not provide an approximation of the fundamental niche. The combination of variables from the archaeological locations themselves might have provided a better approximation of the fundamental niche. The fundamental niche is not used for further analyses.

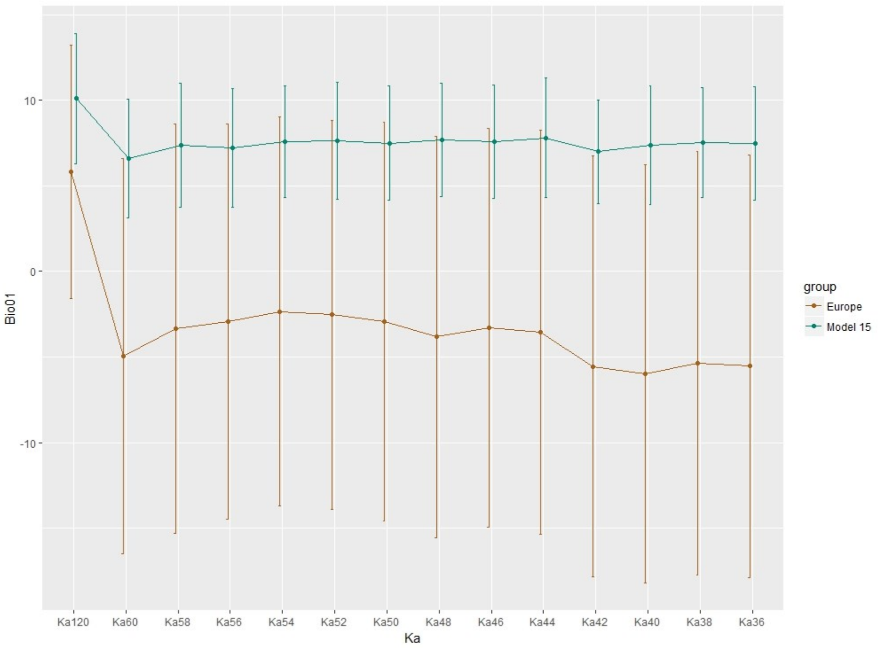

Figure 5-11 Development of the mean for Bio01 through time for the predicted climatic niche of Neanderthal. The brown line is the mean annual temperature of the whole study area of Europe.

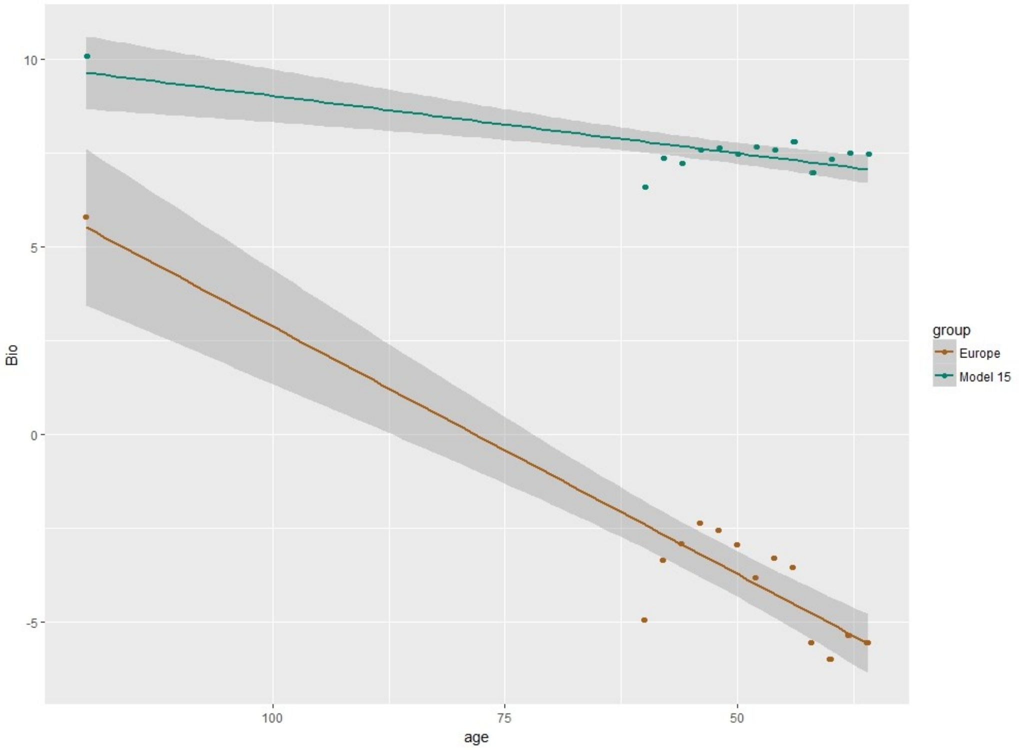

Figure 5-12 Linear regression on the variable Bio01 for Model15 and Europe. Shaded area indicates 95% confidence interval.

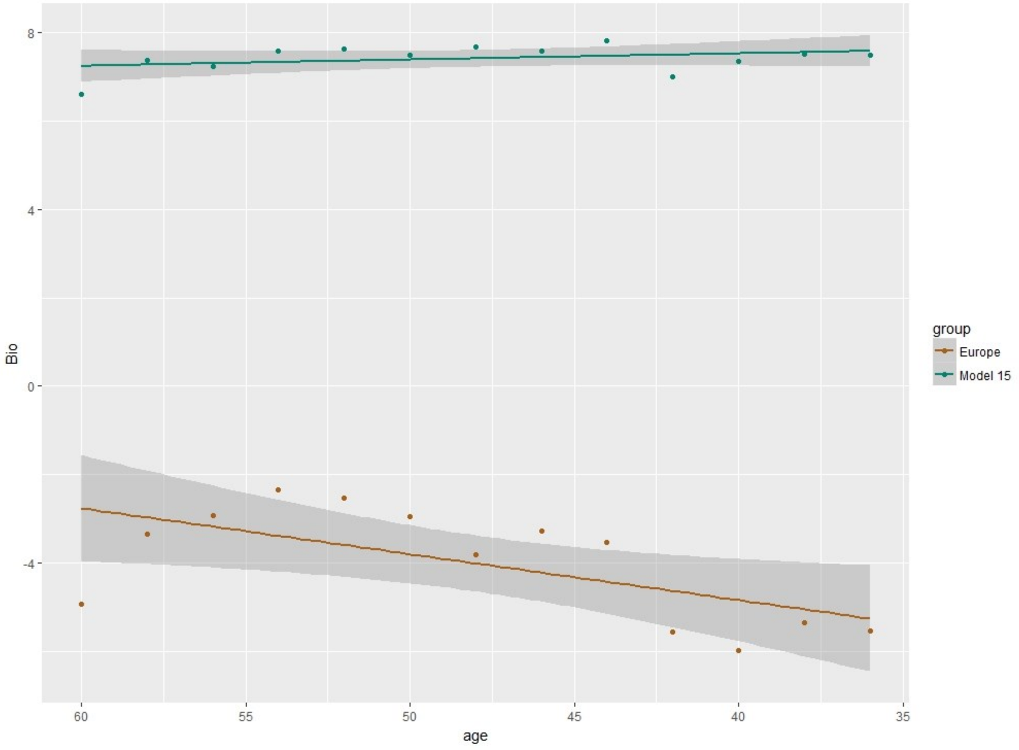

Figure 5-13 Linear regression on the variable bio01 for Model 15 and Europe without 120ka. Shaded area indicates 95% confidence interval.

5.3.10 Development of the Neanderthal niche

The Neanderthal niche remains relatively stable throughout time. Even though the climate is deteriorating in Europe, the mean annual temperature of the Neanderthal niche remains stable at circa 7.4°C during MIS3 (Figure 5-11). This suggests that the Neanderthal did not adapt to the new environment, but instead remained stable in its realised niche and contracted in the direction that the warmer climates contracted to. When looking at the progression of the means through time (investigated by a hierarchical linear regression) between Europe and model 15 (visually presented in Figure 5-12). There is a significant interaction ($b = .05$, $t(116694) = 32.63$, $p <.001$) between the timeframes and Bio01 (entered age, bio01 and the two-way interaction between Europe and model 15).

