Multi-isotopic tracking ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of ancient trophic webs around the time of Neandertal replacement by anatomically modern humans in North-Western Europe

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Paper I (75/100/80/75)

Wißing, C., Matzerath, S., Turner, E., Bocherens, H., 2015a. Paleoecological and climatic implications of stable isotope results from late Pleistocene bone collagen, Ziegeleigrube Coenen, Germany. Quaternary Research 84, 96-105.

Paper II (70/40/80/75)

Wißing, C., Rougier, H., Crevecoeur, I., Germonpré, M., Naito, Y.I., Semal, P., Bocherens, H., 2015b. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. Quaternary International (in press).

Paper III (75/40/80/75)

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List of publications not included but relevant to the topic of the thesis

Bocherens, H., Drucker, D., **Wißing, C.**, 2014. Die Mammutsteppe. Isotopenuntersuchungen in einem vergangenen Ökosystem. Natur – Forschung – Museum 144 (7/8) 2014, 226–231.

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Abstract

The study investigated ecological aspects of the mammoth steppe ecosystem in NW Europe with a special focus on the role of late Neandertals and early modern humans through the analysis of stable isotopes in bone collagen ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$).

Around the time of Neandertal extinction and the arrival of modern humans a diverse community of large herbivorous and carnivorous mammal lived under cold, fluctuating environmental conditions in NW Europe. The study reconstructed the ecological robustness of this ancient ecosystem and its response to oscillating climatic conditions as well as in regard of the ecological participation of Neandertals and early modern humans. The trophic web, the niche partitioning, the ecological flexibility of single species, as well as the general buffer capacity of this biocenosis are objects of investigation.

The Belgium site Troisième caverne of Goyet provided a broad set of directly dated late Neandertal and very early modern human skeletal remains associated with a considerably assemblage of Pleistocene faunal remains. The occurrence of late Neandertals and early modern human skeletal remains at the same place are unique circumstance and allowed a direct comparison of several ecological aspects during a time span with a special relevance for the human evolution.

The site Ziegeleigrube Coenen is contemporaneous with the occurrence of late Neandertals and reflects the ecosystem during or shortly after a cold spell. Even during such phases the structure of the mammoth steppe ecosystem was intact and provided consequently an adequate basis for late Neandertal subsidence. In an ecological context the Neandertals were part of there are no indications for any stress on the structure of the ecosystem.

Through the analysis of $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios in bone collagen of faunal and hominid remains the trophic web was evaluated. Processing of the isotopic data through several statistical approaches allowed a detailed reconstruction of ecological niche partitioning of late Neandertals and early modern humans. Both hominid species occupied the same distinct ecological niche in terms of diet with a clear preference for mammoth and reindeer.

The investigation of the $\delta^{34}S$ composition in Pleistocene bone collagen is a relatively novel approach and provided insights into spatial hominid procurement. The Goyet Neandertals do not reflect the local fauna $\delta^{34}S$ congruously their main prey had an origin different from the neighborhood of the Belgium sites (Scladina, Spy and Goyet). In contrast the $\delta^{34}S$ signal of the Spy Neandertals and the Goyet ancient modern humans corresponds to the values obtained on the local fauna. Potentially different mobility strategies among Pleistocene hominids while exploring the same prey species is the drafted scenario.

The site Lommersum reflects the ecosystem at an initial phase of occupation by modern humans in the area, when Neandertals became already extinct. At this time the regional mammoth population was declining, since the horses entered their niche in distinct region of Western Europe. This study hypothesized that increasing hunting pressure on mammoth by modern humans was the main reason for this, since so far no significant environmental changes on terrestrial ecosystems could be observed in NW Europe.

This study indicates that no distinct ecological change happened through the time of the last Neandertals, even during colder phases of the OIS 3. Potential ecological reasons could not be served as arguments for Neandertal extinction in NW Europe. With the capture of the area by representants of the Aurignacian the mammoth steppe ecosystem started to show evidences for stress, in this case at least partly independently of environmental fluctuations.

Zusammenfassung

Diese Arbeit untersucht durch die Analyse stabiler Isotope ($\delta^{13}C$, $\delta^{15}N$ und $\delta^{34}S$) in Knochenkollagen ökologische Aspekte der Mammutsteppe in NW Europa mit einem besonderen Augenmerk auf die Rolle der späten Neandertaler und frühen modernen Menschen.

In der Zeit, als die Neandertaler ausstarben und die modernen Menschen in NW Europa eintrafen, lebte eine umfangreiche Säugetiergemeinschaft aus Pflanzenfressern und Fleischfressern in kalten, fluktuierenden Umweltbedingungen in dieser Gegend. An dieser Stelle wird die ökologische Robustizität des vergangenen Ökosystems sowohl in Bezug auf die Auswirkungen oszillierender Klimabedingungen, als auch in Anbetracht der ökologischen Partizipation der Neandertaler und frühen moderner Menschen rekonstruiert. Die Trophieebenen, die Nischen Partitionierung, die ökologische Flexibilität einzelner Arten, als auch die grundsätzliche Bufferkapazität dieser Biozönose sind Forschungsgegenstand dieser Arbeit.

Die belgische Fundstelle Troisième caverne of Goyet bietet ein breites Ensemble an direkt datierten späten Neandertalern und sehr frühen modernen Menschen. Die Anwesenheit von Skelettresten des Neandertalers und früher moderner Menschen an einem Ort sind einmalige Umstände und erlauben einen direkten Vergleich verschiedener ökologischer Aspekte in einer Phase von besonderer Relevanz im Zusammenhang mit der menschlichen Evolution.

Die Fundstelle Ziegeleigrube Coenen ist zeitgleich mit der Anwesenheit des späten Neandertalers und reflektiert das Ökosystem während oder kurz nach einer Kaltphase. Auch in solchen Kaltphasen war die Struktur des Mammutsteppenökosystems intakt, so dass die Subsistenzgrundlage der späten Neandertaler gesichert war. In keinem ökologischen Kontext der chronologisch mit der Anwesenheit der späten Neandertaler zusammen fällt, ist in der Struktur des Ökosystems Stress festgestellt worden.

Durch die Analyse der $\delta^{13}C$ $\delta^{15}N$ Isotopenzusammensetzungen des Knochenkollagens von Tieren und Hominiden konnten die verschiedenen Trophieebenen evaluiert werden. Die Verarbeitung der Ergebnisse durch unterschiedliche statistische Verfahren hat es ermöglicht, die ökologische Nische der späten Neandertaler und der frühen modernen Menschen zu beschreiben. Beide Menschenformen besetzten die Gleiche, eindeutige ökologische Nische in Bezug auf ihre Ernährung. Sie favorisierten das Mammut und das Rentier als Hauptbeutetiere.

Die Untersuchung der $\delta^{34}S$ Isotopenzusammensetzung ist eine relative neue Herangehensweise und bot Einblicke in räumliche Aspekte der

Beschaffungsstrategien der Hominiden. Die Goyet Neandertaler reflektieren nicht das δ^{34}S Signal der lokalen Fauna, dem zu Folge hatte der wesentliche Anteil ihrer Jagdbeute eine Herkunft nicht aus der näheren Umgebung der Fundstellen Scladina, Spy und Goyet. Die ist im Gegensatz zu den Neandertalern von Spy und den frühen modernen Menschen von Goyet. Beide Gruppen lieferten Werte, die mit denen der lokalen Fauna korrespondieren. Es wird das Szenario eröffnet, in dem die Raumnutzung der Hominiden unterschiedlich ist, dabei aber die gleichen Beutetiere bevorzug werden.

Die Fundstelle Lommersum reflektiert das Ökosystem in einer anfänglichen Phase der Besiedlung durch den modernen Menschen, als die Neandertaler bereits ausgestorben waren. In dieser Epoche ist ein ökologischer Stress auf die regionalen Mammutpopulationen zu diagnostizieren, so dass in bestimmten Regionen in Europa das Pferd sich in Richtung der ökologischen Nische des Mammuts orientiert kann. Hier ist argumentiert, dass erhöhter Jagddruck auf die Mammute durch den modernen Menschen der Grund für dieses Phänomen sei. Klimatische Faktoren können jedenfalls für den ökologischen Stress, dem das Mammut offensichtlich ausgesetzt war, zu dieser Zeit nicht belegt werden.

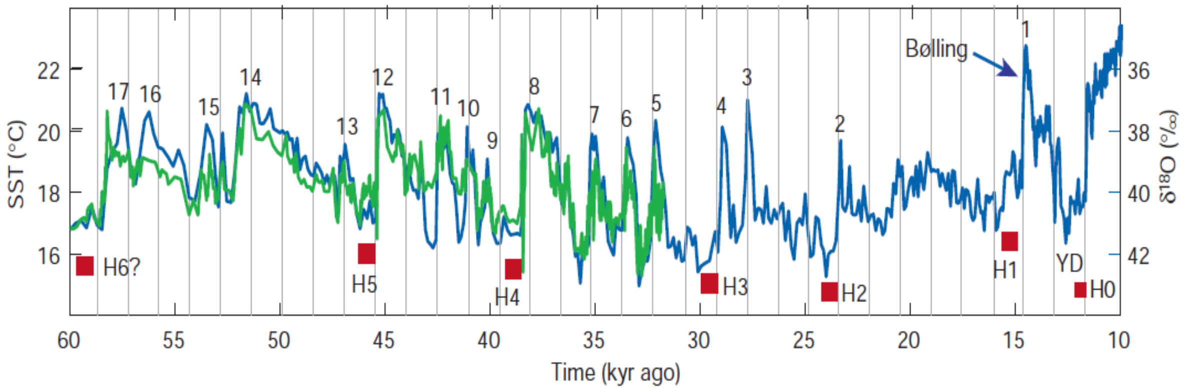
Die Studie veranschaulicht, dass es in der Zeit der letzten Neandertaler, auch während kälteren Phasen des OIS 3, keine eindeutigen ökologischen Veränderungen in der Zusammensetzung und Struktur des terrestrischen Ökosystems in NW Europa gegeben hat. Potentielle ökologische Gründe können nicht herangezogen werden im Kontext des Aussterbens der Neandertaler in NW Europa. Erst mit der Besiedlung durch Menschen des Aurignaciens sind eindeutige Belege für ökologischen Stress des Mammutsteppenökosystems festzustellen, in diesem Fall zumindest teilweise auch unabhängig von Umweltveränderungen.

1. Introduction

1.1. Climatological conditions in Europe

The climatic and environmental conditions in the last ice age (Marine Isotope Stages (MIS) 4, 3 and 2, 73.5–14.7 ka BP,) are complex. The late Pleistocene in Central Europe is not simply a cold stage: the general climatic character can be described by intensive and strong reproducible climatic oscillations from cold stadials to more moderate interstadials. Abrupt warmings with temperatures increasing by 8-16 °C in a few dozen of years (known as Dansgaard–Oeschger (DO) events) can be traced in the Greenland $\delta^{18}O_{ice}$ record (Cacho et al., 1999; Dansgaard et al., 1993). Each DO event was followed by several centuries of gradual cooling, before the temperature dropped sharply back to complete stadial values (Huber et al., 2006; Svensson et al., 2008). Twenty five of these events are documented in the Greenland ice cores in the whole ice age while 15 occurred during MIS 3 around 60-27,000 ka BP.(Van Meerbeeck et al., 2011).

Figure 1



(Rahmsdorf, 2002)

Temperature reconstructions from ocean sediments and Greenland ice

-Proxy data from Atlantic (green) and from the Greenland ice core (blue)

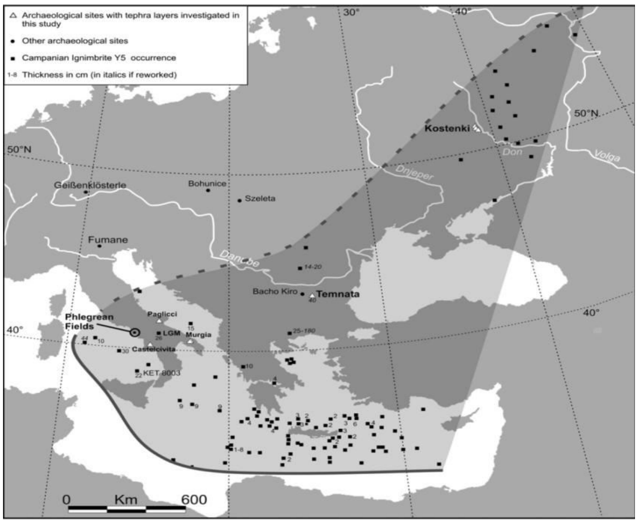
-Dansgaard–Oeschger (D/O) warm events (numbered).

The long lasting DO events were preceded by massive ice flow surges from the northern ice sheets, documented by debris deposits at the North Atlantic floor around the Hudson Strait.

These occasions known as Heinrich (H) events 1 to 6 (Hemming, 2004; Svensson et al., 2008) represent cold spells on the northern hemisphere (Figure 1, red squares). In the context of this study, the potential impacts of such cold spells on the biota are of special interest.

Besides the mentioned repeating climatic oscillations from cold stadials to more interstadial conditions, the environment around 39,000 years in Europe was certainly driven by other mega events as well: The volcanic eruption in the Phlegrean Field (NW of Neaple in Italy) producing the Campanian Ignimbrite (CI)/Y-5 tephra surely impacted the ecosystem. The distal ash fall/rain of CI tephra was widely spread from its source eastward over the Balkans and Black Sea to the Russian plain more than 2200 km distant, and over 1000 km southward to the north African coast (Fedele et al., 2002; Fitzsimmons et al., 2013). Tephra deposits indicate two distinct plume forming phases, Plinian and co-ignimbrite, characteristic of many caldera-forming eruptions (Marti et al., 2016). The total volume of extruded magma is estimated around 300 km^3. The minimum area covered by pyroclastic currents is estimated around 30,000 km^2, while the minimum area directly affected by ash fallout is around 5,000,000 km^2 (Figure 2).

Figure 2



Area covered by Campanian Ignimbrite fallout (Giaccio et al., 2008)

The extensive ash deposits can be recognized as the product of the largest volcanic eruption during the past 200,000 years in the Greater Mediterranean area. This event coincides with the onset of the abrupt cooling Heinrich 4 event. Therefore the scenario of a “volcanic winter” at least in certain areas of Eastern Europe can be assumed (Fedele et al., 2003).

Another global event 40,400 ± 2,000 ka years before present was the Laschamp event (Guillou et al., 2004). The Laschamp event was a complete geomagnetic field reverse, a period during which the magnetic field was reversed for a brief time, but could not generate a stable polarity. Instead, the geomagnetic orientation returned to its former orientation (Valet and Valladas, 2010).

The geomagnetic field excursion can be characterized through a considerably reduced shielding efficiency of the magnetosphere caused by a general weaker distinct magnetic field. As one consequence the earth was more exposed to high energy particle of cosmic and solar origin (Valet and Valladas, 2010). Indeed, the decreased magnetic field intensity caused significantly depletion of ozone in the upper part of the atmosphere. Less ozone caused an increasing UV-B radiation on earth surface (Norval et al., 2007; Valet and Valladas, 2010). This is critical, since UV-B radiation impacts most of the species of the mammal biota directly: Skin cancer (malignancy), Non-melanoma skin carcinomas, acute or long-term damage of the eye and soft tissues including pterygium and cataract and other diseases (Norval et al., 2007) are only some of the potential sanitary risks connected with the Laschamp geomagnetic event.

To conclude, the climatic conditions around 40,000 years BP were complex because of their unstable character. The impact of three mega-events as essential driving factors at this time is still only scarcely understood. The Campanian Ignimbrite eruption, the Heinrich 4 event and the Laschamp geomagnetic event fall relatively close to each other and may have interfered and amplified or compensated each other on a certain level (Fedele et al., 2003).

1.2. Ecological context in Europe

The predominant ecosystem in Europe around 40,000 years ago was the mammoth steppe. This ecozone extended from southwestern Europe until Alaska and was the biggest terrestrial ecosystems around 100,000 to 12,000 years ago. The extinct ecosystem can be characterized through a large community of species which were part of this biome. The extinct mega-herbivorous species (weighing more than 1 ton) like woolly mammoth (*Mammuthus Primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) are surely some of the most typical herbivorous species, but other members of the herbivorous guild like bison (*Bison priscus*), muskox (*Ovibos moschatus*), horse (*Equus ferus*), reindeer (*Rangifer tranadus*) and red deer (*Cervus elaphus*) as well as giant deer (*Megaloceros giganteus*) were part of the mammoth steppe. Also various large predators like the cave lion (*Panthera leo spelaea),* the cave hyena *(Crocuta crocuta spelaea*), wolves (*Canis lupus*) and omnivorous species like the cave bear (*Ursus spelaeus*) and the brown bear (*Ursus arctos*) were characteristic faunal species of this environment. The ecological structure of the mammoth fauna was similar to that of recent faunal communities in the African savannas (Vereshchagin and Baryshnikov, 1992). Most of the extant representants of the mammoth steppe now inhabiting geographically and ecologically distinct natural zones (Pavelkova Ricankova et al., 2014) e.g. the reindeer and muskox, are habitants of subarctic regions, while bison and wolf are recently members of the temperate grass land and forests ecosystems, the horse and saiga antelope (*Saiga tatarica*) in arid steppe environments and the lion and hyena in tropical savanna ecosystems. The reason for such a peculiar mammalian community is probably associated with the unique environmental conditions of the Last Glacial (corresponding to the Weichsel Glaciation) ecosystem (Guthrie, 2001; Stewart, 2008). The non-analogous ecosystem evolved in a dry and cold climate, which is regarded to provide a highly heterogeneous vegetation and mosaic like landscape on a regional scale but not from a continental perspective (Pavelkova Ricankova et al., 2014). This ecosystem covered wide areas of the Northern hemisphere for approximately 100,000 years without major changes and became relatively quickly extinct around 12,000 years before present (Stuart, 2015; Stuart and Lister, 2007; Zimov et al., 2012).

1.3. Hominids in Europe around 40,000 years ago

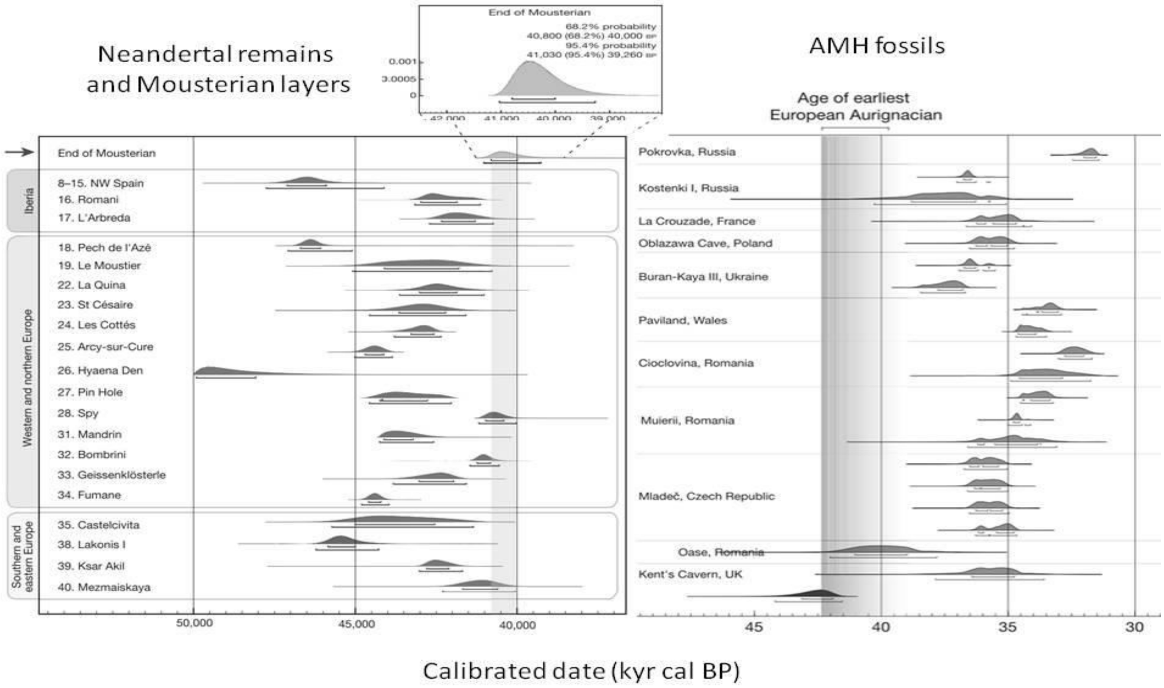
At around 40,000 years ago at least two types of hominins inhabited Europe: the anatomically modern humans (*Homo sapiens*) and the Neandertals (*Homo neanderthalensis*). The Neandertals became extinct approximately 40,000 ago while the anatomically modern humans (AMH) appeared around this time in Europe (Higham et al., 2014; Hublin, 2015; Nigst et al., 2014). The exact timing and spatial disappearance of the Neandertals and the potential chronology of overlapping with the earliest arrival of AMH in Europe are essential question in the field of paleoanthropology (Conard and Bolus, 2003; Conard and Bolus, 2008, 2015; Higham et al., 2011; Higham et al., 2014; Mellars, 2006, 2011). The investigation of spatial and chronological aspects of the replacement of Neandertals by AMHs can provide important insights in a period in which essential aspects of the cultural evolution of AMH evolved considerably (Conard and Bolus, 2003; Conard et al., 2009).

The spread of fully modern behavior (like complex symbolic behavior) demonstrated in complex technologies (like intensive occurrence of organic artifact, musical instruments, distinct stone tool technology) and symbolic communication (seen e.g. in figurative art and ivory jewelry, cave art…), falls in the time range of the arrival of the AMHs and the extinction of the Neandertals (Benazzi et al., 2015; Conard and Bolus, 2015; Higham et al., 2014). The cultural modernity is initially and essentially associated with the stone stool techno complex Aurignacian (Conard and Bolus, 2003) (and possibly other early Upper Paleolithic techno-complexes like the Uluzzian (Benazzi et al., 2015; Zilhao et al., 2015)) which is supposed to be produced by modern humans and not the other possible candidate, the Neandertal (Churchill and Smith, 2000).

But one aspect which has to be considered is the very limited number of AMHs directly dated from the early Upper Paleolithic (UP) (40-28.5 ka BP) across Europe. Most of the specimens were discovered in Eastern Europe, Russia or at the periphery of geographical Europe (Fig.3). It seems the treatment of dead bodies of the “Aurignacian members” was different from later periods like in the Gravettian, so that burial are not known: So far only around one dozen sites in total provided human remains directly dated between 40-28.5 ka BP and most of them are not associated with a diagnostic stone tool techno complex, a clear Upper Paleolithic (UP) inventory, or are excavated at an initial stage of the scientific research without valid stratigraphic attribution (see e.g. Higham et al., 2011) (Figure 3). The Earliest Phase of the Aurignacian has not provided associated human fossils without serious dispute.

Anyhow, final proofs that hominid taxa and lithic cultures, like the Aurignacian, are always related to each other are missing. For example the association of AMH fossils and Middle Paleolithic Mousterian artifacts in the Near East (Qafzeh) (Schwarcz et al., 1988) and North Africa (Taramsa) (Vermeersch et al., 1998), demonstrate the contrast. Also the other way around, an association of Neandertal remains and features supposed to be typical “cultural modern” (see above) occur e.g. in Saint-Césaire and Grotte du Renne (Hublin et al., 1996; Hublin et al., 2012).

Figure 3



Modified after Higham et al., 2011; 2014

End of the Mousterian, the beginning of the Aurignacian and earliest AMH in Europe

But what is certainly providing arguments in the discussion about the transition Middle Paleolithic to Upper Paleolithic (MP-UP) is the possibility that the European Mousterian was, until the very late phase the product of Neandertal cultural behavior: Only Neandertal remains could be discovered in a European MP archeological record, and so far never AMHs. On the other site in UP industries at least from Aurignacian times onward, no Neandertal remains but only AMHs were discovered. This supports my hypothesis that the cultural transition from Middle-to-Upper

Paleolithic in Europe corresponds to a change in hominid type as well. In this study I assume the cultural definition of Middle Paleolithic (MP) is carried by Neandertals, as is the Upper Paleolithic (UP) by anatomically modern humans.

The Mousterian always underlays the Aurignacian and is therefore older at least in all places where both industries occur together. A number of regionally diverse, stratigraphically intermediate technocomplexes, so-called “transitional” are defined by the presence of some key components of the so-called “Upper Paleolithic package” (e.g., specific aspects of stone tool technology, objects of personal ornamentation, bone tools…). These records may shed light in the discussion on potential meetings and potential exchange of cultural and genetic information of both species in Europe (Banks et al., 2008; Benazzi et al., 2015; d’Errico et al., 1998; Finlayson et al., 2004; Zilhão, 2006; Zilhão and d’Errico, 1999).

A direct interaction of both types of hominids is hard to prove based only on the archeological records, but recently more and more details of ancestral relationships between AMH and Neandertals appeared, based on genetic information: Both species (sub-?) species were able to interbreed successfully and have fertile progenies around 40,000 years before present, at least in Eastern Europe (Fu et al., 2015). A direct contact between Neandertals and AMH is therefore given in the broader area of this study. The genetic interrelations among different late Pleistocene hominins are drawing complex pictures with more participants than Neandertals and AMH: The Denisova Cave in Siberia first excavated in 2008 yielded fossil material of a hominid that shares a common ancestor with AMH and Neandertals about 1.0 million years ago based on mtDNA results (Krause et al., 2010) and represents another type of hominid in the late Pleistocene. The final pylogenetic relation of Neandertal and AMH is still part of the current research but not of this study (White et al., 2014; Wood and Lonergan, 2008).

In Central Europe the Neandertals are commonly regarded as typical Pleistocene European hominins and Europe is generally considered as their area of origin (Stringer and Hublin, 1999). Neandertals ranged from Iberia to Russia and from the Mediterranean area to Northern Europe, but beside this “core” area, Neandertal remains were also discovered in Central Asia and Siberia (Krause et al., 2007). Especially Central and West Europe had a relatively long and separate hominid evolution for around 400,000 years and the substitute hominid was the Neandertal

(Hublin, 2015; Stringer and Hublin, 1999). The AMH originated in Africa and migrated through the Levant into Europe (Hershkovitz et al., 2015), while Neandertals became extinct around the same time (Higham et al., 2014; Nigst et al., 2014).

Potential reasons for the downfall of the Neandertals and the success of the AMH are part of the current research. Two main directions are recognizable: first, one which discusses features which are species inherent, like biological and cultural/behavioral aspects (Agustí and Rubio-Campillo, 2016; Banks et al., 2008; Conard and Bolus, 2003; Finlayson et al., 2004; Gilpin et al., 2016); while the other argues external causes (climatic reasons, volcanic eruptions, Laschamp event) forced the Neandertals to extinction (d'Errico and Sánchez Goñi, 2003; Müller et al., 2011; Tzedakis et al., 2007).

Dietary strategies and the related cognitive abilities can provide insights into potential factors in the Neandertal extinction (Bocherens and Drucker, 2006; d'Errico and Sánchez Goñi, 2004; Finlayson et al., 2004; Naito et al., 2014; Naito et al., 2016; Wißing et al., 2015b). In this context several approaches were conducted to reconstruct Neandertal diet, e.g. zooarchaeology (Dusseldorp, 2010; Gaudzinski-Windheuser and Kindler, 2012; Germonpré et al., 2014; Palkopoulou et al., 2016), dental calculus analysis (Hardy et al., 2012; Henry et al., 2011; Henry et al., 2014), dental microwear patterns (Harvati et al., 2013; Pérez-Pérez et al., 2003) and lithic use-wear and residue analysis (Hardy and Moncel, 2011). Furthermore what remains in this dispute, is the role of small mammals or bird and the significance of fresh and/or marine resource exploration in Neandertals and early AMHs diet (Finlayson et al., 2012; Hardy and Moncel, 2011; Pettitt et al., 2003; Richards et al., 2005; Richards et al., 2001; Richards and Trinkaus, 2009). In most of the studies it is hypothesized that Neandertals were limited in their dietary spectrum in comparison to early AMH; this is regarded as one potential reason for the success of AMHs and the demise of the Neandertals.

1.4. Principles of isotopic tracking in a Pleistocene context

In the late Pleistocene context of Europe, the application of stable isotopes for the investigation of ecological aspects increased significantly over the last decades. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio values in bone collagen became an important tool to decipher dietary preferences and niche partitioning among herbivorous and carnivorous species (incl. hominids) (Bocherens, 2015; Bocherens et al., 2015; Bocherens et al., 1991; Fizet et al., 1995; Krajcarz et al., 2016; Naito et al., 2016; Wißing et al., 2015b) and to gain insights into habitat characteristics (Drucker et al., 2008) of key members of the late Pleistocene ecosystem in Europe. The investigation of sulfur isotopic composition in Pleistocene bone collagen is a relatively recent approach. The sulfur isotopic composition ($\delta^{34}S$) in collagen provides insights into the individual's origin and the mobility of single specimens (Drucker et al., 2012; Nehlich, 2015; Nehlich and Richards, 2009) and therefore increased the knowledge of mobility patterns and land use strategies.

The carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) isotope values in terrestrial mammal bone collagen reflect an average of the protein source in the diet of the last years of an individual (DeNiro and Epstein, 1978, 1981; Drucker et al., 2012; Kurle et al., 2014; Nehlich and Richards, 2009). At the bottom of the foodweb the plant isotopic composition differs due to physical and chemical fractionation processes. These fractionation processes are driven by factors such as temperature, water availability, CO_2 concentration, nitrogen disposability for plants, salinity, irradiance and geological background (Farquhar et al., 1989; Minagawa and Wada, 1984). The isotopic signal is reflected through the whole foodweb, from plants to herbivorous and omnivorous species up to carnivores. An essential feature in dietary reconstruction is the enrichment of $\delta^{13}C$ and $\delta^{15}N$ from one trophic level to the next one. $\delta^{13}C$ becomes only slightly enriched with a shift of 0.8-1.3 ‰ between herbivores and carnivores (Bocherens and Drucker, 2003), but reflects therefore habitat information: Since all plants in the mammoth steppe ecosystem used the C3 photosynthesis pathway, the $\delta^{13}C$ ratio provides insights in the general structure of the habitat: an open vs. close landscape (canopy effect) (Drucker et al., 2008) and the role of grass/forbs vs. shrubs in herbivorous species diet (Drucker et al., 2010). Besides habitat aspects

$\delta^{13}C$ ratio can test the significance of meat in omnivorous diet (Hobson et al., 2000), as well as estimate especially quantitative aspects of meat of different prey species in carnivore diet (Bocherens, 2015).

The ^{15}N enrichment is much more intense in contrast to ^{13}C and occurs around 3-5 ‰ from herbivorous to carnivorous species. Therefore the nitrogen isotopic composition allows the reconstruction of different trophic level at a given time and place in the mammoth steppe ecosystem (Ambrose, 1991; Bocherens, 2003; DeNiro and Epstein, 1981).

2. Objectives

This study investigates the late Pleistocene Mammothsteppe ecosystem in NW Europe through the investigation of stable isotopes in faunal and hominid remains. The general objective of the project is to reconstruct the late Pleistocene trophic web and to place the hominins (Neandertals and AMHs) within this framework. Therefore the vulnerability and robustness of the whole ecosystem as well as the investigation of the potential ecological flexibility of single species is part of the study.

The ecological structure in context of fluctuating environmental conditions is one essential part of this study: Since the late Pleistocene has seen dramatic environmental changes in terms of temperature and aridity the aspect of potential impact of these fluctuations on the ecosystem and basically the foodweb is going to be investigated. Especially around the time of the replacement of the Neandertals by AMHs the climatic oscillations were quite distinct. If the general structure of the ecosystem was somehow stressed in the way that species changed their ecology, the climatic aspect played an essential role, probably not only in the Neandertal extinction process. If the structure of the biocenosis was stable and robust enough to be kept under harsher environmental conditions, other reasons may play a more important role in replacement scenarios of Neandertals by AMHs.

After evaluating the impact of environmental changes on the ecosystem, it is needed to test the potential impact of both types of hominids on the structure of the ecosystem. Was the ecology sustainable for both types of hominids, or are there any indications that this was not the case? Became the ecosystem somehow different before and after Neandertal extinction?

After testing the impact of climatic fluctuations and humans on the ecosystem another main objective is to evaluate and describe, through innovative statistical isotope data handling (e.g. Bayesian modeling), the ecological niche partitioning among the key members of the ecosystem. Only then the role of both types of hominids can be evaluated adequately: Each species in general occupied a specific ecological niche in terms of diet and habitat which is represented fundamentally in their stable isotopic composition of the collagen. The niche partitioning of the herbivorous guild as well as the trophic position for particular omnivorous and carnivorous species is reconstructed through stable isotopic compositions in fossil remains. Among the predators in this ecosystem one important aspect is to uncover potential prey preferences, and establishing statistical models of niche partitioning in the predator guild with a focus on both types of hominids. A much more precise qualitative and eminently quantitative estimation of preferred prey through statistical models will allow reconstructing a detailed hominid ecology. Is it possible to determine ecological differences among Neandertals and early AMH which could indicate arguments for the downfall of one of them and the success of the other? Did AMHs behave differently than late Neandertals in terms of dietary and habitat ecology?

3. Material

All sites provided faunal and/or human remains with an age between around 30,000 and 40,000 years. The sites are situated in Central NW-Europe; their maximum distance to each other is around 180km. These sites are essentially Spy, Scladina and Goyet in the Meuse Valley, in Belgium as well as the site Ziegeleigrube Coenen and Lommersum in Germany.

Figure 4

Map of the sites investigated for this study (red dots)

3.1. Ziegeleigrube Coenen

The paleontological loess site Ziegeleigrube Coenen (ZC), district Düren, province Nordrhein Westfalen in Germany (Figure 4), has been reinvestigated between 2009 and 2014 (Matzerath et al., 2014; Matzerath et al., 2012). The stable isotopic results are presented in Wißing et al. (2015a). The faunal remains were collected during 1964, 1967 and 1969 in the clay quarry and as one consequence of this “by chance collecting strategy” the assemblage is considered to be not complete (Matzerath et al., 2012). The paleontological remains consist of seven species of megafauna*:* *Equus sp., Bos/Bison, Coelodonta antiquitatis, Megaloceros giganteus, Mammuthus* *primigenius, Crocuta spelaea* and *Panthera spelaea*. The material is stored and cataloged at the Museum Zitadelle in Jülich.

Earlier AMS radiocarbon analysis (Matzerath et al., 2012) placed ZC in MIS 3, with ages falling between 34 and 43 ^{14}C ka BP. Two additional ages were beyond the limit of the radiocarbon method.

In 1969 Hartwig Löhr also described two stone artifacts which are missing nowadays and no further record is done to validate the potential artifacts. Other potential indications of human activity being two bones displaying modifications, possibly produced during marrow procurement (horse, *Equus sp*., ZC-101 and a large bovid, Bos/Bison,ZC-95: Matzerath et al., 2012, 2014). Taken together at this stage the site cannot be classified unequivocally as “archeological.”

The original find horizon was removed during quarrying activities. However, Matzerath et al. (2014) were able to reconstruct the sequence by comparing profile drawings sketched by W. Krieger, H. Löhr and J. Schalich in 1964 and 1969 with a section opened 100m to the east of the place where the faunal remains have been found in the layer (Matzerath et al., 2014). The sediment in which the faunal remains were embedded was stratified in a sequence of loess deposits some 5.50m below the surface. The remains had been deposited in the gravel and sand infill of a small channel, some 30 cm deep (Matzerath et al., 2014).

3.2. *The “Troisième caverne”* of Goyet

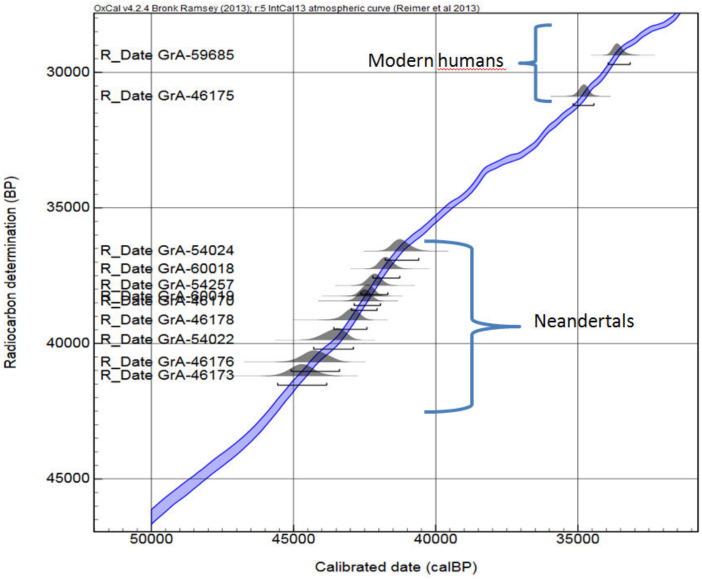
The Rocher de Goyet is located within a limestone massif above the Samson river, a tributary of the Meuse River in the Mozet Commune in the Walloon Region in Belgium (Figure 4). The Goyet site consists out of several caves. In this study all the (sub-) fossil remains came from the “Troisième caverne” of Goyet. Most of the cave sediment was excavated at an early stage of the research by Edouard Dupont in 1868 (Dupont, 1872). Appropriate simplistic are the information about the stratigraphical conditions at the site, following the state of the art at this time. Most of the archaeological material he collected came from 3 of the 5 “fauna-bearing levels” of the 3rd cave. The archeological material was believed to belong to a single archeological cultural group called the “Goyet type”, despite the fact the artifacts came from multiple layers (Di Modica et al., 2016; Dupont, 1872). The presence of human remains was already at least partly published, by Dupont (1872), but Neandertal bones were not identified till 2004 (Rougier et al., 2012; Wißing et al., 2015b). At this point AMH remains could be discovered from all periods of the UP (Rougier et al., 2013). All human and faunal material is hosted in the Royal Belgian Institute of Natural Sciences in Brussels.

Not only the ongoing dating program demonstrated, that each of the five "layers" contains material from different periods, also former studies demonstrated this (Germonpré, 1997; Germonpré and Sablin, 2001; Stevens et al., 2009a). Anyhow the site generated probably one of the richest archeological and anthropological record in the broader geographical area containing several MP and UP industries (Mousterian, Lincombian-Ranisian-Jerzmanowician, Aurignacian, Gravettian, Magdalenian), including a considerable faunal assemblage (Comeyne, 2013; Di Modica et al., 2016; Flas, 2011; Flas, 2015; Otte and Noiret, 2007; Pirson et al., 2012). The stable isotope analysis of Neandertals and AMHs were performed by Wißing et al. (2015b; in prep). 20 hominid specimens are part of this study: 18 Neandertal remains and two AMHs.

The Neandertal remains represent at least five individuals, with four adults represented by four right tibias, and one child represented by a single tooth (Rougier et al., accepted). The tooth was not sampled for stable isotope analysis since it would have been almost entirely destroyed in the process; the four tibias (tibia III represented by specimen Q305-7, tibia IV by Q55-4, tibia V by Q374a-1, and tibia VI by Q57-3) were analyzed. Most of the Neandertal remains are directly dated (Wißing et al., 2015b) and the uncalibrated ^{14}C-ages span between 36,590 + 300, -270 (GrA-54024) and 41,200 + 500, -410 ^{14}C BP (GrA-46173) (Figure 5) with the exception of one Neandertal specimen 2878-2D, dating unexpectedly young, 32,190 ^{14}C BP (GrA-54028). This might be possible due to undetected contamination caused through varnishing. The 2878-2D tooth was part of the samples identified as human by E. Dupont and although we cannot rule out that it was varnished like several other human remains detected while excavating the site. All recently detected hominid remains are not varnished. We consider this date as not valid and exclude it from the discussion.

The two AMH individuals date approximately between 29,370 (GrA-59685) and 30,880 (GrA-46175) ^{14}C uncal. BP (Posth et al., 2016, Rougier et al., accepted) and are clearly younger than the Neandertals (Figure 5). Beside the morphological attribution (Rougier et al., accepted)(Rougier et al., in prep.) mtDNA analysis confirmed the attribution of Neandertals and the presented AMH remains to their specific type of hominid (Posth et al., 2016)

Figure 5



Calibrated dates for Goyet Neandertals and modern humans (modified after Wißing et al in prep.)

The majority of the Neandertal remains have been analysed for stable carbon and nitrogen isotopic composition in the study by Wißing et al. (2015b). Another study in preparation (Wißing et al., in prep.) presents stable carbon, nitrogen and sulfur isotopic data of the two oldest modern humans from the site as well as additionally six Neandertal remains investigated for carbon and nitrogen collagen isotopic composition. The sulfur isotopic results of all Neandertals and AMHs are part of the study in preparation (Wißing et al. in prep.).

The Goyet faunal remains integrated in this study (N=57) have a clear pre-Last Glacial Maximum (LGM) age between around 30,000 and 42,000 years ago, this was either confirmed by direct ^{14}C dates of the remains, by the species composition itself and/or through an ecological approach (Bocherens et al., 2011a). Most of the carbon and nitrogen stable isotopes of the faunal remains have been published by Bocherens et al. (2011). All δ^{34}S faunal values (N=24) are part of this study and are gained on the collagen the δ^{13}C and δ^{15}N values have been measured on (Wißing et al. in prep).

3.3. Spy Cave

The site is one of the richest Palaeolithic stations in Belgium. The small cave is located in the Ardennes, close to the Meuse valley (Figure 4). The Spy cave lies on the left bank of the Orneau, a tributary of the Sambre. In 1885 two Neandertal skeletons were discovered by M. De Puydt and M. Lohest (Semal et al., 2009). All human and faunal material is hosted in the Royal Belgian Institute of Natural Sciences in Brussels. The Neandertal remains from individual Spy I and II have been investigated for carbon and nitrogen stable isotopic composition in the past (Bocherens et al., 2013). These results have been broader contextualized here. In the context of the attached manuscript the carbon and nitrogen isotopic composition of the Spy child (Spy IV), discovered some years ago while examining the collection (Crevecoeur et al., 2010) are presented and discussed. Additionally the sulfur isotopic composition of individuals Spy I and Spy VI (Spy 94a and Spy 646a) are performed for this study. The remains of individual Spy I date approximately 35,810 C^{14} yr BP (GrA-32623), the ones from individual Spy II 33,940 C^{14} yr BP (GrA-32630) and the ones from Spy IV, the child, 32,970 C^{14} yr BP (GrA-32627) (Crevecoeur et al., 2010; Semal et al., 2009). The Spy Neandertals represent the youngest Neandertals in Europe (Higham et al., 2014; Semal et al., 2013; Semal et al., 2009).

This study also integrates carbon and nitrogen values of directly dated faunal remains (N = 8) from the Spy cave (Semal et al., 2013; Semal et al., 2009), the stable isotopic composition was published by Bocherens et al. (2013) and Wißing et al. (2015b). All measurements have been performed on the same collagen.

3.4. Scladina Cave

The Scladina cave site is located in the Condrioz region (commune of Andenne, province of Namur) south of the Sambre and Meuse valleys in Belgium. Scladina lies in a small valley adjacent to the Meuse River in the village Sclayn (Fig. 4). The site was discovered only in 1971 and is since 1978 the subject of still ongoing scientific excavation (Abrams et al., 2010; Bonjean et al., 2015). Scladina is a major occupation site of the Middle Paleolithic in NW Europe and was therefore classified as "*Site exceptionnel de Wallonie*" in 1996. Beside an extensive Late Pleistocene record (Pirson et al., 2006) associated with MP artifact ensembles (Abrams et al., 2013; Bonjean et al., 2015; Di Modica et al., 2016) remains of a Neandertal child were discovered in complex 4A (Toussaint et al., 1998). Anyhow these human remains are significantly older than remains of this study. The Neandertal dated around 86-88,000 BP (Bonjean et al., 2015).

In this study mammothsteppe faunal remains considered came from complex 1A which has an age around 40,000-37,000 ka BP (Bonjean et al., 2009; Pirson et al., 2012). This faunal assemblage is associated with a Mousterian stone tool techno complex (Pirson et al., 2012).

The carbon and nitrogen isotopic composition of a representative ensemble of herbivorous and carnivorous species was already performed in 1997 (Bocherens et al.). The considered species are woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), horse (*Equus ferus*), large bovids, i.e. aurochs (*Bos primigenius*) or steppe bison (*Bison priscus*), cave hyaena (*Crocuta crocuta*), brown bear (*Ursus arctos*) and cave bear (*Ursus spelaeus*)

The analysis of the sulfur isotopic composition is part of the current research study (Wißing et al., in prep) and discussed here. All measurements have been performed on the same collagen.