A simple slope analysis indicated that the Bio01 mean average temperature decreased over time significantly for both Europe and model15. It shows that Neanderthals changed their realised niche to a cooler environment, but not as much as the general deterioration of Europe (Europe: $b = -.13$, $t(116694) = -76.24$, $p < .001$; model 15: $b = -.03$, $t(116694) = -14.03$, $p < .001$). However, when taking the 120ka out of the equation, it can be seen that the Neanderthals did not change their realised niche during MIS3, even though the general climate of Europe cooled significantly (Europe: $b = -.10$, $t(106391) = -21.13$, $p < .001$ and model 15: $b = .01$, $t(106391) = 1.29$, $p = .198$). This could mean that the Neanderthal already lived at the margins of its ecological tolerance during the entirety of MIS3.

To investigate if there is a sub-Milankovitch pattern visible in the Neanderthal realised niche, a comparison was made to the NGRIP ice core data (Svensson et al. 2006, 2008) and the means of Bio01 (Figure 5-14). Since this graph is based on the means of Bio01 of the projected climatic range, caution needs to be taken whilst interpreting the graph because it does not represent local changes in the range and the change represents less than 1.2°C change in total. Overall, there seems to be a tentative pattern. Four Greenland Stadials (GS) seem to have an affect on the mean temperature of the Neanderthal climatic niche during MIS3. The first is GS-18, at the start of MIS3. The mean temperature of the niche is low (6.6°C) and after that an increase in the mean range increases as Europe warms up. There is a small drop during GS-16 and after that the mean temperature for the niche and Europe keeps slowly increasing to 44ka (GS-12). After that a decrease in temperature occurs with a steady decline in European mean temperature. There is a sudden drop in the mean temperature of the climatic niche at 42ka (GS-11). This observed pattern is interpreted below by comparing this pattern to the pattern of niche contraction.

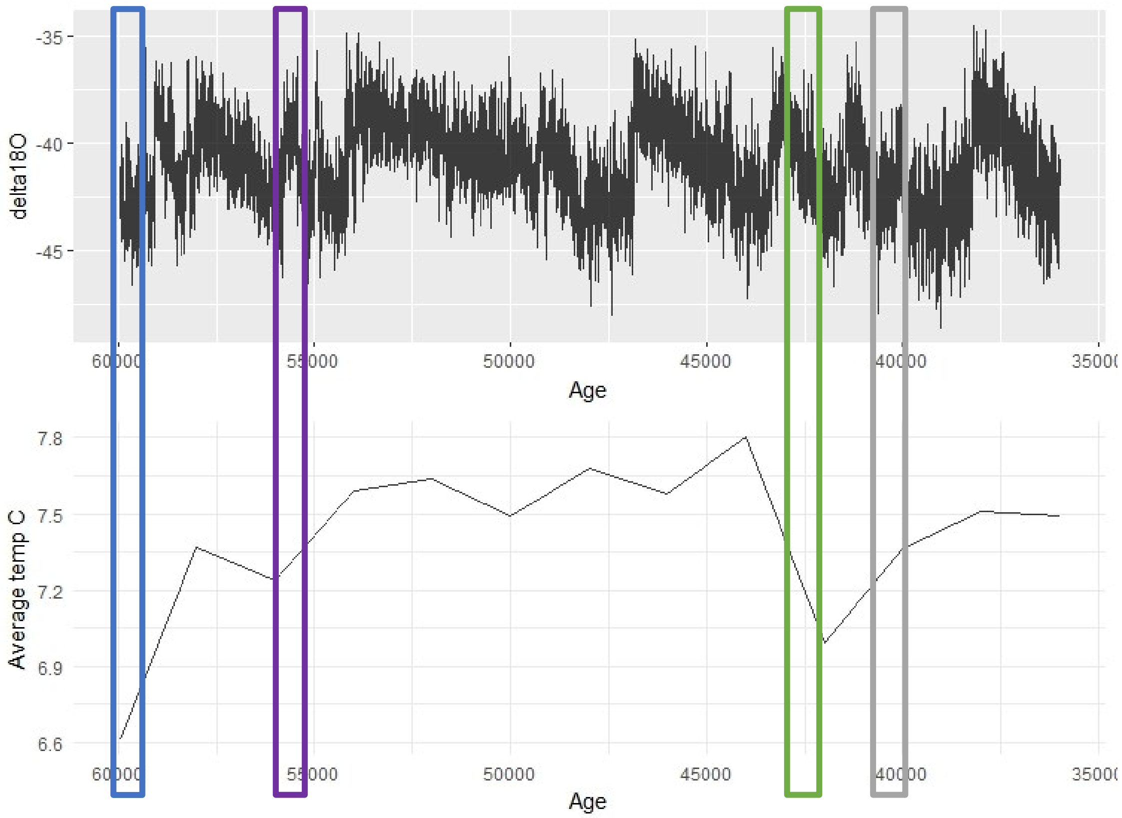

Figure 5-14 Comparison of Bio01 (bottom graph) to the NGRIP ice core (upper graph). The blue bar (first left) represents GS18 purple bar (second left) represents GS-16, the green bar (middle) represents GS-12 and the grey bar (far right) represents GS11. Datapoints for Bio01 are only on the 2000-year intervals starting at 60ka, the connecting lines do not represent additional data.

The predicted climatic niche in geographical space (Figure 5-15) shows a severe contraction and fragmentation at 60ka compared to 120ka, after which the climatic niche expands in geographical space towards most of western and central Europe. Between 44ka and 42ka the niche contracts south and west rapidly and reaches its smallest contraction between 40-36ka.

The contraction and reduced mean temperature at 60ka (Figure 5-15-A) correlate well and likely represent the end of MIS4 and the very long and cold GS-18. The dip in temperature at 54ka (Figure 5-15-D) is geographically observed by a range expansion into more northern and western geography. There is a marked range reduction from the northern margins at 48ka (Figure 5-15-H), which is associated with a small increase in mean temperature (GS-13). There is a larger increase in temperature during ka44 (Figure 5-15-J), where there is a range contraction in the north but an expansion in range in the Levantine area. The contraction in the north and expansion in the south explain the increase in mean temperature, even though the range contraction in Europe continues. The extreme range contraction at 42 (Figure 5-15-K) is a contraction from both the southern and northern margins and correlates well with a cooling of mean temperature of the niche and the cooling of Europe during GS-11. The mean annual temperature increases somewhat, but the range continues to shrink, indicating that there is less area available with the right climatic environment for the Neanderthal. The final contraction of 40-36ka (Figure 5-15-L,M,N) happens after the extinction of the Neanderthal. Even though there is still some suitable area, the niche contraction does coincide with the Neanderthal disappearance.

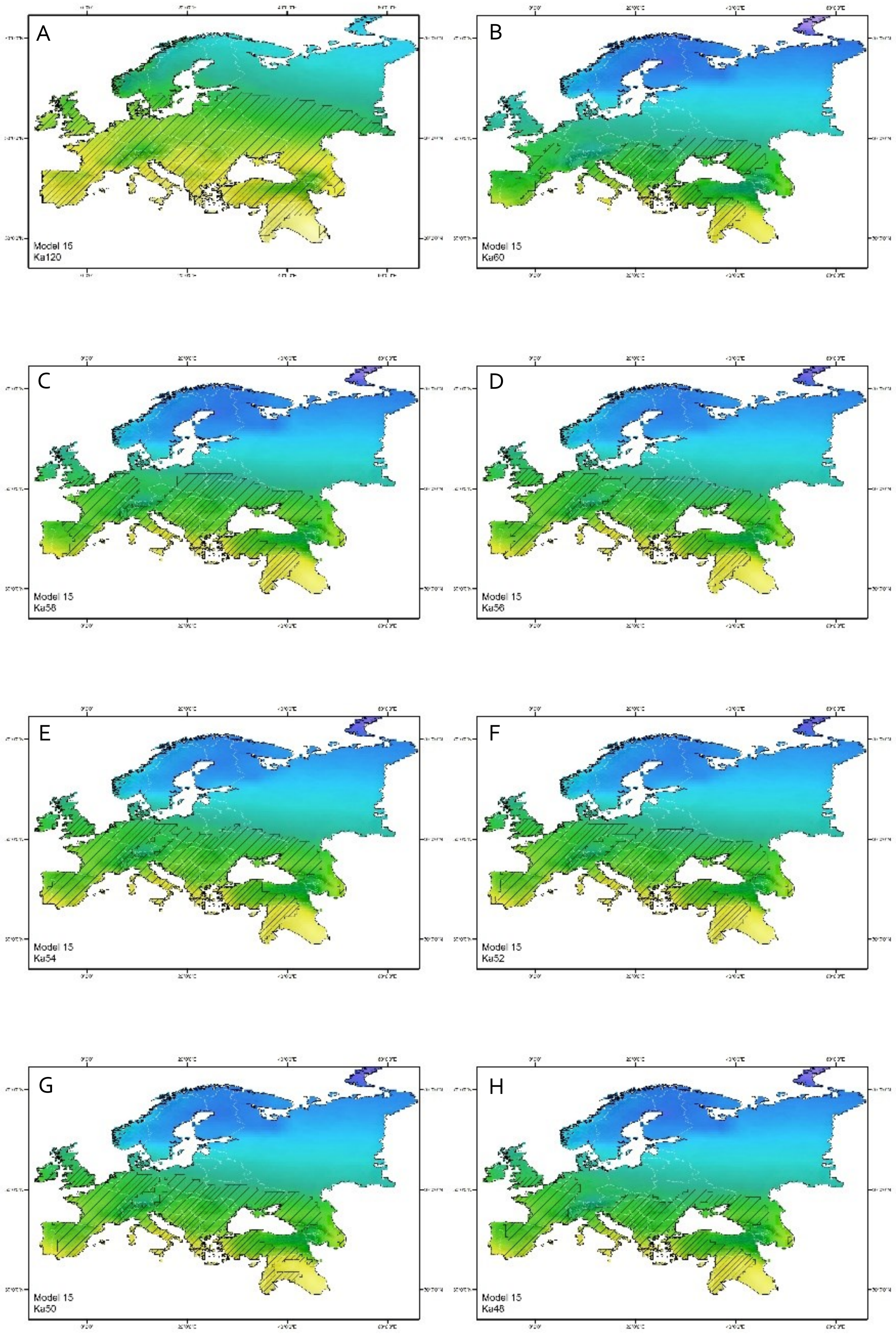

Figure 5.14 Continues on next page. Neanderthal climatic niche prediction of Model 15 shown through time. A=120ka, B=60ka, C=58ka, D=56ka, E=54ka, F=, G=52ka, H=50ka, I=48ka, J=46ka, K=44ka, L=42ka, M=40ka, N=38ka.

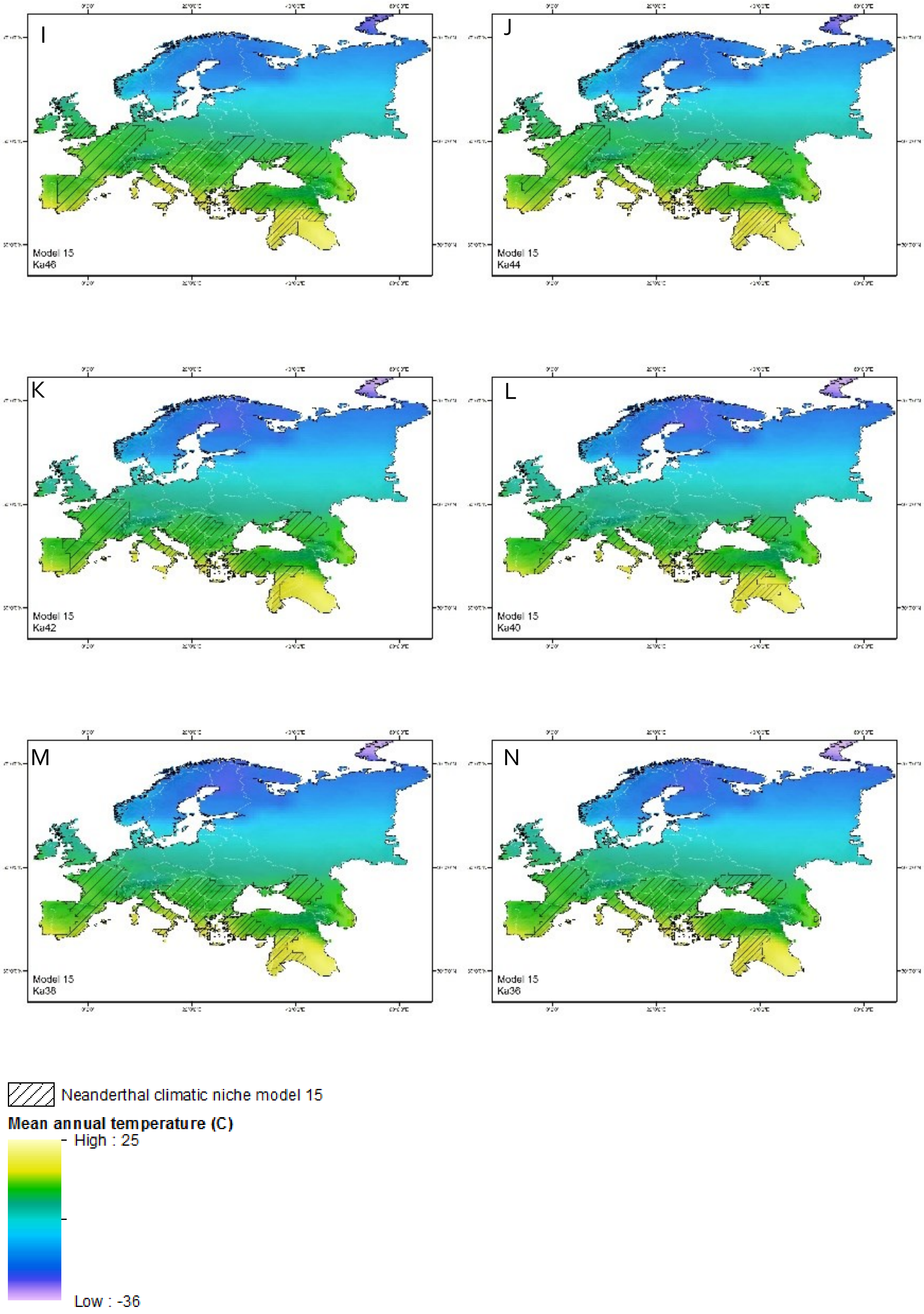

Figure 5-15 Neanderthal climatic niche prediction of Model 15 shown through time. A=120ka, B=60ka, C=58ka, D=56ka, E=54ka, F=, G=52ka, H=50ka, I=48ka, J=46ka, K=44ka, L=42ka, M=40ka, N=38ka.

5.3.11 Comparison to three models

To investigate how the model 15 performs compared to previously published models, a comparison is made between them. The three models have been constructed in slightly different ways (different modelling software, slightly different variables) to the present study and are not fully or directly comparable.