3.5. Lommersum

The open air site Lommersum is situated in a small valley in the foothills of the Eifel around 40 km southwest of Cologne, province Nordrhein-Westfalen (Figure 4). The site is one of the very rare open air Aurignacian sites in Germany (Hahn, 1989; Pastoors and Tafelmaier, 2012). For the northern parts of Central Europe, currently there are almost no sites with adequate quantities of well-preserved faunal remains dating to the early UP.

The site was discovered in 1969 and excavation took place from 1971 to 1974 as well as in 1977 and 1978 by Joachim Hahn. The results are published in a monograph (Hahn, 1989). The archeological horizon IIc is the most important one as it contains the highest artifact density as well as structures like a fireplace (Hahn, 1989). Among the faunal remains the most abundant species are the reindeer (*Rangifer tarandus*) and horse (Equus sp.), but also carnivores such as cave lion (*Panthera spelaea*), wolf (*Canis lupus*), wolverine *(Gulo Gulo)* and fox (*Alopex lagopus*) are represented as single specimens. Mammoth (*Mammuthus primigenius*) is only represented as worked ivory (Hahn, 1989). Latest AMS radiocarbon dates indicate an age between 32,250 ±500 and 35,100 ± 650 C^{14} yr BP (Matthies, 2012). The conventional ^{14}C dates from Lommersum initiated by Hahn span from 29,200±850 up to 33,420±500 C^{14} yr BP. Hahn discussed the age of layer IIc between 29,000 and 32,000 C^{14} yr BP (Hahn, 1989).

For my study I could sample 23 faunal specimens. Since polar fox is represented only through one premolar, it was decided not to samples this species. The same is true for the wolverine. This species is represented by one premolar and one phalange.

Successful stable isotopic carbon, nitrogen and sulfur values were obtained on collagen from reindeer, horse, wolf, cave lion and mammoth remains. All samples originated from layer IIc beside one horse (Equus sp.) (Lom-22) from complex IIb.

4 Methods

4.1. Collagen preparation and isotopic analysis

For each specimen a bone fragment between 200mg and 350mg was carefully sawn using a dremel rotating tool with a diamond-coated blade, after considerable photographic documentation of the specimen. Special care was taken to select only untreated bone.

In some cases the outer bone surfaces were mechanically before the samples were washed in an ultrasonic bath in acetone, rinsed several times with demineralized water, dried at 35 °C for 72 h and crushed to a powder of 0.7 mm grain size. All faunal samples were then measured for the carbon, nitrogen and sulfur content (%C,%N, %S) of the whole bone to generate information about the chemical preservation of the bones and the potential for collagen preservation. Fresh mammal bone contains in average 4% nitrogen, collagen extraction needs a nitrogen content of at least 0.4% nitrogen of the bone to gain collagen on which valid stable isotopes can be measured on. The measurements were performed using a Vario EL III elemental analyser using Sulfanilic acid from Merck as internal standard. The mean standard errors were better than 0.05% for %N.

The collagen was purified according to a well-established protocol (Bocherens et al., 1997; Longin, 1971). All isotopic measurements were performed at the Geochemical unit of the Department of Geosciences at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. Collagen preservation is given and follows general criteria considered for the chemical integrity of this protein (DeNiro, 1985). The chemical preservation of the collagen is expressed by the Ccoll/Ncoll atomic ratio. A range between 2.9 and 3.6 is considered to be suitable for further investigation (DeNiro, 1985), while the nitrogen contend of the collagen should be above 5% (Ambrose, 1990). All isotopic rations are expressed using the "δ" (delta) value as follows:

$\delta^{13}C=[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{reference}-1]x1000‰$

$\delta^{15}N=[(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)^{reference}-1]x1000‰$

$\delta^{34}S=[(^{34}S/^{32}S)_{sample}/(^{34}S/^{32}S)^{reference}-1]x1000‰$

The standard for $\delta^{13}C$ is the internationally defined marine carbonate V-PDB. For $\delta^{15}N$ the atmospheric nitrogen (AIR) is used. $\delta^{34}S$ samples were calibrated relative to international standards NBS 123, NBS 127, IAEA-S-1 and IAEA-S-3. Analytical error based on laboratory standards is ± 0.1 ‰ for $\delta^{13}C$ values, ± 0.2 ‰ for $\delta^{15}N$ results and ±0.4‰ for $\delta^{34}S$ measurements.

Only $\delta^{34}S$ values with atomic C/S_{coll} and N/S_{coll} ratios in the range of 300 to 900 and 100 to 300, respectively, were considered to be valid. (Bocherens et al., 2011b; Nehlich, 2015; Nehlich and Richards, 2009) while the sulfur contend is ranging between 0.13 and 0.24% in collagen. These criteria correspond to values observed on recent mammal collagen (Bocherens et al., 2011b) and fit the theoretical range established on amino acid sequences (Nehlich and Richards, 2009).

4.2. Statistical methods

4.2.1. Cluster analysis

For the identification of any potential pattern in the distribution of individual specimens across the species a cluster analysis based on δ^{15}N and δ^{13}C was performed. This was done using a Ward's minimum variance method with the software SAS JMP version 10. Each cluster represents specific ecological niche in terms diet for all representants regardless the species attribution.

4.2.2. Canonical discriminant analysis

To visualize and describe isotopic variation within and among different species a canonical discriminant analysis was established with the program SAS JMP version 10. This approach is helpful to describe the ecological flexibility of a given species, as well as to evaluate the isotopic distances among all species to each other. The analysis presents isotopic data of a given species in area which include

4.2.3. Bayesian mixing model

To estimate the relative meaning of each animal protein food source for the predators (incl AMHs and Neandertals) a Bayesian mixing model based on multiple isotopic values for multiple sources was applied: SIAR (Stable Isotope Analysis in R), which is a packet for the program R, version 3.0.2. (The-R-CoreTeam, 2013). This Bayesian mixing model has three essential characteristics (Parnell et al., 2010; Parnell et al., 2013):

Uncertainties into input data can be incorporated (standard derivation) as well as in the TEF (trophic enrichment factor). Second, the method provides the proportion densities in terms of probability. For example if a higher amount of a given source species is statistically more probable than a lower amount, in regard of the whole probability range for this source, or not. Third: Through the SIAR package it is possible to produce diagnostic matrix plots in which the statistical dependences between different protein sources are summarized. These correlations have either a negative or positive character. The SIAR software is taking into account these dependences among sources/prey species, which end up in an increasing total probability range. The meaning of this feature has not to be underestimated. In correspondence to several other studies the applied TEF was for +1.1 ± 0.2 ‰ and +3.8 ±1.1‰ for δ^{13}C and δ^{15}N values, respectively (Bocherens and Drucker, 2003; Bocherens et al., 2015; Fox-Dobbs et al., 2007).

Through this approach the consumption of animal protein can be overestimated in relation to the meaning of plant protein. The reason for this is a non-linear isotopic correlation between the most extreme end points of a pure vegetarian and a pure carnivorous feeding behavior: A very small amount of meat in an omnivorous diet would increase the δ^{15}N values of bone collagen extreme: an amount up to 50% plant food results in δ^{15}N values around not lower 1 standard deviation of the collagen of a pure carnivorous species (Bocherens, 2009b), therefore we consider the possibility that a significant amount of the diet could include plant material with low δ^{15}N values. And indeed, latest data imply significant amount of plant protein at least for the Spy Neandertals (Naito et al., 2016).

5 Isotopic results

5.1. Belgium sites

5.1.1. Hominids

All specimens fulfill requirements in their chemical conditions mentioned above for δ^{15}N and δ^{13}C. A detailed summary of chemical characteristic is provided in Table 1. For the Goyet Neandertal specimens the carbon content in collagen ranged between 29.5% (Q48-1) and 47.1% (Q305-4). The nitrogen content in collagen ranges from 10.1 (Q48-1) to 17.0% (Q376-1). The C/N ration in collagen is between 3.3 and 3.4. The conditions for sulfur stable isotopic values mentioned above were not fulfilled for all specimens. In all of these cases the % sulfur in collagen was above the accepted maximum of 0.26%, based on comparison with collagen extracted from fresh bones.

This was the case for Neandertal specimens: Q48-1, Q119-2, Q305-7, Q376-9, and Q376-25 (red in Table 1).

δ^{15}N and δ^{13}C

18 Neandertal specimens from Goyet as well as one individual from Spy represent the Neandertal material analysed for δ^{15}N and δ^{13}C, of this study (Wißing et al., 2015b, in prep). Additionally collagen of two ancient modern humans from Goyet was analysed for δ^{15}N and δ^{13}C (Wißing et al., in prep). The Goyet Neandertals specimens yielded mean δ^{13}C of -19.3‰ (s.d. 0.22‰) and 11.6‰ for δ^{15}N (s.d. 0.43‰). The Spy Neandertal individual yielded values of -19.8‰ for δ^{13}C and 12.5‰ for δ^{15}N (Wißing et al., 2015b, in prep.).

For the AMHs the δ^{13}C values of -19.1‰ yielded individual Q116 and -18.8‰ Q376-3. The δ^{15}N values are 10.9‰ for Q116-1 and 11.4‰ for Q376-3 (Wißing et al., in prep) (Table 1).

δ^{34}S

The δ^{34}S values for the AMHs are 8.6‰ (Q116-1) and 4.4‰ (Q376-3). The values for the Goyet Neandertals (N=11) span between 7.5‰ (Q305-4) and 11.6‰ (Q376-20) with a mean of 10.2‰. The δ^{34}S values for the Spy Neandertals are 3.6‰ for Spy 94a (Spy I) and 2.6‰ for Spy 646a (Spy IV) (Wißing et al., in prep.) (Table 1).

Table 1

ID	Species	Specimen	Dating ID	Date	%C_{coll}	%N_{coll}	C/N	δ^{13}C	δ^{15}N	%S coll (0.13-0.26)	atomic C/Scoll (300-900)	atomic N/Scoll (100-300)	δ^{34} S	References
Site: Goyet														
Q116-1	*Homo sapiens*	Lt humerus diaphysis frag.	GrA-46175	30,880 ± 170	45.6	16.3	3.3	19.1	10.9	0.14	867	266	8.64	1
Q376-3	*Homo sapiens*	Rt humerus diaphysis frag.	GrA-59685	29,370 +180 - 170	43.3	15.4	3.3	18.8	11.4	0.14	814	248	4.43	1
C5-1	*Homo neanderthalensis*	Parietal frag.	-	-	43.0	14.7	3.4	19.7	12.1	0.24	469	138	10.32	1,5
Q48-1	*Homo neanderthalensis*	Lt pubis frag.	-	-	29.5	10.1	3.4	19.6	11.3	2.1	37	11	11.5	1,5
Q53-4	*Homo neanderthalensis*	Rt humerus diaphysis frag. (humerus III)	GrA-54022	39,870 +400, - 350	42.9	15.1	3.3	19.0	11.7	0.19	603	182	9.72	1,2,5
Q55-1	*Homo neanderthalensis*	Lt clavicle frag.	GrA-54257	37,860 +350 - 310	36.9	12.9	3.3	19.2	11.3	0.19	522	157	9.80	1,2,5
Q55-4	*Homo neanderthalensis*	right tibia IV			39.6	14.0	3.3	19.2	11.6	0.24	443	134	11.41	1,2
Q56-1	*Homo neanderthalensis*	Rt femur diaphysis frag. (femur I)	GrA-46170	38,440 +340, - 300	45.4	15.5	3.4	19.5	11.5	0.15	807	236	9.22	1,2, 5
Q57-1	*Homo neanderthalensis*	Lt tibia diaphysis frag. (tibia II)	GrA-46173	41,200 +500, - 410	46.0	16.8	3.2	19.2	11.8	0.2	767	240	10.9	1,2, 5
Q57-2	*Homo neanderthalensis*	Rt femur diaphysis frag. (femur II)	GrA-54024	36,590 +300, - 270	42.7	15.0	3.3	19.1	11.9	0.23	496	149	10.78	1,2,5
Q57-3	*Homo neanderthalensis*	Rt tibia diaphysis frag. VI	GrA-60019	38.260 +350 - 310	43.8	15.4	3.3	19.6	11.2	0.17	693	209	10.88	1,2,5

Table 1

Q 119-2	*Homo neanderthalensis*	rib frag.	-	-	38.9	13.8	3.3	19.3	11.5	0.45	228	69	11.90	1,5
Q305-4	*Homo neanderthalensis*	Lt tibia diaphysis frag. (tibia I)	GrA-46176	40,690 +480, -400	47.1	16.7	3.3	19.4	10.7	0.16	785	239	7.50	1,2,5
Q305-7	*Homo neanderthalensis*	right tibia III	-	-	41.9	14.9	3.3	19.0	11.3	0.29	381	116	11.30	1,2,5
Q374a-1	*Homo neanderthalensis*	right tibia V	-	-	43.1	15.2	3.3	19.1	11.8	0.18	647	196	10.23	1,2,5
Q376-1	*Homo neanderthalensis*	Hand prox. phalanx 2-4	GrA-46178	39,140 +390, -340	46.7	17.0	3.2	19.2	10.9					2,5
Q376-20	*Homo neanderthalensis*	Rt humerus diaphysis frag. (humerus II)	GrA-60018	37,250 +320 -280	39.8	14.0	3.3	19.4	11.8	0.25	429	130	11.57	1,2,5
Q376-9	*Homo neanderthalensis*	Rib frag.	-	-	37.0	13.1	3.3	19.2	11.8	0.85	116	35	12.9	1,5
Q376-25	*Homo neanderthalensis*	Rib frag.	-	-	39.1	13.9	3.3	19.0	11.5	0.33	321	97	11.42	1,5
2878-2D	*Homo neanderthalensis*	Lower lt P4 (mandible 2878-8)	GrA-54028	32,190 +200, -190	41.4	14.4	3.4	19.0	12.5					1,5
Site: Spy														
Spy 94a (Spy I)	*Homo neanderthalensis*	R M3, maxilla frag. attached	GrA-32623	35810 +260, -240	43.7	15.2	3.4	19.4	11.4	0.16	728	217	3.60	1,3, 4
Spy 430a (Spy II)	*Homo neanderthalensis*	Right middle 3rd manual phalanx	GrA-32630	33940 +220, -210	46.8	15.8	3.5	20.3	10.8					3, 4
Spy 92b (Spy II)		Incisor	GrA-32626	36,350 +310/-280	47.1	16.7	3.3	19.8	10.9					3, 4
Spy 572a (Spy II)		Rt scapula	GrA-21546	31,810 +250/-250	41.5	14.4	3.4	19.8	11.0					3, 4
Spy II average					45.1	15.6	3.4	20.0	10.9					
Spy 646a (Neandertal child Spy IV)	*Homo neanderthalensis*	Right hemi-mandible	GrA-32627	32970 +200/-190	43.1	15.4	3.3	19.8	12.5	0.17	676	207	2.60	1, 6

References
1 = Wißing in prep.
2 = Wißing et al. 2015b
3 = Bocherens et al., 2013
4= Semal et al., 2013
5= Rougier et al., submitted
6= Crevecoeur et al., 2010

5.1.2. Faunal remains

The faunal δ^{34}S values from Goyet (N=27) span between -7.2 and 8.4‰ (mean 1.2‰/s.d. 4.1‰). The faunal δ^{34}S values from Scladina (N=23) range from -17.0‰ up to 11.8‰ (mean 2.4‰/s.d. 5.8‰). The δ^{34}S values from Spy horse provided a value of 5.5‰ (sample IV2A 4207) (Table 2). All δ^{34}S values are obtained on same collagen in Wißing et al. (in prep.). δ^{15}N and δ^{13}C data were processed by Bocherens et al. (1997, 2011a, 2013) and Wißing et al. (2015b).

Table 2

ID	Site	Species	Skeletal element	%Cc	%Nc	C/N	%Sc	C/Scoll	N/Scoll	$\delta^{34}S$	$\delta^{13}C$	$\delta^{15}N$	^{14}C-Age	Reference date	Reference for stab. Isotopes
Goyet-A2-7	Goyet	*Panthera spelaea*	*phalanx*	41.3	15.3	3.1					-18.5	8.4			1
Goyet-A3-1	Goyet	*Panthera spelaea*	*astragalus*	44.7	15.5	3.4	0.19	626	185	-2.1	-18.7	8.4			1,5
Goyet-B5-1	Goyet	*Panthera spelaea*	*humerus R*	38.2	13.6	3.3	0.16	629	192	0.6	-18.7	7.3			1,5
Goyet-B5-2	Goyet	*Panthera spelaea*	*humerus R*	34.8	11.7	3.5					-20.7	9.6			1
Goyet-B5-4	Goyet	*Panthera spelaea*	*humerus R*	28.2	10.0	3.3					-19.5	6.3			1
Goyet-A1-6	Goyet	*Crocuta crocuta*	*2nd metacarpus*	41.4	15.2	3.2	0.17	649	204	1.4	-19.7	9.5			1,5
Goyet-A3-5	Goyet	*Crocuta crocuta*	*3rd metatarsus*	44.3	15.5	3.3	0.18	644	192	1.4	-19.2	9.1			1,5
Goyet-A3-6	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.2	15.5	3.2	0.19	612	189	4.5	-19.6	9.4			1,5
Goyet-A3-7	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.8	16.0	3.2	0.17	679	213	2.6	-19.6	9.8			1,5
Goyet-A3-8	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.5	15.8	3.2	0.17	696	216	4.3	-19.4	9.0			1,5
Goyet-B4-1	Goyet	*Crocuta crocuta*	*humerus*	41.9	15.0	3.3					-19.8	7.7			1
SC1800	Scladina	*Crocuta crocuta*	*phalanx I*	42.9	15.6	3.2	0.18	636	198	4.3	-20.2	8.8			2,5
SC1900	Scladina	*Crocuta crocuta*	*phalanx I*	42.6	15.6	3.2	0.16	710	223	1.1	-19.6	10.1			2,5
SC2000	Scladina	*Crocuta crocuta*	*phalanx I*	42.8	15.7	3.2	0.16	713	224	0.1	-19.7	8.2			2,5
SC2100	Scladina	*Crocuta crocuta*	*phalanx I*	42.9	15.6	3.2					-19.4	9.5			2
SC1700	Scladina	*Crocuta crocuta*	*mandible*	39.9	14.6	3.2					-19.8	9.6			2
SC2200	Scladina	*Crocuta crocuta*	*maxillary*	42.0	15.4	3.2					-19.3	9.4			2

Table 2

ID	Site	Species	Skeletal element	%Cc	%Nc	C/N	%Sc	C/Scoll	N/Scoll	δ^{34}S	δ^{13}C	δ^{15}N	^{14}C-Age	Reference date	Reference for stab. Isotopes
IV2A 13534	Spy	*Crocuta crocuta*	*First molar*	42.0	14.2	3.4					-19.90	11.90	42750 +850/-650 (GrA-44547)	Semal 2013	4
Goyet-A3-3	Goyet	*Canis lupus*	*4th metatarsus*	43.5	15.6	3.3	0.18	644	198	1.7	-19.1	6.6			1,5
Goyet-A3-4	Goyet	*Canis lupus*	*4th metatarsus*	43.5	15.3	3.3	0.17	691	208	2.9	-18.8	7.2			1,5
SC30300	Scladina	*Canis lupus*	*Pisiform L*	42.5	14.4	3.4	0.16	709	206	11.8	-20.4	6.6			1,5
Goyet-A2-3	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.9	14.3	3.3					-22.1	4.5			1
Goyet-A2-4	Goyet	*Ursus spelaeus*	*3rd metacarpum*	44.3	15.3	3.4					-21.7	3.4			1
Goyet-A2-5	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.2	13.5	3.4					-21.6	3.1			1
Goyet-A2-6	Goyet	*Ursus spelaeus*	*3rd metacarpum*	38.7	13.3	3.4					-22.1	3.0			1
Goyet-A3-20	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.5	16.0	3.2	0.15	749	236	-5.0	-21.8	2.8			1,5
Goyet-A3-22	Goyet	*Ursus spelaeus*	*3rd metacarpum*	40.7	14.6	3.2	0.16	663	204	-6.6	-21.5	2.6			1,5
Goyet-A3-23	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.4	13.7	3.4	0.16	651	194	-1.5	-21.9	4.3			1,5
Goyet-A3-24	Goyet	*Ursus spelaeus*	*3rd metacarpum*	40.1	14.4	3.2	0.14	759	234	-1.7	-21.5	4.9			1,5
Goyet-A3-25	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	15.7	3.1					-21.4	3.1			1
Goyet-A3-26	Goyet	*Ursus spelaeus*	*3rd metacarpum*	38.8	13.4	3.4					-21.6	5.8			1
Goyet-A3-27	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.5	15.5	3.3					-21.5	4.6			1
Goyet-A3-28	Goyet	*Ursus spelaeus*	*3rd metacarpum*	36.8	13.4	3.2					-22.3	5.3			1
Goyet-B4-9	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	14.9	3.2					-21.3	3.5			1
Goyet-B4-10	Goyet	*Ursus spelaeus*	*3rd metacarpum*	37.9	13.7	3.2					-21.8	4.4			1
Goyet-B4-11	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.3	13.3	3.4					-20.9	4.4			1
Goyet-B4-12	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.7	15.8	3.2					-20.9	3.7			1
Goyet-B4-13	Goyet	*Ursus spelaeus*	*3rd metacarpum*	42.2	15.3	3.2					-21.0	4.8			1
Goyet-B4-14	Goyet	*Ursus spelaeus*	*3rd metacarpum*	42.0	14.9	3.3					-21.8	4.5			1
Goyet-B4-15	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.0	15.3	3.3					-21.0	4.6			1
Goyet-B4-16	Goyet	*Ursus spelaeus*	*3rd metacarpum*	36.4	14.5	2.9					-21.0	6.0			1
Goyet-B4-17	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.8	14.5	3.4					-20.8	3.9			1
Goyet-B4-32	Goyet	*Ursus spelaeus*	*radius*	40.7	14.8	3.2					-21.7	5.2			1
Goyet-B4-34	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	14.1	3.4	0.35	314	92		-22.0	2.7			1,5
SC3100	Scladina	*Ursus spelaeus*	*mandible*	40.9	14.8	3.2	0.15	727	226	0.1	-22.5	3.7			1,5
SC3200	Scladina	*Ursus spelaeus*	*mandible*	42.4	15.2	3.3					-22.1	5.7			1
SC3300	Scladina	*Ursus spelaeus*	*mandible*	43.3	15.8	3.2	0.16	709	222	-2.1	-22.2	6.0			1,5
SC3500	Scladina	*Ursus spelaeus*	*phalanx II*	44.0	16.0	3.2	0.16	731	228	3.4	-21.8	5.1			1,5
SC3600	Scladina	*Ursus spelaeus*	*phalanx II*	42.8	15.6	3.2	0.16	722	225	-17.0	-21.8	3.0			1,5
SC3700	Scladina	*Ursus spelaeus*	*phalanx II*	42.4	15.4	3.2	0.16	699	218	-5.4	-22.0	6.1			1,5
SC3800	Scladina	*Ursus spelaeus*	*phalanx II*	42.5	15.5	3.2	0.15	732	229	-4.2	-22.2	5.0			1,5
Goyet-A2-1	Goyet	*Mammuthus primigenius*	*long bone*	41.0	15.0	3.2	0.13	846	265	-2.6	-20.7	8.1			1,5
Goyet-A3-9	Goyet	*Mammuthus primigenius*	*long bone*	43.9	15.6	3.3	0.16	732	223	4.1	-21.5	7.0			15
Goyet-B4-2	Goyet	*Mammuthus primigenius*	*skull*	41.0	14.6	3.3	0.15	730	223	8.4	-21.6	6.7			1,5
SC600	Scladina	*Mammuthus primigenius*	*tooth fragment*	42.6	15.5	3.2	0.14	830	259	6.0	-20.9	8.4			2,5

Table 2

ID	Site	Species	Skeletal element	%Cc	%Nc	C/N	%Sc	C/Scoll	N/Scoll	$\delta^{34}S$	$\delta^{13}C$	$\delta^{15}N$	^{14}C-Age	Reference date	Reference for stab. Isotopes
SC700	Scladina	*Mammuthus primigenius*	*tooth fragment*	41.5	15.2	3.2	0.13	828	260	6.6	-21.5	9.4			2,5
SC800	Scladina	*Mammuthus primigenius*	*tooth fragment*	41.3	15.1	3.2	0.14	796	249	4.5	-21.6	8.3			2,5
Spy D3 19B 121 1474	Spy	*Mammuthus primigenius*	*Milk molar*	35.1	12.50	3.3					-21.1	11.6	42330 +550/-450 (GrA-32616)	Semal et al. 2009	3
IV2A 13549	Spy	*Mammuthus primigenius*	*Plate of molar*	37.7	13.8	3.2					-21.3	8.1	42950 +800/-650 (GrA-44548)	Semal et al. 2013	4
Goyet-A2-2	Goyet	*Coelodonta antiquitatis*	*unciforme*	43.8	16.2	3.2					-20.0	4.3			1
Goyet-A3-2	Goyet	*Coelodonta antiquitatis*	*scaphoide*	43.8	15.2	3.4	0.18	647	193	-0.1	-20.4	5.7			1,5
Goyet-B4-3	Goyet	*Coelodonta antiquitatis*	*1st metacarpum*	40.0	14.6	3.2					-20.8	5.9			1
SC30100	Scladina	*Coelodonta antiquitatis*	*metatarsal II R*	44.4	15.7	3.3					-21.1	5.5			1
SC900	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.6	15.5	3.2	0.13	874	273	6.9	-20.9	5.5			2,5
SC1000	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.1	15.4	3.2	0.13	872	274	1.9	-20.3	6.9			2,5
SC1100	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.2	15.2	3.2	0.14	822	254	4.6	-20.0	6.4			2,5
SC1200	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	41.2	15.0	3.2	0.14	806	251	2.5	-21.1	5.3			2,5
SC1300	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	41.8	15.2	3.2	0.12	900	281		-20.4	7.5			2,5
SC1400	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	43.1	15.7	3.2					-20.6	5.5			2
Spy 13637 Ulg	Spy	*Cœlodonta antiquitatis*	*Lower P3 or P4*	43.3	14.2	3.6					-20.8	6.8	25670 +130/-120 (GrA-37936)		4
Spy D2 Pal Plateau 4	Spy	*Cœlodonta antiquitatis*	*Milk molar*	40.4	14.4	3.3					-20.1	7.2	44350 +650/-500 (GrA-32613)	Semal et al. 2013	3
Goyet-A3-10	Goyet	*Equus ferus*	*ectocuneiform*	44.9	15.9	3.3	0.15	822	249	0.6	-21.0	5.1			1,5
Goyet-A3-11	Goyet	*Equus ferus*	*ectocuneiform*	41.9	15.4	3.2	0.14	800	252	1.0	-20.7	6.4			1,5
Goyet-A3-12	Goyet	*Equus ferus*	*ectocuneiform*	43.9	15.4	3.3	0.16	746	224	-0.7	-20.8	5.9			1,5
Goyet-B4-4	Goyet	*Equus ferus*	*tibia*	41.0	14.8	3.2					-20.5	6.6			1
SC28400	Scladina	*Equus ferus*	*upper P2 (L)*	33.6	12.9	3					-21.1	6.5			1
SC3900	Scladina	*Equus ferus*	*upper tooth (R)*	42.5	15.6	3.2	0.14	790	248	5.7	-21.7	5.2			2,5
SC4100	Scladina	*Equus ferus*	*upper tooth (R)*	42.6	15.8	3.1	0.13	908	289		-21.7	5.1			2,5
SC4200	Scladina	*Equus ferus*	*upper tooth (R)*	42.8	15.8	3.2	0.13	874	276	2.0	-21.9	5.0			2,5
SC4300	Scladina	*Equus ferus*	*upper tooth (R)*	39.9	14.5	3.2	0.14	781	244	6.2	-21.5	4.8			2,5
SC4400	Scladina	*Equus ferus*	*upper tooth (R)*	40.9	15.0	3.2	0.12	910	286		-21.6	7.0			2,5
IV2E 4207	Spy	*Equus ferus*	*Premolar / Molar*	35.6	14.2	2.9	0.15	633	216	5.5	-20.5	4.5	32810 +250/-230 (GrA-44576)	Semal et al. 2013	4,5
Goyet-B4-6	Goyet	*Bos primigenius*	*centrotarsus*	38.7	14.1	3.2					-20.0	3.8			1
Goyet-A3-13	Goyet	*Bison priscus*	*tibia*	40.9	14.6	3.3	0.16	687	209	-2.8	-20.0	4.1			1,5
Goyet-A3-14	Goyet	*Bison priscus*	*tibia*	41.4	14.6	3.3	0.15	725	219	4.9	-20.4	4.8			1,5
Goyet-B4-5	Goyet	*Bison priscus*	*centrotarsus*	40.9	14.7	3.2					-20.0	5.7			1
Goyet-B4-7	Goyet	*Bison priscus*	*centrotarsus*	38.8	14.1	3.2					-20.4	3.9			1
SC29000	Scladina	*Bison priscus*	*lower M3 (R)*	32.6	11.5	3.3					-20.8	4.4			1
SC29100	Scladina	*Bison priscus*	*lower P4 (L)*	32.1	12.8	2.9					-19.8	5.6			1
SC4500	Scladina	*Bos or Bison*	*lower P (R)*	41.7	15.2	3.2	0.15	764	239	4.1	-20.5	4.8			2,5
SC4700	Scladina	*Bos or Bison*	*lower P3 (R)*	42.7	15.7	3.2	0.14	806	254	8.4	-20.5	4.3			2,5
SC4800	Scladina	*Bos or Bison*	*lower M1(R)*	41.2	15.3	3.1					-19.9	5.3			2
SC4900	Scladina	*Bos or Bison*	*lower P3 (R)*	40.8	15.0	3.2	0.15	725	229	4.5	-20.7	4.4			2,5
SC28800	Scladina	*Bos primigenius*	*lower M3 (L)*	33.9	12.7	3.1					-20.7	4.9			1
SC28900	Scladina	*Bos primigenius*	*lower P4 (L)*	35.0	13.6	3.0					-20.3	4.5			1
Goyet-A3-15	Goyet	*Rangifer tarandus*	*astragalus*	42.3	15.5	3.2	0.17	667	209	7.2	-18.5	2.6			1,5

Table 2

ID	Site	Species	Skeletal element	%Cc	%Nc	C/N	%Sc	C/Scoll	N/Scoll	$\delta^{34}S$	$\delta^{13}C$	$\delta^{15}N$	^{14}C-Age	Reference date	Reference for stab. Isotopes
Goyet-A3-16	Goyet	*Rangifer tarandus*	*astragalus*	43.0	15.1	3.3	0.18	620	187	6.2	-18.5	3.3			1,5
Goyet-A3-17	Goyet	*Rangifer tarandus*	*astragalus*	43.4	15.3	3.3	0.14	803	242	5.1	-18.6	3.4			1,5
Goyet-A3-18	Goyet	*Rangifer tarandus*	*astragalus*	43.9	15.4	3.3	0.15	773	232	6.8	-18.3	3.1			1,5
Goyet-A3-19	Goyet	*Rangifer tarandus*	*astragalus*	44.1	15.2	3.4	0.15	787	232	-7.2	-19.6	4.5			1,5
Goyet-B4-8	Goyet	*Rangifer tarandus*	*centrotarsus*	41.1	14.9	3.2					-18.6	3.9			1
Spy 10640 Ulg	Spy	*Rangifer tarandus*	*First Phalanx*	43.4	14.4	3.5					-19.8	4.9	29040 +180/-160 (GrA-37934)	Semal et al. 2009	4
Spy 13071 Ulg	Spy	*Rangifer tarandus*	*Metacarpal*	35.6	14.1	2.9					-18.4	1.6	36920 +400/-350 (GrA-44546)	Semal et al. 2013	4
Spy D4 19B 121 1480	Spy	*Rangifer tarandus*	*Metacarpal*	39.3	17.4	2.60	0.14	735	279						5
SC29700	Scladina	*Rangifer tarandus*	*tooth*	37.5	12.4	3.5	0.2	625	178	8.3	-17.9	3.5			5
Sc 22400	Scladina	*Rangifer tarandus*	*P2-P4*	35.6	12.9	3.2	0.13	746	232	7.49	-18.7	3.1			5
Sc 22700	Scladina	*Rangifer tarandus*	*M2 inf*	38.8	14.2	3.2	0.14	761	239	8.49	-18.5	5.0			5
Sc 22800	Scladina	*Rangifer tarandus*	*M1 inf*	39.6	14.5	3.2	0.15	706	221	10.52	-17.6	3.6			5
Sc 22900	Scladina	*Rangifer tarandus*	*P4 sup*	39.7	14.6	3.2	0.15	696	219	6.48	-17.8	4.8			5
Sc 23000	Scladina	*Rangifer tarandus*	*M2 sup*	40.9	14.9	3.2	0.14	784	245	13.13	-16.7	7.2			5

1= Bocherens et al., 2011a

2=Bocherens et al., 1997

3= Bocherens et al., 2013

4= Wißing et al., 2015b

5= Wißing et al., in prep

5.2. Ziegeleigrube Coenen

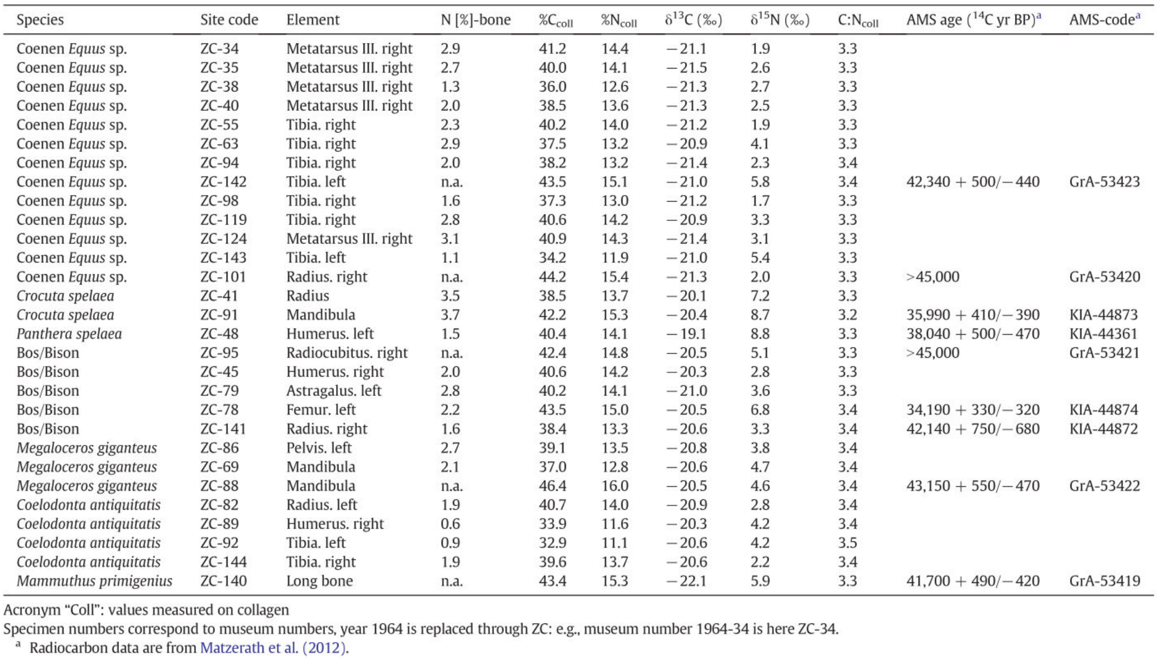
All results are obtained on collagen fulfilled chemical conditions needed (see above). All results are summarized in table 3 and 4.

δ^{15}N and δ^{13}C

The δ^{13}C values obtained for the herbivores ranged between −22.1‰for mammoth (ZC-140) and −20.3‰for Bos/Bison (ZC-45) and woolly rhinoceros (ZC-89). The average δ^{13}C values for the herbivores was−21.0‰ (n=26; s.d. 0.43‰). The carnivores δ^{13}C values ranged from−20.4‰ for hyena (ZC-91) and −19.1‰ for cave lion (ZC-48). The average δ^{13}C values for the carnivores was−19.9‰ (n=3; s.d. 0.7‰) (Wißing et al., 2015a).

The δ^{15}N values for herbivores ranged between 1.7‰ for horse (ZC-98) and 6.8‰ for Bos/Bison (ZC-78), the average δ^{15}N was 3.6‰ (n=26; s.d. 1.4‰). The δ^{15}N values of the carnivores ranged between a minimum of 7.2‰ (ZC-41) for hyena and a maximum of 8.8‰ (ZC-48) for cave lion. The average δ^{15}N value for carnivores was 8.3‰ (n=3; s.d. 0.9‰) (Table 3) (Wißing et al., 2015a) (Table 3).

Table 3



Species	Site code	Element	N [%]-bone	%C_{coll}	%N_{coll}	δ^{13}C (‰)	δ^{15}N (‰)	C:N_{coll}	AMS age (^{14}C yr BP)[a]	AMS-code[a]
Coenen *Equus* sp.	ZC-34	Metatarsus III. right	2.9	41.2	14.4	−21.1	1.9	3.3		
Coenen *Equus* sp.	ZC-35	Metatarsus III. right	2.7	40.0	14.1	−21.5	2.6	3.3		
Coenen *Equus* sp.	ZC-38	Metatarsus III. right	1.3	36.0	12.6	−21.3	2.7	3.3		
Coenen *Equus* sp.	ZC-40	Metatarsus III. right	2.0	38.5	13.6	−21.3	2.5	3.3		
Coenen *Equus* sp.	ZC-55	Tibia. right	2.3	40.2	14.0	−21.2	1.9	3.3		
Coenen *Equus* sp.	ZC-63	Tibia. right	2.9	37.5	13.2	−20.9	4.1	3.3		
Coenen *Equus* sp.	ZC-94	Tibia. right	2.0	38.2	13.2	−21.4	2.3	3.4		
Coenen *Equus* sp.	ZC-142	Tibia. left	n.a.	43.5	15.1	−21.0	5.8	3.4	42,340 + 500/−440	GrA-53423
Coenen *Equus* sp.	ZC-98	Tibia. right	1.6	37.3	13.0	−21.2	1.7	3.3		
Coenen *Equus* sp.	ZC-119	Tibia. right	2.8	40.6	14.2	−20.9	3.3	3.3		
Coenen *Equus* sp.	ZC-124	Metatarsus III. right	3.1	40.9	14.3	−21.4	3.1	3.3		
Coenen *Equus* sp.	ZC-143	Tibia. left	1.1	34.2	11.9	−21.0	5.4	3.3		
Coenen *Equus* sp.	ZC-101	Radius. right	n.a.	44.2	15.4	−21.3	2.0	3.3	>45,000	GrA-53420
Crocuta spelaea	ZC-41	Radius	3.5	38.5	13.7	−20.1	7.2	3.3		
Crocuta spelaea	ZC-91	Mandibula	3.7	42.2	15.3	−20.4	8.7	3.2	35,990 + 410/−390	KIA-44873
Panthera spelaea	ZC-48	Humerus. left	1.5	40.4	14.1	−19.1	8.8	3.3	38,040 + 500/−470	KIA-44361
Bos/Bison	ZC-95	Radiocubitus. right	n.a.	42.4	14.8	−20.5	5.1	3.3	>45,000	GrA-53421
Bos/Bison	ZC-45	Humerus. right	2.0	40.6	14.2	−20.3	2.8	3.3		
Bos/Bison	ZC-79	Astragalus. left	2.8	40.2	14.1	−21.0	3.6	3.3		
Bos/Bison	ZC-78	Femur. left	2.2	43.5	15.0	−20.5	6.8	3.4	34,190 + 330/−320	KIA-44874
Bos/Bison	ZC-141	Radius. right	1.6	38.4	13.3	−20.6	3.3	3.4	42,140 + 750/−680	KIA-44872
Megaloceros giganteus	ZC-86	Pelvis. left	2.7	39.1	13.5	−20.8	3.8	3.4		
Megaloceros giganteus	ZC-69	Mandibula	2.1	37.0	12.8	−20.6	4.7	3.4		
Megaloceros giganteus	ZC-88	Mandibula	n.a.	46.4	16.0	−20.5	4.6	3.4	43,150 + 550/−470	GrA-53422
Coelodonta antiquitatis	ZC-82	Radius. left	1.9	40.7	14.0	−20.9	2.8	3.4		
Coelodonta antiquitatis	ZC-89	Humerus. right	0.6	33.9	11.6	−20.3	4.2	3.4		
Coelodonta antiquitatis	ZC-92	Tibia. left	0.9	32.9	11.1	−20.6	4.2	3.5		
Coelodonta antiquitatis	ZC-144	Tibia. right	1.9	39.6	13.7	−20.6	2.2	3.4		
Mammuthus primigenius	ZC-140	Long bone	n.a.	43.4	15.3	−22.1	5.9	3.3	41,700 + 490/−420	GrA-53419

Acronym “Coll”: values measured on collagen

Specimen numbers correspond to museum numbers, year 1964 is replaced through ZC: e.g., museum number 1964-34 is here ZC-34.

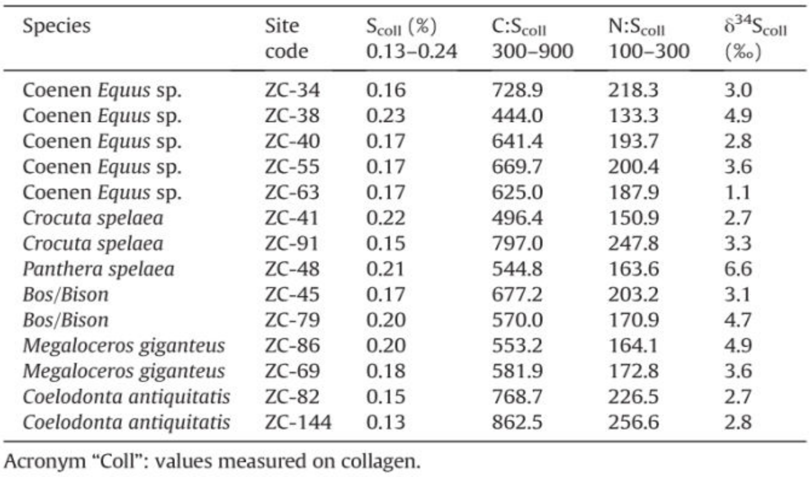
[a] Radiocarbon data are from Matzerath et al. (2012).

Wißing et al., 2015a

δ^{34}S

This study contains 14 δ^{34}S values representing five horses, two individuals of hyena, one cave lion and two specimens of Bos/Bison, giant deer and rhinoceroes respectively. The values ranged from 1.1‰ for the horse (ZC-63) up to 6.6‰for the cave lion sample (ZC-48). The average is 3.6‰ (s.d.1.4‰) (Table 4) (Wißing et al., 2015a).

Table 4



Species	Site code	S_{coll} (%) 0.13–0.24	C:S_{coll} 300–900	N:S_{coll} 100–300	$\delta^{34}S_{coll}$ (‰)
Coenen *Equus* sp.	ZC-34	0.16	728.9	218.3	3.0
Coenen *Equus* sp.	ZC-38	0.23	444.0	133.3	4.9
Coenen *Equus* sp.	ZC-40	0.17	641.4	193.7	2.8
Coenen *Equus* sp.	ZC-55	0.17	669.7	200.4	3.6
Coenen *Equus* sp.	ZC-63	0.17	625.0	187.9	1.1
Crocuta spelaea	ZC-41	0.22	496.4	150.9	2.7
Crocuta spelaea	ZC-91	0.15	797.0	247.8	3.3
Panthera spelaea	ZC-48	0.21	544.8	163.6	6.6
Bos/Bison	ZC-45	0.17	677.2	203.2	3.1
Bos/Bison	ZC-79	0.20	570.0	170.9	4.7
Megaloceros giganteus	ZC-86	0.20	553.2	164.1	4.9
Megaloceros giganteus	ZC-69	0.18	581.9	172.8	3.6
Coelodonta antiquitatis	ZC-82	0.15	768.7	226.5	2.7
Coelodonta antiquitatis	ZC-144	0.13	862.5	256.6	2.8

Acronym “Coll”: values measured on collagen.

Wißing et al., 2015a

5.3. Lommersum

δ^{15}N and δ^{13}C

The δ^{13}C values obtained ranged between -20.9‰ for a horse (Lom-20) up to -18.33‰ for a reindeer (Lom-8) (av. -19.74‰; s.d. 0.9).

The δ^{15}N ranges from 2.0‰ for a reindeer (Lom-7) up to 8.5‰ for the cave lion (Lom-15) (av.4.8‰; s.d. 2.0‰) (Table 5).

δ^{34}S

Seven samples provided collagen which fulfilled the criteria for δ^{34}S values.