The models of the present study agree with the climatic niche models of Benito et al. (2017), henceforth the Benito model, who also observe the warm climatic niche at 120ka. The model of the present study predicts the locations of the archaeological sites used in their study very well. The Benito model used slightly different variables to calculate the Neanderthal niche (Bio5: mean warmest month ~30⁰C, Bio6 mean coldest month >-10⁰C, Bio012 annual rainfall~900mm and Bio018 precipitation warmest quarter >300 mm). For their study, the most important predictor was winter temperature whilst for this study it was the mean annual temperature. The Benito model and the present study agree on the predicted climatic niche. Benito et al. do note that recent discoveries of sites during MIS5e have increased the coastal range to include areas more inland and thus increase the breadth of the climatic niche (Benito et al. 2017). The increased distribution of inland sites generated with the convex-hull for model 15 could therefore be a good approximation to (yet undiscovered) reality and agrees with the Benito model. Though the Benito et al. study (2017) recommends the inclusion of net primary productivity and slope in their models to improve the accuracy at more locals scales, the present study has found no improvement on the inclusion of these variables.

The second model that the present study can be compared to is the one by Melchionna et al. (2018). Their work (named here the Melchionna model) compared the modelled climatic niche of Neanderthal to that of Anatomically Modern Humans during 48-40ka and. They created pooled climatic niches to investigate the range of both hominins and used the archaeological locations to project each of the three time frames. Model 15 agrees with the mean winter temperature for the time frames (mean winter temperature for the Melchionna model: ka44~ -1⁰C, ka40 ~-5⁰C) but the mean summer temperature is a lot higher (mean summer temperature for the Melchionna model: ka44~ 16⁰C, ka40~16⁰C) >5⁰C warmer which indicates that the climatic niche of model 15 is a lot broader. This could be due to the lack of Neanderthal sites in the Near East (since their dataset was built upon Europe), where summer temperatures are high. Both the Melchionna model and model 15 predict the loss of geographic range from the northeast.

The model by Banks et al. (Banks et al. 2008) shows the Neanderthal distribution based on European archaeological sites before and after the Heinrich 4 event (40-38ka). They modelled each time frame based on the respective archaeological locations. The model is now slightly outdated with many younger dates used by the Banks model that have recently been re-evaluated towards the demise of the Neanderthal; these dates no longer represent the last Neanderthals (Higham et al. 2014). Furthermore, their model indicates a much cooler climatic niche (based on mean annual temperature, -1°C - +12°C) than model 15. The continuation of the existence of the Neanderthal climatic niche after the Neanderthal extinction in the Banks model is argued to be an indication that factors other than climate were the cause of the Neanderthal extinction (competition with anatomically modern humans). The model of the present study also shows a continuation of climatic niche, but severely contracted and fragmented. Either method could be used to argue for the survival of the niche past the survival of the actual taxon. Therefore, it could be argued that Neanderthals would have been able to persist without competition with modern humans or that re-expansion from refugia was impossible. The inability to expand from refugia may have been caused by the long term range contraction and fragmentation (as the whole of MIS3 appears to be less suitable for Neanderthals) which led to a diminished Neanderthal population.

5.3.12 Summary of the results

Following the suggestions by Nogués-Bravo (2009) the models have been constructed on different palaeoclimatic reconstructions and explored by using different climatic and abiotic variables. The models have included the timeframe of 120ka, a non-analogous climate in relation to MIS3. Different training data were used and the models were assessed based on archaeological locations as independent validation data from different time frames. The model with the best fit to the archaeological locations and climatic association was chosen: model 15. This model is based on a single time frame (ka52) and projected to all other time frames.

Exploration of the Neanderthal niche was done in climatic space by creating two other models: archaeological locations (done by extracting the climatic values per variable for the archaeological locations), and the approximate fundamental niche (by extracting the climate variables of the niche models for each respective time frame - this is the multitemporal calibration suggested by Nogués-Bravo (2009). These two models were compared to model 15 and the background variable of Europe. The three models showed significant differences with each other. Most notably, the 'fundamental' niche underestimates the cooler end of range whilst the Model15 overestimates this compared to the archaeological reality. Overall, there is a statistically better match between the archaeological locations and Model15 than the fundamental niche. Finally, the modelled niche was explored for niche stability by looking at changes in climatic and geographic space.

Model 15 showed a reasonably stable niche throughout time even though the climatic niche cooled from 120ka to 60ka. During MIS3 the niche remained the same. A comparison to the GS/GI cycles showed that there is a tentative relationship between the occurrence of a GS and the contraction of the range in climatic and/or geographic space.

A comparison with three models using ecological niche modelling show an overall agreement with the Melchionna and Benito model and less so with the Banks model. The model for this study presents a wider but more stable ecological niche, with more inland suitability during MIS5e.

5.4 Discussion

5.4.1 The climatic niche of the Neanderthal

The models created in this study predict that the realised climatic niche of the Neanderthal underwent cooling and contraction between MIS5e and MIS3, after which the climatic niche stabilised but the geographically suitable area contracted during MIS3 until the extinction of the Neanderthal occurred. A tentative link with sub-Milankovitch cycles can be detected, where the cold periods of the Greenland Stadials have a negative effect on the realised climatic niche of the Neanderthals. The models confirm that the realised climatic niche of the Neanderthal was temperate rather than hyper-arctic.

The hyper-arctic adapted Neanderthal was thought to be well adapted to Ice Age Europe with an adapted physiology to deal with the cold (Holliday 1997; Steegmann et al. 2002; Trinkaus et al. 1999; Weaver 2003). This view has now been disproven by physical anthropological studies, faunal association studies and biogeographical studies that all conclude the Neanderthal is in fact more temperate adapted (Benito et al. 2017; Nicholson 2017; Rae et al. 2011; Stewart 2005). The new climatic niche has repercussions on the interpretation of Neanderthal physiology and behaviour. For example, the Neanderthals are deemed to have a higher metabolic rate and energy consumption in order to keep warm (Steegmann et al. 2002). Based on the high metabolic rate, the 'less mobility strategy' postulates Neanderthals needed larger home ranges in cooler northern Europe because of the reduction in available biomass (hunting becomes more important), this would lead to an increase in energy expenditure due to prolonged foraging activities (Verpoorte 2006). When compared to modern humans under equal conditions, the Neanderthals were not able to move as far north as modern humans (Verpoorte 2006). This theory was dismissed by arguing for more frequent, but less intense, movement throughout the home range that would have enabled Neanderthals to cope (Verpoorte 2006).

The high metabolic rate also called for high-energy foods and tied in with the high meat consumption found in the stable isotope studies (Richards and Trinkaus 2009; Wißing et al. 2016). The high meat consumption required hunting larger game and thus it was thought that Neanderthals were hyper-carnivores that only hunted the larger game (Niven et al. 2012; Richards et al. 2008; Stiner et al. 2000). Evidence has slowly been building that Neanderthals explored more food stuffs than previously thought, especially plants, smaller animals and marine resources which are found in the archaeological record associated with Neanderthals (Fiorenza et al. 2015; Henry et al. 2014; Stringer et al. 2008). The exploitation of marine sources fits well with the ecological niche model by Benito and colleagues that shows a higher suitability in coastline habitats (Benito et al. 2017). The suitability of coastal areas of their models does not agree with the previous views of Neanderthals being hunters of large mammals on the cold and vast European plains (Benito et al. 2017). Their model however still agrees with the view that Neanderthals were better suited to the more open coastal areas during warm phases because the Neanderthals did not like the dense forests of inland Europe (Gaudzinski-Windheuser et al. 2014; Gaudzinski-Windheuser and Roebroeks 2011). The present study does suggest inland Europe was suitable for the Neanderthals during MIS5e. This is supported by the notion that the shorter limbs in Neanderthal were not adaptations to the cold, but rather an adaptation to more forested environments (Stewart 2005). This is supported by the associated taxa found on Neanderthal sites that prefer closed environments (Stewart 2005; Stewart et al. 2003). The most forested environments in MIS3 are regarded to be in the south of Europe (Bennett et al. 1991; Willis et al. 2000). The contraction of the Neanderthal range to the south may thus be tied to the contraction of the forests rather than the actual temperature tolerances of the Neanderthal. A better understanding of the vegetation of Europe is needed during MIS5e and MIS3 before the relationship between Neanderthals and a forested environment can be investigated via climatic niche models.