The four samples without valid results contain a higher % sulfur in collagen (>0.26%) and are therefore excluded for discussion. The maximum δ^{34}S was obtained on the reindeer Lom-4 (4.7‰) while the lowest value was provided by Lom-2 (1.4‰). The average is 3.4‰ (s.d. 1.5‰)(Table 5).

Table 5

ID	Species	Part	%C_coll	%N_coll	C/N	δ^{13}C	δ^{15}N	%S coll (0.13-0.26)	atomic C/Scoll (300-900)	atomic N/Scoll (100-300)	δ^{34} S
Lom-1	*Equus*	Radius r	11.67	5.02	2.71	-21.18	1.70				
Lom-2	*Rangifer tarandus*	Humerus	41.88	15.34	3.18	-19.14	3.70	0.23	488.60	153.45	1.43
Lom-3	*Rangifer tarandus*	Radius r	44.48	16.05	3.23	-19.19	3.78	0.21	553.51	171.17	4.20
Lom-4	*Rangifer tarandus*	Radius r	39.37	14.38	3.19	-18.95	3.19	0.20	537.13	168.16	4.73
Lom-5	*Rangifer tarandus*	Radius r dist.	40.00	14.00	3.30	-19.40	3.30	0.28	383.08	114.92	6.92
Lom-6	*Rangifer tarandus*	Radius r dist.	43.51	15.73	3.23	-18.35	3.30	0.20	593.53	183.89	2.57
Lom-7	*Rangifer tarandus*	Radius r dist.	18.20	6.80	3.10	-19.90	2.00	0.38	127.05	40.69	8.96
Lom-8	*Rangifer tarandus*	Radius r dist.	45.18	16.43	3.21	-18.33	3.43	0.18	675.90	210.73	5.59
Lom-9	*Rangifer tarandus*	Radius r dist.	38.28	14.06	3.18	-18.79	3.60	0.27	371.41	116.90	6.15
Lom-10	*Rangifer tarandus*	Radius r dist.	39.35	14.29	3.21	-18.97	2.97	0.32	332.90	103.61	6.96
Lom-11	*Rangifer tarandus*	Radius r dist.									
Lom-12	*Equus ferrus*	Radius r	43.97	15.87	3.23	-20.62	6.64	0.16	723.99	223.92	2.00
Lom-13	*Equus ferrus*	Radius r medial	41.80	15.37	3.17	-20.68	7.31	0.20	555.17	174.93	3.45
Lom-14	*Canis Lupus*	Tibia distal.	35.38	12.46	3.31	-20.23	7.68				
Lom-15	*Panthera leo*	Incisive	38.00	13.50	3.30	-19.20	8.50				
Lom-16	*Equus ferus*	Tibia distal.	38.77	13.68	3.31	-20.88	4.21				
Lom-17	*Equus ferus*	Tibia distal.									
Lom-18	*Equus ferus*	Tibia distal.									
Lom-19	*Mammuthus primigenius*	Ivory	27.0	9.1	3.5	-20.6	7.6				
Lom-20	*Equus ferus*	humerus r.	39.2	13.8	3.3	-20.9	5.0				
Lom-21	*Equus ferus*	radius r.	42.4	14.9	3.3	-20.7	6.3				
Lom-22	*Equus ferus*	humerus r.	40.9	14.5	3.3	-20.4	4.5				
Lom-23	*Equus ferus*	radius r.?									

6. Discussion

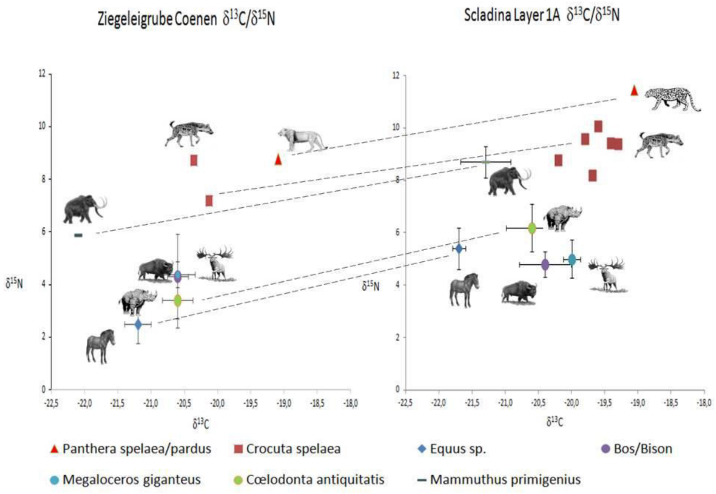
6.1. Impact of climatic fluctuations and the impact of hominids on the mammothsteppe ecosystem

The Marine Isotope Stage (MIS) 3 is characterized through several sort term climatic fluctuations (Heinrich events) (Svensson et al., 2008). One key question in understanding hominid ecology at this time in Europe is the impact of such cold spells on the structure of the whole ecosystem. Another striking feature is the potential impact of hominids on the ecosystem structure. Both factors, climate and hominids, are basal in understanding of their potential impacts on dynamics of the ecosystem structure in the late Pleistocene.

6.1.1. Impact of climatic fluctuation on the structure of the mammothsteppe

While interpreting the δ^{15}N and δ^{13}C values of the site Ziegeleigrube Coenen (ZC) these values are compared with the ones obtained from the Scladina layer 1A complex. This complex yielded a very similar species composition (Bocherens et al., 1997). The complex 1A has been dated to between 37,300 + 370/−320 ^{14}C yr BP (GrA-32633) and 43,150 +950/−700 ^{14}C yr BP (GrA-32581) (Pirson et al., 2012), unfortunately dating of the ZC with the same precision is not performed at this point. The ^{14}C-dates clearly fall in the MIS 3 complex, while the dates span between 34,190+330/−320 ^{14}C yr BP (KIA-44874) and 43,150+550/−470 C^{14} yr BP (GrA-53422). Some dating attempts yielded results beyond the limit of the radiocarbon method, meaning older than 45,000 ^{14}C yr BP (GrA-53420 and GrA-53421) (Matzerath et al., 2012). It has to be considered that radiocarbon ages in this range are extremely sensitive to contamination by recent carbon (Wood et al., 2010). All younger ZC dates are from the Kiel laboratory, where the chemical characteristics of the dated collagen are not provided. It seems possible, that the site is older 45,000 years, this scenario is supported by the limited variation in isotopic values: Even if the ^{14} C-dates scatter, the faunal remains have the same ecological background (Wißing et al., 2015a). No shifts in δ^{15}N values in correspondence with the radiocarbon dates were observed. All together this indicates somehow a contemporaneity at least from an ecological point of view. To investigate the chronological positioning more in detail a dating program with participation of several laboratories is ongoing these days.

Figure 6



2D-scatter plot of Ziegeleigrube Coenen and Scladina Layer 1A. Herbivores are represented by average values with standard deviation, carnivores are represented by single individuals (Wißing et al., 2015b).

The structure of the ZC ecosystem is still intact, like in Scladina layer 1A (for a detailed discussion of the structure of the mammoth steppe see section “Niche partitioning in the late Pleistocene“). The relative values are corresponding from one site to the other (Figure 6). The ecological niches for the herbivores are very similar, even the carnivorous hyenas and felids occupied a very similar niche at both sites. The separation of the niche of hyenas and Pleistocene felids is a common feature of the ecosystem and observed elsewhere as well. This phenomenon is affiliated to different hunting strategies (Bocherens, 2015). If any of the species would produce significant different relative isotopic values this would indicate ecological stress.

Climatic fluctuations have an impact on the isotopic composition on the bottom of the foodweb, the plants. The limiting factor for plants is the mean annual temperature (MAT). MAT is essential since in frozen soils the nitrogen fixation and turnover rate of nutrients are dramatically reduced (Hobbie and Hogberg, 2012). A decrease of accessible nutrients in cooler periods/or shortly after results in a depletion in soil/plant $\delta^{15}N$ (Stevens and Hedges, 2004). On the other site increasing MAT in a (semi-) glacial context causes elevated $\delta^{15}N$ (Brenner et al., 2001). Decreasing $\delta^{15}N$ in herbivorous collagen is therefore related to a decreasing MAT/a cold spell (Ambrose, 1991; Heaton et al., 1986).

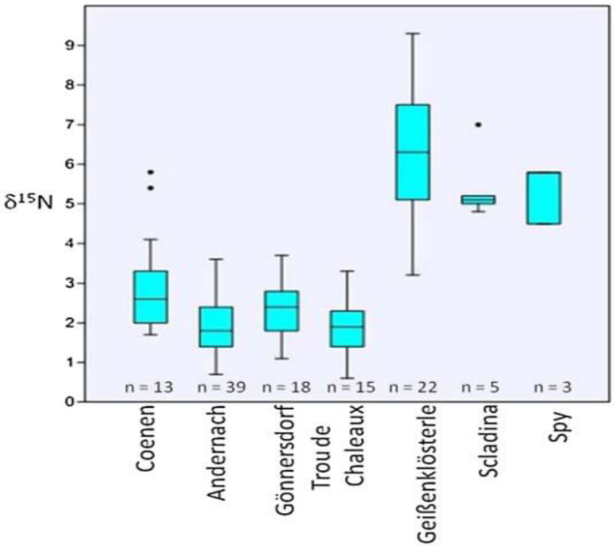
A comparison of all $\delta^{15}N$ bone collagen values from ZC (Wißing et al., 2015a) and Scladina layer 1A (Bocherens et al., 1997) showed, that although the relative isotopic position for each species was similar, the absolute values are around 3‰ lower for the mammoth, horse, and rhinoceros and felids at ZC (Figure 6). The lower $\delta^{15}N$ values of ZC represent a cooler habitat than Scladina complex 1A, the biocenosis we compared ZC directly with. Despite any chronological uncertainties both sites are clearly in MIS 3 but represent different environmental conditions.

Similar phenomena (low $\delta^{15}N$ values) could be observed after the Last Glacial Maximum (LGM) in MIS 2 of Europe (Drucker et al., 2003, Richards and Hedges, 2003; Stevens and Hedges, 2004; Stevens et al., 2008). But at this time the classic mammoth steppe ecosystem was already disappearing since many key species became extinct in Europe or survived only in some refugia (Stuart, 2015; Stuart and Lister, 2007).

In order to examine more in depth the understanding of ecological variability and especially to gain insights in the potential capacity to puffer environmental stress within the mammothsteppe ecosystem in MIS 3, we focused on the most abundant species in ZC, the horse. Horses are exclusively herbivores with no changing significant metabolic processes in MIS 3 and 2 which could cause different $\delta^{15}N$ values. Differences in $\delta^{15}N$ values are the result of changing isotopic composition of plant isotopic signal in their diet (Rodière et al., 1996). The inter site comparison (from sites with MIS 2 and MIS 3 age) showed that there are two groups defined by their

mean $\delta^{15}N$ values (Figure 7).

Figure 7



δ^{15}N values of horse collagen from pre- and post-LGM sites: pre-LGM: Ziegeleigrube Coenen, Geißenklösterle, Scladina and Spy; post-LGM: Andernach–Martinsberg, Gönnersdorf, Trou de Chaleaux. δ^{15}N values include standard error (whisker length indicates 95% interval) (Wißing et al., 2015a)

All post LGM sites (Andernach-Martinsberg, Gönnersdorf, Trou de Chaleaux) provided δ^{15}N values which are relatively low. This is related to the limited soil activity recently after the LGM (Stevens et al., 2009b). In Central Europe there are some general chronological trends in horse δ^{15}N values observed: Values are very low between 13,500 ^{14}C yr BP and 12,000 ^{14}C yr BP and increased to around 4–5‰ by 10,000 ^{14}C yr BP (Stevens and Hedges, 2004). Increasing δ^{15}N values are associated with the recovery of the soil activity. All post LGM sites discussed here, chronologically fall in the phase before soil recovery could took place.

The second group is constituted by sites with clearly higher δ^{15}N values (Scladina, Geißenklösterle, Spy (Figure 7). All these sites date pre LGM and are relatively close in age to each other.

It is striking, that the δ^{15}N horse values of the pre LGM site ZC are closer to the ones observed in post LGM sites. As mentioned above the nitrogen isotopic values can hint at chronological classifications according to some general trends in Europe

(Drucker et al., 2003, Richards and Hedges, 2003; Stevens and Hedges, 2004). We can exclude that ZC is very close in age to the other pre LGM sites, otherwise we expect a similar environmental background, which would be represented in similar δ^{15}N values in horse collagen. The environmental conditions or at least the soil activity was different in ZC from all other pre LGM sites, but more similar to conditions shortly after the LGM. The ecological data suggest a stadial date most reasonable around the Heinrich 5 event around 46,000 years ago (Cacho et al., 1999; Sánchez Goñi et al., 2008; Svensson et al., 2008). This is consistent with the obtained ^{14}C dates.

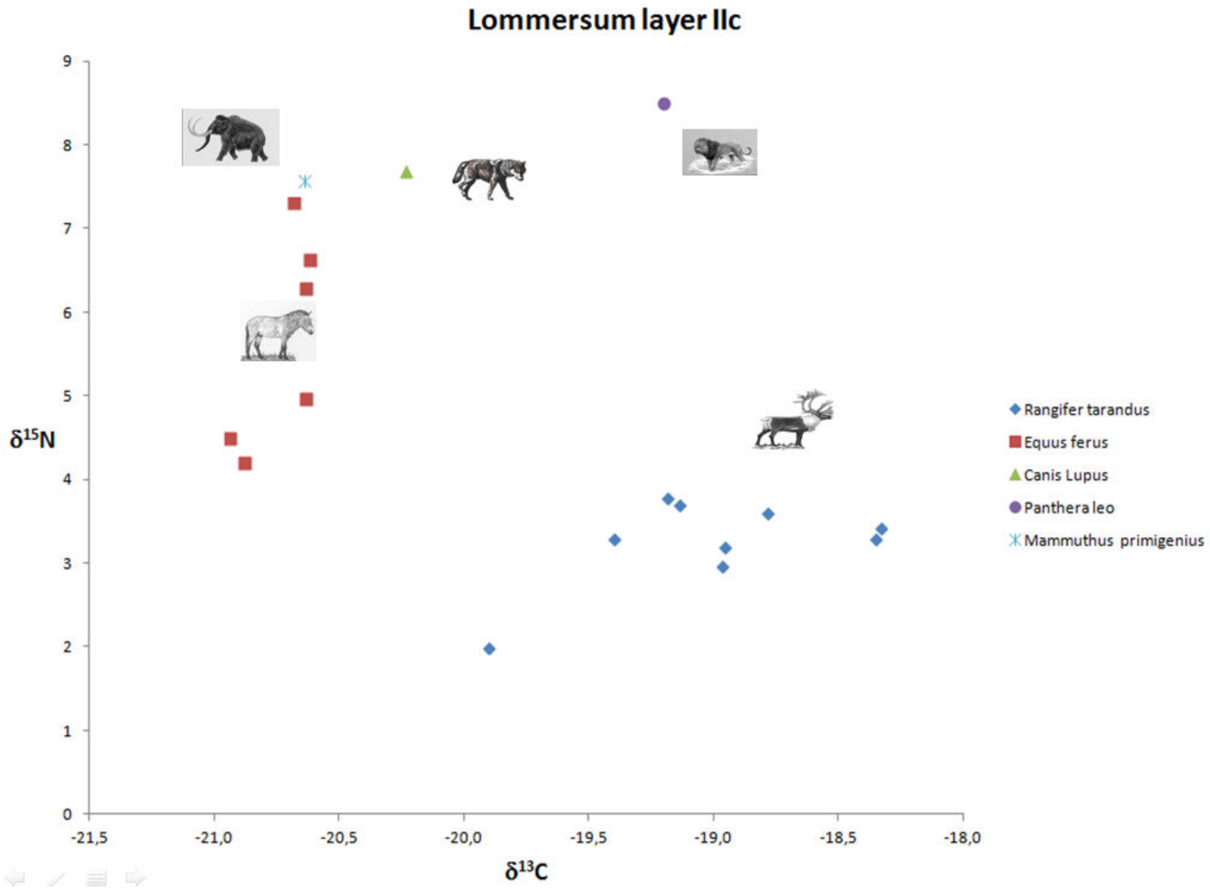
Under the estimation, the proposed chronological association is not wrong, it would indicate, that the Heinrich 5 event had an impact on the biogeochemical cycle of nitrogen in soils, reflected by lower δ^{15}N values. However the impact must been less intense than the LGM, where almost no large mammals or even humans are around in this area.

In this context most important is, that this cold spell event was not harsh enough to disrupt the structure of the mammoth steppe ecosystem, either for the herbivorous or carnivorous species. The typical niche partitioning among the participants of the ecosystem could still be observed (see section “Niche partitioning in the late Pleistocene“). No ecological stress could be diagnosed. Particularly for the Neandertals the intact ecosystem could provide the basis for their subsistence. The meanings of these conclusions are especially important in understanding fluctuations of late Neandertal populations in response to climatic shifts in MIS 3.

6.1.2. Impact of human activity on the mammothsteppe ecosystem

Through the site ZC we could exclude significant stress on the ecosystem caused by climatic aspects at the time when the last Neandertals were around in NW Europe. The site Lommersum is significantly younger: something between 29,000 and 32,000 C^{14} yr BP (Hahn, 1989), potentially slightly older (Matthies, 2012). What matter here, is that the site yielded an Aurignacian industry which is supposed to be produced by AMHs after the extinction of the Neandertals. The site produced mainly reindeer and horse remains which represent the preferred hunting prey. Mammoth is only represented by worked ivory(Hahn, 1989). Predators are very not very abundant at the oldest Aurignacian open air site in Germany (Hahn, 1989). The below discussed isospaces (see section “Niche partitioning in the late Pleistocene”) typically the species occupied in this ecosystem, is in Lommersum only partly visible (Figure 8).

Figure 8



2D-scatter plot of Lommersum

The mammoth yielded the highest $\delta^{15}N$ values and low $\delta^{13}C$ values while the reindeer produced very high $\delta^{13}C$ and low $\delta^{15}N$ values. The canid and the felid occupied the expected niche (Bocherens, 2015). What is striking it the circumstance that all horses fall rather in the expected range for mammoth (Figure 8). Some horse individuals still present relative low $\delta^{15}N$ but associated with $\delta^{13}C$ values as low as expected for mammoth. The consumption of similar plants for mammoth and horses (more concrete a mix-diet for horses, with only partly grazing on the same plants than the mammoths, because of the spectrum of $\delta^{15}N$ horse values) seems to be a reasonable explanation. A similar phenomenon has been observed in the Aurignacian and Gravettian in the Swabian Jura (Geißenklösterle) as well (Drucker et al., 2015). Drucker et al. (2015) showed through the investigation of $\delta^{18}O$ of horse remains with different $\delta^{15}N$ values, there was no environmental contrast. There was no correlation between $\delta^{18}O$ and $\delta^{15}N$. The high ^{15}N abundance of horses at Lommersum and contemporaneously in the Swabian Jura suggests a possible direct competition between mammoth and horses for the same forage and/or forage growth seasonal conditions. It seems the mammoth could not anymore fully occupy/defending ecologically their niche so that the horse could enter in it (Drucker et al., 2015). Since environmental factors could not be consulted convincingly, the most reasonable hypothesis is a declining mammoth population, caused by human pressure with the beginning of the Upper Paleolithic/beginning of the presence of modern humans in the area of research. This is in contrast to the time of the ecosystem the late Neandertals were still part of (Bocherens, 2009b; Bocherens et al., 2005; Bocherens et al., 2013; Wißing et al., 2015b). In all studies the structure of the ecosystem was still preserved without any clear signs for stress. So far only in an archeological context when modern humans are around ecological stress especially on the mammoth population could be observed (Drucker et al., 2014; Drucker et al., 2015). In the Aurignacian and the following techno-complex the Gravettian this phenomenon occurs at the beginning only locally, especially in areas east of Central Europe it seems the mammothsteppe structure, more concrete the mammoth populations, are probably more robust against human hunting pressure (Bocherens et al., 2015).

Finally it seems plausible to hypothesize that climatic changes between 50,000 and 30,000 have not significantly impacted the general character of the ecosystem in NW-Europe. Also the Neandertals have not caused a significant ecological stress on the biocenosis in terms of stable isotopes. Only when modern humans entered the area the ecosystem started to change enduring. The decline of mammoth population caused by modern human hunting activity seems reasonable. This giant herbivorous species with low reproduction rate is vulnerable for overhunting especially in a context of increasing human population density with the beginning of the Upper Paleolithic (Flores, 2014; Sandom et al., 2014).

6.2. Niche partitioning in the late Pleistocene

Preconditions

To investigate ecological aspects through the stable isotope approach some prerequisites have to be fulfilled. The niche partitioning and associated trophic relations can only be investigated in an ecological context. That means not only one single species has to be investigated but as many antagonists of the biocenosis as possible to refine the context. Isolated isotopic values of a given specimen do not provide deep insights, but the relative isotopic compositions of different species are adequate to perform ecological understanding of an ecosystem.

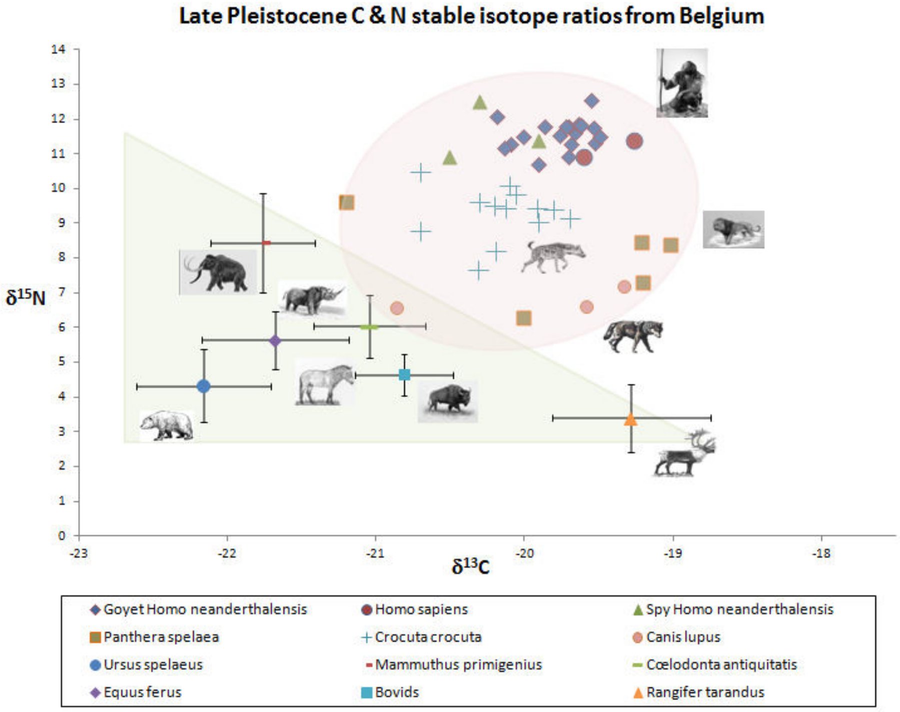
Beside a broad herbivore and carnivore species spectrum it is essential to compare isotopic data performed on specimens lived under the same abiotic conditions like temperature, aridity, elevation and so on, since these factors also drive the isotopic baseline (see above). In an optimal case all remains should come from a single site and should be contemporaneous. Of course in an archeological context this is in general not case. For the study of hominid ecology the Belgium sites (Goyet, Spy, and Scladina) provide the unique possibility to investigate a very rich faunal assemblage associated with Neandertals and very early AMH. The sites are very close by to each other and chosen faunal material has the same ecological background and a clear pre-LGM age. The Troisième Caverne of Goyet is the only site known where both hominid types are represented in the fossil record at the same place. Here the conditions to investigate Late Pleistocene hominid ecology are therefore unique.

6.2.1. 2D-scatter plot ($\delta^{13}C$ versus $\delta^{15}N$)

The most classic way to presents late Pleistocene isotopic results is the 2D-scatter plot (Figure 9). For the Belgium sites, the classic mammothsteppe pattern is preserved and structured like observed in Europe in other contexts as well (Bocherens, 2003, 2015; Bocherens et al., 2005; Bocherens et al., 2011a; Bocherens et al., 2015; Yeakel et al., 2013).

Based on stable carbon and nitrogen isotopic composition no dietary or habitat inducted stress can be diagnosed (Wißing et al., 2015b) (Figure 9).

Figure 9



2D-scatter plot (Wißing et al., in prep.)

6.2.1.1. Herbivores

Differences in herbivorous isotopic compositions are essentially connected to particular preferences for different plant diet. The mammoth yielded the highest δ^{15}N values and relatively low δ^{13}C values. Mammoths consumed an isotopically distinct food source, reflective of aridity, dung fertilization, and (or) plant selection. This dietary signal suggests that woolly mammoths occupied one of the most distinct habitat or forage niche relative to other Pleistocene herbivores. (Schwartz-Narbonne et al., 2015). Mammoth may preferred mature plant material which is in general elevated in δ^{15}N (Bocherens and Drucker, 2003). Even if δ^{15}N values can be as high as in carnivores, δ^{13}C values are always significantly lower in bulk collagen. The trophic positioning of mammoth as a pure herbivore is demonstrated by the study of single amino acids in collagen just recently (Naito et al., 2016; Schwartz-Narbonne et al., 2015). Among bovids, rhinoceros and horses the species related differences are less distinct (Figure 9). Rhinoceros are in general slightly higher than both other species (Bocherens et al., 2011a).

On the contrary reindeer has a very characteristic isotopic signal. Their highest δ^{13}C and lowest δ^{15}N values among the herbivores is caused by consumption of lichen, a well observed phenomenon (Drucker et al., 2012) (Stevens et al., 2008; Yeakel et al., 2013). The cave bear is clearly in the range of a pure vegetarian, and in general yield very low δ^{13}C and δ^{15}N. The vegetarian dietary strategy of this species has been intensively debated several times (Bocherens, 2009a; Bocherens et al., 2014c; Richards et al., 2008).

6.2.1.2. Carnivores

Based on stable isotopic fractionation from one trophic level to the next higher one carnivores in generally yield higher δ^{13}C and especially δ^{15}N values.

The hyenas yielded on average the highest δ^{15}N values among the carnivorous species. The most reasonable explanation for this is the more intensive exploitation of mammoth and woolly rhinoceros as herbivores with the highest δ^{15}N values (Wißing et al., 2015b). Also predating on other carnivores and omnivores would cause the relative elevated δ^{15}N values. The centered position of the hyenas indicates general access to a broad spectrum of prey. Additionally striking is that all other predators seem to pattern around the hyenas (Figure 9). This indicates avoiding direct competition between different carnivorous species. It is likely that the relative isotopic composition of the hyenas is not the result of selective scavenging but of active hunting (Bocherens et al., 2011a). General scavenging would result in overlapping isotopic values through species (Wißing et al., 2015b). All hyenas plot relatively close to each other; the reason for this was probably hunting in a collective and therefore accessing the same dietary resources.

The cave lions produced a pattern more divers on the left and right edge of the isospace the hyenas occupy (Figure 9). No cave lion is in the range of the hyena. The individual differences within this species and in comparison to the hyenas indicate a solitary way of life of cave lions. The ecological relations among both species observed in Belgium are well distributed features through the ecosystem (Bocherens, 2015; Bocherens et al., 2011a). In all cases when cave hyenas are present they occupied the central position in the predators' guild and no other species are interfering with them. It seems this species was the top faunal predator of the mammothsteppe.

The wolf is a flexible species in terms of hunting strategies (Bocherens, 2015; Fox-Dobbs et al., 2007; Muro et al., 2011). This is demonstrated by the isotopic data observed on the specimens in the late Pleistocene record at the Belgium sites as well. One specimen yielded relatively low δ^{13}C and δ^{15}N values; this could indicate a preference for cave bear and/or small mammals, while two other individuals yielded values corresponding to a preference for reindeer.

To summarize: among the herbivores there is a specific dietary preference for each species, recognizable through plotting the δ^{15}N and δ^{13}C values in a 2D scatter plot. All herbivores occupied a distinct ecological niche in terms of diet. The same is true for the carnivores. Each species inhabited a distinct ecological niche based on preferred prey. The observed pattern in Belgium is characteristic for this kind of ecosystem. If one of these species produced clearly different relative values, this would indicate distinct ecological faulting or at least a certain level of ecological stress in terms of habitat and diet for that particular species.

6.2.1.3. Hominids

Neandertals:

In figure 9 the Neandertals from Goyet and Spy are plotted. The Neandertals occupied a very specific ecological among the predators. All Neandertals yielded the highest δ^{15}N values and relatively high δ^{13}C values. No other predator showed such high δ^{15}N values.

The isospace occupied by Neandertals can be described as limited in expansion since the standard deviations (0.47‰ for δ^{15}N and for δ^{13}C 0.28‰) is relatively small. The individual differences in diet are only minor and are smaller to each other than to other species. The isospace is typically for so far all analyzed late Neandertals and is dued to a special preference on megaherbivores like mammoth (e.g. Wißing et al., 2015b).

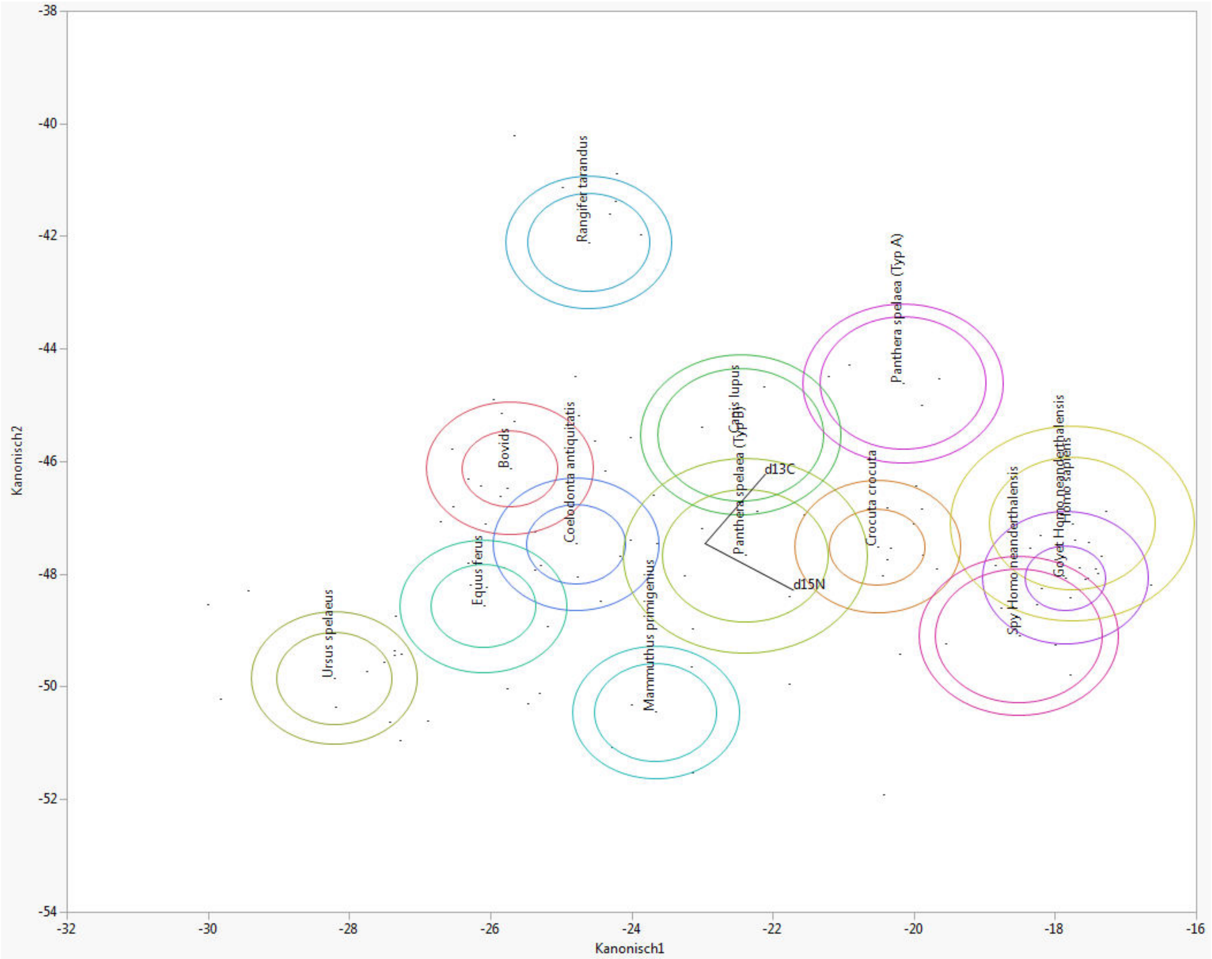
Modern humans:

The analysed AMH specimens fall in the range of Neandertals (Figure 9). The δ^{13}C values are slightly higher and the average values may indicate an increasing meaning of reindeer for the modern humans in contrast to Neandertals. Most striking is the similarity of isotopic values of both hominid species (Figure 9). The ecological placement of the AMH in the faunal context visualized in the 2D-scatter plot shows high similarities between both types of hominids.

6.2.2. Discriminant analysis

The discriminant analysis is way to present isotopic data from a statistical perspective. The inner areas contain 50% of the points for a given species; the outer corresponds to a 95% confidence limit for the mean (Figure 10).

Figure 10



Discriminant analysis (modified after Wißing et al., in prep.)

The essential information are the spatial relations of the isospaces to each other. The closer they are, the closer the ecological niche in terms of preferred diet is. The niche partitioning described in section “2D scatter plot” can be found again. The herbivorous and carnivorous species are separated with on minor exception. Within the herbivores rhinoceros, bovids and the horses are close to each other, while the mammoth, the reindeer and the cave bear a clearly separated without interfering with other species. The three species form endpoints of the herbivorous guild.

Among the carnivorous species a niche partitioning can be observed. The wolf and the hyenas are clearly separated without any overlap. The cave lions are divided into two groups without any overlap: one with low $\delta^{13}C$ values (type A) and the other group with high $\delta^{13}C$ values (type B). Cave lion individuals in the presents of hyenas focus either on reindeer (type A) or on cave bear mainly (type B) (Figure 10)(Bocherens et al., 2011a). Averaging the values of both groups would indicate a too expanded isospace. Type B is overlapping with the rhinoceros. This is probably a statistical issue, since this group consists only out of two specimens, one of them even with relatively low $\delta^{15}N$ values. The case of this cave lion could mean that some prey species with low $\delta^{15}N$ are not present in the study. Small mammal species such as rodents and lagomorphs could exhibit lower $\delta^{15}N$ than the big herbivores and are therefore potential candidates for the missed prey fraction (Drucker, 2001). Another possibility to explain this low $\delta^{15}N$ value is that this specimen could be chronologically younger and of post-LGM age. Similar values are observed in the Jura and Paris Basin in a Post LGM context (Bocherens et al., 2011a). Direct dating would help to solve this issue.

As soon as cave hyena is not part of the mammoth steppe ecosystem (like in Siberia), it seems cave lion explored prey with lower $\delta^{13}C$ values and/or had at least access to a broader species spectrum. It seems the collective hunting species like wolf (especially in post-LGM context) and cave hyena (in pre-LGM context) were at an advantage and been dominant predators to cave lions (Bocherens, 2015).
Taken together, the three predator species occupies distinct ecological niches which present the different prey preference for each of them.
A special focus of attention is paid on the hominids: The hominids in general do not interfering with other potential animal competitor. There is only a very minor overlapping with the hyena and AMH as well as the Spy Neandertals. The hominids occupied a very specific ecological niche in terms of isospace within the carnivorous guild. While debating within the hominids group, the Spy Neandertals, the ones from Goyet and the AMHs are overlapping intensively to each other. This overlapping pattern is the most extensive in this context. The Spy Neandertals share half of their isospace with the one from Goyet. The Goyet Neandertal isospace is close to complete within the variation of the Goyet AMH. The Goyet Neandertals and AMH from Goyet are more similar to each other in terms of isospace, than the Spy

Neandertals to the Goyet ones. Only by stable carbon and nitrogen isotopic composition it is not possible to distinguish both types of hominids.

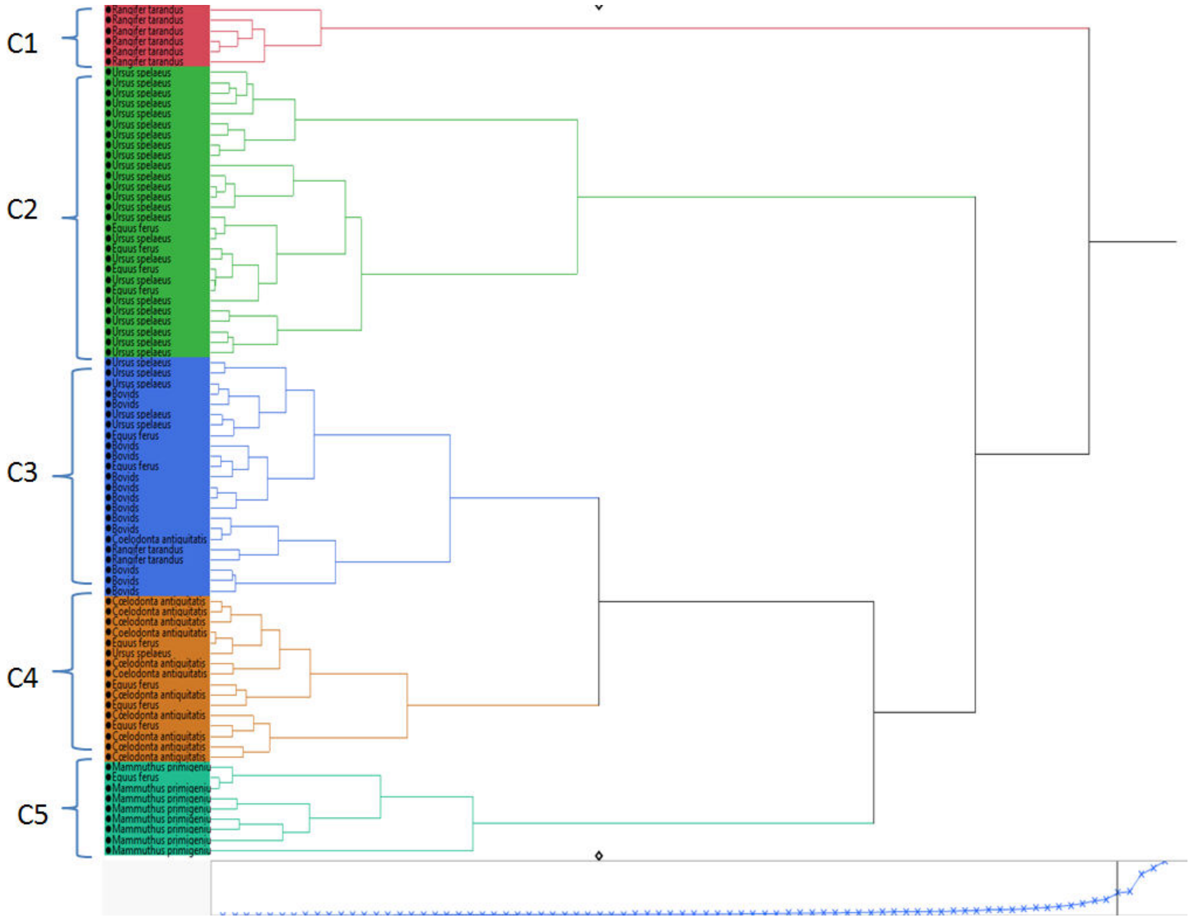
6.2.3. Cluster Analysis

The cluster analysis presents isotopic values of single individuals regardless of their species attribution. Each cluster represents similarities in dietary terms. This approach provides interesting insights in the general niche partitioning of the ecosystem. If a cluster is exclusively constituted by one species, this indicates e.g. a very high degree of specialisation for this species. Or the other way around, if a given species is represented in several cluster this would indicate a higher degree of dietary flexibility. Each cluster represents a distinct ecological niche which can be exhausted by an optional number of species.

6.2.3.1. Herbivores

The herbivorous species yielded 5 different clusters (Figure 11).

Figure 11



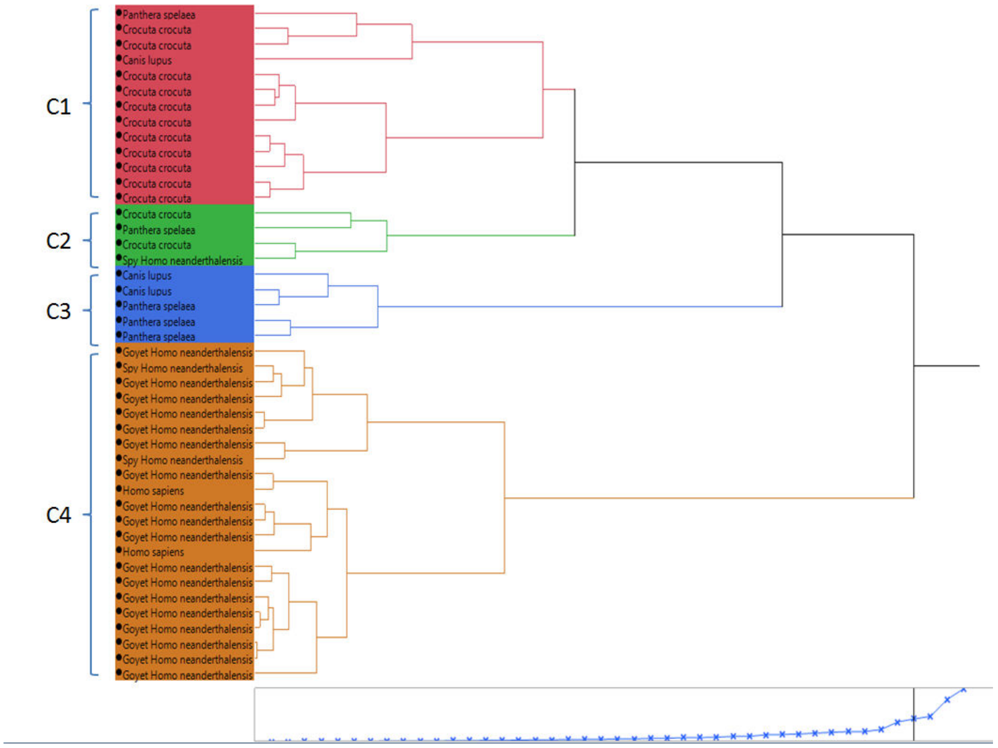
Clusteranalysis herbivores (Wißing et al. in prep.)

The first cluster represents only reindeer. The characteristic isotopic signal is based on their preference on lichen; only two individuals are in cluster 3. The second cluster contains essentially cave bears and contains 24 out of a total of 29 cave bear individuals. The only other taxa represented in cluster 2 is the horse (N=4). The ecological niche of the cave bear is reflected through this cluster. Cluster 3 contains a broad spectrum of species with a clear dominance of the bovids (13 out of 23). All bovids are represented only within this cluster, therefore it describes the typical niche for bovids. However, this niche is not restricted to one species only. Five different taxa are represented in there. Bovids occupied a niche other species could step in easier than in cluster one and two. Cluster 4 is dominated by woolly rhinoceros all representatives of this species are within this cluster with the exception of one individual, from cluster three. This ecological niche is more specialized than the third cluster since the number of species and individuals are quite limited, consequently the niche rhinoceroses occupied can be characterized as relatively specific since the overlap with the others seems to be limited. Cluster 5 contains all mammoth specimens, beside one horse exclusively mammoth is represented here. The mammoth inhabited a clear, specific niche.

All together I can postulate different degrees of flexibility for different species, based on the clusteranalysis.
Reindeer, mammoth and cave bear occupied very specific dietary niches. In the typical cluster of these species the presence of other individuals is very limited. In contrast the horses are much more flexible, since they occur in 4 out of 5 clusters. The cluster of the bovids and the one where almost all rhinoceroses appear have a more general character, and are not exclusive.

6.2.3.2. Carnivores

Figure 12



Cluster analyses Carnivores (Wißing et al in prep.)

The carnivores produced 4 clusters (Figure 12). The first cluster is constituted out of 13 specimens and the majority (N= 11) is representing different hyena individuals. This cluster reflects the typical ecological niche, in terms of carbon and nitrogen stable isotopic composition, of the hyenas. All hyena specimens beside two are within this cluster, therefore is seems plausible to name the cluster “hyena cluster”. The second cluster contains the smallest number of specimens (N=4) while three different species are represented: two hyenas, one cave lion and one Neandertal specimen from Spy. One characteristic commonality the four specimens have, are the lower δ^{13}C values in combination with (in relation to other representatives of the same species) lower δ^{15}N values. These individuals are more intensively relying on cave bears, than on reindeer, this tendency is especially true for the first two specimens, the hyena and the cave lion. The other hyena specimen and the Spy Neandertal are in the relative context of their specific species less intensive explorating the reindeer. Each representative within this cluster is not part of the cluster where the majority of their species is represented. It seems to be a relatively fragile mammoth steppe predator cluster with a slightly refusal for reindeer and a minor preference for cave bear. Anyhow, the small number of specimens and the high diversity of species is what characterizes the cluster and implies an intensive competition among representatives of this cluster. Based on this the cluster is preliminary named the “cluster of the outcasted”.

The third cluster consists out of two wolves and three cave lions. All individuals that belong to this cluster have a clear preference for reindeer. This is especially true for the three cave lion specimens, like discussed above. This cluster represents the classical reindeer hunter and is therefore named the “reindeer hunter cluster”.

The last cluster contains all hominids beside one specimen from Spy which was discussed above. No other species are present in cluster 4. Both types of hominids cluster intermixed to each other. An important visualization can be seen in the general patter of the whole cluster analysis: The first brench-off in the diagram (Figure 12) divided the hominids (except one) from the rest of the carnivorous species. All carnivorous animals are closer to each other, than to Neandertals and AMH. The early brench–off of the hominids demonstrate that within the carnivorous guild both types of hominids played the same, extreme specific role. Cluster 4 is consequently named the “hominid cluster”.

6.2.4. Summary niche partitioning

The niche partitioning among herbivores and carnivores in the mammothsteppe ecosystem was distinct. This can be evaluated through the stable carbon and nitrogen composition in bone through different ways to process the data. The Late Pleistocene in Belgium for around 30,000 and 50,000 years provided an intact ecosystem without any indications for dietary or habitat inducted stress. Among the herbivores the reindeer, the mammoth and the cave bear occupied the most special niche. The rhinoceros and bovids occupied a niche which was not exclusively occupied by them. The horse is probably the most flexible herbivorous species. Among the carnivores each species had a special prey preference with only limited overlap with other potential predators. The hyena was the dominant faunal predator; these in packs hunting species outcompeted other species like the cave lion and wolf. The cave lion scatters in general around the niche occupied by hyenas and was relaying either in cave bear or on reindeer. The individually scattered isotopic values indicate a solitary hunting strategy. The wolf is relatively flexible in terms of diet. The specimens part of this study are either focused on reindeer, or on cave bear/small mammals.The hominids occupied the most special niche in the carnivorous guild. Neandertals and modern humans are not distinguishable through their isotopic values.

6.3. Hominid prey preference

To establish quantitative and qualitative concepts of preferred prey in hominids diet a Bayesian method (SIAR V4, Stable Isotope Analysis-package in R) was used. The impact of proteins derived from meat is overestimated (see section methods). For the detection of plant food in omnivorous diet the analysis of amino acids like glutamic acid and phenylalanine is a much more precise tool and has been performed on the Spy Neandertals (Naito et al., 2016). The study by Naito et al. (2016) was the first application of this approach on Neandertal collagen and demonstrated, that the Spy Neandertals relayed for up to ~20% of their protein source on plants. The omnivorous character of Neandertal diet has been directly proven and quantified in this important study by Naito et al. (2016). Not only in the light of these results, the diet reconstructions based on bulk collagen values have to be regarded as relative estimations, not absolute ones. Three different graphs were produced presenting the results.

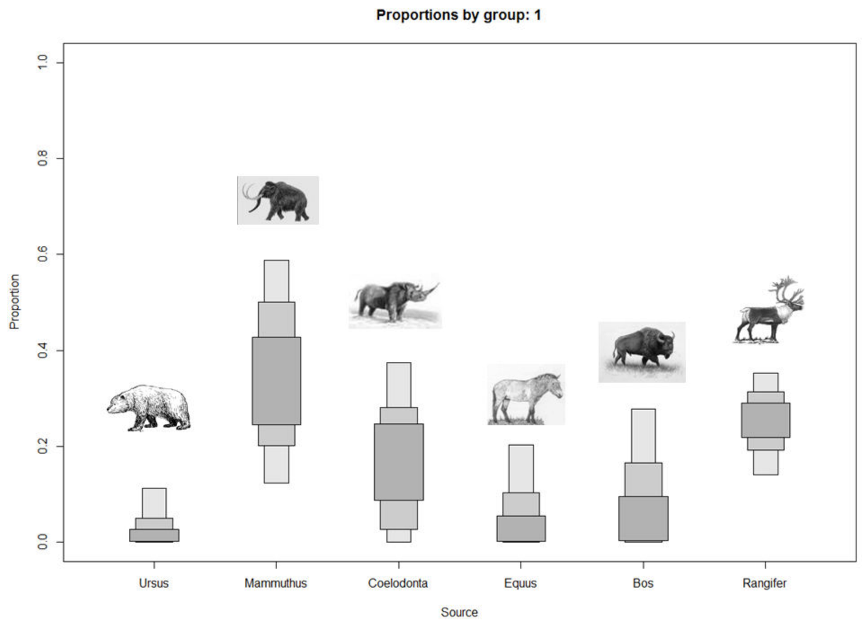
First, the proportion box plots: there are three different grey scales shown. The lightest grey represents a probability of 95%, the medium grey 75% and the darkest grey 25%; equivalent to this a violin plot was drawn for the AMHs (the black boxes and whiskers show median with 1st and 3rd quartiles and ranges with 1.5 times length of the interquartile range above the 3rd quartile or below the 1st quartile, respectively. The shaded area indicates Karnel density plot of the probability density of prey proportions.

Second, the probability density curve which shows the probability for a given relative amount. Third, for a better understanding of the statistical dependences between each potential prey to all the others, their statistical dependences are expressed against each other through a diagnostic matrix plot. There can be either a positive or negative correlation between two or more species. The SIAR software provides results taking into account these correlations among species, in this case an increasing probability range for the potential prey. Not only can the preferred prey be reconstructed, but also the other way around: who was predating on whom.

6.3.1. Neandertals

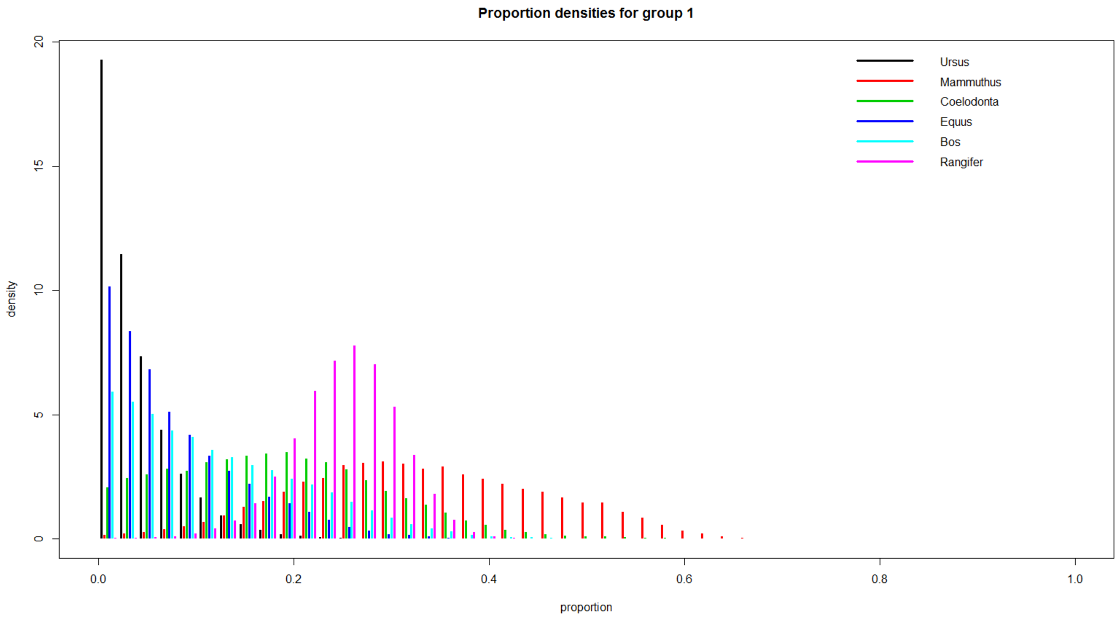
The Neandertals diet preference in drafted in figure 13. It is obvious that the relative meaning of species is different. The cave bears were the most unimportant species in Neandertals diet. The highest probability proportion is around 0 and decreases rapidly down to around 0% probability at an amount of 20%. In contrary the mammoth contributed most, with an amount between 15 and 60% (Figure 13) and the highest probability in the range between 30 and 40% (Figure 14). In figure 15 it becomes also clear that the probability density for a certain amount cannot be encircled more in detail, since there are some negative correlations with other species, like rhinoceros, horses and bovids.

Figure 13



Species Proportion of Neandertals (modified after Wißing et al., 2015b)

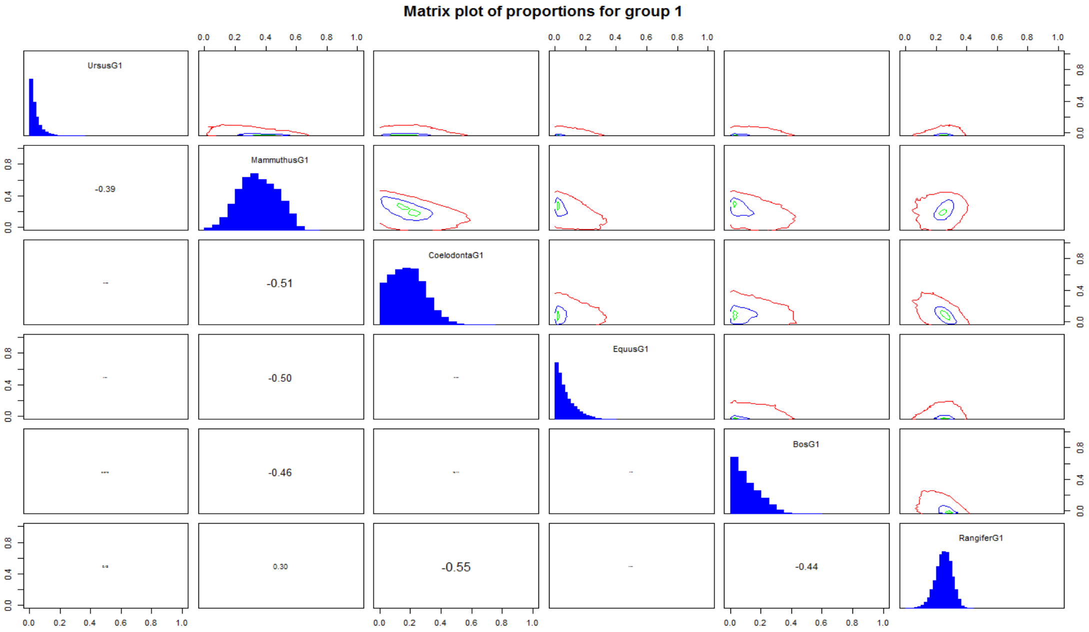
Figure 14



Property density for Neandertal preferred diet (Wißing et al., 2015)

This implies if these species were less represented in their proportions, the probability for a higher amount of mammoth would increase (Figure 15). From a statistical point of view it is even somehow more complex, since there is a strong negative correlation between rhinoceros and reindeer as well (Figure 15).

Figure 15



Matrix plot Neandertals (Wißing et al., 2015b)

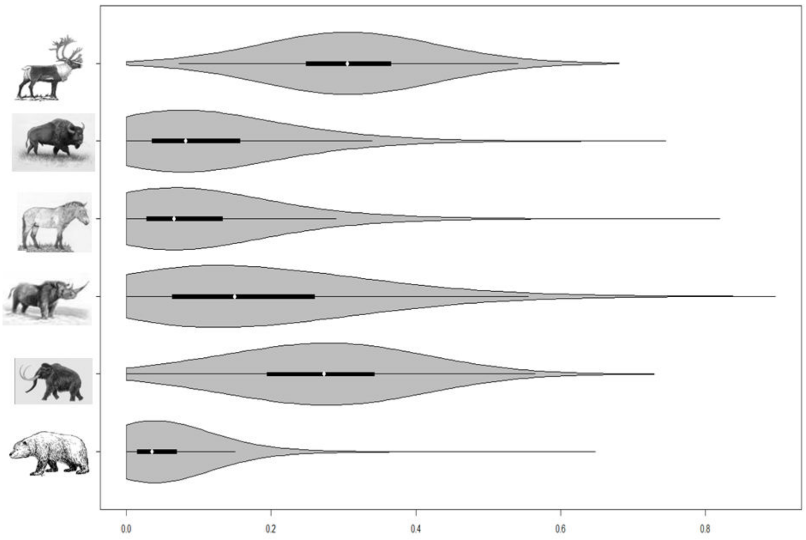
The relative amount of rhinoceros was around 20%. The amount of reindeer in Neandertals diet can be estimated at around 25% with the highest proportion density even at this level. The statistical correlations indicate that a less amount of reindeer would result in a higher amount of rhinoceros (and vice versa) in Neandertals diet. The positive correlation between reindeer and mammoth is indicating that a higher amount of reindeer would need a higher amount of mammoth in the Neandertals prey spectrum. Bovids and horses played only a minor role in Goyet Neandertals' prey choice.

The most important prey species for the Goyet Neandertals were the mammoth, and the reindeer, followed by rhinoceros. Cave bear contributed the less to the Goyet Neandertals' diet.

6.3.2. Modern humans

Since the stable isotopic composition of the AMHs is very similar to the values obtained on the Neandertals the preferred prey species is similar as well for AMH specimens Q116-1 and Q376-1 (Figure 16).

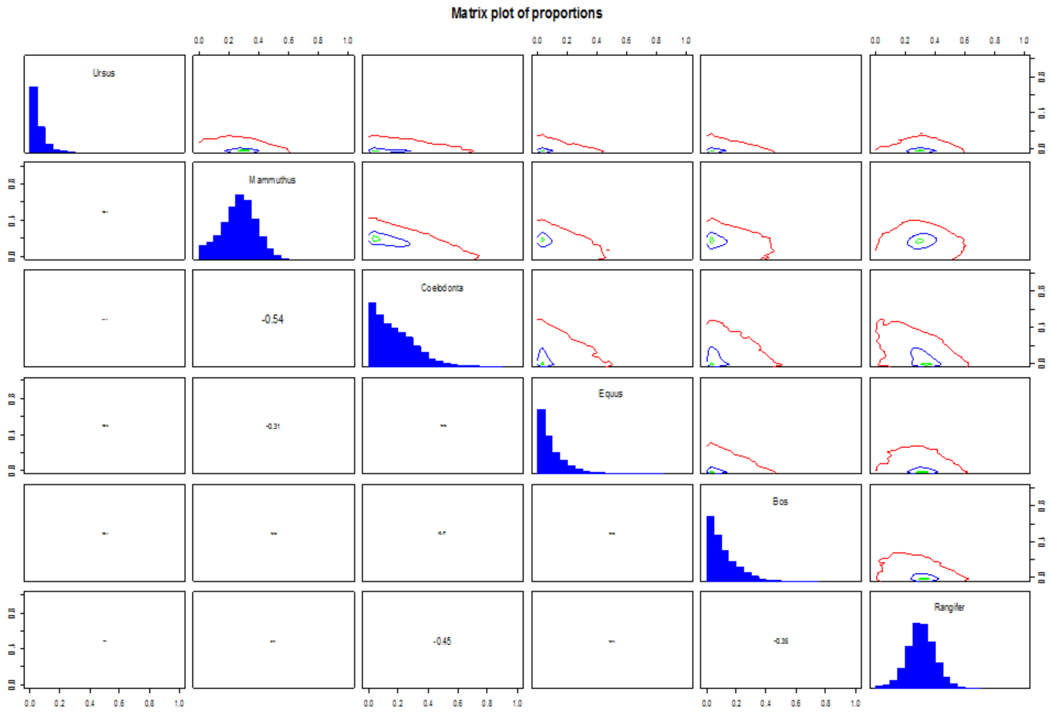
Figure 16



Violin plot Prey preferences modern humans (Wißing et al, in prep.)

The statistical dependence between potential prey species are very similar to what has been observed for the Neandertals (Figure 17). The highest correlations are between the mammoth and the rhinoceros, between the rhinoceros and the reindeer and between the bovids and the reindeer. The negative correlation among mammoth and rhinoceros implies a higher amount of mammoth would need a lower amount of rhinoceros or an increasing amount of rhinoceros followed by a lower quantity of mammoth (Figure 17). The strongest correlation is between mammoth and rhinoceros. By considering further the negative correlation between rhinoceros and reindeer, it becomes clear, that a lower amount of rhinoceros would imply a higher amount of reindeer and mammoth at the same time, since there are negative correlations between rhinoceros and mammoth and rhinoceros and reindeer. Beside these uncertainties which result always in increased probability ranges the relative ranking of preferred prey is similar for both types of hominids.

Figure 17



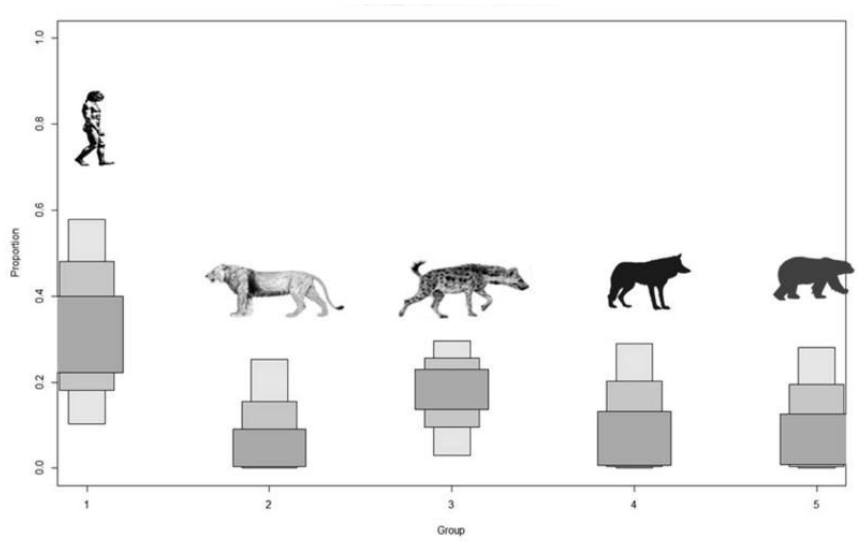
Matrix plot modern humans (Wißing et al, in prep.)

6.3.3. The role of mammoth as prey

Mammoth was for both, Neandertals and modern humans, the most important protein source. The abundance of this key species in the ecosystem is therefore directly associated with the subsistence of prehistoric humans. Like discussed above, all carnivorous species occupied a distinct ecological niche. Predation on mammoth was in general a characteristic of hominids subsistence strategy in the late Pleistocene (Figure 18).

No other species had so regular access to this megaherbivore. The only species with a reasonable amount of mammoth in their diet was the cave hyena. It seems reasonable hypothesize that hyena hunted juvenile mammoths, had probably access on carcasses left by hominids and scavenged on perished mammoth remains. The high amount of mammoth in hominids diet would only hard to be explained only by scavenging on mammoth. This would imply the humans could take possession of the mammoth killed by other predators/hyenas in an amount that these predators could not reach δ^{15}N as high as the scavenging hominids.

Figure 18



Predation on mammoth (Wißing et al., 2015b)

Basically the high δ^{15}N values of the hominids are the result of the intake of diet with high δ^{15}N, the mammoth. The ecological niche of hominids and hyenas is clearly separated. Considering these argument both types of hominids were active, selective hunters with a certain specialisation on mega herbivorous species, especially the mammoth.

Through the analysis of the site Lommersum it could be uncovered, that horses already at the time of the first humans can yield isotopic values which are roughly in the range of mammoth. If I assume, AMHs hunted horses with a similar isotopic composition than the mammoth, it would not be possible to distinguish both sources through stable isotopic analysis of bulk collagen.

Especially important here, the ^{15}N content can reach the same level like in mammoth, anyhow this does not imply that horses always occupied completely the mammoth niche, in contrast. In Lommersum the horse δ^{13}C values are lower than horse values seen e.g. in Belgium; already as low as for the analysed Lommersum mammoth ivory. The ivory yielded relative low $\delta^{15}N$ value of 7.6‰ in comparison to the Belgium mammoth remains (av. 8.5‰) and values obtained at the Geißenklösterle by Drucker et al. (2015).

In the pre-LGM context, the niche of the mammoth can be described as very distinct based on isotopic composition. The horses in contrast are very flexible herbivores. The horses of Lommersum yielded a broad spectrum of $\delta^{15}N$ values, which could never be seen for the mammoth in this kind of chronological and ecological context.

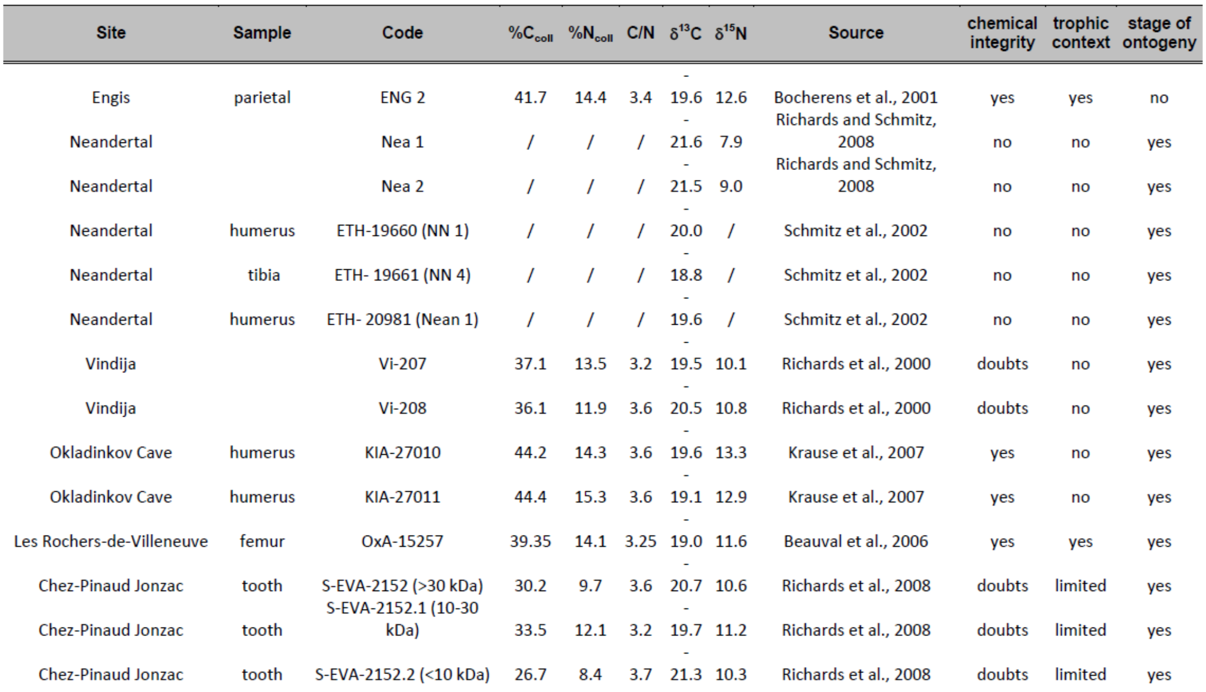
The characteristic of the scattered $\delta^{15}N$ horse values up to the range expected for mammoth in an Upper Paleolithic context could be observed for the horses in the Ach valley as well, not exclusively in Lommersum (Drucker et al., 2015). The horses never entered completely and most important not exclusively the ecological niche of the mammoth. In an ecological context where probably no mammoths are around like in the final Gravettian epoch in SW France (Drucker et al., 2015), the niche of the mammoth is disappearing as well and the horse just adjust to the same niche they occupied in a context where mammoth population was undisturbed. The horses can only step into this niche, when mammoth is around, but not so numerous. Mammoth are impacting the landscape through their mechanical (feeding, trampling, and digging) and biological actions (incomplete digestion, dung rejection) shaped the landscape and enhances finally the ecosystem productivity. This species created at least partly their own niche (Haynes, 2012; Zimov et al., 2012) in which horses never went in completely.

If modern humans from Goyet would have preferred horses instead of mammoth, the average isotopic signal would be lower than the observed values and not as high as demonstrated for the Neandertals. Anyhow an underestimation effect of the intake of horse meat in AMHs cannot be ruled out at this point.

6.3.4. Review of isotopic signatures of late Neandertals

To reconstruct dietary aspects of prehistoric hominids, certain requirements should be met: the chemical characteristics of the collagen must fit established criteria for valid collagen, the stage of ontogeny should be considered with a special attention on nursing (one trophic level higher than the mother) and an ecological context is needed to place the hominids in. Only a limited numbers of studies were perform following these criteria (Table 6).

Table 6



Site	Sample	Code	$\%C_{coll}$	$\%N_{coll}$	C/N	$\delta^{13}C$	$\delta^{15}N$	Source	chemical integrity	trophic context	stage of ontogeny
Engis	parietal	ENG 2	41.7	14.4	3.4	-19.6	12.6	Bocherens et al., 2001	yes	yes	no
Neandertal		Nea 1	/	/	/	-21.6	7.9	Richards and Schmitz, 2008	no	no	yes
Neandertal		Nea 2	/	/	/	-21.5	9.0	Richards and Schmitz, 2008	no	no	yes
Neandertal	humerus	ETH-19660 (NN 1)	/	/	/	-20.0	/	Schmitz et al., 2002	no	no	yes
Neandertal	tibia	ETH- 19661 (NN 4)	/	/	/	-18.8	/	Schmitz et al., 2002	no	no	yes
Neandertal	humerus	ETH- 20981 (Nean 1)	/	/	/	-19.6	/	Schmitz et al., 2002	no	no	yes
Vindija		Vi-207	37.1	13.5	3.2	-19.5	10.1	Richards et al., 2000	doubts	no	yes
Vindija		Vi-208	36.1	11.9	3.6	-20.5	10.8	Richards et al., 2000	doubts	no	yes
Okladinkov Cave	humerus	KIA-27010	44.2	14.3	3.6	-19.6	13.3	Krause et al., 2007	yes	no	yes
Okladinkov Cave	humerus	KIA-27011	44.4	15.3	3.6	-19.1	12.9	Krause et al., 2007	yes	no	yes
Les Rochers-de-Villeneuve	femur	OxA-15257	39.35	14.1	3.25	-19.0	11.6	Beauval et al., 2006	yes	yes	yes
Chez-Pinaud Jonzac	tooth	S-EVA-2152 (>30 kDa)	30.2	9.7	3.6	-20.7	10.6	Richards et al., 2008	doubts	limited	yes
Chez-Pinaud Jonzac	tooth	S-EVA-2152.1 (10-30 kDa)	33.5	12.1	3.2	-19.7	11.2	Richards et al., 2008	doubts	limited	yes
Chez-Pinaud Jonzac	tooth	S-EVA-2152.2 (<10 kDa)	26.7	8.4	3.7	-21.3	10.3	Richards et al., 2008	doubts	limited	yes

Comparison of late Neandertals (Wißing et al., 2015b)

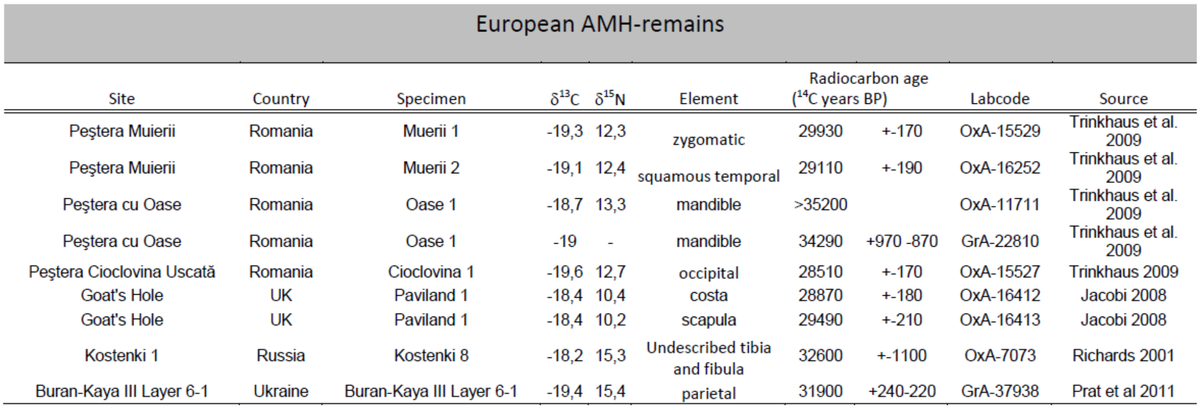
The remains from Engis (Bocherens et al., 2001), the analysis done on the remains from Les Rochers-de-Villeneuve (Beauval et al., 2006) and the Neandertal remains from Les Pradelles as well as from Saint-Césaire (Bocherens et al., 2005) are the only data fulfilling the conditions for valid dietary reconstruction. In all cases the Neandertals occupied the same ecological niche like drafted here. They were top predators with a clear preference for the terrestrial megaherbivores. Their ecological niche was very similar in Western and Central Europe. Unfortunately the collagen preservation in late Neandertal remains of sites outside the typical mammoth steppe for example in Southern Europe is not given. It could be important in the context of potential adaption strategies and cultural dynamics how Neandertals' ecology may changed in response to different environments. Maybe they tended to include smaller mammals like lagomorphs and birds (Finlayson et al., 2012) or the amount of plants in the diet was higher due to a broader offer (Fiorenza, 2015; Hardy and Moncel, 2011). In some circumstances also the exploitation of aquatic resources has been hypothesized (Bocherens et al., 2014a).

For me it seems plausible that Neandertals had a dietary ecology essentially driven by environmental and ecological circumstance and embedded in a complex cultural context.

6.3.5. Review of isotopic signatures of ancient modern humans

Like discussed above the presents of earliest modern humans in Europe is limited in terms of fossils in Europe. The initial upper Paleolithic complexes are not doubtless associated with human remains in Europe (see Figure 3). Beside the lack of skeletal material, not all remains were analysed for stable isotopic composition. The ones analysed are provided here in table 7.

Table 7



European AMH-remains

Site	Country	Specimen	$\delta^{13}C$	$\delta^{15}N$	Element	Radiocarbon age (^{14}C years BP)		Labcode	Source
Peştera Muierii	Romania	Muerii 1	-19,3	12,3	zygomatic	29930	+-170	OxA-15529	Trinkhaus et al. 2009
Peştera Muierii	Romania	Muerii 2	-19,1	12,4	squamous temporal	29110	+-190	OxA-16252	Trinkhaus et al. 2009
Peştera cu Oase	Romania	Oase 1	-18,7	13,3	mandible	>35200		OxA-11711	Trinkhaus et al. 2009
Peştera cu Oase	Romania	Oase 1	-19	-	mandible	34290	+970 -870	GrA-22810	Trinkhaus et al. 2009
Peştera Cioclovina Uscată	Romania	Cioclovina 1	-19,6	12,7	occipital	28510	+-170	OxA-15527	Trinkhaus 2009
Goat's Hole	UK	Paviland 1	-18,4	10,4	costa	28870	+-180	OxA-16412	Jacobi 2008
Goat's Hole	UK	Paviland 1	-18,4	10,2	scapula	29490	+-210	OxA-16413	Jacobi 2008
Kostenki 1	Russia	Kostenki 8	-18,2	15,3	Undescribed tibia and fibula	32600	+-1100	OxA-7073	Richards 2001
Buran-Kaya III Layer 6-1	Ukraine	Buran-Kaya III Layer 6-1	-19,4	15,4	parietal	31900	+240-220	GrA-37938	Prat et al 2011

Stable isotopes of early modern human (Wißing et al., in prep.)

Beside the specimen from Goat's Hole (Paviland 1) (Jacobi and Higham, 2008) all remains came from the periphery of Europe, basically from Eastern Europe. Paviland 1 yielded clearly the lowest $\delta^{15}N$ and highest $\delta^{13}C$ values.

The remains from Romania (Peştera Muierii, Peştera cu Oase and Peştera Cioclovina Uscată) (Trinkaus et al., 2009) as well as the one from Russia (Kostenki 1)(Richards et al., 2001) and the ones from the Crimea Peninsula (Buran-Kaya III) (Prat et al., 2011) yielded higher $\delta^{15}N$ values than obtained from all the analysed Neandertals.

Through direct comparison of single isotopic data some authors (Pettitt et al., 2003; Richards et al., 2001; Richards and Trinkaus, 2009) concluded that basically AMHs had a greater reliance on marine and freshwater resources and in general a broader food spectrum. (Aquatic ecosystems can yield higher $\delta^{15}N$ values based on a longer foodchain). The difficulties and limitations to compare directly single isotopic values instead of relative ones ,embedded in an ecological context, has been described in detail above. A chronological and spatial shift of the isotopic baseline is a well observed phenomenon in this time range (Bocherens et al., 2014b; Wißing et al., 2015a). None of the sites where ancient modern skeletal remains could be discovered, late Neandertal remains have been found as well. But the sites in Romania produced Middle Paleolithic industries in which the faunal composition is very similar to the one in layers supposed to be the result of AMH activity (Trinkaus et al., 2009), this does not imply major dietary difference between Neandertals and modern humans at these places.

A study performed on the remains of Buran-Kaya III (Prat et al., 2011) provided an adequate ecological background for the AMH and it was clearly demonstrated, that the isotopic baseline is higher than in the Neandertal cases. All analyzed herbivorous species are enriched in $\delta^{15}N$ relatively to the sites investigated for Neandertal diet. The authors of this study conclude that the isotopic composition of this AMH composed of mainly terrestrial resources (Prat et al., 2011). This conclusion corresponds with the results obtained on the early AMH from Goyet.

6.3.6. Summary diet reconstruction for hominids

The late Neandertals and the first modern humans in the Late Pleistocene mammothsteppe ecosystem of NW Europe yielded very similar relative stable isotopic carbon and nitrogen isotopic values of bulk bone collagen. The ecological niche both types of hominids occupied was very similar in terms of diet and habitat. Both focused on terrestrial herbivore meat with a special preference for the megaherbivores like mammoth. For both hominids the mammoth and the reindeer played an essential role (Wißing et al., 2015b). Since the analysis of bulk collagen does not allow the reconstruction of plant food, the study of Naito et al. (2016) showed that even in the mammothsteppe the Spy Neandertals had an intake of around 20% plant protein in their diet. A broader dietary spectrum for modern humans in contrast to late Neandertals cannot be consulted.

6.4. Aspects of habitat and mobility

6.4.1. Context

Only very initial research has been processed to investigate the δ^{34}S isotopic compositions of Pleistocene bone collagen.

The sulfur isotopic composition of terrestrial mammals is mainly driven by the bedrock (see section 1.4.). In the archeological record, the local spectrum of δ^{34}S values should be evaluated to recognize any potential specimens with different origin. The Belgium sites form the background for this study since Goyet and Spy provided the hominid material.

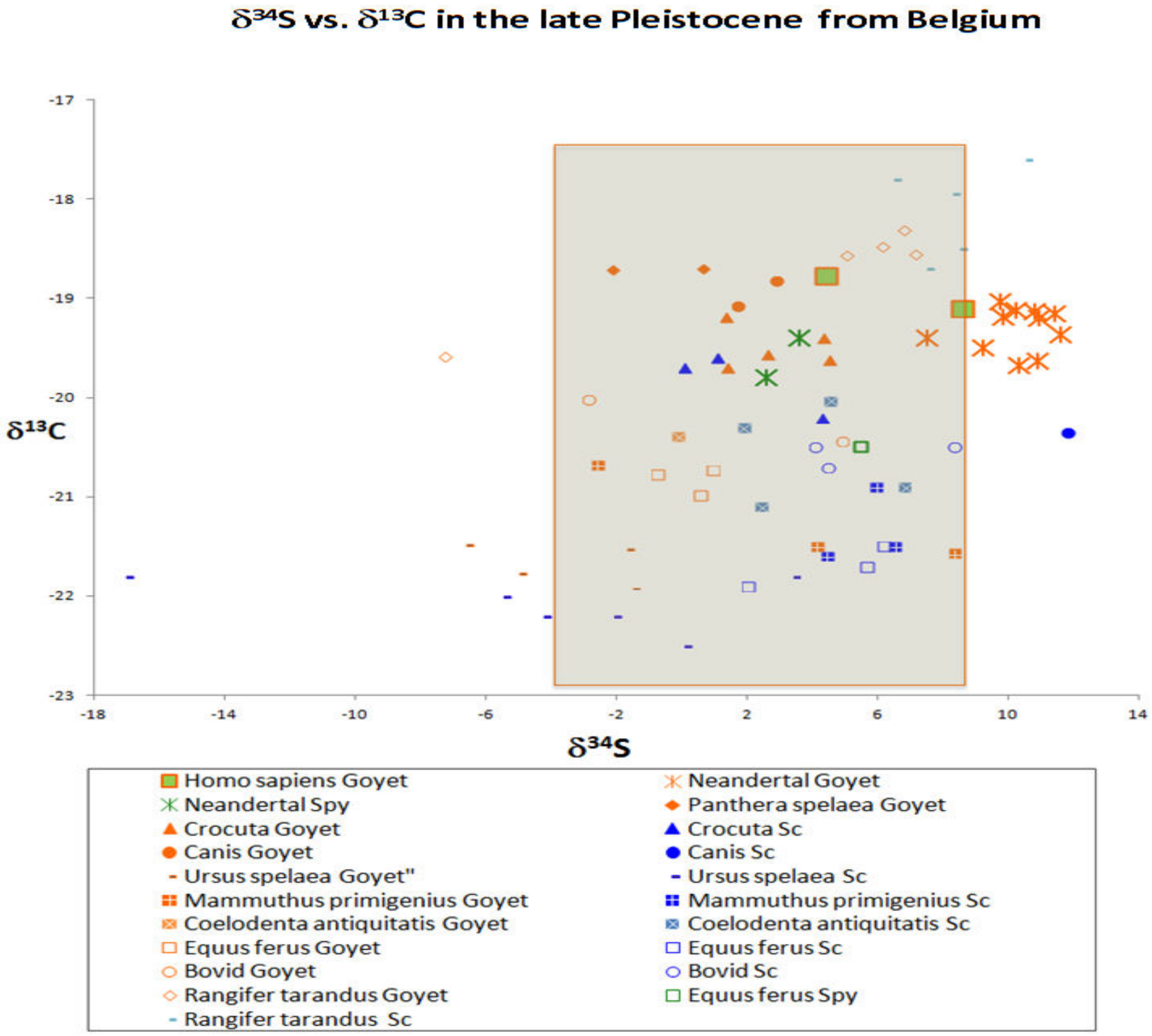
The total isotopic ranges observed from Belgium late Pleistocene sites have been investigated in some other similar contexts as well: In the Moravian Plain the site of Predmostí was investigated for δ^{34}S isotopic composition (av. 2.25‰; N=14) (Bocherens et al., 2015), at the Geißenklösterle in the Ach Valley in SW-Germany (av. 0.24‰; N=8; exclusive one non-local reindeer specimen) (Drucker et al., 2015). Furthermore the sites Ziegeleigrube Coenen (av. 3.6‰; N=15) (Wißing et al., 2015a) and Lommersum (av. 3.4‰; N=7) were investigated for δ^{34}S. The site with the highest δ^{34}S values for herbivorous species is Abri Pataud in Dordogne (SW-France) with an average of 10.3 ‰ (Drucker et al., 2015).

Each site/area represents their typical, local characteristic δ^{34}S. The Belgium sites provided the broadest ensemble of δ^{34}S for the whole Pleistocene so far.

6.4.2. late Pleistocene faunal remains Belgium

In figure 19 the δ^{34}S and δ^{13}C are plotted against each other. The faunal remains plot in essential between -3‰ and 8.5‰ (av. 2.5‰, N=60) (grey background in fig.19). some cave bears from Scladina and Goyet as well as one reindeer provided values which are clearly lower. One cave bear from Scladina even yielded a value of -17‰ δ^{34}S. It is striking that cave bear it the species with the lowest δ^{34}S values (av. -4.0‰) of the late Pleistocene in Belgium. This indicates the special ecological niche this species is occupying. It is reasonable to hypothesize not only the diet of this species is special, also the microhabitat. Since all cave bear specimens yielded low values, indifferently from which site, I exclude that all cave bear individuals were invaders in this region. They seem to be local in this region, but preferred a special microhabitat exclusively. Further investigation is needed to test if similar pattern can be recognized in other places as well. Unfortunately in none of the above mentioned sites cave bear has been investigated for δ^{34}S. In total no cave bears (*Ursus Spelaea*) beside the ones presented here were ever analysed for δ^{34}S.

Figure 19



2D-Scatter plot of the late Pleistocene in Belgium (Wißing et al, in prep)

Only one reindeer specimen from Goyet yielded δ^{34}S values similar to the ones observed for cave bear. In contrast to cave bear the reindeer is a migratory species and I conclude this specimen has probably another origin.

The “local” sulfur isotopic signal was only roughly constructed, basically on the faunal carnivores, especially the hyenas and additionally the main field of herbivorous species. The hyenas of Goyet and Scladina are relatively centered in the grey field. Since they have access to all species (Wißing et al., 2015b), they represent average $\delta^{34}S$ composition of the area. The horse is a none-migrating species, at least not seasonally, and is therefore supposed to reflect the local $\delta^{34}S$ signal as well.

One canid and some reindeer tooth specimens from Scladina yielded $\delta^{34}S$ values higher the main field. In most of the cases the $\delta^{34}S$ values for the Goyet specimens are slightly higher, than the ones obtained on the site Scladina. I expect this phenomenon represents differences in the microhabitat.

In both cases, when specimens appear with lower or higher $\delta^{34}S$ isotopic composition than the main field this implies other habitats in the mobility circumference for this species, probably with the exception of the cave bear. A comparison of tooth dentin collagen and bone collagen of the same individual could indicate intra-individual mobility aspects. Dentin isotopic composition reflects the signal catches during the time of tooth formation, while bone collagen reflects the average of the last years of a given species. Especially in the case of reindeer this approach could result in deeper understanding of mobility of this species in this area in the late Pleistocene, since they yielded the most extreme values among the herbivores and provided a reasonable portion in hominids diet. Seasonal migrating pattern of this species has been documented in SW-France (Jonzac) at the same time through strontium isotopic analysis (Britton et al., 2011).

6.4.3. late Pleistocene human remains Belgium

This study presents $\delta^{34}S$ of three different local hominid groups: The Neandertals from Goyet, the ones from Spy and the modern humans from Goyet (Figure 12).

6.4.3.1. Neandertals

The Spy Neandertals yielded values of 3.6 and 2.6‰ $\delta^{34}S$ and are therefore centered in the field defined as reflecting the local signal (Figure 19). The main prey of both individuals had an origin in the neighborhood of the Spy site. Their values correspond to the ones obtained on carnivores like hyenas and canids from Goyet.

The Goyet Neandertals in contrast yielded the highest average $\delta^{34}S$ values of the ecosystem. No other species beside one canid and some reindeer tooth specimens (both Scladina) yielded similar values (Figure 19). The $\delta^{34}S$ composition is relatively homogeneous which indicates the homogeny of the whole group in terms of origin. Only one individual (Q305-4) yielded slightly lower $\delta^{34}S$ values (7.5‰). Interestingly enough this specimen also provided the lowest $\delta^{15}N$ values of all hominids (10.7‰). Based on the $\delta^{34}S$ isotopic composition, an assumption about a geographical origin different from the local faunas is robust. The non-local Neandertal group was entering the area, maybe in the context of seasonal migration: In this case the stay and intake of protein has to be limited in time and amount otherwise these Neandertals would accumulate the local signal. Another hypothesis is that the Neandertals visited the area only for a short time and potentially even for their first time. The Goyet place was surely the place they visited the last time in their life. The role as foreign invaders becomes even more intriguing while considering that most of the Goyet Neandertals show evidence for cannibalism (Rougier et al., 2012, accepted) while this not the case for the local Spy remains. A more concrete geographical origin for the Goyet Neandertals is so far not really possible. I exclude an origin close by to all Belgium and German sites mentioned here, since all of them provided $\delta^{34}S$ values much lower. The only area where similar $\delta^{34}S$ values could be obtained was in the Dordogne in SW-France (Drucker et al., 2015).

6.4.3.2. Modern humans

Both AMHs yielded $\delta^{34}S$ values lower the ones obtained on the Goyet Neandertals. Only Neandertals specimen Q 305-4, discussed above, has slightly lower $\delta^{34}S$ than AMH individual Q116-1. AMH individual Q 376-3 is relatively centered in the field defined as local $\delta^{34}S$ signal. If we would hypothesize AMH had a higher intake of aquatic resources in their diet this could explain the difference between AMHs and Neandertals, but only in combination with higher $\delta^{15}N$ and $\delta^{13}C$ values. Since this is not the case, it is more robust to hypothesize that Neandertals and modern humans had an intake of main prey from different regions, while they exploited very similar prey species. It was the hunting ground which was different for the Goyet Neandertals and the Goyet AMH, in contrast to the Neandertals the AMHs relied on fauna closer by the site their skeletal remains could be discovered.