5.4.2 Contraction of the Neanderthal range

This is the first study to compare the climatic niche of the MIS5e Neanderthal populations and the climatic niche of the populations during MIS3. Our model suggests a development in the climatic niche that is cooler in MIS3 than during MIS5e. The cooling of the climatic niche from

MIS5e to MIS3 is combined with a large reduction in range. The model shows the most severe range reduction and fragmentation is at 60ka, suggesting that the Neanderthal is in full refugial state during MIS4. This change in climatic niche and geographic range may correlate to a presumed bottleneck, or extinction event before 48ka (and likely during MIS4), where most the northern European population went extinct and was replaced by an eastern population (Dalén et al. 2012; Fabre et al. 2009). The eastern population may have developed a tolerance to cooler climates and introduced this to the European group. It could also be that the cooler climatic niche found in MIS3 was not expressed during MIS5e because the Neanderthal population was small and so did not expand to the marginal edges of the climatic niche, or the cooler niche was not predicted in the model during MIS5e due to a lack in archaeological sites in more northern areas. The climatic niche of the model does predict a more northern and eastern geographic range than any of the models in the literature. Since the model agrees well with the archaeology of all time frames, the preferred view here is that the model of the present study provides a realistic view of the Neanderthals realised niche and that archaeological sites could be expected to be found in the Central European Plains dating to MIS5e.

The Neanderthals have lived through the transition from interglacial to glacial a number of times, and it is often argued that, because the glacial-interglacial cycles before the cooling to OIS2 did not pose a problem for Neanderthal survival, something else -like competition with anatomically modern humans- must have contributed to the extinction of the hominin (Banks et al. 2008; d'Errico and Sánchez Goñi 2003) . However, the transitions from interglacial to glacial are different for each cycle (Barnosky et al. 1996). And the transition from MIS5e to OIS2 (the Last Glacial Maximum) is different due to the increase and amplitude in millennial variability (Wolff et al. 2010). The ice-core records show a severe cooling during MIS4 and a slow warming during early MIS3, a slow overall cooling but highly variable middle MIS3 and a rapid cooling in late MIS3 towards OIS2 (Rasmussen et al. 2014). During MIS3 the climatic niche of the model remains relatively stable and does not follow the same cooling trend as the general European climate. This indicates that the Neanderthal may have contracted geographically to the remaining suitable climatic niche rather than expanding its climatic niche by remaining in the geographically less suitable areas. Even though the climatic niche of the Neanderthal does not change significantly during MIS3, a tentative correlation between the changes in mean temperature and the Greenland Stadials could be made, where the Greenland Stadials have a negative impact on the climatic niche and geographic range. The Neanderthal climatic niche mean annual temperature drops most markedly during GS18 and GS11. The mean temperature rises during GS12, this can be explained by the expansion of the

Neanderthal range into the Levantine area, but there still is a contraction in range in northern Europe. It has been argued that human presence in northern Europe may have been short-lived and only occurred during interstadials (Jacobi and Higham 2011). In reverse this means local extinction or habitat tracking to more suitable areas during stadials.

The cold periods of Heinrich events caused a turnover of cultural systems (and populations) for anatomically modern humans in Iberia (Bradtmöller et al. 2012; Schmidt et al. 2012). Behavioural change may have aided survival in the new environments, and effectively increased breadth of the climatic niche for Anatomically Modern Humans. Cultural change can also be observed within the Neanderthals over time and space. During MIS5e in Europe there is the Mousterien de Tradition Achaeulien (MTA) which is then followed by the Quina tradition between 70-40ka (Wragg Sykes 2017). More localised signals are also found; for example, the southwest of France shows the recurrent succession of three groups of the Mousterian: Ferrassie, Quina and Mousterien de Tradition Achaeulien (MTA) (Turq et al. 2013). In Spain the Quina is superseded directly by transitional industries or Upper Palaeolithic assemblages. In Central Europe the Keilmessergruppen (KMG) are the local Mousterian varieties and they change regionally and temporally during MIS5e and MIS3 (Richter 2016; Roebroeks and Soressi 2016). Finally, the largest technological change is the occurrence of transitional industries all over Europe at the end of the Neanderthal reign. The most known (and debated) transitional industry, the Châtelperronian is now attributed to the Neanderthals (Welker et al. 2016). These changes in stone tool production may relate to the changes in Neanderthal populations (perhaps even genetic turnovers) and to the expansion and contraction of the Neanderthal range during the climatic variability of MIS3. Even though there is archaeological evidence for behavioural change, the overall climatic niche of the Neanderthal did not expand according to the model.

Furthermore, the model shows that the geographic contraction started halfway through the time frames used for MIS3 (after 50ka) and thus suggest a slow but steady contraction well before the emergence of anatomically modern humans. The contraction of the Neanderthals by local extinction rather than habitat tracking has been suggested by studies of archaeological evidence, demographic studies and the loss of genetic diversity through time (Bocquet-Appel and Degioanni 2013; Fabre et al. 2009; Finlayson and Carrión 2007; Hublin and Roebroeks 2009; Sørensen 2011).

5.4.3 Extinction of the Neanderthal

The ultimate contraction of the Neanderthal range lead of course to the extinction of the species. The model shows a severe range fragmentation towards 40ka and beyond with very small pockets of suitable area. The range fragmentation is considered to be a main driver of Neanderthal extinction (Melchionna et al. 2018). However, the suitable area in the model does persist beyond the extinction of the Neanderthal to 36ka (youngest time frame modelled). The persistence of the range has been interpreted to suggest that other drivers may have had an influence in the final years of Neanderthal survival (such as competition with modern humans (Banks et al. 2008). However, the continuous contraction and fragmentation of the Neanderthal climatic niche since 50ka suggests that the retreat in the southern refugia was so severe that there were no viable populations left in Europe to recolonise with amelioration of the climate. A similar pattern has been observed for carnivores in Iberia, that occur in low population densities and have large home ranges. The contraction of their range was so severe that the refugia were too small to sustain viable populations and thus lead to the extinction of the taxa (O'Regan 2008; O'Regan et al. 2002). The temporal and geographical scale used in this study does not offer enough detail to argue for other drivers or simply climatic deterioration as a cause for Neanderthal extinction.

The general observed pattern of range contraction (as agreed by the model from the present study) goes from northeast to southwestern Europe. However, the persistence of the northernmost archaeological locations in western Europe, do not agree with this trend. Late surviving northern Neanderthals at sites such as Spy in Belgium and Geißenklösterle in Germany do fit within the presented model, but they may also signify different ecological processes. It may be, that these last Neanderthals were not part of a viable population anymore, but groups of Neanderthals experiencing the dead clade walking syndrome, or extinction debt (Jablonski 2001; Tilman et al. 1994). These last groups of Neanderthals may have persisted the unfavourable conditions but have been cut off from a viable population that has contracted into its southwestern refugium by 44ka. On the other side, another ecological process could explain their late survival. The late survival in northern areas may indicate that cryptic northern refugia were involved (Stewart and Lister 2001). Northern refugia have been suggested by genetic research and by ecological niche modelling for several species (Deffontaine et al. 2005; Edwards et al. 2014; Hofreiter and Stewart 2009; Kotlík et al. 2006; Moore et al. 2015; Sommer and Zachos 2009). The late survival of Neanderthals in northern Europe may have occurred during multiple glacial-interglacial cycles and aided fast reoccupation of northern territories. However, recolonization out of northern refugia towards the end of the Neanderthal existence did not occur and local extinction took place. Therefore, when evaluating the Neanderthal niche, the inclusion of the very last Neanderthals may portray an unsuitable niche and provide no ecologically meaningful answers for the taxon.

The present study focusses on Europe mostly because there is very little archaeological evidence in the east. The fossil record of Neanderthal remains is limited to Western Europe whilst some genetic evidence is available for Asian sites (Krause et al. 2007; Roebroeks and Soressi 2016; Slon et al. 2017). There is a research bias towards Western Europe, partly because of the preservation circumstances (presence of caves) and partly due to historic interest in areas such as south-western France. A study has shown that this has a large influence on the interpretations of the patterns (Maxwell et al. 2018). As rightly observed by Roebroeks and Soressi (2016) the eastern and northern sides of the Neanderthal range are largely unknown. It is likely that Europe only represents the margins of the Neanderthal range and that the core population is situated in Asia. This is attested by the influx of an genetically eastern population into Europe (Dalén et al. 2012). A similar pattern of population turnovers has been observed on collared lemming, where genetically distinct populations moved repeatedly into Europe from Asia (Brace et al. 2012). It may therefore be proposed that Neanderthals survived for longer in the core area of their range in Asia than in Europe and that the documented extinction of the Neanderthal is only the regional extinction of the European population. The hint for late surviving Neanderthals in the east is documented in Armenia and Georgia (Adler et al. 2008; Chataigner et al. 2003; Pinhasi et al. 2012), though the core of the range may be as far as Kazakhstan. Obviously, a research focus on Neanderthals in Asia is needed.

5.4.4 Improving the models

Like all models, this model only approximates reality. Care has been taken to create and choose the best-fitting model to the present-day knowledge of archaeological sites and their absolute dates. The use of one timeframe to predict other timeframes has been shown to be a good fit to the archaeological reality and it may come near to the fundamental niche of the European Neanderthal. The merging of climatic values of several time frames based on archaeological locations to create the approximate fundamental niche has proven unsuccessful because the fundamental niche had less broad climatic ranges than the sites themselves. Furthermore, the prediction of each time frame separately based on the archaeology from that time is more likely to show a (autocorrelated) change in niche breadth. Therefore, the selection of one timeframe used to projected onto other time frames and evaluated with independent archaeological data is the preferred method.

As discussed in the previous chapter (Chapter 4) the temporal (less than 2000 year intervals) and geographical variability (smaller than 50x50km cells) in the climatic record cannot yet be captured in the climatic simulations (Burke et al. 2017). This may mean that range fragmentation (though the Melchionna model is promising), contraction and dispersal ability are difficult to recreate at the needed resolution. However, the model could be improved by incorporating the genetic and demographic evidence as a start. A further consideration is the inclusion of the eastern range of the Neanderthal. Currently, little is known about the Neanderthal populations in Asia and few archaeological sites exist (Krause et al. 2007). The inclusion of the Asian Neanderthals in the model will likely increase the realised niche (due to more continental climates with more severe winters and warmer summers). Finally, separate modelling of the different Neanderthal clades may show the adaptations of populations to the climatic niche.

5.5 Conclusion

The exploration of the Neanderthal niche has been conducted by developing a climatic niche model through time (120ka, 60-36ka). This study found that the climatic niche from MIS5e experienced a cooling towards MIS3, although within MIS3 the climatic niche of the Neanderthal remained relatively stable compared to the climatic deterioration of Europe as a whole. A tentative negative link between Greenland stadials and the climatic niche of the Neanderthals has also been observed for MIS3. The steady contraction from 50ka onwards in geographic space, together with the relative stability of the Neanderthal niche suggests that behavioural change detected in the archaeological record did not aid the Neanderthals' survival. Therefore, it may be concluded that this model approximates the stable realised niche of Neanderthals through time.

5.6 References

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6 Discussion

6.1 Original contribution to knowledge

The climate is changing, and it is more pressing than ever to start to understand the past so that there is a way to prepare for future changes in mammalian ranges. The best period to study these changes is the Late Pleistocene, where there are changes in species composition and range contractions accompanied by extinctions. This research focused on Europe from 60-10 ka and analysed under-researched topics regarding mammalian climatic niches.

Having systematically reviewed the literature to extract data from archaeological and palaeontological studies on mammals in Europe, a scheme was developed for quantifying the reliability of radiocarbon dates (Chapter 2). This was then applied to the database of mammalian fossil data to extract only the most reliable mammalian data (Chapter 2). Furthermore, present-day geographical information of mammals was collected and used to create a quantifiable framework of climatic associations to use for palaeoenvironmental reconstructions (Chapter 3). The results from the present-day mammalian framework and the most reliable past mammalian data were combined to investigate the existence of non-analogue mammalian communities during the Late Pleistocene (Chapter 4). Finally, the climatic niche of one key taxon in detail was studied: the Neanderthal was investigated in the last chapter (Chapter 5).

6.1.1 Chapter 2: Improving the reliability of published radiocarbon dates

Knowledge gap

The continuous development of the radiocarbon dating techniques have increased the reliability of the resulting dates (Wood 2015). Many archaeological chronological studies use radiocarbon dates of varying reliability. There is a lack in consistency in the developed auditing methods (Graf 2009; Pettitt et al. 2003). The resulting need for a comprehensive auditing method was addressed in this chapter (research question 1).

Methods

Flowcharts for the main materials used for radiocarbon dating (collagen, charcoal and wood, shell carbonates) were made based on a review of the methodological literature. The flowcharts lead to a methodological assessment of each radiocarbon date: good, fair, poor, or unusable. A further flowchart was made to assess the contextual integrity of the sample which either upgraded or downgraded the methodological assessment. The combination of these two flowcharts provide the researcher with a final assessment of the reliability of each radiocarbon date. These flowcharts were compared to another quantitative method (Pettitt et al. 2003) for three archaeological sites to see if the assessments are in line with each other.

Findings

The developed quantitative method to assess the methodological and contextual reliability of each radiocarbon date assigned a grade to each carbon date of poor, fair or good. This quantitative method performed well in a comparison to a quantitative method used by Pettitt et al. (2003) showing that it is a simple and effective way to assess quality of radiocarbon dates.

Implications

The use of this method allows for a quantitative analysis of the quality of radiocarbon dates, producing a better dataset to analyse patterns in the past and make them comparable between studies. Chapters 4 and 5 use this method to select appropriate radiocarbon dates for model-building and -evaluation. This chapter successfully met objective 1.

6.1.2 Chapter 3: distribution of modern mammals

Knowledge gap

Reconstruction of past environments when using mammals as a proxy is based on their current distribution, or on comparison of other past faunal communities and their environmental associations (Stewart et al. 2003). However, it is often hard to trace how authors obtained the climatic association of the taxa. When the climatic associations are based on current distributions of mammalian taxa, it may not reflect their full fundamental niche and therefore the environments that could have been occupied in the past, because their current ranges are severely impacted by human pressure (Faurby and Araújo 2018). The knowledge gap is that we do not have a reliable idea of how the current distributions of important mammals reflects back to the past environments for which they are used as indicators of environmental conditions (research question 2).

Methods

Present-day distribution data of 74 mammalian species were collected from the Red List and GBIF on a world-wide scale. These distribution data were cleaned and merged using ArcMAP 10.3, and random points were placed within the combined polygon. Climatic data were obtained for each point from BioClim. Bioclim variables which correlated with a correlation coefficient <0.7 were selected for developing a climatic niche model. The random points were used as training data for climatic niche modelling in MaxEnt with the selected BioClim variables as predictor variables. The resulting climatic niche models were turned into polygons (indicating likely presence per taxon, using ArcMAP 10.3) according to the maximum training sensitivity level plus specificity logistic threshold for each taxon. Area overlap between niche models and different climatic zones of the Köppen-Geiger climate classification was then calculated and a percentage area of polygon per climate group was calculated. This was then used to give each taxon a broad climate classification (such as cold-arid).