7. Conclusions

The Troisième caverne of Goyet provided the most considerable late Neandertal assemblage in Northern, Central and Western Europe, as well as very early modern humans. The skeletal remains are associated with an extended set of herbivorous and carnivorous Pleistocene species. The site is embedded in an archeologically rich landscape. All bone material is chemically well preserved for stable isotopic analysis. These circumstances to investigate the ecological aspects of late Neandertals and early modern humans in Europe are unique.

This study demonstrated that the mammothsteppe ecosystem between 30,000 and 50,000 NW Europe was of an ecologically robust structure, even through phases with harsher environmental conditions. During the time of the late Neandertals, no ecological stress could be observed in the structure of the foodweb, therefore the ecosystem provided the basis for late Neandertal subsistence also in colder phases of the OIS 3.

With the initial arrival of modern humans, ecological stress was detected on mammoths. Both types of hominids were essentially relying in the same manner on terrestrial mammals, mainly mammoth and reindeer. Hominids were the species with the most regular access to mammoth meat among the whole predator guild. No other predator competed directly with them. An increasing modern human population combined with more intensive mammoth exploitation than in previous times produced stress on the population dynamics of this megaherbivorous species, but not to the extent that mammoths disappeared totally during the Aurignacian in this area.

The ecological niche both types of hominids occupied is nearly identical in terms of diet. There are no indications for a broader subsidence strategy in AMHs ecology and therefore no potential dietary based arguments for the success of the one type of hominid and the decline of the other one during the late Pleistocene in NW Europe. These finds are especially important for the reason that other factors probably became even more relevant in Neandertal extinction process. If ecological reasons were negligible, cultural differences (especially aspects like social networks for information transfer/knowledge exchange) and mobility (of people and ideas) may have played a more significant role and provided advantages for the AMHs. The initial study of mobility aspects in this study already indicated that there are indeed some distinct complex differences among different groups and different types of late Pleistocene hominids.

Neandertals and modern humans occupied the identical ecological niche with the same preferences for diet but potentially different land-use strategies. Neandertals were ecologically replaced by modern humans. No ecological reasons can evidently be documented in the Neandertal extinction process in the studied area.

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Paleoecological and climatic implications of stable isotope results from late Pleistocene bone collagen, Ziegeleigrube Coenen, Germany

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ABSTRACT

Climatic and ecological conditions during Marine Oxygen Isotope Stage (MIS) 3 are complex and the impact of cold spells on the ecosystems in Central Europe still needs to be investigated thoroughly. Ziegeleigrube Coenen (ZC) is a late Pleistocene MIS 3 locality in the Lower Rhine Embayment of Germany, radiocarbon-dated to >34 ^{14}C ka BP. The site yielded a broad spectrum of mammal species. We investigated the carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) isotope signatures of bone collagen, since these are valuable tools in characterizing ecological niches, environmental conditions and aspects of climate and mobility. By comparison with pre- and post-Last Glacial Maximum (LGM) sites in Central Europe we show that ZC belongs in a cold event of MIS 3 and was climatically more similar to post-LGM sites than to pre-LGM sites. However, the trophic structure resembled that of typical pre-LGM sites in Belgium. This cold event in MIS 3 changed the bottom of the foodweb, but do not seem to have had a direct impact on the occurrence of the mammalian species and their ecological distribution. Apparently the (mega-) faunal community could adapt also to harsher environmental conditions during MIS 3.

Introduction

The late Pleistocene in Central Europe is characterized by intensive climatic oscillations and corresponding changes in environmental conditions (Dansgaard et al., 1993; Svensson et al., 2008). Even during the period between 50 and 30 ka ago, significant environmental fluctuations have been demonstrated by different approaches (pollen analysis, lake sediments, cave speleothems, among others) (Roucoux et al., 2005; Bohncke et al., 2008; Van Meerbeeck et al., 2011). Despite these changes, assemblages of large mammals in NW and Central Europe are strikingly monotonous, including herbivores such as woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), horse (*Equus* sp.), large bovines (*Bos*/*Bison*), giant deer (*Megaloceros giganteus*) and reindeer (*Rangifer tarandus*), as well as carnivores such as cave hyena (*Crocuta spelaea*), cave lion (*Panthera spelaea*) and wolf (*Canis lupus*). This faunal assemblage is characteristic of the “mammoth-steppe fauna” and seems to be resilient to a certain degree of climatic changes. One of the most interesting aspects of the Pleistocene is the adaptation of these species to such abiotic processes. Techniques such as stable isotope analysis of fossil bones or tooth microwear analysis can be due to gain dietary information for these large mammal species and to evaluate their ecological flexibility (e.g., Rivals et al., 2009; Bocherens et al., 2011a; Drucker et al., 2014).

Over the past decades, stable carbon and nitrogen isotope ratio values in bone collagen have been used successfully to decipher dietary preferences and niche partitioning among herbivorous and carnivorous species of the late Pleistocene in Europe (Fizet et al., 1995; Bocherens and Drucker, 2003; Bocherens et al., 2011a). The analysis of sulfur ($\delta^{34}S$) provides insights about the individual origin and mobility of the specimen (Drucker et al., 2012). The overall goal of the present study is to apply the carbon, nitrogen and sulfur isotope approach to finds from the recently reinvestigated paleontological site of Ziegeleigrube Coenen (Matzerath et al., 2012), and to present these results in the context of mammal ecology and their flexibility within Marine Oxygen Isotope Stage (MIS) 3 and MIS 2 at seven sites in Central Europe.

In order to generate paleoecological information on aspects such as soil activity, herbivore habitat characteristics, niche partitioning of the mammal assemblage and site integrity, it was necessary to compare the faunal spectrum of ZC to assemblages from sites of similar age located in neighboring regions (Fig. 1). Scladina Cave layer 1A (Bocherens et al., 1997) in Belgium was chosen, since it is approximately the same age as ZC and is located ~100 km away. This comparison will provide an example for the ecological variability within assemblages from the

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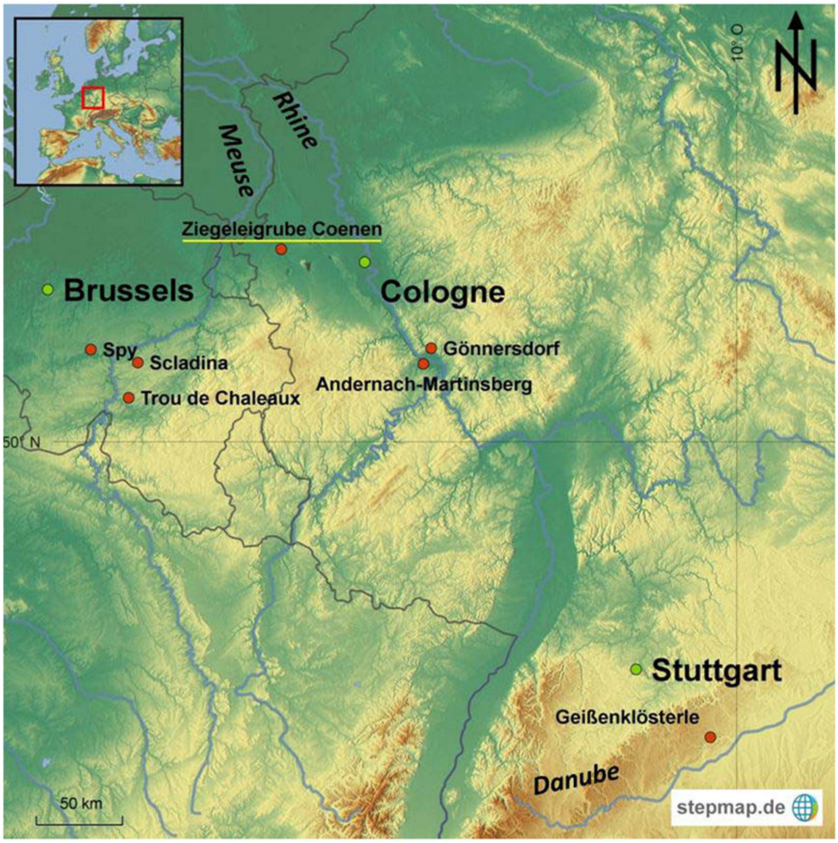

Figure 1. Location of the sites described in the paper (red dots).

late Pleistocene, since most of the terrestrial mammalian species mentioned here are represented at both sites.

The horse (*Equus* sp.) is the most common species at ZC, and δ^{13}C and δ^{15}N isotope values from these horses will be compared to existing isotope data of equids with secure stratigraphical, chronological and environmental contexts at other sites. These sites include the late glacial open-air settlements of Gönnersdorf and Andernach–Martinsberg, located in the Central Rhineland of Germany, and the late-glacial occupation level at the Trou de Chaleaux cave site in Belgium. Additional data are included from pre-LGM occupations at Spy, Scladina (Belgium) and Geißenklösterle (South Western Germany).

Principles of isotopic ecology of late Pleistocene fauna

Plant materials differ in the composition of their carbon, nitrogen and sulfur isotope values due to isotopic fractionation during chemical and physical processes, which depend on abiotic factors such as temperature, water availability, CO_2-concentration, nitrogen availability, salinity and irradiance and the geological background. The plant isotopic signature is passed on to the animal isotopic signature and then through the whole trophic web up to the top predators (Minagawa and Wada, 1984). Carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S) isotope values in terrestrial mammal bone collagen reflect an average of the isotopic composition of dietary protein consumed during the last few years of an individual's life (DeNiro and Epstein, 1978, 1981; Nehlich and Richards, 2009; Drucker et al., 2012).

In terrestrial ecosystems stable carbon isotopes are powerful tools in distinguishing between C3 or C4 photosynthesis pathway-based foodwebs (Farquhar et al., 1989; Cerling et al., 1998). In boreal and temperate ecosystems, where C4-plants are more or less absent, different values of δ^{13}C have been recorded for C3 plants, depending on whether the plants are growing in open or closed habitats. This phenomena is due to the canopy effect (Drucker et al., 2008). A vertical gradient in the δ^{13}C values of forest plants, with higher δ^{13}C values at the top of the canopy and lower values at the bottom, is typical of the canopy effect (Dawson et al., 2002; Drucker et al., 2008). However, it should be noted that a significant degree of forest closure is necessary to trigger detectable depletion in the δ^{13}C values of understory plants. Furthermore, a minor enrichment in δ^{13}C values can be observed through the trophic web. Some authors (Bocherens and Drucker, 2003) suggest a shift of 0.8 to 1.3‰ between herbivores and carnivores.

^{15}N isotope enrichment of around 3–5‰ occurs at every trophic level, providing an instrument to reconstruct different trophic levels within the same ecosystem at a given place and time (DeNiro and Epstein, 1981; Ambrose, 1990; Bocherens and Drucker, 2003). In general δ^{15}N values also underlying climatic conditions such as temperature and humidity (Heaton et al., 1986). Soil and plant δ^{15}N values systematically decrease with increasing mean annual precipitation (MAP) and decreasing mean annual temperature (MAT) (Amundson et al., 2003). Several studies have shown that some excursion of the baseline δ^{15}N values did take place in the late Pleistocene, shifting the whole terrestrial foodweb (e.g., Fizet et al., 1995; Drucker et al., 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004; Fox-Dobbs et al., 2008; Stevens et al., 2008; Bocherens et al., 2014; Stevens et al., 2014).

Sulfur stable isotope values (δ^{34}S) can be used to distinguish between marine and terrestrial resource exploitation (terrestrial animals usually have δ^{34}S values around 5–10‰ while marine organisms have a relatively constant δ^{34}S value of 20‰) and as an indicator for freshwater resource consumption (range between −22 and +22‰) (Peterson and Fry, 1987). In purely terrestrial contexts, they are also useful as indicators of a geographical/geological origin (Drucker et al., 2012; Nehlich, 2015). The majority of the sulfur is taken up through the roots as sulfate, which originates either from the bedrock or is deposited by rain. Plants receive the majority of their sulfur through their roots as sulfate, which is derived from the weathering of local geological formations. Therefore sulfur isotope analysis can be used analogous to, e.g., strontium isotopes as a geographical/geological indicator (Nehlich, 2015; Richards et al., 2003).

Material

Between 2009 and 2014 the paleontological assemblage from the loess site "Ziegeleigrube Coenen" (ZC), district of Düren, province Nordrhein–Westfalen in Germany, has been undergoing reinvestigation (Matzerath et al., 2012; Matzerath et al., 2014). In this paper we present 29 isotope values from ZC and discuss their ecological and climatic implications in the context of other pre- and post-LGM sites.

The faunal remains from the ZC were collected intermittently during 1964, 1967 and 1969 and consequently the assemblage is not complete (Matzerath et al., 2012). The paleontological remains consist of seven species of megafauna (2013): *Equus* sp., *Bos*/*Bison*, *Coelodonta antiquitatis*, *Megaloceros giganteus*, *Mammuthus primigenius*, *Crocuta spelaea* and *Panthera spelaea* (Table 1). The material was stored and cataloged at the Museum Zitadelle Jülich. Here we use sample numbers according to the inventory numbers of the museum, except that we replaced "1964-" by "ZC-" (Tables 2 and 3). Earlier AMS radiocarbon analysis (Matzerath et al., 2012) placed ZC in MIS 3, with ages falling between 34 and 43 ^{14}C ka BP. Two additional ages were beyond the limit of the radiocarbon method (Table 2).

Apart from the faunal remains, Hartwig Löhr also described two stone artifacts (now missing) from this site in 1969. With the only other trace of human activity being two bones displaying modifications possibly produced during marrow procurement (horse, *Equus* sp., ZC-101 and large bovid, *Bos*/*Bison*, ZC-95: Matzerath et al., 2012, 2014) the site cannot be classified unequivocally as "archeological."

The original find horizon was removed during intense quarrying activities. However, Matzerath et al. (2014) were able to reconstruct the sequence by comparing profile drawings sketched by W. Krieger, H. Löhr and J. Schalich in 1964 and 1969 with a section opened 100 m to the east of the place where the faunal remains have been found in the layer (Matzerath et al., 2014). The sediment in which the faunal remains were embedded was stratified in a sequence of loess deposits some 5.50 m below the surface. The remains had been deposited in the gravel and sand infill of a small channel, some 30 cm deep (Matzerath et al., 2014). Processes of erosion and accumulation characterized the deposit and the channel had probably cut through different sediment units in the course of its formation, resulting in a channel fill comprising mixed materials from maybe more than one stratigraphic layer. This mixing could explain the range in radiocarbon ages, discussed in the Discussion section below.

Methods: bone collagen extraction and isotopic analysis

Bone pieces between 200 mg and 350 mg were cut with a diamond-tipped cutting wheel set on a Dremmel rotating tool. Although care was taken to select untreated specimens, two of the bone samples, ZC-35 and ZC-91, have possibly been conserved with linseed oil (Matzerath et al., 2014). Collagen was extracted from 24 samples by the Biogeology working group in Tübingen University. Five additional collagen samples were extracted at the Center for Isotope Research, Groningen University, and sent to Tübingen for isotopic analysis. All stable isotope analyses were performed in the Department of Geosciences in Tübingen University following standard methods (Bocherens et al., 2011a,b). The outer bone surfaces of all samples were mechanically abraded, the bone pieces were washed twice in an ultrasonic bath in acetone and several times with distilled water, then dried and powdered to a homogeneous sample with a particle size less than 0.7 mm.

A preliminary determination of the whole bone nitrogen (N) content was performed following Iacumin et al. (1996, 1997) and Bocherens et al. (2005) to characterize the potential collagen preservation. Fresh bone contains around 4% nitrogen (e.g., Bocherens et al., 1991). The collagen extraction protocol was performed following a method modified from Longin (1971) as described by Bocherens et al. (1997). Some 250 mg of the bone powder was decalcified in 1 M HCl during 20 min at around 20°C and filtered through a 5 μm filter. The amount of bone powder depended on the nitrogen content of the bone, which approximately reflects the collagen yield. The residue was soaked in 0.125 M NaOH for 20 h at around 20°C. Afterwards the rinsed residue was heated in a closed container at 100°C for 17 h in a HCl solution with pH 2 until the collagen gelatinized. After filtration through a 5 μm filter, the liquid containing the gelatin was freeze-dried. The yield was calculated and expressed relative to the bone weight in mg g^{-1} (Bocherens et al., 1997). Elemental analysis (C_{coll}, N_{coll}, S_{coll}) was conducted at the Department of Geosciences at the University of Tübingen using an NC2500 CHN-element analyzer coupled to a Thermo Quest Delta + XL mass spectrometer. The chemical preservation of the collagen is expressed by the C_{coll}/N_{coll} atomic ratio (Table 2). A C:N atomic ratio of between 2.9 and 3.6 (DeNiro, 1985) and a nitrogen percentage of collagen (N_{coll}) above 5% (Ambrose, 1990) are considered to indicate well preserved collagen. The standard for δ^{13}C is the internationally defined marine carbonate (V-PDB). The standard for δ^{15}N is the atmosphere (AIR). Analytical error based on laboratory standards is ± 0.1‰ for δ^{13}C values and ± 0.2‰ for δ^{15}N. Samples were calibrated to δ^{34}S values relative to international standards NBS 123, NBS 127, IAEA-S-1 and IAEA-S-3. The reproducibility is ± 0.4‰ for δ^{34}S measurements, and the error on amount of S measurement is 5%. Only δ^{34}S values of samples for which the atomic C/S_{coll} and N/S_{coll} ratios were in the range of 300 to 900 and 100 to 300, respectively, were retained (Nehlich and Richards, 2009; Bocherens et al., 2011b; Nehlich, 2015). In modern mammals, the collagen sulfur content was found to vary from 0.14 to 0.33% (Bocherens et al., 2011b), which generally fits the theoretical range of 0.14 to 0.29% based on DNA and amino acid sequence (Nehlich and Richards, 2009). This study presents only δ^{34}S values derived from samples with a sulfur content in collagen between 0.13 and 0.24% (Table 3). Comparable methods of collagen extraction were applied to bone samples at all the other sites discussed in this paper.

Table 1
Faunal remains from Ziegeleigrube Coenen.

Faunal remains	NISP (number of individual specimens)	MNI (minimum number of individuals)
Equus sp.	78	5
Bos/*Bison*	9	1
Coelodonta antiquitatis	5	1
Megaloceros giganteus	4	1
Mammuthus primigenius	2 (3?)	1
Crocuta spelaea	2	2
Panthera spelaea	1	1
Not defined	6	–
Total	107	11

Results

The isotopic results are summarized in Tables 2 and 3. Collagen was successfully extracted for isotope analysis from all of the ZC bone specimens. The atomic C/N ratios for the extracted collagen ranged from 3.2 to 3.5 and none of the %N in collagen is lower than 11%, indicating that all of the extracted collagen was well-preserved.

The δ^{13}C values obtained for the herbivores ranged between -22.1‰ for mammoth (ZC-140) and -20.3‰ for *Bos*/*Bison* (ZC-45) and woolly rhinoceros (ZC-89). The average δ^{13}C values for the herbivores was -21.0‰ ($n = 26$; s.d. 0.43‰). The δ^{13}C values for the carnivores ranged from -20.4‰ for hyena (ZC-91) and -19.1‰ for cave lion (ZC-48). The average δ^{13}C values for the carnivores was -19.9‰ ($n = 3$; s.d. 0.7‰). Cave lion (ZC-48) produced the highest δ^{13}C values (-19.1‰) of the whole fauna, while the lowest value was yielded by mammoth with -22.1‰.

Table 2
Ziegeleigrube Coenen.

Species	Site code	Element	N [%]-bone	%C$_{\text{coll}}$	%N$_{\text{coll}}$	δ^{13}C (‰)	δ^{15}N (‰)	C:N$_{\text{coll}}$	AMS age (^{14}C yr BP)[a]	AMS-code[a]
Coenen *Equus* sp.	ZC-34	Metatarsus III. right	2.9	41.2	14.4	−21.1	1.9	3.3		
Coenen *Equus* sp.	ZC-35	Metatarsus III. right	2.7	40.0	14.1	−21.5	2.6	3.3		
Coenen *Equus* sp.	ZC-38	Metatarsus III. right	1.3	36.0	12.6	−21.3	2.7	3.3		
Coenen *Equus* sp.	ZC-40	Metatarsus III. right	2.0	38.5	13.6	−21.3	2.5	3.3		
Coenen *Equus* sp.	ZC-55	Tibia. right	2.3	40.2	14.0	−21.2	1.9	3.3		
Coenen *Equus* sp.	ZC-63	Tibia. right	2.9	37.5	13.2	−20.9	4.1	3.3		
Coenen *Equus* sp.	ZC-94	Tibia. right	2.0	38.2	13.2	−21.4	2.3	3.4		
Coenen *Equus* sp.	ZC-142	Tibia. left	n.a.	43.5	15.1	−21.0	5.8	3.4	42,340 + 500/− 440	GrA-53423
Coenen *Equus* sp.	ZC-98	Tibia. right	1.6	37.3	13.0	−21.2	1.7	3.3		
Coenen *Equus* sp.	ZC-119	Tibia. right	2.8	40.6	14.2	−20.9	3.3	3.3		
Coenen *Equus* sp.	ZC-124	Metatarsus III. right	3.1	40.9	14.3	−21.4	3.1	3.3		
Coenen *Equus* sp.	ZC-143	Tibia. left	1.1	34.2	11.9	−21.0	5.4	3.3		
Coenen *Equus* sp.	ZC-101	Radius. right	n.a.	44.2	15.4	−21.3	2.0	3.3	>45,000	GrA-53420
Crocuta spelaea	ZC-41	Radius	3.5	38.5	13.7	−20.1	7.2	3.3		
Crocuta spelaea	ZC-91	Mandibula	3.7	42.2	15.3	−20.4	8.7	3.2	35,990 + 410/− 390	KIA-44873
Panthera spelaea	ZC-48	Humerus. left	1.5	40.4	14.1	−19.1	8.8	3.3	38,040 + 500/− 470	KIA-44361
Bos/Bison	ZC-95	Radiocubitus. right	n.a.	42.4	14.8	−20.5	5.1	3.3	>45,000	GrA-53421
Bos/Bison	ZC-45	Humerus. right	2.0	40.6	14.2	−20.3	2.8	3.3		
Bos/Bison	ZC-79	Astragalus. left	2.8	40.2	14.1	−21.0	3.6	3.3		
Bos/Bison	ZC-78	Femur. left	2.2	43.5	15.0	−20.5	6.8	3.4	34,190 + 330/− 320	KIA-44874
Bos/Bison	ZC-141	Radius. right	1.6	38.4	13.3	−20.6	3.3	3.4	42,140 + 750/− 680	KIA-44872
Megaloceros giganteus	ZC-86	Pelvis. left	2.7	39.1	13.5	−20.8	3.8	3.4		
Megaloceros giganteus	ZC-69	Mandibula	2.1	37.0	12.8	−20.6	4.7	3.4		
Megaloceros giganteus	ZC-88	Mandibula	n.a.	46.4	16.0	−20.5	4.6	3.4	43,150 + 550/− 470	GrA-53422
Coelodonta antiquitatis	ZC-82	Radius. left	1.9	40.7	14.0	−20.9	2.8	3.4		
Coelodonta antiquitatis	ZC-89	Humerus. right	0.6	33.9	11.6	−20.3	4.2	3.4		
Coelodonta antiquitatis	ZC-92	Tibia. left	0.9	32.9	11.1	−20.6	4.2	3.5		
Coelodonta antiquitatis	ZC-144	Tibia. right	1.9	39.6	13.7	−20.6	2.2	3.4		
Mammuthus primigenius	ZC-140	Long bone	n.a.	43.4	15.3	−22.1	5.9	3.3	41,700 + 490/− 420	GrA-53419

Acronym “Coll”: values measured on collagen

Specimen numbers correspond to museum numbers, year 1964 is replaced through ZC: e.g., museum number 1964-34 is here ZC-34.

[a] Radiocarbon data are from Matzerath et al. (2012).

The δ^{15}N values for herbivores ranged between 1.7‰ for horse (ZC-98) and 6.8‰ for *Bos/Bison* (ZC-78) and the average δ^{15}N were 3.6‰ (n = 26; s.d. 1.4‰). The δ^{15}N values of the carnivores ranged between a minimum of 7.2‰ (ZC-41) for hyena and a maximum of 8.8‰ (ZC-48) for cave lion. The average δ^{15}N value for carnivores was 8.3‰ (n = 3; s.d. 0.9‰). At ZC there are no shifts in δ^{15}N values in correspondence with the radiocarbon age.

The horse (*Equus* sp.) is of special interest since it is the most common species in ZC (NISP = 78; MNI = 5). Horse δ^{15}N values ranged from 1.7‰ (ZC-98) to 5.8‰ (ZC-142) with an average of 3‰ and a standard deviation of 1.3‰ (n = 13). Two samples are conspicuously high in value, samples ZC-142 and ZC-143 with δ^{15}N values of 5.8‰ and 5.4‰, respectively. These samples were actually taken at different places on the same bone/individual. If we exclude this individual (samples ZC-142 and ZC-143), the average δ^{15}N horse value is 2.5‰ and the standard deviation is only 0.7‰ (n = 11).

Table 3
Ziegeleigrube Coenen δ^{34}S values.
Source: this work.

Species	Site code	S$_{\text{coll}}$ (%) 0.13–0.24	C:S$_{\text{coll}}$ 300–900	N:S$_{\text{coll}}$ 100–300	δ^{34}S$_{\text{coll}}$ (‰)
Coenen *Equus* sp.	ZC-34	0.16	728.9	218.3	3.0
Coenen *Equus* sp.	ZC-38	0.23	444.0	133.3	4.9
Coenen *Equus* sp.	ZC-40	0.17	641.4	193.7	2.8
Coenen *Equus* sp.	ZC-55	0.17	669.7	200.4	3.6
Coenen *Equus* sp.	ZC-63	0.17	625.0	187.9	1.1
Crocuta spelaea	ZC-41	0.22	496.4	150.9	2.7
Crocuta spelaea	ZC-91	0.15	797.0	247.8	3.3
Panthera spelaea	ZC-48	0.21	544.8	163.6	6.6
Bos/Bison	ZC-45	0.17	677.2	203.2	3.1
Bos/Bison	ZC-79	0.20	570.0	170.9	4.7
Megaloceros giganteus	ZC-86	0.20	553.2	164.1	4.9
Megaloceros giganteus	ZC-69	0.18	581.9	172.8	3.6
Coelodonta antiquitatis	ZC-82	0.15	768.7	226.5	2.7
Coelodonta antiquitatis	ZC-144	0.13	862.5	256.6	2.8

Acronym “Coll”: values measured on collagen.

The large variation in the δ^{15}N values from the hyena samples (ZC-41 and ZC-91) is an unequivocal indication we are dealing here with bones from two animals, since the difference (1.5‰) is too great for variation within one individual. Trophic enrichment from one level to another has also been detected at ZC: carnivorous species are enriched in δ^{13}C by about 1.5‰, and in δ^{15}N by about 4.5‰, in comparison to herbivorous species (Table 2).

We were able to obtain 14 δ^{34}S values from bones representing five horses, two individuals of hyena, one cave lion and two specimens of *Bos/Bison*, giant deer and rhinoceroes respectively, that were consistent with the chemical conditions mentioned above. The values ranged from 1.1‰ for one of the samples from horse (ZC-63) up to 6.6‰ for the cave lion sample (ZC-48). The total values have an average of 3.6‰ and a standard deviation of 1.4‰.

Discussion

Previous radiocarbon ages

AMS radiocarbon analyses were earlier performed on collagen extracted from nine samples from the Ziegeleigrube Coenen site (Matzerath et al., 2012). Those nine uncalibrated ^{14}C ages are given in Table 2. Analyses were done at two laboratories, in Kiel (KIA) and Groningen (GrA). The ^{14}C ages likely place ZC in MIS 3, with seven heterogeneous uncalibrated ages between 34,190 + 330/− 320 ^{14}C yr BP (KIA-44874) and 43,150 + 550/− 470 ^{14}C yr BP (GrA-53422). Two additional ages were beyond the limit of the radiocarbon method, both being older than 45,000 ^{14}C yr BP (GrA-53420 and GrA-53421).

Radiocarbon ages in this time-range are commonly imprecise and are also extremely sensitive to even very small amounts of contamination by modern carbon (e.g., Wood et al., 2010). Currently an accurate dating of the site has not been achieved and, for this reason, ZC has been included in an ongoing comparison of ^{14}C datings between the laboratories in Kiel (KIA), Groningen (GrA) and Oxford (ORAU).

Since all the younger ages from ZC are from the Kiel laboratory and the quality of the Kiel-collagen has not been controlled in the chemical sense, it seems possible that all the samples may be older than 45 ^{14}C ka BP. This scenario is supported by the limited variation in isotopic values for the species (Fig. 2). On the basis of the radiocarbon ages alone the fauna could not be confidently associated with either a warmer (interstadial) or a cooler (stadial) phase within MIS 3.

Site integrity of Ziegeleigrube Coenen: implications from isotopic results

It is necessary to consider the geographical origin of the different specimens when examining site integrity. A common local origin would indicate homogeneity of the assemblage and, in order to detect this, the sulfur isotopic composition of the collagen was analyzed. A clear separation in sulfur isotopic values would be present if the species derive from different regional/geological backgrounds. This is not the case at ZC, and the sulfur isotopic values are relatively homogenous (sd. 1.4‰) in contrast to studies with values from different sites from the Jura Mountains (Drucker et al., 2012). It is worth mentioning that there is no linear correlation of the nitrogen isotopic values and the sulfur isotopic composition ($R^2 = 0.0992$).

During MIS 3, short-term climatic fluctuations (Heinrich events) (Svensson et al., 2008) may have had a marked impact on the isotopic composition of soils and plants. In fact, previous work has documented shifts in the δ^{15}N value of whole ecosystems during this time range, at least in Southwestern France (Bocherens et al., 2014). At ZC there are no shifts in δ^{15}N values in correspondence with the radiocarbon dates, which implies a common ecological background for the remains.

Ecological implications

The faunal assemblage of ZC was compared with the fauna from Scladina Cave layer 1A in order to obtain additional details about the ecosystem. The complex 1A has been dated to between 43,150 + 950/− 700 ^{14}C yr BP (GrA-32581) and 37,300 + 370/− 320 ^{14}C yr BP (GrA-32633) (Bonjean et al., 2009; Pirson et al., 2012) and faunal composition at both sites is very similar (Figs. 2 and 3) (Bocherens et al., 1997).

A comparison of all δ^{15}N bone collagen values from ZC and Scladina layer 1A (Bocherens et al., 1997) demonstrated that although the relative isotopic position for each species was similar at both sites, the absolute values are around 3‰ higher for herbivores such as mammoth (*M. primigenius*), horse (*Equus* sp.) and woolly rhinoceros (*C. antiquitatis*) at Scladina (Fig. 2). An exception is the giant deer (*M. giganteus*) which has an average of 4.0‰ at Scladina and 4.4‰ at ZC. A similar trend can be observed for the carnivores. The average δ^{15}N value of the two hyenas (*C. spelaea*) from ZC is 1.3‰ lower than the specimens from Scladina. A comparable pattern was observed for the felids, where the ZC sample is around 2.8‰ lower in δ^{15}N than the one from Scladina. In combination with the δ^{13}C results, this indicates specific niche which is similar for the hyenas and felids at both sites. The ecological niche of hyena and cave lion are clearly separated. This affiliated to different hunting strategies of both species and observed elsewhere (e.g., Bocherens, 2015). If one of these species produced clearly different relative values, this would indicate separate ecological niches or at least a certain level of ecological stress for that particular species (Drucker et al., 2014).

Within the mammoth steppe ecosystem during the pre-LGM period in Europe regular patterns are seen in fauna δ^{15}N and δ^{13}C values (Bocherens et al., 1997; Bocherens, 2003; Bocherens et al., 2011a; Yeakel et al., 2013; Bocherens, 2015; Bocherens et al., 2015). Among the herbivores, woolly mammoth yielded the highest δ^{15}N values and relatively low δ^{13}C values. Bovids, horses and rhinoceroses have relatively similar values and, in most cases, could not be clearly distinguished individually by their stable carbon and nitrogen collagen isotope ratios. In contrast, reindeer can easily be identified by isotopic analyses due to their high δ^{13}C values, which at other sites had been attributed to lichen consumption (Bocherens, 2003; Drucker et al., 2003). So far the isotopic composition for all the ZC species reflects a typical mammoth–steppe ecosystem.

Climatic and chronological implications

In the mammoth steppe ecosystem of Central Western Europe the main limiting factor for the plants is the mean annual temperature

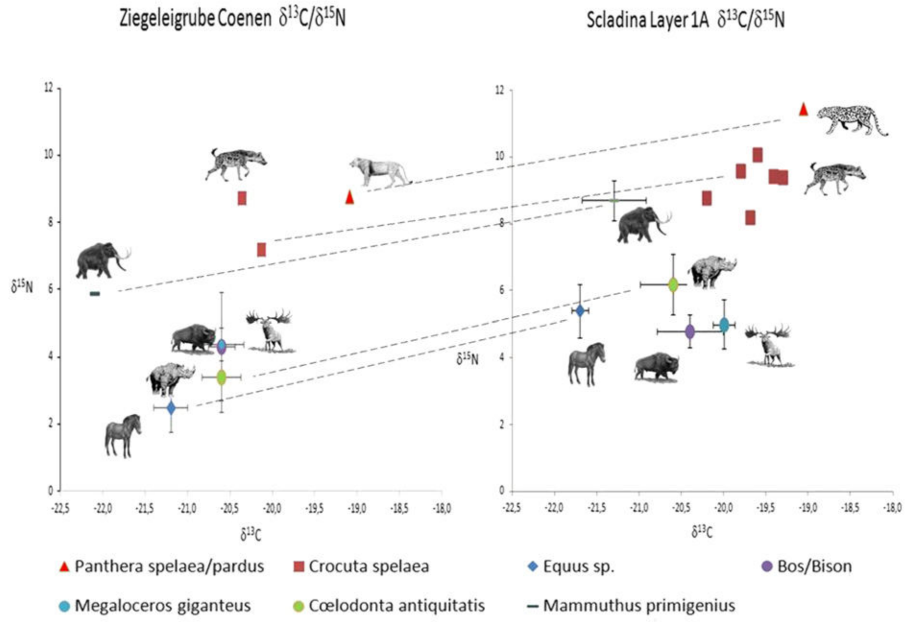

Figure 2. δ^{13}C and δ^{15}N graphs of Ziegeleigrube Coenen and Scladina Layer 1A and comparison of δ^{15}N values from both sites. Herbivores are represented by average values with standard deviation, carnivores are represented by single individuals.

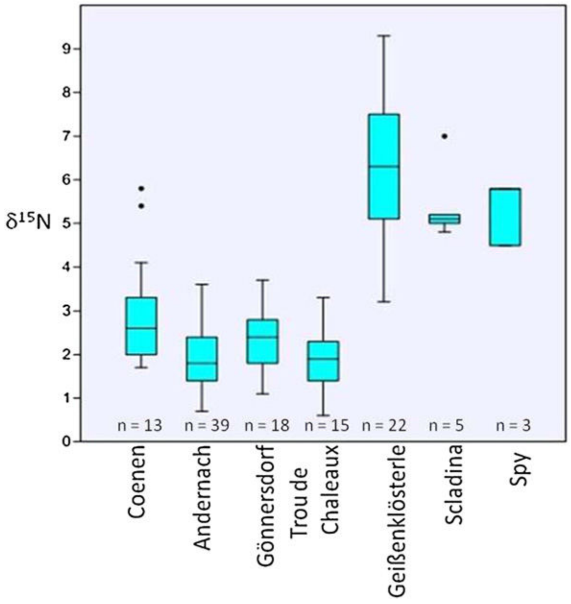

Figure 3. $\delta^{15}N$ values of horse collagen from pre- and post LGM sites discussed in the text: pre-LGM: Ziegeleigrube Coenen (the two dots are specimens from the same bone), Geißenklösterle, Scladina and Spy; post-LGM: Andernach–Martinsberg, Gönnersdorf, Trou de Chaleaux. $\delta^{15}N$ values include standard error of horse collagen (whisker length indicates 95% interval).

(MAT). MAT is an essential factor, since in frozen soils the growth of plants/nitrogen fixation and the turnover rate of nutrients are extremely reduced. The $\delta^{15}N$ values of plants are determined by the source of nitrogen they access, its chemical form and, in particular, influence of mycorrhizae (Hobbie and Hogberg, 2012). Mycorrhizae and micro-organisms make organic nitrogen available for plants. Leguminous plants are an exception to this since they fix nitrogen from the atmosphere with microbe-symbionts. A decrease in available nutrients throughout the glacial period intensifies the impact of the developments of the mycorrhiza and results in a depletion in soil/plant $\delta^{15}N$ (Stevens and Hedges, 2004). Soil activity in (semi-) permafrost ecosystems is limited in comparison to that observed under warmer conditions, and it is recognized that soil $\delta^{15}N$ values increased with increasing mean annual temperature (Brenner et al., 2001). On the contrary, decreasing temperatures in a (semi-) glacial context, with low soil activity due to the occurrence of permafrost, can be related to decreasing $\delta^{15}N$ values of herbivore collagen over time and space (Heaton et al., 1986; Ambrose, 1991; Drucker et al., 2003). Consequently the lower $\delta^{15}N$ collagen values from the late Pleistocene site ZC represent a cooler habitat with harsher conditions than those found at other pre LGM sites such as Scladina layer 1A or Geißenklösterle and Spy (Table 4). At this stage of research it is not possible to quantify the differences but further investigation, in particular the δ^{18} O values from bones, could provide some hints about relative temperature changes in this context.

We focused on horse $\delta^{15}N$ values in order to examine and understand the ecological characteristics of different sites dating to MIS 3 and 2. Horses are an exclusively herbivorous species and, in general, any differences in $\delta^{15}N$ values in horse bone, correspond to differences in the isotopic values of the plants in their diet (Rodières et al., 1996) and the metabolic processes. We assume that there were no significant differences in the metabolic processes of horses during the Pleistocene and consequently changes in the $\delta^{15}N$ values correspond to differences in values of the horse diet.

The inter-site comparison shows two groups defined by their mean values (Fig. 3). The first group has relatively low $\delta^{15}N$ values, including ZC (mean: 2.5‰ if samples ZC-142, 143 are excluded), Andernach (mean: 1.9‰), Gönnersdorf (mean: 2.3‰) (Stevens et al., 2009b) and Trou de Chaleux mean: 1.9‰ (Table 5) (Stevens et al., 2009a). These sites are post LGM in age with the exception of ZC, which is clearly pre-LGM. ZC yielded values which correspond to those observed at the younger Late Glacial sites. This pattern indicates similar environmental conditions or at least a comparable degree of soil activity. Stevens et al. (2009b) argued that we may be dealing with a pre-interstadial period with stadial–interstadial warmer conditions, at least in Gönnersdorf and Andernach–Martinsberg (Stevens et al., 2009b). They place the onset of the occupation at these sites prior to the warming of Greenland Interstadial GI 1e (Stevens et al., 2009b). We assume a similar situation in Trou de Chaleux (Fig. 3).

Some general trends in $\delta^{15}N$ horse collagen values can be observed at least in Central Europe. There is a dramatic rise of $\delta^{15}N$ values from around 13,500 ^{14}C yr BP or even earlier, until around 10,000 ^{14}C yr BP. Values are very low between 13,500 ^{14}C yr BP and 12,000 ^{14}C yr BP and increased to around 4–5‰ by 10,000 ^{14}C yr BP (Stevens and Hedges, 2004). This phenomenon can be correlated with a recovery of soil activity and soil features. Strictly speaking, a gradual shift from ecto- and ericoid mycorrhiza to arbuscular mycorrhizae. In addition, the predominant form of nitrogen changes from organic to inorganic and whereas phosphorous is abundant, availability of nitrogen is limited. All these factors are connected with increasing temperatures after the Last Glacial Maximum. It is important to mention that a general depletion of $\delta^{15}N$ during and after the Younger Dryas cannot be recognized (Stevens and Hedges, 2004; Drucker et al., 2011). Lower temperatures and all their consequences for plant and soil activity during and after the LGM had a much stronger impact on the ecosystem in Europe rather than e.g., conditions occurring during the Younger Dryas. It is however important to keep in mind that the $\delta^{15}N$ variation does not directly track temperature fluctuations.

The second group consists of sites with a relatively higher nitrogen horse collagen isotopic composition. All of the sites pre-date the LGM, Scladina Layer 1A has a mean $\delta^{15}N$ value of 5.4‰ (Bocherens et al., 1997), Spy 5.1‰ (Bocherens et al., 2013) and Geißenklösterle 6.4‰ (Bocherens et al., 2011a) (Fig. 3). The sites are relatively close in age. It appears that the herbivorous megafauna at all of the pre-LGM Ardenne and Swabian Jura sites dating to around 40,000 to 24,000 ^{14}C yr BP occupied comparable ecological niches in terms of their diet (comparable pattern) according to $\delta^{15}N$ and $\delta^{13}C$ in bone collagen (Bocherens et al., 2011a). It is interesting that ZC yielded relatively low $\delta^{15}N$ values. As mentioned above the nitrogen isotopic values can hint at chronological classifications according to some general trends in Europe (Richards and Hedges, 2003; Stevens and Hedges, 2004; Drucker et al., 2011). We can exclude that ZC is very close in age to the other pre-LGM sites, otherwise we would expect comparable $\delta^{15}N$ values and the same ecological frame. We consider that either the environment or at least the soil activity with all its associated consequences, e.g., lower $\delta^{15}N$ values in a colder phase and higher in a warmer context, was not the same as in the other pre-LGM sites. Local differences caused by different types of bedrocks can be excluded; this is strongly supported by the homogeneous sulfur isotopic values.

Consequently the ecological information derived from the stable isotope data suggest a stadial date, which argues for a MIS 3/Heinrich 5 date (Cacho et al., 1999; Sánchez Goñi et al., 2008; Svensson et al., 2008). The scattered radiocarbon data are consistent with the MIS 3 assignment. If this chronological association is correct, it would mean that the Heinrich 5 event must have been cold enough to have an impact on the biogeochemical cycle of nitrogen in soils, as reflected by the decrease of $\delta^{15}N$ values at the base of the ecosystem. However, it must have been less severe than the LGM, during which time Western Germany was more-or-less totally deserted by humans and large mammals. Moreover, the Heinrich 5 event would not have been harsh enough to disrupt the trophic structure of the ecosystem, either for the herbivores or their predators. This conclusion is particularly important in understanding the fluctuations of prehistoric human populations, in this case Neanderthals, in response to the climatic shifts during MIS 3.

Table 4
Pre-Last Glacial Maximum sites: Scladina, Geißenklösterle and Spy.
Sources: 1 = Bocherens et al. (1997). 2 = Bocherens et al. (2011a). 3 = Stevens and Hedges (2004). 4 = Conard and Bolus (2008). 5 = Germonpré et al. (2014).

Species	Site code	Element	%C_{coll}	%N_{coll}	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N_{coll}	Source	AMS age (^{14}C yr BP)	AMS-code
Site: Scladina										
Crocuta spelaea	SC1800	Phalanx I	42.9	15.6	−20.2	8.8	3.2	1		
Crocuta spelaea	SC1900	Phalanx I	42.6	15.6	−19.6	10.1	3.2	1		
Crocuta spelaea	SC2000	Phalanx I	42.8	15.7	−19.7	8.2	3.2	1		
Crocuta spelaea	SC2100	Phalanx I	42.9	15.6	−19.4	9.5	3.2	1		
Crocuta spelaea	SC1700	Mandible	39.9	14.6	−19.8	9.6	3.2	1		
Crocuta spelaea	SC2200	Maxillary	42.0	15.4	−19.3	9.4	3.2	1		
Panthera pardus	SC30700		40.5	14.1	−19.1	11.5	3.4	2		
Mammuthus primigenius	SC600	Tooth	42.6	15.5	−20.9	8.4	3.2	1		
Mammuthus primigenius	SC700	Tooth	41.5	15.2	−21.5	9.4	3.2	1		
Mammuthus primigenius	SC800	Tooth	41.3	15.1	−21.6	8.3	3.2	1		
Cœlodonta antiquitatis	SC900	Lower P2 (R)	42.6	15.5	−20.9	5.5	3.2	1		
Cœlodonta antiquitatis	SC1000	Lower P2 (R)	42.1	15.4	−20.3	6.9	3.2	1		
Cœlodonta antiquitatis	SC1100	Lower P2 (R)	42.2	15.2	−20.0	6.4	3.2	1		
Cœlodonta antiquitatis	SC1200	Lower P2 (R)	41.2	15.0	−21.1	5.3	3.2	1		
Cœlodonta antiquitatis	SC1300	Lower P2 (R)	41.8	15.2	−20.4	7.5	3.2	1		
Cœlodonta antiquitatis	SC1400	Lower P2 (R)	43.1	15.7	−20.6	5.5	3.2	1		
Equus ferus	SC3900	Upper tooth (R)	42.5	15.6	−21.7	5.2	3.2	1		
Equus ferus	SC4100	Upper tooth (R)	42.6	15.8	−21.7	5.1	3.1	1		
Equus ferus	SC4200	Upper tooth (R)	42.8	15.8	−21.9	5.0	3.2	1		
Equus ferus	SC4300	Upper tooth (R)	39.9	14.5	−21.5	4.8	3.2	1		
Equus ferus	SC4400	Upper tooth (R)	40.9	15.0	−21.6	7.0	3.2	1		
Bison priscus	SC29000	Lower M3 (R)	32.6	11.5	−20.8	4.4	3.3	2		
Bison priscus	SC29100	Lower P4 (L)	32.1	12.8	−19.8	5.6	2.9	2		
Bos or *Bison*	SC4500	Lower P (R)	41.7	15.2	−20.5	4.8	3.2	1		
Bos or *Bison*	SC4700	Lower P3 (R)	42.7	15.7	−20.5	4.3	3.2	1		
Bos or *Bison*	SC4800	Lower M1 (R)	41.2	15.3	−19.9	5.3	3.1	1		
Bos or *Bison*	SC4900	Lower P3 (R)	40.8	15.0	−20.7	4.4	3.2	1		
Bos primigenius	SC28800	Lower M3 (L)	33.9	12.7	−20.7	4.9	3.1	1		
Bos primigenius	SC28900	Lower P4 (L)	35.0	13.6	−20.3	4.5	3.0	2		
Megaloceros giganteus	SC2300	Tarsal bone	41.6	15.2	−20.2	4.0	3.2	1		
Megaloceros giganteus	SC2500	Upper tooth	43.7	15.9	−20.2	5.0	3.2	1		
Megaloceros giganteus	SC29800	Lower P4 (R)	40.9	13.5	−19.7	5.9	3.5	2		
Site: Geißenklösterle										
Equus sp.	EQ-GK 313	Radius	39.2	14.1	−19.8	4.1	3.2	2		
Equus sp.	EQ-GK 314	Tibia	43.2	15.7	−20.7	8.7	3.2	2		
Equus sp.	EQ-GK 316	Humerus	41.5	14.6	−20.6	7.3	3.3	2		
Equus sp.	EQ-GK 317	Femur	36.3	13.5	−20.7	5.5	3.1	2		
Equus sp.	EQ-GK 318	Tibia	42.8	14.3	−21.8	3.4	3.5	2		
Equus sp.	EQ-GK 319	Tibia	42.2	14.8	−21.4	4.2	3.3	2		
Equus sp.	EQ-GK 321	Tibia	37.8	13.9	−20.1	8.5	3.1	2		
Equus sp.	EQ-GK 322	Tibia	36.3	13.7	−20.8	6.3	3.1	2		
Equus sp.	EQ-GK 323	Tibia	36.1	13.6	−20.7	6.1	3.1	2		
Equus sp.	EQ-GK 325	Tibia	41.6	14.4	−20.8	7.1	3.3	2		
Equus sp.	EQ-GK 326	Humerus	42.9	15.3	−21.0	6.1	3.2	2		
Equus sp.	EQ-GK 327	Tibia	41.6	15.0	−20.9	5.9	3.2	2		
Equus sp.	EQ-GK 329	Tibia	40.7	15.5	−20.8	6.9	3.0	2		
Equus sp.	EQ-GK 330	Tibia	28.6	10.9	−21.6	6.9	3.0	2		
Equus sp.	EQ-GK 331	Tibia	43.8	16.2	−20.6	6.1	3.1	2		
Equus sp.	OxA-4857	–			−20.0	9.2	3.0	3	27,500 ± 550	OxA-4857
Equus sp.	OxA-5227	–			−20.7	9.3	3.2	3	28,050 ± 550	OxA-5227
Equus sp.	OxA-5707	–			−20.6	7.5	3.1	3	33,200 ± 800	OxA-5707
Equus sp.	OxA-4856	–			−20.6	5.1	3.2	3	30,950 ± 800	OxA-4856
Equus sp.	TUB-77	Femur	39.3	14.6	−21.1	3.2	3.1	4	36,490 + 350/−340	KIA-17303
Equus sp.	TUB-78	Humerus	39.7	14.2	−21.2	8.5	3.3	4	31,870 + 260/−250	KIA-8958
Equus sp.	TUB-79	Radius	41.4	14.9	−21.8	4.7	3.2	4	36,700 + 450/−430	KIA-17299
Site: Spy										
Equus sp.	Spy 14038 Ulg	–	44.3	14.0	−21.4	5.8	3.2	1 + 5	34,580 + 330/−290	GrA-37932
Equus sp.	IV2E 4207	–	35.6	14.2	−20.5	4.5	2.5	1 + 5	32,810 + 250/−230	GrA-44576

acronym “Coll”: values measured on collagen.

Conclusion

The fauna from the Ziegeleigrube Coenen (ZC) is potentially significant for understanding the paleoecological context of northwestern Europe during a critical period of human evolution in Europe, before and around the time of Neanderthal replacement by anatomically modern humans (Conard and Bolus, 2008; Flas, 2011; Higham, 2011; Higham et al., 2012, 2014; Pirson et al., 2012). It seems that cooling events in MIS 3 like Heinrich events had not significantly impacted the megafaunal composition in parts of Central Europe. Hence, these regions could provide the preferred prey of Neanderthals during such cold spells. In contrast to the many cave sites from this period, ZC is one of the few late Pleistocene sites in an open air loess context. Due to the extraordinary preservation of the ZC remains, this site yielded a considerable spectrum of Pleistocene faunal material comprising several carnivores and herbivores. The chemical bone preservation is good and, consequently, the collagen content and preservation was acceptable for extraction and could be processed successfully. Applying radiocarbon and isotopic

Table 5
Post-Last Glacial Maximum sites: Andernach, Gönnersdorf and Trou de Chaleux.
Source: 1 = Stevens et al. (2009b). 2 = Stevens et al. (2009a).

Species	Site code	Element	%C_{coll}	%N_{coll}	δ^{13}C (‰)	δ^{15}N (‰)	C:N_{coll}	Source	AMS age (^{14}C yr BP)	AMS-code
Site: Andernach										
Equus sp.	A/AND/B/35	–	38.8	13.8	−20.1	2.4	3.3	1		
Equus sp.	A/AND/B/43	–	39.9	14.3	−21.1	1.1	3.3	1		
Equus sp.	A/AND/B/24	–	37.7	13.3	−21.0	3.6	3.3	1		
Equus sp.	A/AND/B/40	–	35.2	12.5	−21.0	2.0	3.3	1		
Equus sp.	A/AND/B/44	–	39.6	14.1	−21.3	0.9	3.3	1		
Equus sp.	A/AND/B/1	–	38.7	13.8	−20.9	2.0	3.3	1		
Equus sp.	A/AND/B/2	–	35.2	12.6	−21.2	1.7	3.3	1		
Equus sp.	A/AND/B/4	–	32.6	11.6	−20.9	1.3	3.3	1		
Equus sp.	A/AND/B/6	–	30.1	10.8	−20.7	1.6	3.2	1		
Equus sp.	A/AND/B/14	–	37.4	12.8	−21.1	1.3	3.4	1		
Equus sp.	A/AND/B/15	–	36.4	13.3	−21.1	3.5	3.2	1		
Equus sp.	A/AND/B/16	–	37.7	13.2	−21.2	2.1	3.3	1		
Equus sp.	A/AND/B/17	–	33.5	12.1	−21.1	1.3	3.2	1		
Equus sp.	A/AND/B/18	–	39.2	14.0	−20.8	1.7	3.3	1		
Equus sp.	A/AND/B/19	–	33.9	12.1	−20.7	0.7	3.3	1		
Equus sp.	A/AND/B/20	–	34.5	12.3	−21.0	2.0	3.3	1		
Equus sp.	A/AND/B/21	–	38.7	14.7	−21.0	1.3	3.1	1		
Equus sp.	A/AND/B/22	–	35.2	12.6	−20.7	1.7	3.3	1		
Equus sp.	A/AND/B/23	–	41.0	14.4	−21.1	2.8	3.3	1		
Equus sp.	A/AND/B/26	–	28.1	10.1	−20.9	2.8	3.3	1		
Equus sp.	A/AND/B/27	–	38.9	13.5	−21.2	1.6	3.4	1		
Equus sp.	A/AND/B/28	–	37.0	13.1	−21.2	2.3	3.3	1		
Equus sp.	A/AND/B/29	–	44.0	15.4	−21.0	1.4	3.3	1		
Equus sp.	A/AND/B/30	–	37.3	13.2	−20.5	2.4	3.3	1		
Equus sp.	A/AND/B/31	–	34.6	12.5	−21.2	3.2	3.2	1		
Equus sp.	A/AND/B/32	–	30.4	11.2	−21.3	2.1	3.2	1		
Equus sp.	A/AND/B/33	–	34.3	12.2	−20.9	2.6	3.3	1		
Equus sp.	A/AND/B/34	–	37.6	13.4	−21.2	1.1	3.3	1		
Equus sp.	A/AND/B/36	–	36.5	12.7	−21.1	1.2	3.3	1		
Equus sp.	A/AND/B/37	–	38.8	13.9	−20.8	1.5	3.3	1		
Equus sp.	A/AND/B/38	–	39.4	14.0	−21.2	1.8	3.3	1		
Equus sp.	A/AND/B/39	–	38.7	13.9	−21.2	2.0	3.3	1		
Equus sp.	A/AND/B/41	–	40.3	14.1	−21.4	1.8	3.3	1		
Equus sp.	A/AND/B/42	–	41.5	14.9	−21.3	2.7	3.3	1		
Equus sp.	A/AND/B/45	–	37.1	13.8	−21.2	1.9	3.1	1		
Equus sp.	A/AND/B/46	–	32.4	11.2	−21.7	1.9	3.4	1		
Equus sp.	A/AND/B/47	–	34.9	12.6	−20.6	1.8	3.2	1		
Equus sp.	A/AND/B/48	–	37.7	13.3	−20.9	1.4	3.3	1		
Equus sp.	A/AND/B/49	–	38.7	13.8	−20.4	2.5	3.3	1		
Rangifer tarandus N = 11	max δ^{13}C −19.2	max δ^{15}N 2.8			av −19.8	av 2.1		1		
	min δ^{13}C −21.2	min δ^{15}N 1.4								
Site: Gönnersdorf										
Equus sp.	A/GON/B/18	–	39.7	14.1	−21.0	1.1	3.3	1		
Equus sp.	A/GON/B/12	–	38.9	13.6	−20.6	3.1	3.3	1		
Equus sp.	A/GON/B/7	–	35.0	12.6	−21.0	1.1	3.3	1		
Equus sp.	A/GON/B/8	–	38.3	13.0	−21.0	1.9	3.4	1		
Equus sp.	A/GON/B/11	–	34.1	12.0	−20.6	1.9	3.3	1		
Equus sp.	A/GON/B/13	–	41.9	14.7	−20.3	2.0	3.3	1		
Equus sp.	A/GON/B/14	–	37.0	12.3	−21.4	2.1	3.5	1		
Equus sp.	A/GON/B/16	–	31.1	10.2	−21.3	1.7	3.5	1		
Equus sp.	A/GON/B/17	–	36.1	12.7	−20.4	2.9	3.3	1		
Equus sp.	A/GON/B/20	–	38.4	13.8	−20.4	2.4	3.2	1		
Equus sp.	A/GON/B/21	–	38.9	13.2	−20.7	2.5	3.4	1		
Equus sp.	A/GON/B/22	–	35.9	12.3	−20.5	3.1	3.4	1		
Equus sp.	A/GON/B/23	–	43.0	15.2	−21.0	2.7	3.3	1		
Equus sp.	A/GON/B/24	–	38.1	13.8	−20.7	1.8	3.2	1		
Equus sp.	A/GON/B/25	–	39.1	13.5	−20.9	2.7	3.4	1		
Equus sp.	A/GON/B/27	–	31.1	11.0	−20.9	3.7	3.3	1		
Equus sp.	A/GON/B/28	–	39.0	13.6	−21.0	2.8	3.4	1		
Equus sp.	A/GON/B/29	–	37.5	13.2	−20.6	1.5	3.3	1		
Rangifer tarandus N = 22	max δ^{13}C −19.0	max δ^{15}N 3.0			av −19.7	av 1.7		1		
	min δ^{13}C −20.2	min δ^{15}N 0.6								
Site: Trou de Chaleux										
Equus sp.	A/CX/B/28	–	19.7	6.3	−21	2.4	3.6	2		
Equus sp.	A/CX/B/29	–	38	13.5	−20.9	1.4	3.3	2		
Equus sp.	A/CX/B/30	–	42.4	15.2	−20.7	2.2	3.3	2		
Equus sp.	A/CX/B/31	–	36.6	12.6	−20.8	2.3	3.4	2		
Equus sp.	A/CX/B/32	–	38.5	13.7	−20.9	3.3	3.3	2		
Equus sp.	A/CX/B/33	–	39.3	14.1	−20.6	1.9	3.3	2		
Equus sp.	A/CX/B/34	–	42.5	15.3	−20.8	1.9	3.2	2		
Equus sp.	A/CX/B/35	–	40.4	14.4	−21	1.6	3.3	2		
Equus sp.	A/CX/B/36	–	42.6	15.4	−21.1	2.1	3.2	2		

(*continued on next page*)

Table 5 (*continued*)

Species	Site code	Element	%C_{coll}	%N_{coll}	δ^{13}C (‰)	δ^{15}N (‰)	C:N_{coll}	Source	AMS age (^{14}C yr BP)	AMS-code
Site: Trou de Chaleux										
Equus sp.	A/CX/B/37	–	50.2	17.8	−20.9	1.9	3.3	2		
Equus sp.	A/CX/B/40	–	36.5	13.1	−20.9	1.3	3.2	2		
Equus sp.	A/CX/B/42	–	21.1	7.7	−21	0.6	3.2	2		
Equus sp.	A/CX/B/43	–	19.1	6.8	−21.1	2.3	3.3	2		
Equus sp.	A/CX/B/45	–	39.7	14.2	−20.7	1.3	3.3	2	12,880 ± 100	OxA-3633
Equus sp.	A/CX/B/46	–	43.6	15.9	−21.1	2.1	3.3	2	12,790 ± 100	OxA-3632

Acronym "Coll": values measured on collagen.

tracking to the large mammal bones, we established the integrity and authenticity of the assemblage more in detail, even though the finds were recovered under poor conditions, without systematic documentation and excavation. It was possible to identify a coherent food web and a relatively homogenous ecological affiliation for all of the species.

The δ^{15}N and δ^{13}C values of the mammalian species reflect the typical niche partitioning observed in the mammoth steppe ecosystem (e.g., Bocherens et al., 1997; Bocherens, 2003; Bocherens et al., 2011a; Yeakel et al., 2013). There are no indications of any ecological stress. The δ^{15}N isotope composition of horse collagen from the sites considered in this paper can be clearly distinguished into relatively high δ^{15}N values from the pre-LGM sites and relatively low δ^{15}N values from post-LGM sites. The δ^{15}N values of horse at the site ZC are clearly closer to those from post-LGM sites mentioned in the paper, indicating environmental conditions during phases of MIS 3 which were similar to those prevailing during the post-LGM sites. We could ascertain that the ecological framework is consistently different from the one represented at other pre-LGM sites mentioned here, while the faunal composition is the same. It is the δ^{15}N baseline of the ecosystem that is responsible for the lower values.

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Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe

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ABSTRACT

The Late Pleistocene site "Troisième caverne" of Goyet (Belgium) has yielded the broadest set of Neandertal remains in North-Western Europe and is associated with a rich and diverse large mammal assemblage. We reconstructed the dietary ecology at the site using stable isotope tracking ($\delta^{13}C$ and $\delta^{15}N$) of bone collagen. The $\delta^{13}C$ and $\delta^{15}N$ values of all species are consistent with those observed in other "mammoth steppe" sites. The relative contribution of potential prey species to the diet of carnivores (including Neandertals) was evaluated using a Bayesian model. The distribution of individuals from herbivorous species and carnivorous ones was determined through cluster analysis in order to identify ecological niches, regardless of the individual species attribution. The Neandertals within the predator guild and the mammoth and reindeer as representatives of the herbivores occupied the most specific and most narrow ecological niches. The "Troisième caverne" of Goyet can be regarded as a key site for the investigation of Late Pleistocene Neandertal ecology north of the Alps.

1. Introduction

Neandertals went extinct approximately 40,000 years ago (Higham et al., 2014), around the time anatomically modern humans (AMH) began to replace the previous Neandertal populations (Hublin, 2015; Nigst et al., 2014). The dietary strategies and the related cognitive abilities can provide insights into potential arguments for the Neandertal extinction (e.g. d'Errico and Sánchez Goñi, 2004; Finlayson et al., 2004; Bocherens and Drucker, 2006; Bocherens et al., 2014b). Several approaches were conducted to reconstruct Neandertal diet, e.g. zooarchaeology (Gaudzinski-Windheuser and Kindler, 2012a,b; Germonpré et al., 2014), dental microwear patterns (Pérez-Pérez et al., 2003; Harvati et al., 2013), tooth calculus analysis (Henry et al., 2011; Hardy et al., 2012), lithic use-wear and residue analysis (Hardy and Moncel, 2011) and the investigation of stable carbon and nitrogen isotopes of bone and teeth collagen (e.g. Bocherens et al., 1991, 2001, 2005b; Bocherens, 2009b; Bocherens et al., 2013; Richards et al., 2000; Richards and Schmitz, 2008; Richards and Trinkaus, 2009). All the different projections present different, in some cases even on the first view apparently contradictory, results equivalent to their specific possibilities. Nevertheless, there is common agreement of the regular consumption of large ungulate meat. In the current state of research, it has been accepted that Neandertals were able to hunt actively (e.g. Richards et al., 2000; Bocherens and Drucker, 2006; Serangeli and Bolus, 2008; Rendu et al., 2012; Gaudzinski-Windheuser and Kindler, 2012a,b; Germonpré et al., 2014), in contrast to around two decades ago (e.g. Binford, 1985; Stiner, 1991; Marean, 1998).

What remains in dispute is the potential role of smaller mammals or birds in Neandertal diet, as well as the significance of fresh and/or marine resource exploration (e.g. Richards et al., 2001; Hardy and Moncel, 2011; Blasco and Fernández Peris, 2012a,b;

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Bocherens et al., 2014d). Another striking point is the significance of plant food consumption. Several interpretations have been proposed about plant food consumption: Did it occur just by chance, very regularly, only in certain ecosystems, or even for medicinal reasons (e.g. El Zaatari et al., 2011; Henry et al., 2011, 2014; Hardy et al., 2012; Salazar-García et al., 2013)?

The archaeological and anthropological record in Belgium provides a unique situation: the several previously presented remains from Spy, Scladina, Walou, Trou de l'Abîme at Couvin and Engis (e.g. Bocherens et al., 2001, 2013; Draily, 2004; Toussaint et al., 2006; Semal et al., 2009, 2013; Toussaint et al., 2010; Germonpré et al., 2014) emphasized the richness of Neandertal fossils with associated artifacts and faunal remains in this area. The "Troisième caverne" of Goyet (Belgium) contributed significantly to the archaeological record. The site yielded the most extensive assemblage of Neandertal remains in terms of numbers of specimens and individuals in Northern Europe (Rougier et al., 2012, in prep.) providing the rare opportunity for a valid reconstruction of the ecology of Neandertals at this site, and more generally in the region. Not only a considerable spectrum of Neandertal remains have been identified in the last years, but also a broad spectrum of herbivorous and carnivorous species from the same ecosystem. The ecological context allows to reconstruct the trophic structures through the investigation of stable isotopic composition. Furthermore, the chemical preservation of the organic parts of the bone material is excellent in contrast to most of the sites in, for example, Southern Europe.

Altogether, this site provides one of the best opportunities to reconstruct the ecology of Neandertals within their ecosystem through stable isotopic investigation.

The stable isotopic composition of collagen is directly correlated to the isotopic signature of consumed dietary protein. We applied statistical analysis of the Neandertal results and their potential prey to establish a quantitative and qualitative estimation of the composition of their diet. Since the isotope composition of bone collagen reflects the average protein input of the most recent years of an individual, we can estimate ecological behavior on a long term scale, in contrast to methods providing insights as snapshots or short term time ranges (e.g. tooth wear analysis, residue analysis on stone tools, investigation of the species composition of the faunal assemblage in the site).

Here we also provide information about the general structure of this ecosystem in the broader frame of the mammoth steppe ecosystem; we highlight aspects such as niche partitioning among herbivores and among carnivores with a special focus on the contribution of different prey species in the protein part of the Neandertal diet. While doing this we evaluated potential competition with other predators and highlight the relations among the carnivores guild. These results will be compared directly with the Neandertal results from Spy (Bocherens et al., 2013).

Paleodietary reconstruction using stable carbon and nitrogen isotopic signatures of collagen of European Pleistocene humans is an established technique that was first implemented on Neandertal remains from Marillac (Charente, France; today designated as "Les Pradelles") (Bocherens et al., 1991; Fizet et al., 1995). Since this early research, several Neandertal remains have been the subject of investigation using stable isotopes: early Late Pleistocene remains from Scladina cave in Belgium (Bocherens et al., 1999); the Late Pleistocene remains from Vindija in Croatia (Richards et al., 2000); Spy and Engis in Belgium (Bocherens et al., 2001, 2013); Saint-Césaire, Les Pradelles and Les Rochers-de-Villeneuve in France (Bocherens and Drucker, 2003a; Bocherens et al., 2005b; Beauval et al., 2006). Neandertal in Germany (Richards and Schmitz, 2008) and Okladnikov Cave from South Siberia (Krause et al., 2007) have all been used to investigate Neandertal diet through the stable carbon and nitrogen isotopes of their remains. We will discuss our results in the context of previously published results to emphasize the pertinence of the Goyet site.

This paper focused on two essential aspects: the first is to describe the ecological background within the mammoth steppe ecosystem, and the second is to detail the ecology of the Goyet Neandertals and the potential implications.

2. Material and methods

2.1. The "Troisième caverne" of Goyet

The Goyet caves are located in the Mozet Commune in the Walloon Region in Belgium around 20 km away from the Spy site (Fig. 1) and consist of several archaeological sites. The "Troisième caverne" of Goyet is located within a karstic system on the bank of the Samson Valley, a tributary of the Meuse River. Most of the sediment was excavated by Edouard Dupont in 1868 (Dupont, 1872), without the methods used by modern excavators although the fieldwork was somehow advanced if we consider the standards for Paleolithic sites investigations at the time. Most of his work was recorded in writing (e.g. Dupont, 1872) and most of the artifacts were labeled. Dupont described five "fauna-bearing levels" at the site, which were originally considered to correspond to chronological units. However, the "fauna-bearing levels" consist of a mix of remains from different periods (e.g. Germonpré, 1997, 2001; Stevens et al., 2009a). Efforts were therefore made to directly date the human remains (Rougier et al., in prep.). Altogether the "Troisième caverne" yielded rich Late Pleistocene occupations from the Middle and Upper Paleolithic (Mousterian, Lincombian-Ranisian-Jerzmanowician, Aurignacian, Gravettian, and Magdalenian) including a considerable faunal assemblage (e.g. Germonpré, 1997; Germonpré and Sablin, 2001; Otte and Noiret, 2007; Flas, 2011; Pirson et al., 2012).

2.2. Comparison sites

To get a broader ecological dataset, we integrated the sites of Scladina and Spy to our study (Fig. 1). Both yielded material with a very similar ecological and temporal background to Goyet. Spy was excavated more than a century ago. The stratigraphic attribution of the remains it yielded does not follow modern standards (e.g. Pirson et al., 2012; Germonpré et al., 2014), therefore all of the faunal material in the present study is directly dated. The situation at Scladina is different. The faunal remains from the site are not directly dated but come from a well-stratified context. The site was discovered in 1971 and is still under investigation. All of the material considered in this study comes from complex 1A and is associated with a Mousterian technocomplex (Bonjean et al., 2009).

2.3. Skeletal material

2.3.1. Goyet

The human material studied was collected during the excavations of E. Dupont in 1868 and identified as Neandertal during the reassessment of the "Troisième caverne" collections by Rougier et al. (in prep.). The Neandertal remains represent at least five individuals, with four adults represented by four right tibias, and one child represented by a single tooth (Rougier et al., in prep). The tooth was not sampled for stable isotope analysis since it would have been almost entirely destroyed in the process; the four tibias (tibia III represented by specimen Q305-7, tibia IV by Q55-4, tibia V by Q374a-1, and tibia VI by Q57-3) were analyzed (Table 1). In addition to these four identified individuals, stable carbon and nitrogen analyses were performed on eight diagnostic Neandertal

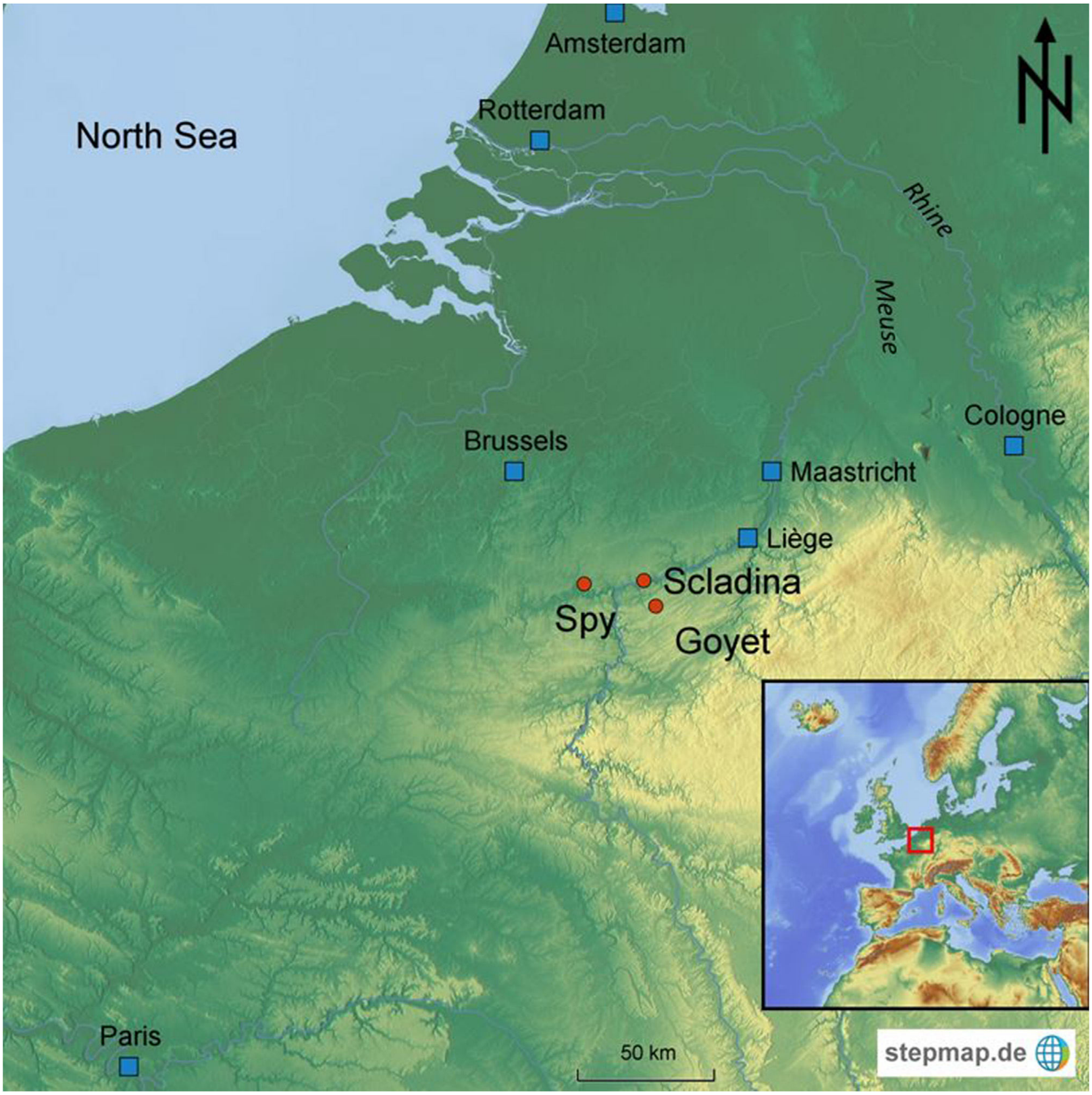

Fig. 1. Map of the Belgian sites included in this study.

bones without any clear assignment to a specific individual (Table 1). Most of the Neandertal remains from Goyet are all directly dated (Rougier et al., in prep.). The uncalibrated ^{14}C-ages span between 36,590 + 300, −270 (GrA-54024) and 41,200 + 500, −410 ^{14}C BP (GrA-46173) (Table 1). All stable carbon and nitrogen isotopic analyses of the Neandertal remains were performed in the context of this study.

The faunal remains from Goyet underlying this study have a clear pre-LGM age between around 25,000 and 40,000 years ago. This has either been confirmed by direct radiocarbon dates or demonstrated through their ecological background (Bocherens et al., 2011) and, in general, by the species composition itself. Species with a clear pre-LGM age are also considered in this study, e.g. cave hyena that became extinct in Belgium about 27,000 years ago (Germonpré, 1997; Stuart and Lister, 2007), as well as cave bear that became extinct around 25,500 years ago (Bocherens et al., 2014a). For our purpose, an attribution to a pre-LGM age is sufficient. The stable carbon and nitrogen isotopic values for the faunal remains from Goyet were obtained by Bocherens et al. (2011) and are given in S1.

2.3.2. *Spy*

The Spy Neandertal remains that are part of this study have been investigated for stable carbon and nitrogen isotopic composition in Bocherens et al. (2013). Most of the faunal data from Spy integrated into this study have also been published (Bocherens et al., 2013).

One remain from Spy I and one remain from Spy II were analyzed. Both have been directly dated respectively to approximately 35,810 ^{14}C BP (GrA-32623) and 33,940 ^{14}C BP (GrA-32630; Semal et al., 2009).

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Table 1
Goyet and Spy Neandertal isotopic data.

ID	Specimen	Dating ID	Date	$\%C_{coll}$	$\%N_{coll}$	C/N	$\delta^{13}C$	$\delta^{15}N$	Reference
Q53-4	Rt humerus diaphysis frag. (humerus III)	GrA-54022	39,870 + 400/−350	42.9	15.1	3.3	−19.0	11.7	Rougier et al. (in prep.); this study
Q55-1	Lt clavicle frag.	GrA-54257	37,860 + 350/−310	36.9	12.9	3.3	−19.2	11.3	Rougier et al. (in prep.); this study
Q55-4	Rt tibia diaphysis frag. (tibia IV)			39.6	14.0	3.3	−19.2	11.6	Rougier et al. (in prep.); this study
Q56-1	Rt femur diaphysis frag. (femur I)	GrA-46170	38,440 + 340/−300	45.4	15.5	3.4	−19.5	11.5	Rougier et al. (in prep.); this study
Q57-1	Lt tibia diaphysis frag. (tibia II)	GrA-46173	41,200 + 500/−410	46.0	16.8	3.2	−19.2	11.8	Rougier et al. (in prep.); this study
Q57-2	Rt femur diaphysis frag. (femur II)	GrA-54024	36,590 + 300/−270	42.7	15.0	3.3	−19.1	11.9	Rougier et al. (in prep.); this study
Q57-3	Rt tibia diaphysis frag. (tibia VI)	GrA-60019	38,260 + 350/−310	43.8	15.4	3.3	−19.6	11.2	Rougier et al. (in prep.); this study
Q305-4	Lt tibia diaphysis frag. (tibia I)	GrA-46176	40,690 + 480/−400	47.1	16.7	3.3	−19.4	10.7	Rougier et al. (in prep.); this study
Q305-7	Rt tibia diaphysis frag. (tibia III)			41.9	14.9	3.3	−19.0	11.3	Rougier et al. (in prep.); this study
Q374a-1	Rt tibia diaphysis frag. (tibia V)			43.1	15.2	3.3	−19.1	11.8	Rougier et al. (in prep.); this study
Q376-1	Hand prox. phalanx 2-4	GrA-46178	39,140 + 390/−340	46.7	17.0	3.2	−19.2	10.9	Rougier et al. (in prep.); this study
Q376-20	Rt humerus diaphysis frag. (humerus II)	GrA-60018	37,250 + 320/−280	39.8	14.0	3.3	−19.4	11.8	Rougier et al. (in prep.); this study
Spy 94a (Spy I)	Rt M3, maxilla frag. attached	GrA-32623	35,810 + 260/−240	43.7	15.2	3.4	−19.4	11.4	Bocherens et al. (2013)
Spy 430a (Spy II)	Rt hand middle phalanx 3	GrA-32630	33,940 + 220/−210	46.8	15.8	3.5	−20.3	10.8	Bocherens et al. (2013)

Additionally, we analyzed the stable carbon and nitrogen isotopes of previously directly ^{14}C dated faunal remains from Spy (Semal et al., 2009, 2013; see S1) (*Rangifer tarandus* N = 2, *Coelodonta antiquitatis* N = 1, *Mammuthus primigenius* N = 1, *Equus* sp. N = 1, *Crocuta crocuta* N = 1).

2.3.3. Scladina

All of the faunal remains that are part of this study come from a stratified context, complex 1A, which has an age approximately between 37,300 (GrA-32633) and 43,150 (GrA-32581) ^{14}C BP (Pirson et al., 2012). Stable $\delta^{13}C$ and $\delta^{15}N$ isotopic analyses were performed by Bocherens et al. (1997, 2011; S1).

2.4. Principles of carbon and nitrogen stable isotopic tracking in a Pleistocene context

The analysis of stable carbon and nitrogen isotope ratios is an excellent tool in the investigation of several ecological aspects of this time period (Yeakel et al., 2013; Bocherens et al., 2014b). For example, it is very easy to distinguish between C3, C4 and CAM photosynthesis pathways. However, C4 and CAM plants are absent in the Late Pleistocene mammoth steppe ecosystem, where all plants used the C3 photosynthesis pathway. In a pure C3 environment, this approach allows the description of the general character of the habitat such as: open vs. closed landscape (Drucker et al., 2008); the ecological niche in terms of diet (MacFadden and Shockey, 1997) such as grass/forbs vs. trees/shrubs in herbivore diet (e.g. Drucker et al., 2010; Bocherens et al., 2015b); the contribution of animal proteins to omnivore diet (e.g. Hobson et al., 2000); and the meat of different prey in carnivore diet (e.g. Bocherens et al., 2015a).

The isotopic composition of bone collagen reflects an average of the protein source in the diet of the last few years of an individual (e.g. DeNiro and Epstein, 1978, 1981; Ben-David and Flaherty, 2012; Kurle et al., 2014). At the bottom of a foodweb, the plant carbon and nitrogen stable isotopes differ due to isotopic fractionation during chemical and physical processes. These fractionation processes depend on factors such as temperature, water availability, CO_2 −concentration, nitrogen availability, salinity, irradiance, and the geological background (Minagawa and Wada, 1984; Farquhar et al., 1989). Through the consumption of herbivores, omnivores and carnivores will also express these specific isotopic signatures, which will thus be reflected through the whole trophic web.

For dietary reconstruction the enrichment of $\delta^{13}C$ and $\delta^{15}N$ from one trophic level to the next one is an essential feature. The $\delta^{13}C$ values become slightly enriched through the trophic web, with a shift of 0.8–1.3‰ between herbivores and carnivores (Bocherens and Drucker, 2003b). In contrast to $\delta^{13}C$ values, $\delta^{15}N$ enrichment is much more intense. Heavy nitrogen isotope (^{15}N) enrichment occurs around 3–5‰ for every trophic level and allows the reconstruction of different trophic levels within one ecosystem at a given time and place (DeNiro and Epstein, 1981; Ambrose, 1991; Bocherens and Drucker, 2003a,b).

2.5. Methods

2.5.1. Collagen preparation and isotopic analysis of the Goyet Neandertal remains

For each specimen a fragment was carefully sawn using a dremel rotating tool with a diamond-coated blade, after considerable documentation of the specimen. All of the analyses were performed at the Department of Geosciences of Tübingen University (Germany). The samples were washed in an ultrasonic bath in acetone, rinsed several times with demineralized water, dried at 35 °C for 72 h and crushed to a powder of 0.7 mm grain size. Most samples were then measured for the carbon, nitrogen and sulfur content (%C, %N, %S) of the whole bone to get an insight about the chemical preservation of the bones and the potential for collagen preservation (Bocherens et al., 2005a). Fresh mammal bone contains around 4% nitrogen, and ancient bone with less than 0.4% typically does not yield a reasonable amount of well-preserved collagen (Bocherens et al., 2005a). These measurements were performed with a Vario EL III elemental analyser (Elementar) (mean standard error 0.02%, 0.05%, and 0.03% for %C, %N and %S, respectively). Collagen extraction was performed following a method modified from Longin (1971) as described in Bocherens et al. (1997). Isotopic measurements were done using an elemental analyser NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. The degree of chemical preservation of the collagen can be expressed by the C_{coll}/N_{coll} atomic ratio (Table 1). Only collagen with a C/N ranging between 2.9 and 3.6 is suitable for further investigation (DeNiro, 1985). The nitrogen percentage of the collagen (N_{coll}) should be higher than 5% (Ambrose, 1990). The isotopic ratios are expressed using the "δ" (delta) value as follows: $\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{reference} - 1] \times 1000‰$, $\delta^{15}N = [(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{reference} - 1] \times 1000‰$. The standard for $\delta^{13}C$ is the internationally defined marine carbonate V-PDB. For $\delta^{15}N$ the atmospheric nitrogen (AIR) is used. Analytical error based on laboratory standards is ±0.1‰ for $\delta^{13}C$ values and ±0.2‰ for $\delta^{15}N$.

2.5.2. Statistical methods

All isotopic data in this study were first analyzed through a cluster analysis, performed with the software JMP version 10.0

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(SAS). This aimed at recognizing clusters within the herbivore and carnivore guilds with comparable ecological niches in terms of their diet.

The statistical analysis of the relative quantification of each food source for predators including Neandertals was carried out using SIAR (Stable Isotope Analysis in R), a Bayesian mixing model based on multiple isotopic values for multiple sources (Parnell et al., 2010), with the program R, version 3.0.2 (The-R-CoreTeam, 2013). The advantage of this approach in contrast to other mixing models (e.g. Bocherens et al., 2005b) is the possibility to integrate uncertainties in input data, and therefore to produce true probability densities for the proportion estimates of each prey species to the predators' diet. However this approach should be used with caution since SIAR will always be able to construct a model based on the analyzed prey, consequently the calculated proportions of potential prey species have to be seen as tendencies and not as absolute values. Finally, we can never be sure that all the species available as prey during the lifetime of a predator are represented in the fossil record. Here we only incorporated the large herbivorous mammal representatives as potential prey. Finally, we excluded the possibility that a significant (in terms of impact on the isotopic composition) amount of protein was obtained from other carnivores through intraguild predation or scavenging. The results have to be interpreted as a general trend, the relative differences being the most revealing aspects in this study. Following previous works (Bocherens and Drucker, 2003b; Fox-Dobbs et al., 2007; Bocherens et al., 2015a) we estimated a Tropic Enrichment Factor (TEF) of +1.1 ± 0.2‰ and +3.8 ± 1.1‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

3. Results

3.1. Chemical preservation of the bones and bone collagen

All specimens analyzed for this study fulfill the requirements in their chemical conditions mentioned above (Section 2.5.1). Consequently we consider that all of the extracted collagen was well preserved. The isotopic results for the Neandertals are summarized in Table 1 and those for the faunal remains in S1.

For the Neandertal specimens, the carbon content in collagen ranged between 39.6 and 47.1%, the content of nitrogen ranged between 12.9 and 17.0%. This is in the range of fresh collagen (Rodière et al., 1996). The C_{coll}/N_{coll} atomic ratio spans between 3.2 and 3.4. The analyzed Spy faunal remains yielded carbon contents in collagen between 35.6% and 44.3%, nitrogen contents between 13.2% and 14.4%, and their C_{coll}/N_{coll} atomic ratio ranged between 2.9 and 3.6.

3.2. Isotopic results of bone collagen according to species

3.2.1. Neandertals

The four Neandertal tibias yielded $\delta^{13}C$ values between −19.6‰ and −19.1‰, with a mean value of −19.2‰ and a standard deviation of 0.27‰. The $\delta^{15}N$ ranged from 11.2‰ up to 11.8‰ with a mean value of 11.5‰ and a standard deviation of 0.29‰. When adding the other Neandertal specimens lacking an individual attribution, the $\delta^{13}C$ values range between −19.0‰ and −19.6‰ with a mean value of −19.2‰ and a standard deviation of 0.19‰, and the $\delta^{15}N$ values range between 10.7‰ and 11.9‰ with a mean of 11.5‰ and a standard deviation of 0.39‰.

3.2.2. Faunal remains

The six analyzed Spy faunal remains yielded $\delta^{13}C$ values and $\delta^{15}N$ values ranging from −21.3‰ to −18.4‰ and from 1.6‰ to 10.5‰, respectively. All the new specimens represent herbivorous species except for one hyena. The herbivorous individuals present $\delta^{13}C$ values from −21.3‰ (mammoth) to −18.4‰ (reindeer) and their $\delta^{15}N$ values range from 1.6‰ (reindeer) up to 8.1‰ (mammoth). The hyena from Spy yielded tooth dentin results of −19.9‰ ($\delta^{13}C$) and of 11.9‰ ($\delta^{15}N$). This equates to bone equivalent values of −20.2‰ for $\delta^{13}C$ and 10.5‰ for $\delta^{15}N$, following the correlation between tooth and bone values for carnivorous species from Bocherens (2015). The complete faunal results are summarized in S1.

4. Discussion

4.1. Reconstruction of the ecological niches

4.1.1. Preconditions

To reconstruct the ecological aspects of a site through the investigation of stable isotopes, some prerequisites have to be fulfilled (Bocherens, 2009b, 2015; Bocherens et al., 2014c). To remodel ecological niches of herbivores and carnivores, remains of these species from the same ecosystem should be compared to each other. The faunal specimens should have lived under the same abiotic conditions (e.g. temperature, aridity, moisture, elevation above sea level) since they have a direct impact on the isotopic baseline in the ecosystem (e.g. Stevens et al., 2009a, 2009b; Bocherens et al., 2014b; Wißing et al., 2015). In a theoretical optimal case, all remains should be contemporaneous and from a single site. In this study we include material from several sites close by (Goyet, Scladina and Spy) with the same ecological background and a clear pre-LGM age (Fig. 1).

4.1.2. Ecological niches

To recognize different patterns of isotopic values, we plotted the $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2) and performed a cluster analysis for the carnivore (Fig. 3) and herbivore species (Fig. 4). Different plant or prey diets during the pre-LGM period in Europe produced regular patterns of $\delta^{13}C$ and $\delta^{15}N$ values within the mammal representatives of the mammoth steppe ecosystem (e.g. Bocherens, 2003; Bocherens et al., 2011; Yeakel et al., 2013). As long as this pattern is preserved, there are no indications for dietary stress within the ecosystem (e.g. Drucker et al., 2014b).

4.1.3. Herbivores

The isotopic pattern within the herbivore guild is most likely linked to a particular preference for different plants for each herbivorous species in the mammoth steppe. Within the herbivore guild, the woolly mammoth always yielded the highest $\delta^{15}N$ values and relatively low $\delta^{13}C$ values (Bocherens, 2003). The mammoth specimens yielded ^{15}N values as high as some carnivores, but had clearly lower $\delta^{13}C$ values. If we take into account the average values and standard deviations of this species ($\delta^{13}C = -21.3‰ \pm 0.3‰$ and $\delta^{15}N = 8.45‰ \pm 1.4‰$), we see no overlap with other species (Fig. 2 and S1). This is the typical ecological niche of the mammoth in an intact ecosystem (e.g. Drucker et al., 2014a, 2014b). The reason for $\delta^{15}N$ values 3‰–5‰ higher than horse and reindeer in mammoth collagen remains under debate. Some hypotheses concerning this have been proposed: It could be physiological adaptations to handle water and food shortage (Heaton et al., 1986), differences in diet like mature grass (Bocherens, 2003), and coprophagy (Clementz et al., 2009). Since a change in ^{15}N abundance to lower values can be correlated with a general decline of the mammoth steppe such as in Mezhyrich in Central Ukraine (Drucker et al., 2014a), the phenomenon of high ^{15}N values is interpreted as the result of dietary specialization, in this case probably mature grass (e.g. Schwartz-Narbonne et al., 2015).