Findings

These models show that the taxa classed as temperate in archaeological the literature are able to deal with the cooler environments of Europe much better than typically assumed in the literature. These 'temperate taxa' could not be classed as a purely temperate but were often more cold adapted. The climatic niches of most taxa were broader than currently typically recorded in literature dealing with environmental reconstructions in the Late Pleistocene.

Implications

The implications of this study are that environmental reconstruction based on mammals is less straight forward than previously presented in the literature. Most European mammals seem to have a wide climatic tolerance (thus testing the hypothesis of research objective 2). In particular, it may be problematic to use large mammals to indicate the presence of temperate environments, because the mammals considered indicators for a temperate environment have been modelled to inhabit a much wider, especially cooler, climatic niche. It is therefore harder to accurately reconstruct a temperate environment using mammals as a proxy. The framework provided by this study should aid with more accurate environmental reconstructions of Late Pleistocene studies.

6.1.3 Chapter 4: The case for non-analogue faunas. Modelling the impact of Late Pleistocene climate change to species-specific distributions.

Knowledge gap

There is a longstanding debate on the occurrence of non-analogue faunas in the Pleistocene (e.g. Stewart 2009). The discussion entails whether the non-analogue faunas are a true faunal community (Stafford et al. 1999) or if the observations are an artefact of dating imprecision and stratigraphic mixing (Coope 2006). This gap in knowledge relates to research question 3.

The combination of improved dating methods and species distribution modelling may help further this debate.

Methods

Possible non-analogue mammals were selected, based on the existing literature and outcomes of the climatic niche models in Chapter 3. Climatic niche models were made in MaxEnt based on the modern distribution data collected in Chapter 3. The climatic niches were projected to past time frames (60-10ka bp). These niches were processed in ArcMap 10.3, and were turned into polygons based on the maximum training sensitivity plus specificity logistic threshold per taxon. The taxa were split into three groups based on their modern distribution (southern, eastern or northern group). The percent overlap of each taxon with the taxa from the other groups was then calculated per time frame in ArcMap10.3. The models were then compared to the independent data set on past mammalian presence in archaeological sites. Further models were run for reindeer to assess the sensitivity of the models by changing the training data (presence points) and variable input (climatic simulations) in MaxEnt and processed the same way in ArcMap 10.3.

Findings

The species distribution models conducted for this study showed that based on the present distribution of the specific taxa deemed non-analogue in the past, the taxa did not overlap substantially in the past (thus meeting research objective 3). This disputed the non-analogue faunal communities' existence. However, the models of past distributions based on current distributions did not match the archaeological locations of the matching taxa, suggesting that past populations of the taxa may have had a different realised niche to their current one. This mismatch appeared especially in eastern and northern taxa. Several models were run for reindeer, but none were fully supported by archaeological data.

Implications

The models predicted that the southern taxa remained relatively stable in their realised niche. That the non-analogue combinations were not picked up by the models, may be attributed to a lack of precision in radiocarbon dating and the lack of variability in climatic simulations. The calibrated age range of the radiocarbon dates often cover several hundred years, which may include the appearance and disappearance of a taxon in an area. The variability in palaeoclimatic simulations is twofold: the existing simulations reconstruct the climate in large geographic space (cells of 50x50km) averaging localised changes in climate. Furthermore, the time frames only simulate one year every 2000 to 1000 years. Severe climatic change occurred more frequently within a 2000-year time slot than is currently captured in such large time slices. Finally, the mismatch between the archaeology and the models suggest that the combinations between the non-analogue taxa may have been fleeting, which may be explained by several biogeographic principles. This could be due to the seasonal migration capabilities of some taxa (e.g. reindeer is a highly migratory taxon), different dispersal abilities per taxon, local extirpations and extinction of populations or survival in cryptic refugia. A combination of these factors would be able to create an overlap of taxa that normally would not be sympatric, for example the lingering of a nearly extinct population of saiga antelopes and the fast dispersal of reindeer into the same area.

6.1.4 Chapter 5: The predicted Neanderthal stable realised niche and the contraction of its geographic range.

Knowledge gap

The assumed climatic tolerances of the Neanderthal have changed drastically in the past two decades. The Neanderthal was originally thought to be hyper-arctic (i.e. Steegmann et al. 2002) whilst there is now a growing body of literature claiming that the Neanderthal is more temperate adapted (i.e. Rae et al. 2011; Stewart 2005). Most research into the climatic niche of the Neanderthal has focused on the time of extinction (Banks et al. 2008; Melchionna et al. 2018). However, little research has been done on how climate changes affected the Neanderthal temperate climatic niche and distribution through time (research question 4).

Methods

Archaeological locations were selected from four time frames (120ka, 52ka, 44ka and 42ka). Six climatic niche models were run in MaxEnt on the 120ka archaeological locations with different abiotic variables from different climatic simulations. The best performing combination of variables was chosen to then assess the sensitivity of the climatic niche models to different training data (presence points). The model with the best-performing training data was chosen to project to all available time frames (120ka and 60ka to 36ka at 2000-year intervals). The climatic variables were extracted from the model and compared statistically to the climatic variables of the archaeological locations, constructed fundamental niche and the background climate of the study area Europe at the four selected time frames (with ANOVA and subsequent pairwise comparisons of the models). Finally, the climatic niche and the geographic range of the best performing model (model 15) was statistically analysed through all the time frames (regression analysis).

Findings

This chapter explored the Neanderthal realised niche by creating different models to investigate the effect of different climatic and landscape variables. A final model (model 15) was chosen that shows that the fundamental niche of Neanderthals did not change, but the realised niche moved to a slightly cooler environment between MIS5e and MIS3. During MIS3 the realised niche was not predicted to change, leading to geographic contraction of the Neanderthal. A tentative observation has been made on the impact of short-lived climatic cycles of the Greenland Stadials and Interstadials. The Greenland Stadials seem to have a negative impact on the climatic niche and geographic distribution of the Neanderthals throughout MIS3.

Implications

The use of a time frame far outside the time frames of interest (i.e. well before Neanderthal extinction and when the taxon was not in refugial state) shows the true process within Neanderthal range contraction. This study shows that Neanderthals were possibly living on the margins of their climatic tolerance in MIS3, which is supported by their small population size and frequent population turnovers during MIS3 as shown by genetic studies. There is a tentative interpretation from the models that the Greenland Stadials has a negative effect on the climatic niche and distribution of the Neanderthals. The combination of the reduced climatic niche and geographic range during MIS3 topped up with the climatic deterioration of sub-Milankovitch cycles may have put extra stress on the survival-ability of the taxon. The assessment of different models and the inclusion of time frames (MIS5e) outside of the time of interest (MIS3) has resulted in a better understanding of the Neanderthal realised and fundamental niche (meeting research objective 4).

6.2 Research limitations

Specific research limitations are covered in each chapter and addressed accordingly. Below is a short summary of the limitations encountered.

6.2.1 Selection of sites, taxa and radiocarbon dates

The constructed database (Chapter 2) with archaeological and palaeontological sites, published radiocarbon dates and identified taxa is likely to have missed some sites, new radiocarbon dates, or faunal studies. Records published after 2015 have not been added to the database. This may have an impact on the studied distribution of the different taxa (Chapters 4 & 5). However, the new data is unlikely to change the interpretation of the data. The selection of radiocarbon dates may have been too stringent, where dates may meet the criteria to qualify for a good standard they were classed as less good because the available published data were not adequate. This may have led to an underrepresentation of archaeological sites. The stringent selection of data has been supported by other studies (Dinnis et al. 2016). Faunal remains publications used for the distribution studies may have misidentified the taxa, since some are very difficult to separate (e.g. *Bos/Bison*). The distributions of taxa on Red List and GBIF data may be incorrect (these are continuously updated), the Red List polygons may include climatically unsuitable areas in some cases, and the identification of taxa on GBIF may be incorrect because some observations are recorded via citizen science (although steps were taken in the studies of this thesis to remove obvious errors). Even though, the modelled distribution may not be comprehensive, given the stringent data cleaning, comparison to other studies and use of appropriate analyses this thesis has provided the best research possible within its limitations.