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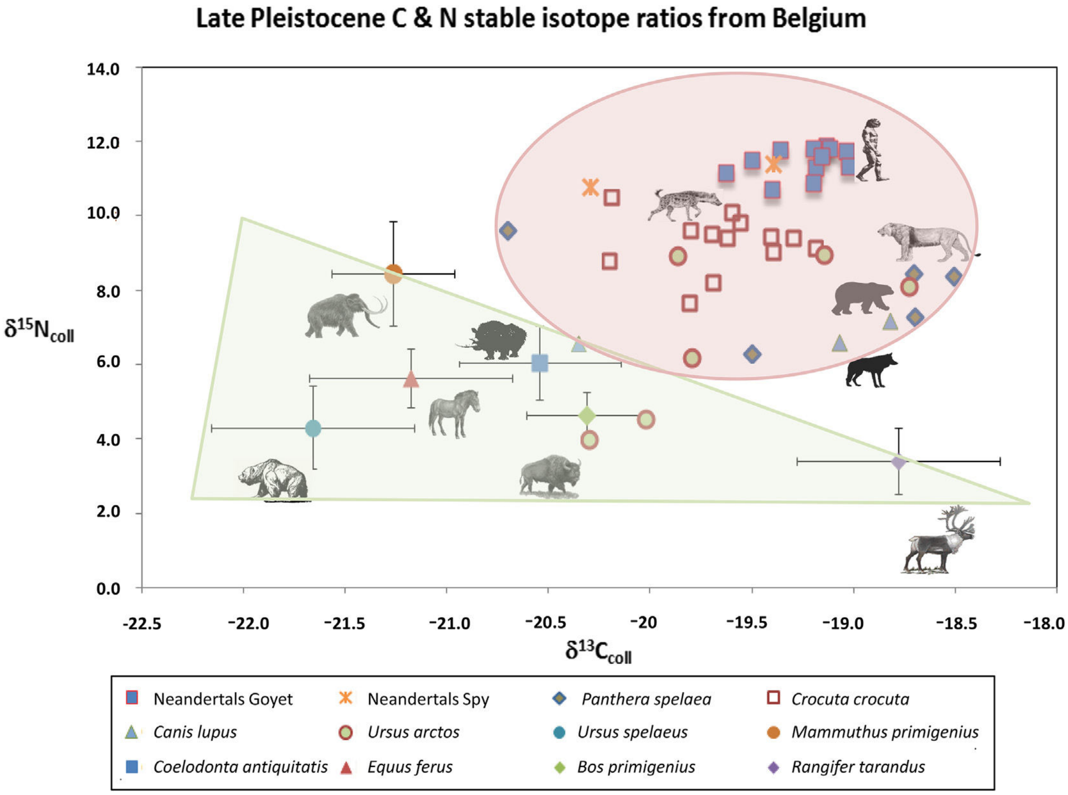

Fig. 2. δ^{13}C and δ^{15}N scatter plot of the Scladina, Goyet and Spy Late Pleistocene remains.

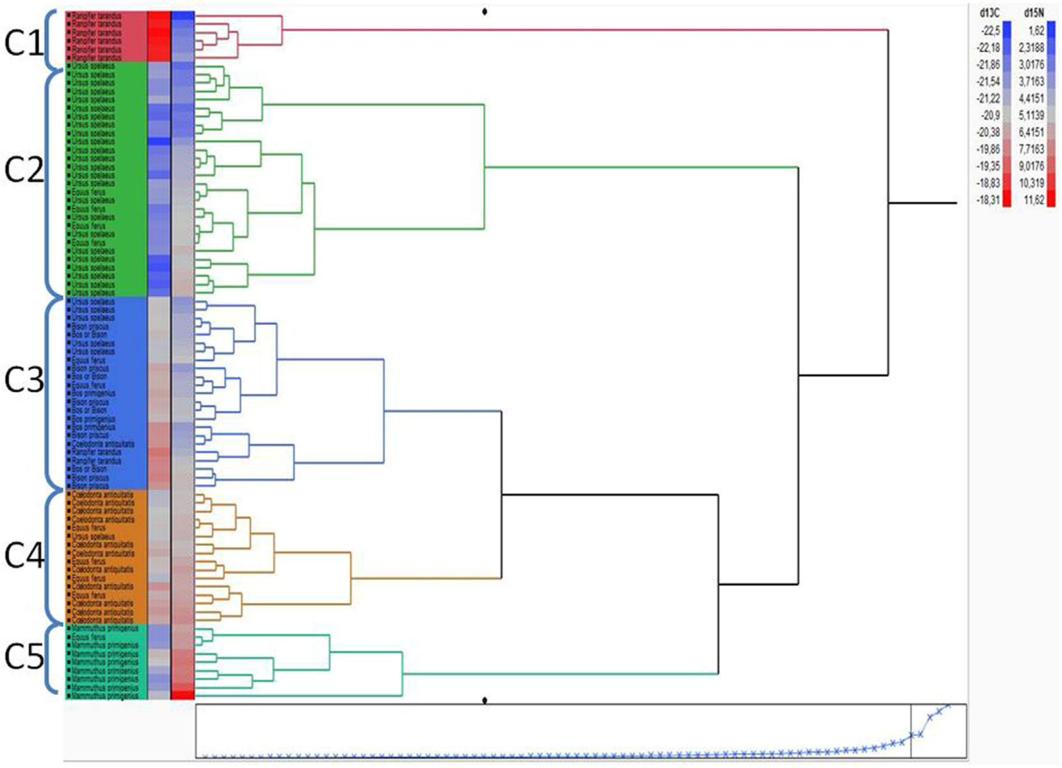

Fig. 3. Cluster analysis of the δ^{13}C and δ^{15}N values of the herbivore guild from the analyzed Belgian sites.

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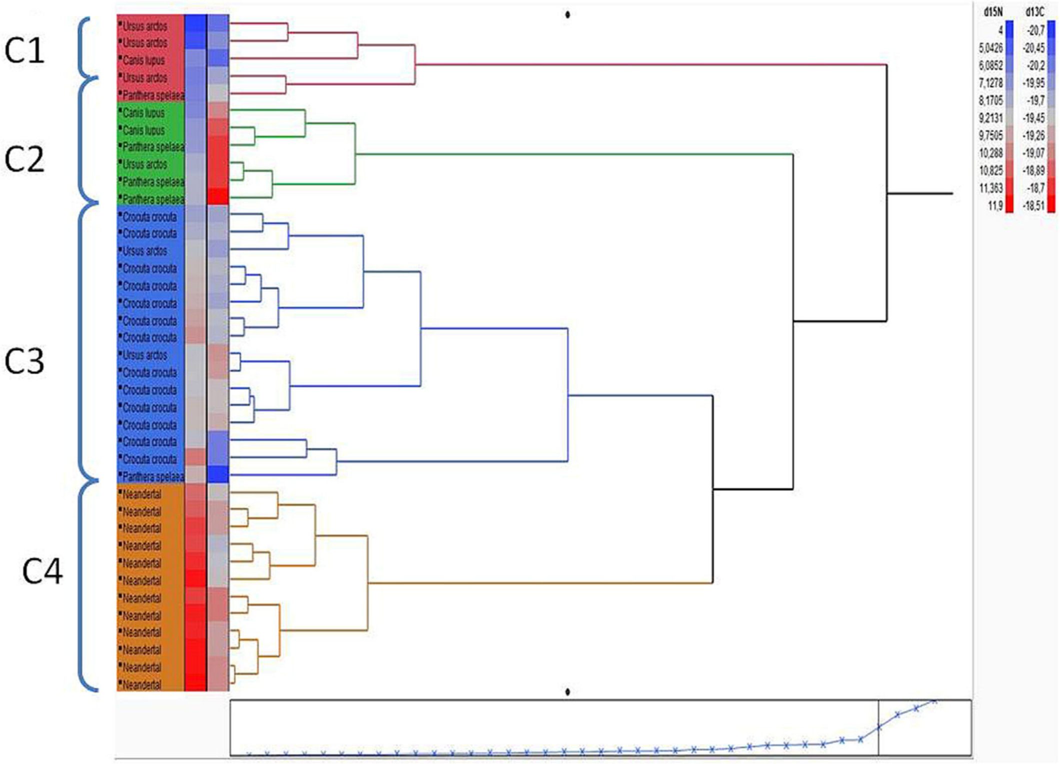

Fig. 4. Cluster analysis of the $\delta^{13}C$ and $\delta^{15}N$ values of the carnivore guild from the analyzed Belgian sites.

The bovids, rhinoceros and the horses in general plot relatively close to each other and consequently could not be distinguished individually through this approach. However, their mean values and the range of their standard deviations are clearly different. These three species are in the center of the herbivore range, with means in between the mammoth and reindeer values (bovids: $\delta^{13}C = -20.3 \pm 0.3‰$ and $\delta^{15}N = 4.65 \pm 0.6‰$; rhinoceros: $\delta^{13}C = -20.5 \pm 0.4‰$ and $\delta^{15}N = 6.04 \pm 1.0‰$; horse: $\delta^{13}C = -21.2 \pm 0.5‰$ and $\delta^{15}N = 5.64 \pm 0.8‰$).

In general the $\delta^{15}N$ values of rhinoceros are slightly higher than for the other two species (Bocherens et al., 2011). This phenomenon can be seen here as well. The reindeer presented the most positive $\delta^{13}C$ values ($-18.8 \pm 0.5‰$) and the lowest average $\delta^{15}N$ values ($3.4 \pm 1‰$). This is due to their consumption of lichen, a well-known and observed feature (e.g. Bocherens, 2003; Stevens et al., 2008; Drucker et al., 2012).

The cave bear is clearly in the range of the herbivores. This species yielded the lowest $\delta^{13}C$ values ($-21.7 \pm 0.5‰$) as well as second lowest average $\delta^{15}N$ values ($4.3 \pm 1.1‰$). The herbivorous diet of this species has been previously discussed (Richards et al., 2008a; Bocherens, 2009a) and demonstrated several times through the investigation of stable isotopic composition (Bocherens et al., 2006, 2014a; Bocherens, 2015). To conclude, among the herbivorous species there is a specific diet preference for each species recognizable through plotting their $\delta^{13}C$ and $\delta^{15}N$ values; the observed pattern is similar to the one already observed for this kind of ecosystem (Fig. 2) (e.g. Yeakel et al., 2013; Bocherens, 2015).

4.1.4. Cluster analysis: niche deviation (herbivores)

In Fig. 3 the cluster analysis presents the $\delta^{15}N$ and $\delta^{13}C$ values of each single herbivore individual according to their $\delta^{15}N$ values. Each cluster represents a similarity in terms of the protein source. This is an important aspect of the ecological niche if, for example, only single individuals from different species or only one species is represented in a certain cluster. The clusters describe on the one hand the ecological flexibility of a given species and on the other hand the range and “distances” among the different ecological niches (based on diet), and most likely more interesting, the species.

Altogether there are five main clusters (C1 to C5 starting from above) (Fig. 3). The first cluster (with a red (in the web version) background) represents only reindeer specimens. Since these animals have a special kind of diet (e.g. lichen, see above) their special niche is clearly visible within this cluster, consequently we named it the “reindeer cluster”. The only other reindeer specimens are represented in C3 (N = 2). The second cluster (C2) (green background) consists mainly of cave bear specimens (N = 24) and includes most of the representatives of this taxon; consequently we named this cluster “cave bear cluster” although it also includes four horses. Five cave bear specimens are not represented in this cluster but in the next one (upper part of C3), relatively close to the C2 cluster. One cave bear is also represented in C4. Altogether, cluster C2 is the largest cluster with the largest number of representatives.

Cluster C3 (blue background) contains a broad spectrum of species. The majority of the specimens are bovids (N = 13). The second most represented species is cave bear with five specimens. The remaining species in this cluster include horse (N = 2), rhinoceros (N = 1) and reindeer (N = 2). With a clear dominance of the bovids (13 out of 23), we describe the C3 cluster as the “bovid cluster”. All of the bovid specimens are represented only within this cluster. We can hypothesize that this C3 cluster represents the typical ecological niche for bovids. However, this niche is not restricted to one species only. Altogether, five species are represented here. Since this cluster is constituted by several species, we assume a certain ecological expansion in terms of diet within this cluster. Other species developed obviously similar dietary habits to that of bovids, or the other way around.

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The C4 cluster is clearly dominated by the woolly rhinoceros with 11 out of 16 specimens, followed by the horse with four specimens and one cave bear. Since the cluster is dominated by the woolly rhinoceros, it was named the "woolly rhinoceros" cluster. All representatives of this species are within this cluster with the exception of one individual, which is in the C3 cluster. This ecological niche is more specialized than the C3 cluster since the number of species and individuals from other species than rhinoceros are quite limited. The niche rhinoceroses occupied is relatively specific and the overlap with the others seems to be limited. Finally, the C5 cluster contains all mammoth specimens. In addition, this cluster contains one horse sample. The mammoth ecological niche is within the mammoth steppe ecosystem, which is clearly visible here through the stable isotopic approach corroborating previous studies (see above).

From the cluster analysis we see that the horse is the most diverse species, as it is represented in all clusters with the exception of the reindeer cluster C1. The second most flexible species is the cave bear. It appears in C2, C3 and C4 with a clear concentration in C2. The bovids and the woolly rhinoceros are both limited to one cluster, with the exception of one woolly rhinoceros sample which appears in C3. For both taxa, it is relevant to mention that other species are also abundant in their cluster, so their niche is not exclusive. The reindeer and the mammoth seemed to be the most specialized species. Within the reindeer cluster C1, no other species is represented, but some reindeer specimens ($N = 2$) can be found in the C3 cluster. The mammoth is limited to one cluster (C5) and only one other specimen is also part of the C5 cluster (horse). The mammoth occupied the most specific niche of this ecosystem within the herbivorous guild.

4.1.5. *Carnivores/omnivores*

The carnivorous species yielded generally significantly higher δ^{15}N and δ^{13}C values (Fig. 2). This reflects the expected stable isotopic fractionation from one trophic level to the next higher one.

The omnivorous brown bears have a quite diverse isotopic pattern (Fig. 2). Some individuals are in the range of herbivores, especially specimen Goyet-B4-36, whereas the other five specimens yielded results in between the carnivorous and herbivorous values or in the carnivorous range of values. This pattern reflects their ecological flexibility in terms of their protein source. For example, specimen D1 227 9D-E from Spy yielded the highest δ^{13}C values, which indicates a diet with a high amount of reindeer meat. Interestingly, the brown bears are the only species where some individuals ($N = 2$) are roughly in the range of hyenas. The individual differences and/or flexibility of the whole species are the most striking features of this taxon.

The three wolf specimens also showed certain flexibility in their protein source reflected by a wide range of their carbon and nitrogen stable isotopes. Specimen SC30300 from Scladina yielded relatively low δ^{13}C values in contrast to the other ones from Goyet, which suggests that it had a significant amount of reindeer in its diet.

The hyenas yielded on average the highest δ^{15}N values among the carnivorous species; this can only be caused by a diet with higher δ^{15}N values. One reasonable explanation for higher δ^{15}N values is the more intensive exploitation of mammoth and woolly rhinoceros as herbivores with the highest δ^{15}N values. It is also possible that this species was a predator of other carnivorous animals or that it scavenged rotten carcasses that could have different isotopic values than fresh meat (Diedrich, 2009, 2011). We also considered the possibility that a unique feeding strategy consuming tissues that are not available or common for other predators (e.g. bone collagen, some intestines) could result in elevated δ^{15}N (Naito et al., in press).

It seems that hyenas had access to all available prey animals since all the other animal predators had only limited access to mammoth and rhinoceros. This implies a special ecological position of this species within the predator guild, additionally considering that the other predators also seem to scatter around the isospace occupied by hyenas (Fig. 2). This indicates an avoidance strategy at least in terms of diet/prey choice. It is difficult to suggest that this hyena pattern occurred by pure selective scavenging of the prey from other carnivores. It is more likely that hyenas were active predators (Bocherens et al., 2011) since if they had mostly scavenged the prey of other predators, their values would clearly overlap.

The five analyzed cave lions yielded a very diverse pattern. Despite the small sample size, their standard deviation is the highest within the pure carnivorous guild (0.8‰ for δ^{13}C and 1.1‰ for δ^{15}N). Not one cave lion specimen is within the isotopic range of the hyenas. The individual differences within this species and in comparison to the hyenas can be linked to the solitary habits of cave lions in contrast to the collective behavior of the cave hyenas (Bocherens et al., 2011).

The 12 Goyet Neandertal specimens represent at least 4 different adult individuals (Rougier et al., in prep.). The Neandertals yielded the highest nitrogen (average $\delta^{15}N = 11.5‰$) and relatively high carbon isotopic values (average $\delta^{13}C = -19.2‰$). The diet of these individuals was in general very similar in terms of averages and consists of prey/average protein source with a very high ^{15}N composition (Fig. 2). Having the highest nitrogen isotopic values within the predator guild does not mean that Neandertals were more carnivorous than for instance the hyena, but it implies that the protein fraction of their diet had higher δ^{15}N values.

Interestingly, no other carnivorous species is in the range of the Goyet Neandertals. Not a single individual has values comparable with the Neandertals. This proves that Neandertals occupied a special ecological niche.

4.1.6. *Cluster analysis: niche deviation (carnivores)*

In Fig. 4 the cluster analysis represents the δ^{15}N and δ^{13}C values according to their δ^{15}N values of each single carnivore specimen and the omnivorous brown bear, including the Neandertals from Goyet. The dendrogram shows four main clusters (C1 to C4). The intra-cluster diet similarity is greater than the inter-cluster similarity.

C1 represents the omnivorous brown bear ($N = 3$), one wolf and one cave lion. All these individuals are characterized by relatively low δ^{15}N values (Figs. 2 and 4), which does not automatically mean that the wolf and the cave lion were omnivorous. We have to keep in mind that not all potential prey animals are represented in our study. For example, rodents and lagomorphs are not represented in this study, but they usually exhibit lower δ^{15}N than ungulates (Drucker, 2001; Bocherens et al., 2011). We interpret this cluster as the one of the "small game hunters" with a slight tendency in the direction of reindeer.

C2 contains three out of five cave lions, two wolves and one brown bear (Fig. 4). This cluster represents the cluster of individuals with a clear preference for reindeer (Fig. 2). For instance, the cave lion has been shown in several cases to be a species with a special preference either for this cervid or for cave bear (Bocherens et al., 2011). The extinction of this species coincides chronologically with the extinction of species mentioned above in Western Europe (Stuart and Lister, 2011; Bocherens et al., 2014a; Sommer et al., 2014). Thus this cluster represents the typical "reindeer hunter" niche.

C3 consists mainly of cave hyena ($N = 13$). All individuals of this species are represented within C3. Additionally, two brown bears and one cave lion are represented. Since there is only very limited overlap in the average values of the hyena with other species (Fig. 2), and their isotopic values are limited in range and standard deviation, we describe this cluster as the typical "hyena cluster". This cluster represents top predators with access to all available prey in this ecosystem. Representatives of this cluster focus on mammoth and woolly rhinoceros as protein sources.

All the Neandertal specimens are in C4 (n = 12) (Fig. 4). Their high level of homogeneity in terms of species within all carnivore clusters is due to two observations: first, the Neandertal values are grouped relatively close to each other (Fig. 2), and second they are clearly separated from the other species (Fig. 4). This implicates that the ecological niche of these Neandertals in terms of protein source is the most specific of all the analyzed species in the carnivore guild. This result indicates a certain kind of prey choice that is not or only hardly explainable through scavenging of prey that other predators hunted down. The hyena was the only predator that regularly had access to mammoth and rhinoceros, the mammals which played an important role in the Neandertals' diet. Unspecific scavenging from hyenas would result in an isotopic signature similar to the one of hyenas. To base their dietary strategy only on scavenging specific prey of the other predators (mammoth, rhinoceros) instead of all the available prey does not seem reasonable. The most likely procurement strategy of Neandertals seems to be an active and selective hunting. The ecological niche is engaged only by Neandertals and is interlaced with typical representatives of the mammoth steppe like mammoth and rhinoceros. Their abundance within the ecosystem is directly reflected on this cluster.

4.2. *Reconstruction of consumed prey*

In order to obtain a more precise picture of the potential prey of all carnivorous species, we calculated the potential proportion of consumed prey using a Bayesian method (SIAR V4, Stable Isotope Analysis-package in R) (Parnell et al., 2010; The-R-CoreTeam, 2013).

It is worth to point out that we underestimate the consumption of plant food with this approach. The analysis of the nitrogen stable isotope ratios in single amino acids of the collagen seems to be a more precise tool for this kind of investigation (Naito et al., in press, 2014). This avenue of research has just started for Pleistocene contexts. It is not to be underestimated that there is a non-linear isotopic variation between the most extreme end points of a pure vegetarian and a pure carnivorous feeding behavior, meaning that even a very small amount of meat immediately increases very significantly the δ^{15}N values of the bulk collagen. The contribution of plant food up to 50% of the total proteins in an omnivore diet results in δ^{15}N values that are not lower than 1 standard deviation of the collagen of a pure carnivore (Bocherens, 2009b). We consider that for Neandertals, for example, the whole diet could include a significant amount of plant food with low δ^{15}N values (as high as half the dry weight of the dietary intake) (Bocherens, 2009b). Consequently, we provide data on the relative protein source contribution of the different prey for each of the predator species, not absolute values.

There are three important advantages of this analysis: first of all, the possibility to incorporate uncertainty (standard deviations) into input data as well as into the enrichment factor from one trophic level to the next one (TEF). Second, the method provides not only a range of protein source proportions (proportion box plots), but also the probability distribution (proportion densities). Within the proportion box plots, three different grey scales are shown. The lightest grey represents a probability of 95%, the medium grey 75% and the darkest grey 25% (Fig. 5–10). Finally, to have a better understanding of the statistical dependences between each potential prey to all the others, their relationship is expressed against each other through a diagnostic matrix plot. There are several possibilities if there is either a positive or negative correlation between two or more species. The SIAR software provides results taking into account these correlations among species, in this case an increasing probability range for the potential prey (Parnell et al., 2010). Here we will discuss the prey choice for all the carnivore species including the Neandertals and the omnivorous brown bear. We calculated the average values of each species, taking their standard deviation into account. For the Neandertals, we also analyzed the individual values. We reconstructed the potential predators of the mammoth to get a better idea of the potential hunters of this species.

The cave lion protein sources can be described as follows (Fig. 5). Cave bear was part of their diet for around 20%, and the proportion of mammoth was the lowest with values between 0% and 10% of the total dietary protein, the highest probability density being around 0% and then decreasing continuously (S2). The amounts of rhinoceros and horse are close to each other and span on average between 5 and 20% (Fig. 5). The amount of bovids can be described in the same way as the one for cave bear, with a maximum probability of around 20–25% (S2). Reindeer as a protein source played on average the most important role for the cave lions (Fig. 5). This contribution has the highest probability expressed in density maximum around 25–28% (S2). It is worth mentioning here that there is no strong correlation between the amounts of several species (S2). The strongest correlation is a negative one between the bovids and the horses, meaning that an increased horse contribution requires less bovids, and vice versa.

The hyena diet can be summarized as shown is Fig. 6. Immediately visible is the average composition of their diet. This reflects the availability of all potential prey species for the hyena. The only species with a slightly lower amount is the reindeer. The highest probability around 15% is expressed through the highest density (S2). Between the reindeer and the bovids is a strong negative correlation (S2), which means that if the amount of reindeer increases, less bovid is necessary or, if the hyena consumes more bovids, less reindeer is necessary to gain the isotopic composition the hyena specimens have in average. The same is true for cave bear and horse since they are negatively correlated as well (S2). On the other hand, there is a positive correlation between mammoth and reindeer, indicating that more reindeer requires a higher contribution of mammoth protein to gain the measured isotopic values.

The protein sources of wolf are visualized in Fig. 7. Reindeer and cave bear seem to have played an important role; their dietary contribution is above 20% each with a slightly higher amount of reindeer. The probability for reindeer as one main diet component is the highest around 25% (S3). The consumption of mammoth was the lowest. The highest density of probability is close to 0% and decreases significantly until a maximum of around 10%. There is a negative correlation between the amount of rhinoceros and reindeer; the more reindeer, the less rhinoceros is necessary to get the average wolf signal (S3). However, intra-wolf diversity is relatively high (as discussed above) and consequently, these average values have to be taken within this context. One of the most important general features of the prey choice of this species is the very low consumption of mammoth and the statistical possibility to "replace" some of the rhinoceros with reindeer. This species does not rely very intensively on the two largest herbivore species in this ecosystem. Altogether the statistical correlations between potential prey species are in comparison limited.

The brown bear yielded results similar to the wolf (Fig. 8). The preferred prey were reindeer and cave bear, but only slightly. These species yielded the highest probability density around 20%. For the bovid, the horse and the rhinoceros, the probability density is stretched wider (S3). One of the most important results is again the

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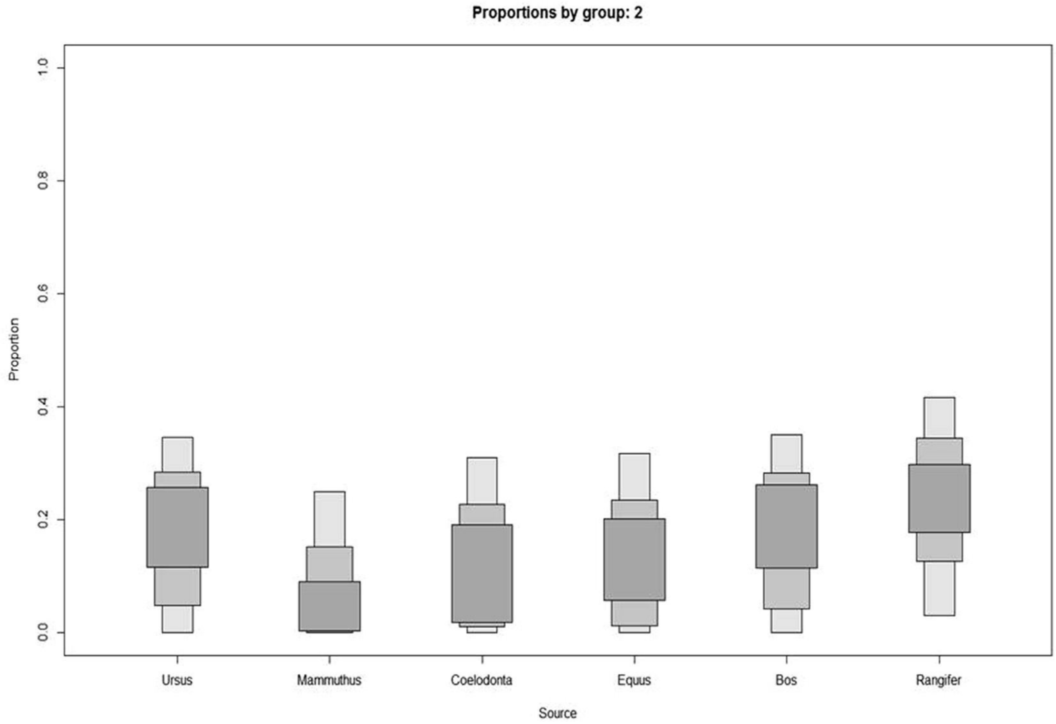

Fig. 5. Species proportions of cave lion diet.

very low contribution of mammoth. The highest probability is close to 0% and decreases continuously (S3). There is a slightly negative correlation between the bovids and the reindeer (S3). Again, the average values have to be taken with the corresponding background since the brown bear is quite a flexible feeder (see above). The general independency of this species on the typical megaherbivores of the mammoth steppe (mammoth and rhinoceros) is similar to the wolf individuals.

Finally, we reconstructed the proportion of each potential prey for the Neandertals. Following Fig. 9, cave bears played more or less

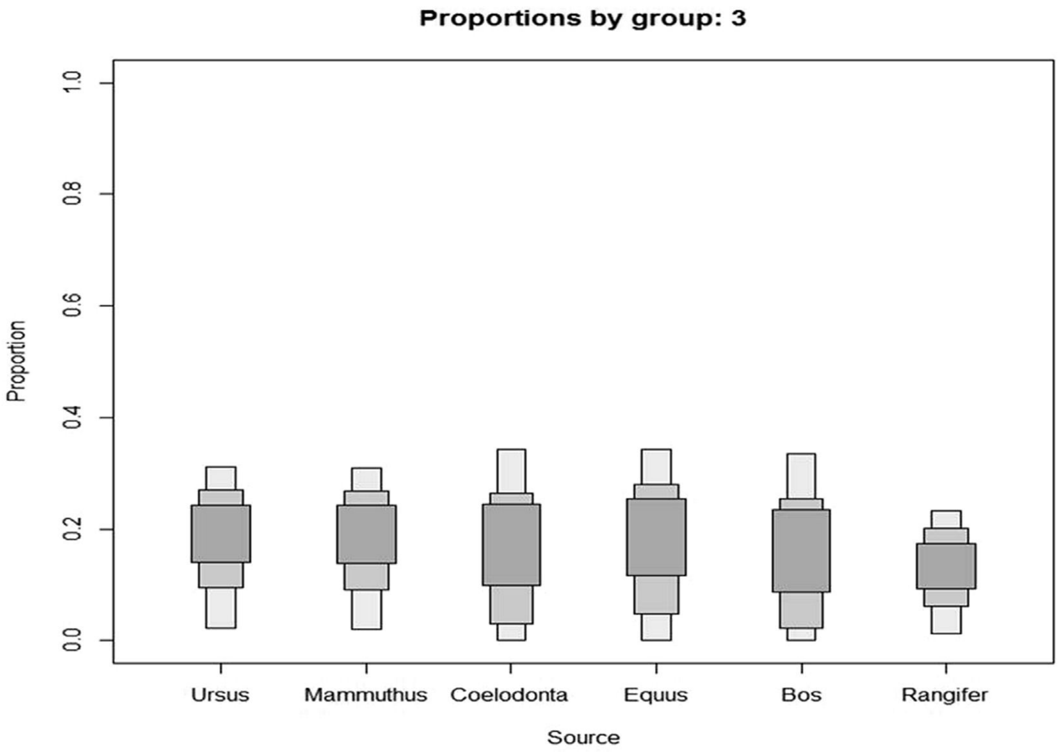

Fig. 6. Species proportions of hyena diet.

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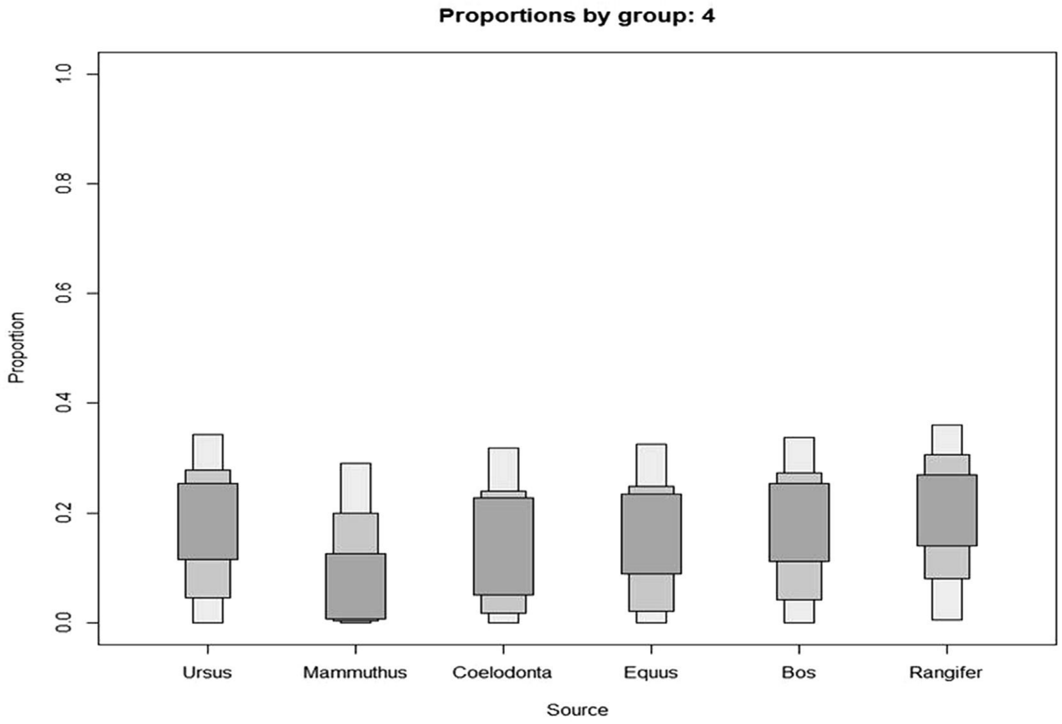

Fig. 7. Species proportions of wolf diet.

no role as protein source. The highest probability proportion is around 0 and decreases rapidly down to around 0% probability at an amount of 20% (S4). In contrast, with a 95% probability the amount of mammoth meat contribution was between 15% and 60% (Fig. 9), with the highest probability in the range between 30 and 40%. Unfortunately, we cannot define a more precise probability for this species because there are some negative correlations with other species, like rhinoceros, horses and bovids (S4). This means that if these species were to decrease in their proportions, the probability for a higher amount of mammoth in the diet would increase. The

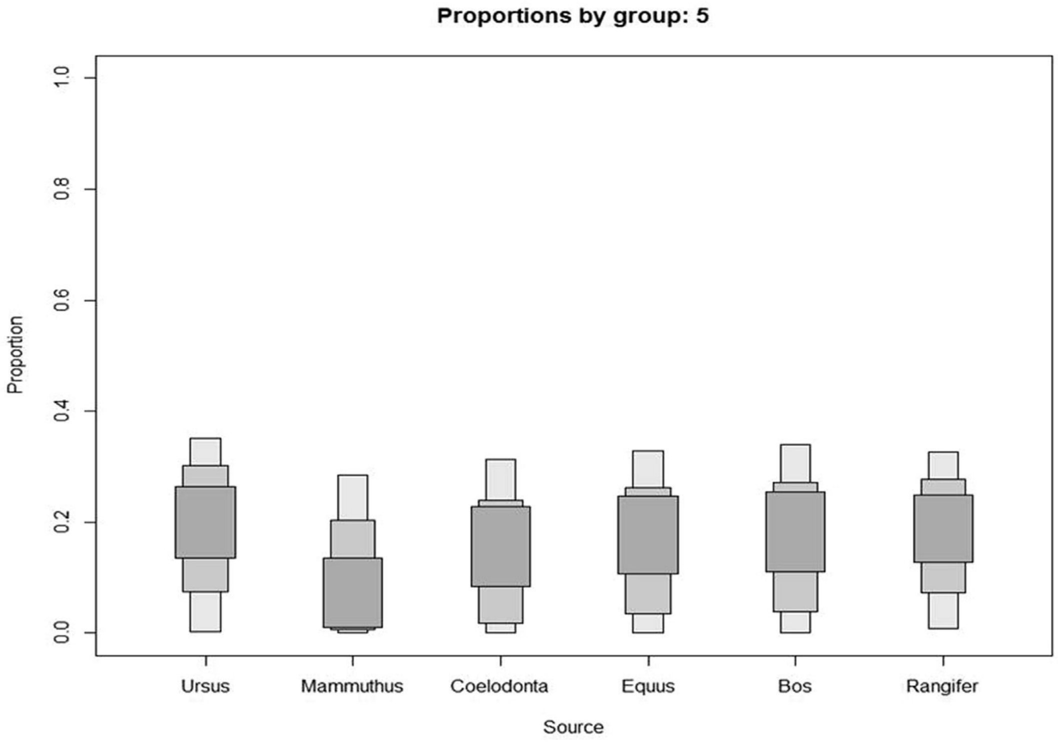

Fig. 8. Species Proportions of brown bear diet.

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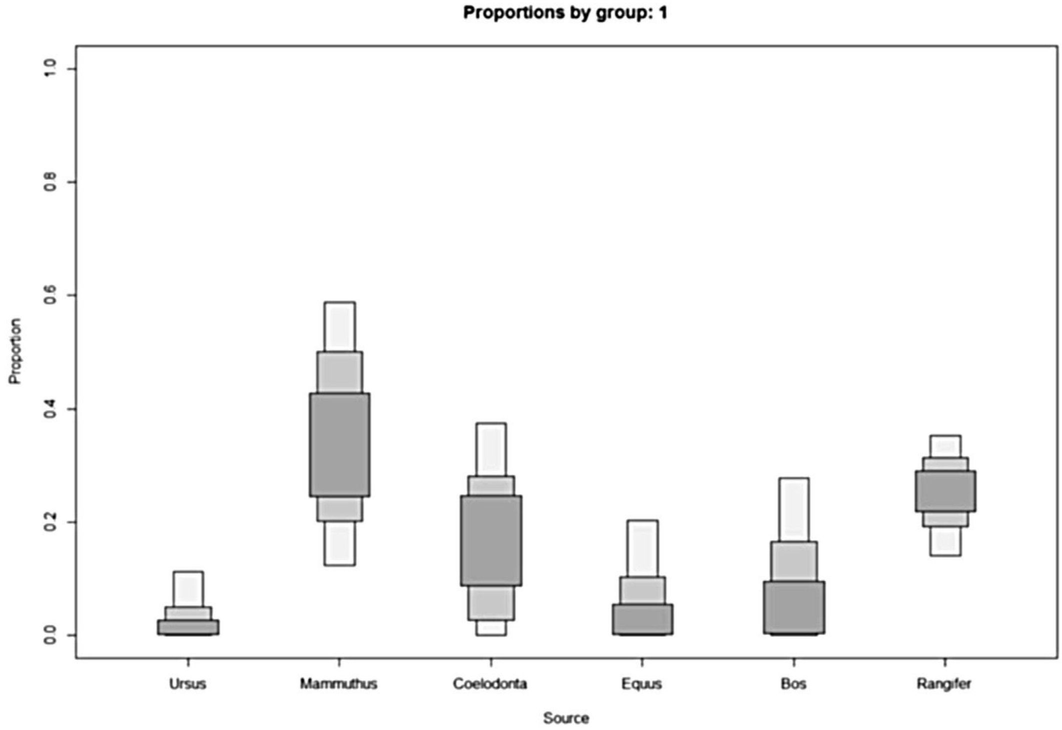

Fig. 9. Species Proportions of Neandertal diet at Goyet.

situation is somehow complex since there is a negative correlation between rhinoceros and reindeer as well (S4). Rhinoceros and reindeer yielded a very strong correlation (S4). The amount of rhinoceros was around 20% (the highest density of probability at this point). The amount of reindeer can be estimated at around 25% with the highest proportion density even at this level (S4). If Neandertals had less reindeer in their diet, they had to increase the proportion of rhinoceros, and vice versa. However, the high negative correlation between mammoth and rhinoceros means that a decreasing amount of rhinoceros would need an increasing amount of mammoth (S4). Finally, a higher contribution of reindeer would mean more mammoth is also required since there is a positive

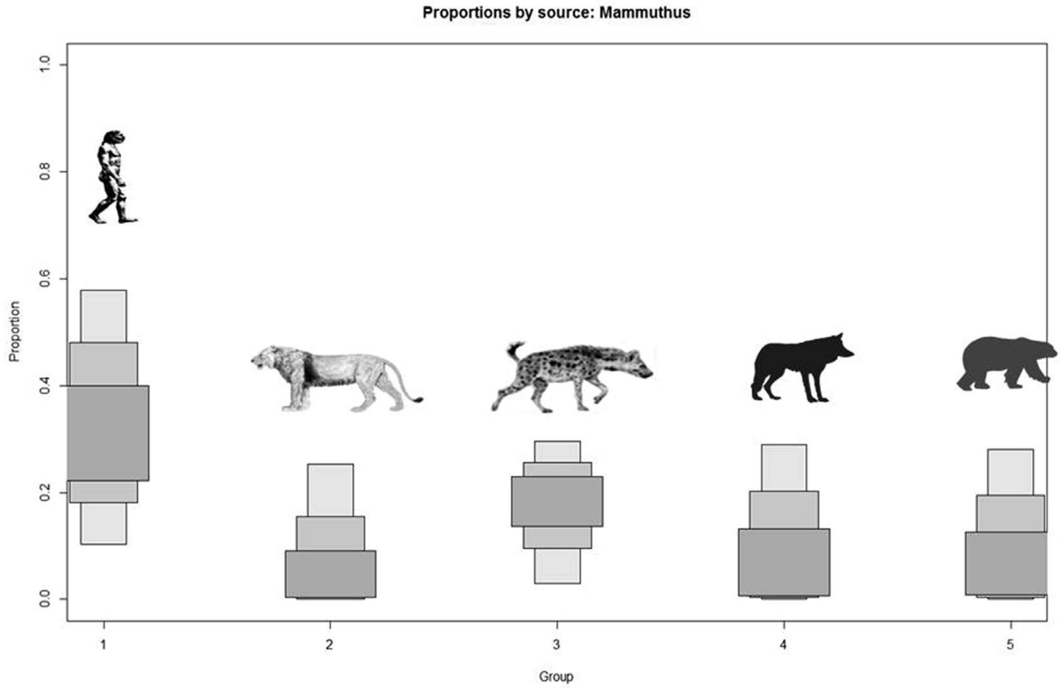

Fig. 10. Predation pressure on mammoth at Goyet in relative proportions.

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correlation between both species. The amount of horse and bovid meat in the Neandertal diet is relatively low, between 0 and 10%, whereas bovids played a slightly more important role than horses (S4). This is important since there is nearly no correlation between these species (S4), which improves the statistical precision.

4.2.1. *Analysis of single Neandertal individuals*

To get an insight in the individual dietary differences among the Neandertal group, the individuals identified based on their right tibias (tibias III, IV, V and VI) were separately analyzed with the SIAR approach (S5 to S8). We see nearly the same results as those of the average Neandertal values (incl. standard deviation) since all the individuals plot relatively close to each other (Fig. 2). However, there are some slight differences that can play an important role in solving the uncertainties caused by the negative correlations between the average proportions of potential prey species (see above). Reindeer is represented between 30% and 10%. Cave bear was more or less not a protein source for the different individuals, in contrast to the mammoth, which most likely played the most important role as protein source for every individual. The probability for a high amount of rhinoceros as part of the diet is again relatively high. However, the grade of uncertainty for this species is very prominent, since there are negative correlations between rhinoceros and mammoth as well as negative correlations between rhinoceros and reindeer. The only exception where we do not see such a high negative correlation between these species is for the individual represented by tibia VI (S8). The individual with the lowest uncertainties based on the lowest grade of correlations yielded the lowest amount of reindeer protein in their diet. For this individual, the most important prey animals are, in order of appearance: mammoth, rhinoceros, horse and bovids (with similar proportions), reindeer (around 10%), and cave bear (S8).

4.2.2. *Analysis of the Neandertal remains Spy I and Spy II*

Since Spy and Goyet are relatively close in time and space, it seems reasonable to investigate the adult individuals Spy I (represented by specimen Spy 94a) and Spy II (Spy 430a) with the same statistical approach and data background used for the Neandertal remains from Goyet. When comparing both sites, the stable isotope values are relatively close to each other with a low level of difference (Table 1). The most interesting points are the slightly lower δ^{13}C values (average −19.85‰) for the Spy specimens in comparison with the ones from Goyet (average 19.2‰) (Fig. 2). If we compare the dietary strategies for both Spy specimens (S9 and S10), we see that for both individuals mammoth was the most important prey with the highest density of probability at a proportion of around 30% for Spy I and 40% for Spy II (S9 and S10).

For Spy I the second most significant prey was most likely the rhinoceros with the highest density of probability at a proportion of around 25%, followed by reindeer around 15% and horse and bovids. For horse and bovids, the probability increases the lower the amount is (S9), and on average, these species contributed less than 10% of the total protein intake. Again, cave bear does not play any role as prey. The probability to have close to no cave bear is high and decreases with a theoretical increase of the proportion of this species (S9).