6.2.2 Species distribution modelling

Species distribution models, as the name suggests, are models and thus approximate representations of reality. The models provide insight where the actual process or pattern is unobservable. Such models can never incorporate all the different biotic and abiotic factors that affect species distribution, but they are the most reliable way of investigating patterns beyond known distributions.

The nature of archaeological and palaeontological data is that it is easier to provide proof of presence than of absence (Roebroeks 2006). Absence could signify a real absence or be a result of other processes (abundance of the taxon during its life, excavation or sampling techniques, preservation ability of the location and type of fossil, research interests and ability to locate sites etc). Therefore, only few modelling methods are suitable for this kind of data. MaxEnt (maximum entropy) software works well with presence-only data but is limited to the variables that can be put into the model. The model does not take into account biotic factors such as dispersal ability or competition (Merow et al. 2013). The variables on which the climatic niche models were built were suitable for use on different temporal and geographic scales (for example 2000-year time intervals and 50km^2 cells for climatic variables). It may be that the changes in the faunal (and hominin) record happened on a much finer scale, both geographically and temporally, than the studies presented here were able to detect (Gillingham et al. 2012). Furthermore, the presence data of the taxon that goes into the model (training data) can be compiled in multiple ways and the analyses in Chapter 4 and 5 have shown what difference the input training data make to the resultant climatic niche model of the taxa. Finally, factors that may be important to changes in the realised climatic niche are not always observable in the records of the past. For example, the ability to hibernate to become fossorial so as to retain heat in cold periods, as observed for water voles today (Giraudoux 1997), the ability to migrate long distances or stay resident depending on where populations live (Dalén et al. 2017; Morganti et al. 2017), changes in time budgets and group sizes to increase flexibility (Korstjens and Hillyer 2016; Lehmann et al. 2010) and changes in material culture of Neanderthals that aid survival(Sørensen 2009). These characteristics are not often preserved in the archaeological record. If factors like these play a role in the distribution of a taxon, it would mean that the climatic niche predictions made would underestimate the fundamental niche of the taxon and that the models of realised niche for different time frames are underestimates of their true potential distributions.

6.3 Recommendations for future research

The studies in this thesis have focused on two main things, improving the use of 'big data' in Pleistocene studies, and the patterns of distribution of extant and extinct taxa in the Pleistocene based on the evaluated data sources.

Big data is dirty. Large datasets often contain errors; misspellings, misidentifications, double entries, incomplete entries etcetera. Cleaning and assessing data from online databases are of vital importance (Vamberger and Fritz 2018). The first recommendation therefore is to publish radiocarbon dates following the strict guidelines published by Millard (Millard 2014). This enables all researchers to assess the methodological aspects of the radiocarbon dates. Leading on from this is the recommendation to incorporate all these presented variables into the main online databases (as is done for ORAU), such as the INQUA database (ORAU 2018; Vermeersch 2017). And finally, a measure of evaluation (as presented in Chapter 2) and noting the redating of sites would decrease the misuse of radiocarbon dates. The use of big data in ecology and palaeoecology has been frequently addressed and the platforms of the IUCN Red List and GBIF are under continuous improvement (Arnaud et al. 2016; Butchart et al. 2007; Keith et al. 2015). However, not all problems are easily solved, for example: the GBIF database incorporates another database PANGAEA (Data Publisher for Earth & Environmental Science 2018), which details museum collections and researchers have to be aware that the location data saved with the observations often locate the museum rather than where the specimens were found. Another recommendation is the use of a standardised way of reporting faunal remains in publications (Morin et al. 2017a, 2017b) and using quantitative sources for reconstructing Late Pleistocene environments, this would create a more realistic and comparative dataset (Hernández Fernández 2001). Since these analyses are generating big data, the more accurate they are the better meta-analyses will be.

The second set of recommendations are those for avenues of future academic research based on the outcomes of Chapter 4 and 5. Firstly, it is clear from Chapter 4 that the debate around the existence of non-analogue fauna is not resolved and more focused research is needed here. A combination of targeted radiocarbon dates on faunal remains identified to species and from the same geological horizon from multiple sites, together with a more integrative modelling approach could start to address this issue. The more integrative modelling approach is slowly becoming more widespread where genetic population studies are incorporated with the species distribution modelling (Alvarado-Serrano and Knowles 2014; Lagerholm et al. 2017; Lorenzen et al. 2011). However, the modelling will not resolve the issues without developing climate simulations at adequate geographic and temporal scales. Downscaled palaeoclimate simulations in geographic space (to 15x15km^2) are being developed (Latombe et al. 2017). Temporal scales are more difficult to validate to past proxies due to the imprecision of absolute dating methods. Another way to investigate the possibilities of the existence of non-analogue faunal combinations is by exploring the power of individual-based models or agent based models to explore the individualistic responses of populations to past climate change and to see if the taxa could co-occur (DeAngelis and Grimm 2014; Panzacchi et al. 2015). Although these models are harder to create for extinct taxa, since many required variables cannot be derived from the fossils (behaviours, dispersal ability, impact of competition etc.) these individual based models can also prove useful for past extinct taxa (Hölzchen et al. 2016). Investigating non-analogue combinations of taxa is not only relevant for the past. The ability for non-analogue combinations to exist in the past also indicates the expression of these ecological tolerances in the future, with the taxa facing different scenarios of climate change (Maguire et al. 2015; Nogués-Bravo et al. 2016).

Investigating the existence of non-analogue communities does not only provide us with insight to taxa that are currently extant, but also taxa that went extinct. The models of Chapter 4 show the range contractions that are in accordance with the disappearance of the taxa from Europe (even though the models do not work completely and show that the modelled climatic niche retained some geographic space, so the taxa were projected to persist). In a way, these taxa are the most non-analogue taxa imaginable, since they have gone extinct and there is no modern analogue available. One of these taxa is a fellow hominin, the Neanderthal. Chapter 5 was the first study to incorporate the MIS5e and MIS3 data into one species distribution model, showing the time of the classic Neanderthal and the period of its demise. The models show a shift in the realised niche of the Neanderthal from the MIS5e to

MIS3, suggesting that MIS3 might not have been as suitable as previously predicted. The detection of the shift in the realised niche indicates that there is a limit to our understanding of the potential fundamental niche of the Neanderthal. The model also shows a tentative negative link on the influence of the Greenland Stadials on the predicted climatic niche and geographic range of the Neanderthal. The analyses suggest that the Neanderthal remained in refugial state initiated during MIS4 all the way throughout MIS3 and that the frequent climatic deteriorations impacted on the resilience of the taxon. More research with climatic niche modelling into MIS4 would show if the Neanderthal was indeed in refugial state during MIS4 and have implications for the interpretations of the patterns in MIS3. The use of the MIS5e data has shown that the modelling of deep time distributions does provide insight into processes otherwise unobservable. It is thus suggested that the MIS5e (or other suitable periods) ranges should be explored for the Neanderthal and other taxa in similar ways. These models could explore moments where changes in behaviour or physiology may have occurred to deal with climatic change (indicated by a shift in realised niche). Similar to the non-analogue taxa mentioned above, an integrated approach of genetic, demographic and (individual/niche) models would provide a more holistic view. Furthermore, a combined approach between climatic niche models of the prey species of the Neanderthal and the Neanderthal niche may show similar or divergent patterns, depending on the flexibility of the Neanderthals and is an interesting avenue to explore. However, none of these models will make complete sense until we have dealt with the mammoth in the room: the unknown geographic range of the Neanderthal. The gap in research in Asia is slowly being filled in (Adler et al. 2014; Krause et al. 2007; Slon et al. 2017), but much more research is needed to find the total distribution and thus potential climatic tolerances of the Neanderthal. As always, more archaeological and palaeontological sites, more precise dates and better models are needed.

6.4 References

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