The individual Spy II yielded the lowest δ^{13}C values of all Neandertal remains we included in this study, which most likely indicates the lowest amount of reindeer for this individual. Indeed the highest density of probability is around 5% and decreases rapidly with an increasing amount of reindeer in the diet of this specimen (S10). Bovids did not play an important role either (around 5–10%) with a decreasing density of probability when increasing above 5%. For horse, the density of probability between 0% and 25% does not change, which means that we cannot estimate a more precise amount of this potential prey. One reason for this is the negative correlation between cave bear and horse (S10), which is the strongest within this matrix. The similarity of density of probability for both species is very high (S10). If we consider the results of all other analyzed Neandertal specimens, which always yielded a very low amount of cave bear in the diet, we can assume that the probability for a more intensive exploitation of horse in contrast to cave bear is reasonable. The second highest negative correlation is between mammoth and horse. This implies that the already high amount of mammoth in the diet (around 40%) could increase with a lower amount of horse connected with an increasing amount of cave bear (S10). For reasons stated previously, we assume this is not the case. This high amount of mammoth protein represents the maximum of the amount of mammoth since a significant higher exploitation of cave bear is not reasonable, at least for this individual.

The analysis of the two Spy adult Neandertal remains confirmed the general results obtained at Goyet but in addition, this approach yielded the possibility to clarify certain statistical inadequacies due to several negative or positive correlations among species.

4.2.3. *Predation on megaherbivores at Goyet*

The isotopic composition of the Late Pleistocene Goyet Neandertals cannot be explained without a high contribution of herbivore mammal meat. However, it is still under debate as to what the role of megaherbivores played in general as potential prey species for Neandertals (see for instance Smith, 2014). In all previous studies so far, Neandertals are clearly in the range of carnivores and never overlap with the range/area of omnivorous or even herbivorous species. In each case, the δ^{15}N values of the Neandertals are 1–2‰ more positive than those of the contemporaneous predators.

In Fig. 10 we reconstructed the different proportions of prey that each carnivore consumed in reference to the mammoth. Here, some clear trends are visible: Neandertals were the species that most intensively relied on mammoth in comparison with all the other carnivorous species. With a 95% probability of an amount between around 10% and 60% and the highest probability between around 20% and 40%, the mammoth played a more important role for the Goyet Neandertals than for all other carnivorous species. For the cave lion, the mammoth played only a very minor role. With a probability of 95% for an intake of mammoth between around 0% and 25% (with a maximum probability around 0 and 10%), this species was definitely not focused on hunting or scavenging mammoth. Hyena has the second highest proportion of mammoth for dietary protein with a proportion between 5% and 28% (95% probability). The highest probability is around a proportion of 20%. Wolf and brown bear most likely did not rely on mammoth. Both species have very similar prey preferences concerning the mammoth. An amount between 0% and around 28% of this species (95% probability) was part of their diet. For wolf and brown bear, the higher probabilities are in the range between 0 and 10%.

The fact that no other herbivore occupied the distinct ecological niche the mammoth filled produced an isotopic signature that can be clearly described in the context of all other contemporaneous herbivorous species (discussed above). Their hunters, the Neandertals, accumulated their unique isotopic signature, which can be seen in their collagen isotopic carbon and nitrogen stable isotopic composition. Neandertals have clearly the highest amount of mammoth in their diet in comparison with all other carnivorous species (e.g. Fig. 10). If we hypothesize that the Neandertals would have scavenged from the hyena (the only other predator with a reasonable amount of mammoth in their diet) in a significant amount, the isotopic compositions of both predators would clearly overlap. Since they do not, it is unlikely that Neandertals selectively scavenged only the mammoth in significant amounts from the hyena. We also have serious doubts that the Neandertals would have taken away all of the mammoth from hyenas, which would be the only possibility to explain the recurring results of hyenas having lower δ15N values than Neandertals. Instead, we were able to clearly demonstrate that, within the predator guild, the Neandertals were the main predators of mammoth (e.g. Fig. 10). There is no other predator in the ecosystem eating mammoth meat in comparable amounts. Furthermore, we demonstrated the specific ecological niches of both Neandertals and hyenas, which are clearly different with no overlap of the bulk collagen isotopic carbon and nitrogen composition. Given these arguments, we argue that the Neandertals were selective and active mammoth hunters. Through this model, it can be hypothesized that mammoth was, for the Neandertals, the most important species, at least in an ecosystem like this. For the other carnivorous or omnivorous species, the mammoth played a much less important direct role. The abundance of mammoth in the ecosystem most likely played an important role for the Goyet Neandertals. The ecological implications for the cave site of Spy are very similar due to the similarities of the Neandertal isotopic values. At Spy, Germonpré et al. (2014) proposed on the basis of an archaeozoological study that Neandertals and not other carnivores were responsible for the large number of mammoth remains at the site. A special preference, most likely for dietary reasons, has to be taken into account for the collection of juvenile mammoth skull elements at Spy. The same observation has been made in other archaeological contexts elsewhere, possibly due to proboscidean heads having a particular nutritional potential (e.g Broadhurst et al., 2002; Agam and Barkai, 2015). Mammalian brain tissue is one of the richest terrestrial sources of long chains of omega-3 polyunsaturated fatty acids (n-3 LC-PUFAs) (Broadhurst et al., 2002). A minimum intake of about 0.5 g of n-3 LC-PUFAs per day is required in the human diet to avoid signs of deficiency (Rustan and Drevon, 2005). However, n-3 LC-PUFAs are very susceptible to oxidation. Their rate of degradation is influenced by light, heat, and oxygen concentration; oils rich in n-3 LC-PUFAs stored in the dark at 4 °C reached a level of oxidisation beyond human consumption after one month of storage (Pak, 2005; Albert et al., 2013). In addition to the arguments proposed by Germonpré et al. (2014) for the hunting of mammoths by the Neandertals of Spy, the fact that the brain of a dead mammoth would spoil very quickly implies that the Neandertals must have had very rapid access to the carcasses, which is not in favor of them scavenging dead mammoths. The presence of gnawed mammoth long bones at Spy suggests that hyenas got later access to the mammoth remains that the Neandertals had transported to the cave.

4.3. *Review of $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures of Late Pleistocene Neandertals*

In general, isotopic analysis of prehistoric humans for dietary reconstruction must meet certain requirements: the chemical composition of the collagen must be reliable, the stage of ontogenesis must be considered (with special attention to the nursing effect) and finally, a broad set of contemporaneous herbivorous and carnivorous species from the same site/area must be analyzed in order to reconstruct the trophic structure of the foodweb.

A specimen very similar in time and space to those analyzed in the present study is Engis 2 (Bocherens et al., 2001). This is a young individual with an age probably around 4–6 years (Tillier, 1983) and consequently, we cannot exclude that this specimen still has an isotopic signature impacted by nursing, especially since the $\delta^{15}N$ values are enriched in relation to all adult specimens from Goyet and Spy. For this reason, the Engis 2 individual is not suitable for direct comparison (Table 2).

Table 2
Late Neandertal isotopic comparison.

Site	Sample	Code	$\%C_{coll}$	$\%N_{coll}$	C/N	$\delta^{13}C$	$\delta^{15}N$	Source	Chemical integrity	Trophic context	Stage of ontogeny
Engis	parietal	ENG 2	41.7	14.4	3.4	−19.6	12.6	Bocherens et al. (2001)	yes	yes	immature
Neandertal	humerus	Nea 1	/	/	/	−21.6	7.9	Richards and Schmitz (2008)	no	limited	mature
Neandertal	humerus	Nea 2	/	/	/	−21.5	9.0	Richards and Schmitz (2008)	no	limited	mature
Neandertal	humerus	NN 1	/	/	/	−20.0	/	Schmitz et al., 2002	no	limited	mature
Neandertal	tibia	NN-4	/	/	/	−18.8	/	Schmitz et al. (2002)	no	limited	mature
Neandertal	humerus	Nean 1	/	/	/	−19.6	/	Schmitz et al. (2002)	no	limited	mature
Vindija	mandible	Vi-207	37.1	13.5	3.2	−19.5	10.1	Richards et al. (2000)	doubtful	no	mature
Vindija	parietal	Vi-208	36.1	11.9	3.6	−20.5	10.8	Richards et al. (2000)	doubtful	no	mature
Okladnikov Cave	humerus	KIA-27010	44.2	14.3	3.6	−19.6	13.3	Krause et al. (2007)	yes	no	mature
Okladnikov Cave	humerus	KIA-27011	44.4	15.3	3.6	−19.1	12.9	Krause et al. (2007)	yes	no	mature
Les Rochers-de-Villeneuve	femur	RdV 1	39.35	14.1	3.25	−19.0	11.6	Beauval et al. (2006)	yes	yes	mature
Chez-Pinaud Jonzac	tooth	S-EVA-2152 (>30 kDa)	30.2	9.7	3.6	−20.7	10.6	Richards et al., (2008a,b)	doubtful	limited	mature
Chez-Pinaud Jonzac	tooth	S-EVA-2152.1 (10–30 kDa)	33.5	12.1	3.2	−19.7	11.2	Richards et al., (2008a,b)	doubtful	limited	mature
Chez-Pinaud Jonzac	tooth	S-EVA-2152.2 (<10 kDa)	26.7	8.4	3.7	−21.3	10.3	Richards et al., (2008a,b)	doubtful	limited	mature
Les Pradelles	skull fragment	M300	41.1	14.7	3.3	−19.1	11.5	Bocherens et al. (2005b)	yes	yes	mature
Les Pradelles	mandible	M400	37.6	13.1	3.3	−19.5	11.4	Bocherens et al. (2005b)	yes	yes	mature
Les Pradelles	skull fragment	M100	18.9	7.0	3.2	−21.8	8.4	Bocherens et al. (2005b)	yes	yes	mature

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The Neandertal type specimen and another confirmed Neandertal individual from the Feldhofer Grotte were also analyzed for stable carbon and nitrogen isotopes (Richards and Schmitz, 2008). These samples were associated with results obtained on only six faunal samples without stratigraphic context (Richards and Schmitz, 2008). Since the chemical collagen preservation is an important aspect to be considered (six out of 12 faunal remains yielded valid collagen), the %C and %N of the collagen would have been interesting to review but this information is not provided (see Richards and Schmitz, 2008). The $\delta^{13}C$ values of both Neandertal specimens are lower than all terrestrial mammal values at the site, which has never been documented elsewhere. The assumed predators, in this case Neandertals, would never yield lower $\delta^{13}C$ values than the average composition of their prey. The $\delta^{13}C$ values for the Neandertals presented in another article in 2002 (Schmitz et al., 2002) are significantly higher and rather in the range of the expected values for Neandertals, but the chemical validity of this collagen cannot be checked since the C/N ratio in collagen is not provided (Table 2).

Vindija is an important Southern European Neandertal site in Croatia that yielded a broad set of hominin and faunal remains. Two Neandertal specimens (Vi-207 and Vi-208) have been analyzed for stable carbon and nitrogen isotopes (Richards et al., 2000) (Table 2). Two faunal specimens from the same layer, one cervid and one cave bear, were used for trophic reference as well as one bovid and another cave bear from the older layer G3. No carnivorous animal collagen could be extracted due to preservation reasons (Richards et al., 2000). For this reason, Richards and colleagues included faunal collagen results from typical mammoth steppe sites several hundred kilometers north in the Czech Republic: Dolni Věstonice II, Milovice and Brno-Francouzská. The complex G in Vindija has an ecological background most likely different from typical Czech Republic sites. Following Janković et al. (2011) and Miracle et al. (2010), it appears that the Neandertal remains were deposited during relatively temperate conditions and the ungulate remains from complex G were most likely deposited during temperate conditions within MIS 3 (Miracle et al., 2010; Janković et al., 2011). The Gravettian open air mammoth sites in the Czech Republic reflect somewhat different conditions (Beresford-Jones et al., 2011). In this case, a direct comparison of the stable isotopes with the aim of reconstructing trophic relationships is difficult since the ecological background of the Neandertals is not the same as that of the faunal remains from the Czech sites. In addition to the lack of comparable faunal material, the collagen preservation at Vindija is not good and the ^{14}C dates published in 2000 by Richards et al. are not reliable (Higham et al., 2006). For the different reasons presented above, these specimens from Vindija cannot be included for further comparisons with the remains from Belgium (Table 2).

The Okladnikov sequence in the Altai region of Siberia also yielded Neandertal remains which contain collagen (Krause et al., 2007). The stable carbon and nitrogen isotopes are provided (Table 2). However, these results are unfortunately not contextualized, meaning that no faunal material was investigated as required for stable isotope analysis. Due to this lack of information, these data cannot be interpreted in ecological terms.

Another isotopic study performed by Beauval and colleagues in 2006 (Beauval et al., 2006) presented stable isotopic carbon and nitrogen values from Les Rochers-de-Villeneuve (Lussac-les-Châteaux, Vienne) in South-East France (Table 2). The collagen fits all necessary chemical criteria; consequently, the stable isotopic results are valid. Unfortunately, beside one hyena sample, no contemporaneous faunal assemblage has been analyzed for stable isotopes. Therefore the results were directly interpreted in the context of stable isotopic investigations carried out on the site of Les Pradelles, around 100 km southwest of Lussac-les-Châteaux (Beauval et al., 2006). To conclude, this study provides valid Neandertal collagen isotopic results that are embedded in an ecological context and therefore fulfills the requirements for a diet reconstruction.

A study performed by Richards et al. analyzed the stable isotopic carbon and nitrogen composition of Neandertal and faunal remains from the site of Chez-Pinaud at Jonzac (in Charente-Maritime, South-Western France) (Richards et al., 2008b) (Table 2). The Neandertal values are derived from tooth collagen and consequently do not reflect the average years of the individual but the time span of tooth formation. The collagen yields are relatively low, including yields between 0.1% and 0.3%, hence the use of ultrafiltration to improve the extraction and isolation of intact collagen (Richards et al., 2008b). However, it is surprising that collagen (>30 kDa fraction) stated to be unreliable due to carbon contamination is still considered, especially when the $\delta^{13}C$ values are significantly lower than the values from the 10–30 kDa fraction. The 10–30 kDa fraction is much better preserved and has a C/N ratio of 3.2 (Richards et al., 2008b). If we consider only the C/N ratios, both values can be considered to be valid, but since the $\delta^{13}C$ values are different, it is difficult to interpret which is the more probable result. Dietary reconstruction models would be different if we considered either one or the other Neandertal values, especially regarding the meaning of reindeer and horse as prey.

Richards et al. (2008b) also analyzed faunal material from layers 6 to 8 of Jonzac. The Neandertal tooth came from layer 7, but as no other contemporaneous carnivore species from layer 7 could be integrated into this study, one hyena from layer 8 was analyzed. Due to the lack of predator values, an estimation of the role the Neandertals had within the predator guild is so far not possible. Regardless, the conclusions of Richards et al. (2008b) based on the herbivores and the Neandertal remain from level 7 do not change significantly, even when data from level 8 were included. The Neandertal was a top-level carnivore with a prey preference on large herbivorous mammals like bovids and horses, a similarity found among the Neandertals in general (Richards et al., 2008b).

The French sites Saint-Césaire and Les Pradelles (South-Western France) provided late Neandertal collagen with contemporaneous faunal remains from the sites themselves and from sites with similar ages at Camiac and La Berbie, 120–150 km south-east of Saint-Césaire. Bocherens and colleagues analyzed Neandertal remains from Saint-Césaire (Bocherens and Drucker, 2003a) and Les Pradelles (Bocherens et al., 2005b). Bocherens et al. (1991) also presented the collagen isotopic composition of Neandertals with ambiguous chemical compositions from Les Pradelles. In the study from 2005 (Bocherens et al., 2005b), all the Neandertal collagen results are based on reliable collagen since the percent determinations of carbon and nitrogen in collagen are provided (Table 2). The studies of the Neandertal remains from Saint-Césaire and Les Pradelles are, beside those from Goyet and Spy, some of the very few suitable for detailed investigations concerning trophic relations and dietary habits of the late Neandertals. Therefore, we analyzed these data with our statistical approach to increase the accuracy of our results and to obtain deeper insights into the potential correlations between prey species (see S11 and S12). Bocherens et al. (2005b) found that the Saint-Césaire Neandertal also relied heavily on mammoth meat (between around 15% and 55% (S11) of the proteins). Mammoth was the most important prey species for this individual (Bocherens et al., 2005a,b). Interestingly, hyenas at this site had a much lower amount of mammoth in their diet in comparison to the hyenas from Belgium (S12). This supports the above discussed assumption that Neandertals did not scavenge mammoth remains hunted by hyenas on a regular basis, and were instead active selective hunters at this site as well. The probability density for mammoth in the Saint-Césaire Neandertal diet has a bell shape, with the highest probability around 35% of the protein intake (S11). For all other species the probability density decreases exponentially, therefore a lower contribution is more probable than a higher one (S11). This observation is particularly distinctive for reindeer. This species contributed the least to the total meat protein intake of the Neandertal specimen. Horses and rhinoceroses contributed very similarly, with the highest probability between 0% and 20% of the protein intake (S11). In contrast to some of the Goyet Neandertals, we do not see the above discussed negative correlations between reindeer and bovid, reindeer and rhinoceros, and between mammoth and rhinoceros (S11). Such correlations are less abundant and comparable with the ones for the Spy individuals (S9 and 10). This points to a more statistically secure preference for mammoth even for the Goyet Neandertals.

It is striking that the isotopic results from Saint-Césaire and Les Pradelles are very close to the ones observed at the Belgian sites. The Neandertals exhibit $\delta^{15}N$ values significantly more positive than those of other animal predators, i.e. an enriched prey, in average for the last years of the individual's life, in comparison to all other predator species (the herbivores with the highest $\delta^{15}N$ values being in general the mammoth and rhinoceros). If we consider the similarities of the general pattern within the herbivore/carnivore guild in South-Western France and at the Belgian sites, we can postulate a similar trophic ecology. The comparison of the isotopic patterns of these late European Neandertals points to a trophic position as active, selective top predators in an open environment, and with limited variation.

Unfortunately, Neandertal remains from Southern European sites have not provided deeper insights into their ecology through the composition of stable isotopes in collagen. It would be interesting to see how Neandertals may differ in their dietary ecology in other ecological contexts than a typical mammoth steppe. From other evidence, it seems that dietary strategies in Southern Europe, in regions outside of the mammoth steppe, are somehow different for the Late Pleistocene Neandertals (e.g. Salazar-García et al., 2013). Furthermore, others have also hypothesized that in a context like this, a tendency towards a preference for a broader spectrum of prey species including smaller animals like lagomorphs and birds may have occurred (e.g. Brown et al., 2011; Finlayson et al., 2012). Similarly, an increasing amount of plant food consumption has been postulated in less harsh environments such as on the Iberian Peninsula or Italy (e.g. Hardy et al., 2012; Salazar-García et al., 2013; Fiorenza et al., 2015; Fiorenza, 2015). Neandertals most likely had a diverse hunting and occupation behavior, which is most likely impacted by climate/ecological conditions.

5. Conclusions

Stable carbon and nitrogen isotope investigation into the ecology and diet of the Late Pleistocene Neandertals and contemporaneous herbivore and carnivore collagen was performed successfully. The “Troisième caverne” of Goyet (Belgium) has yielded the broadest set of Neandertal individuals, contextualized with faunal remains, in Northern Europe and is therefore perfectly suitable for this kind of approach.

With statistical approaches, we have demonstrated the existence of ecological niches either occupied by single species or by several species. We further demonstrated that all Neandertals belonged to the group of carnivores and occupied a very specific niche. The diversity among the Neandertal individuals is the lowest in this ecosystem. Most of the dietary protein was derived from megaherbivores. Neandertals were the species in the mammoth steppe ecosystem relying most heavily directly on mammoth. The abundance of this species had most likely a direct impact on Neandertal subsistence strategy. Our results support an active hunting activity in contrast to a general scavenging strategy. This study also reviews a set of previously published Neandertal collagen stable isotopic values and in many cases, either the chemical reliability or the ecological background is not satisfactorily provided. When the necessary requirements were met, the ecological results and interpretation are very similar to the results we obtained. The Neandertals in the mammoth steppe ecosystem during the Late Pleistocene had, at least in Northern and Western Europe, very similar hunting strategies. The numerous Neandertal remains embedded in a rich archaeological context makes the “Troisème caverne” site a key-site for the understanding of late Neandertal ecology in North-Western Europe.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2015.09.091.

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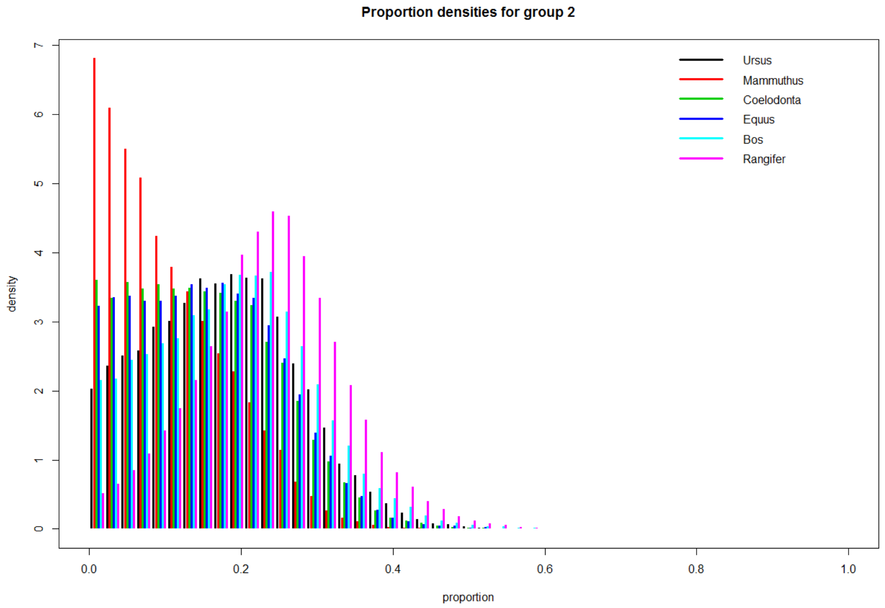
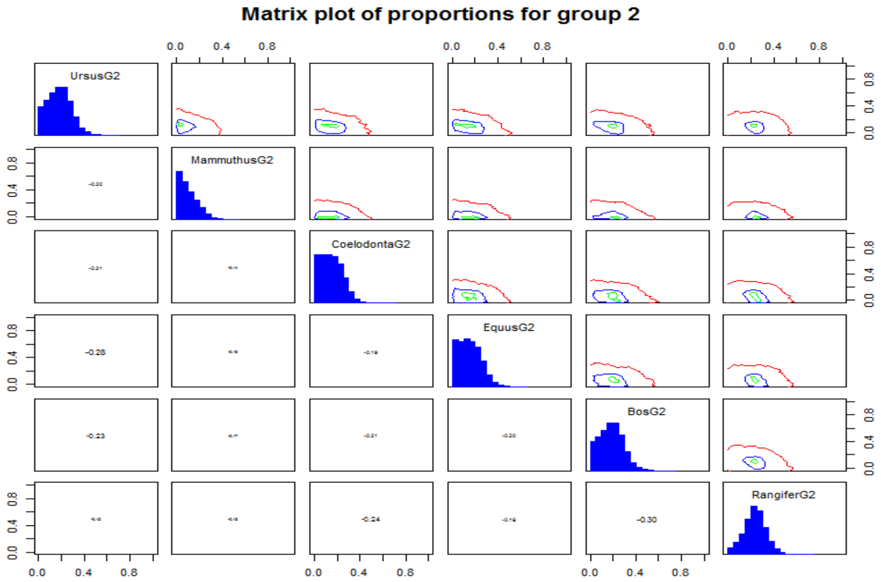
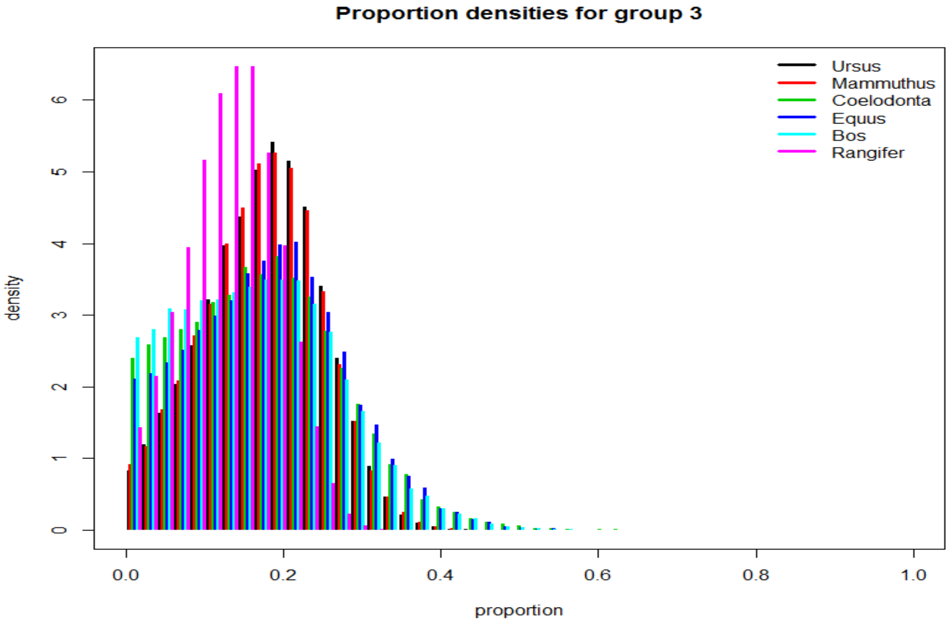
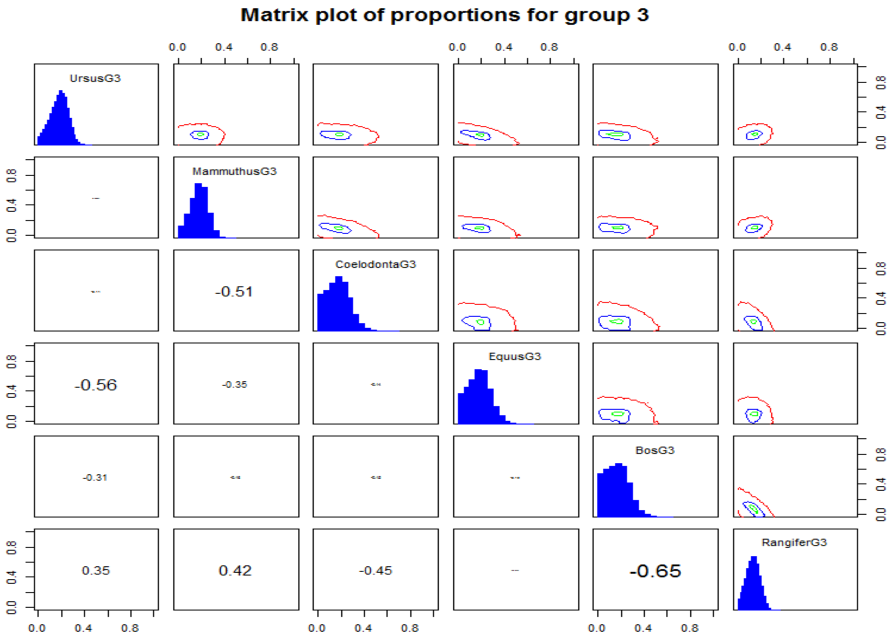
S1 Proportion densities and matrix plot for cave lion and hyena

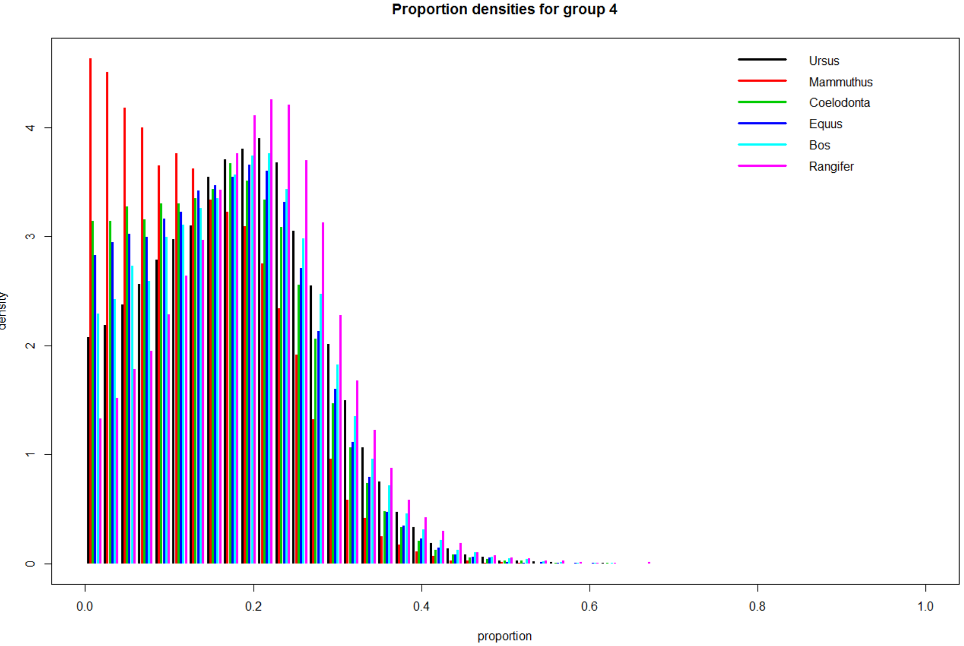

Proportion densities for group 2

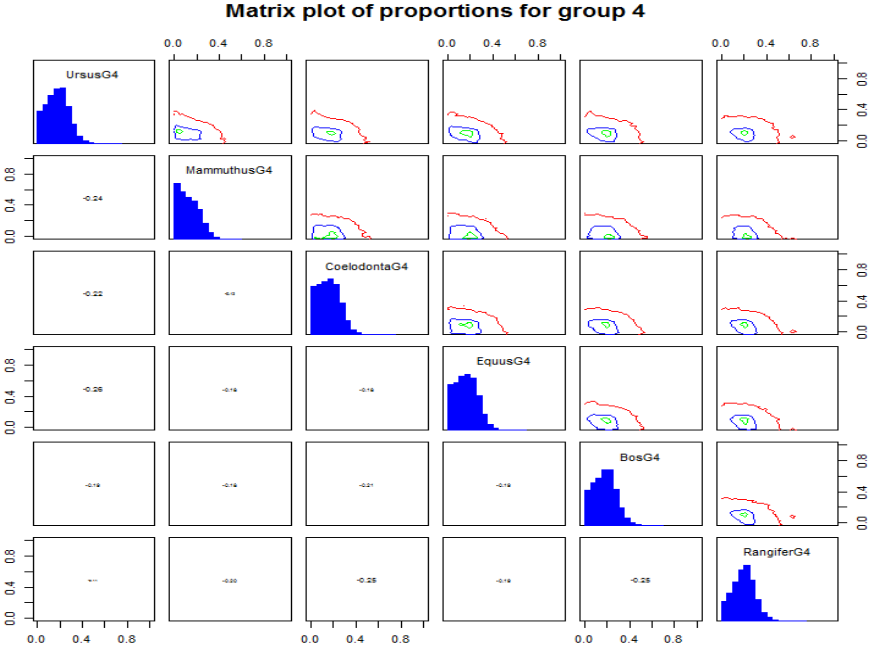

Matrix plot of proportions for group 2

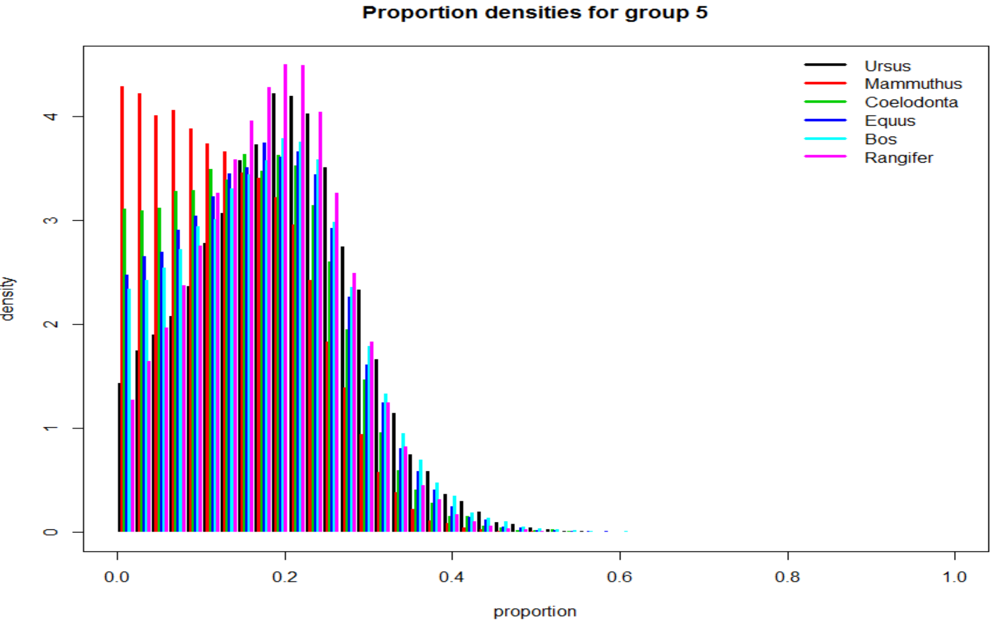

Proportion densities for group 3

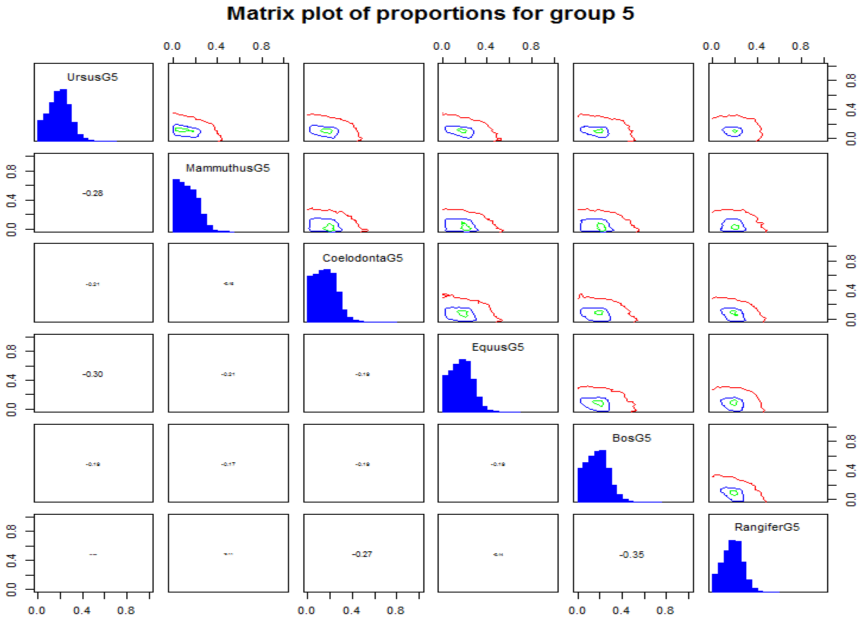

Matrix plot of proportions for group 3

S2 Proportion densities and matrix plot for wolf and brown bear

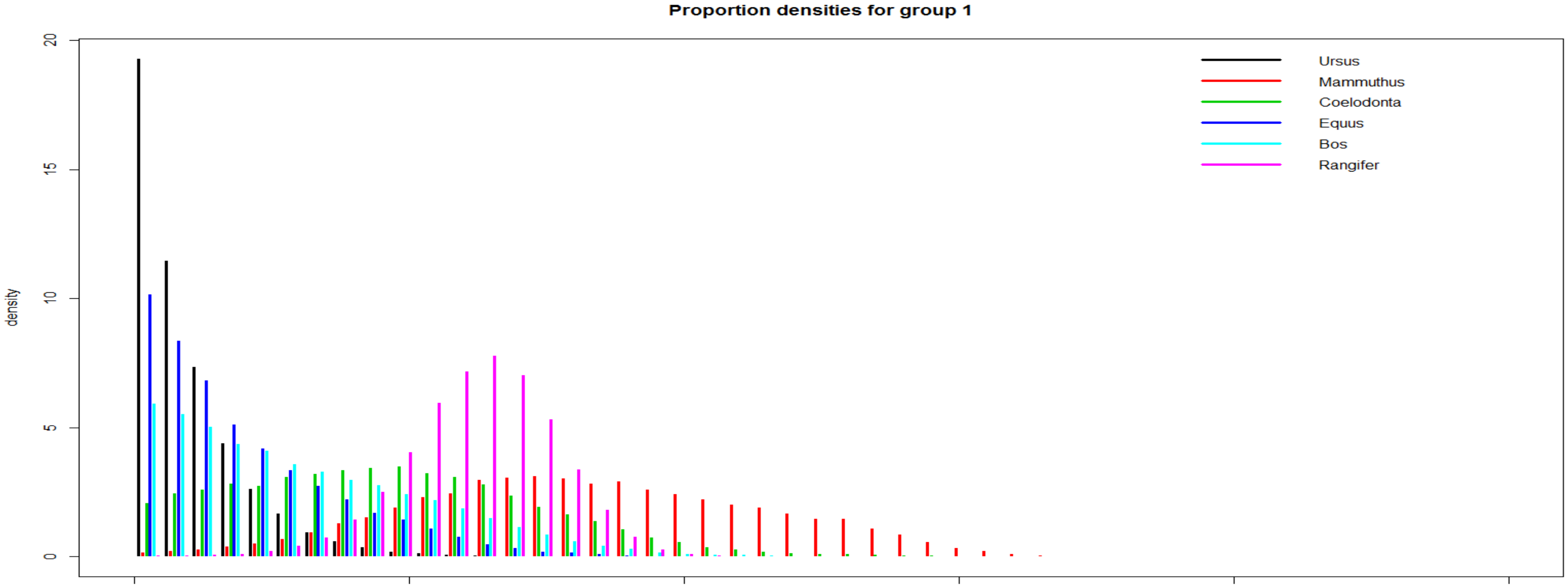

Proportion densities for group 4

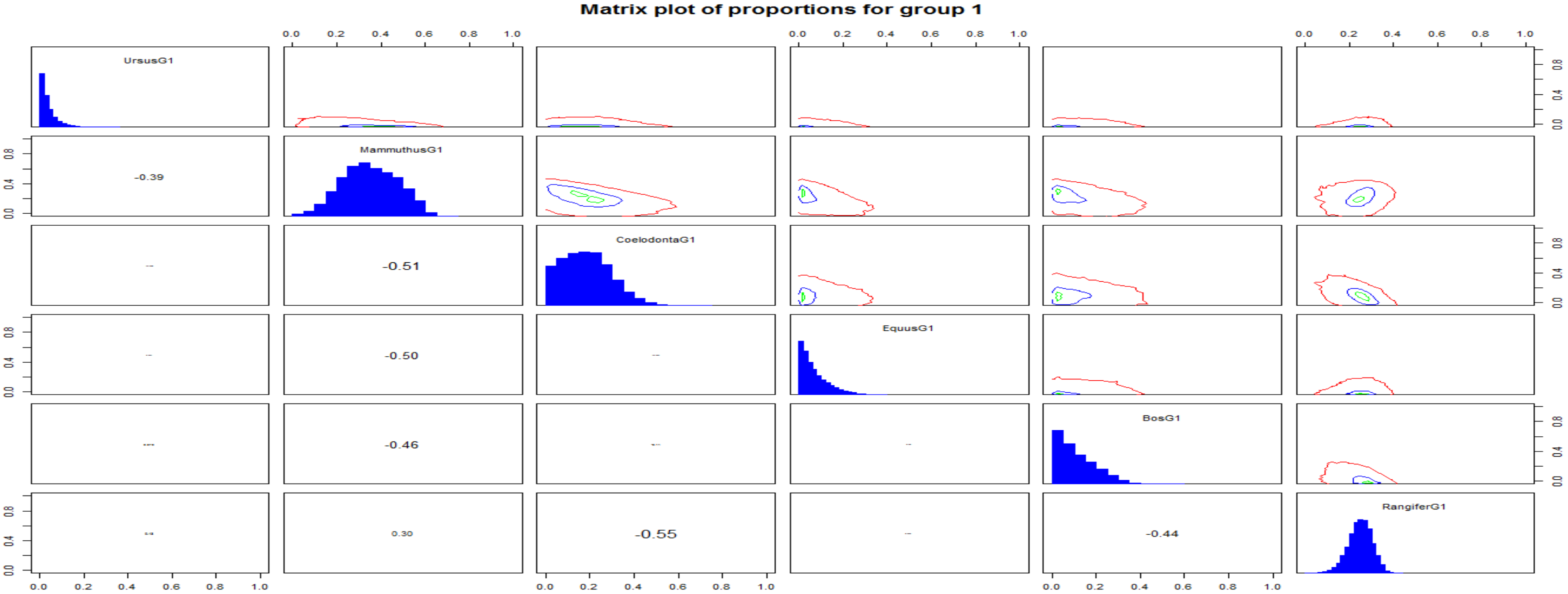

Matrix plot of proportions for group 4


Proportion densities for group 5

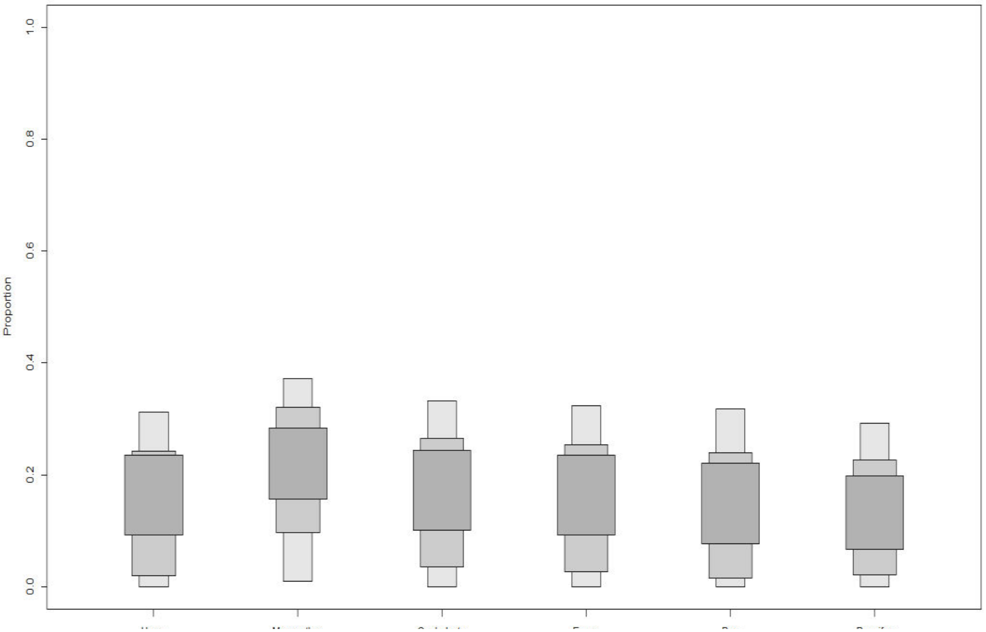

Matrix plot of proportions for group 5

S3: Proportion densities and matrix plot Neandertals


Proportion densities for group 1


Matrix plot of proportions for group 1

S4 Proportion, proportion density and matrix plot of Tibia I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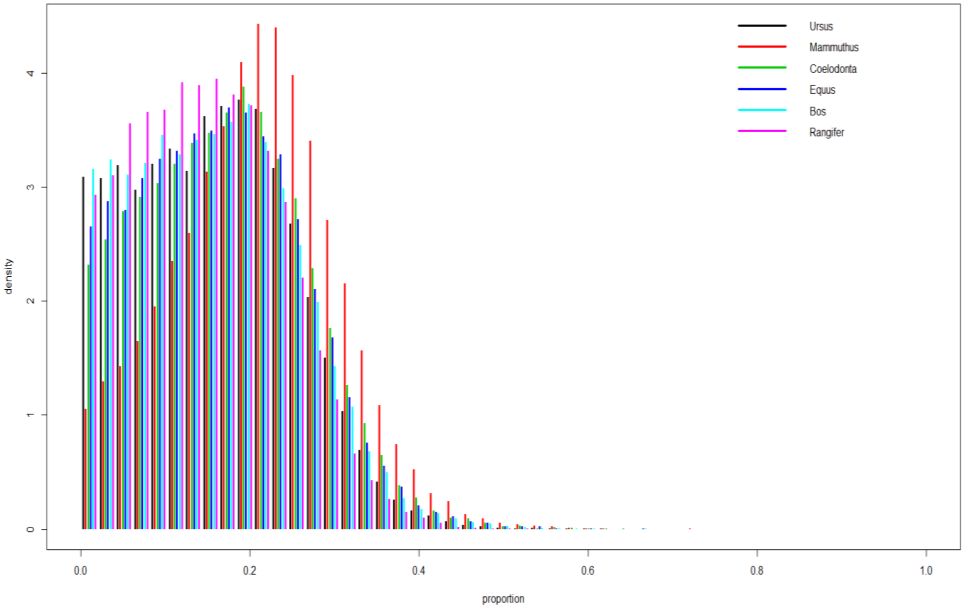
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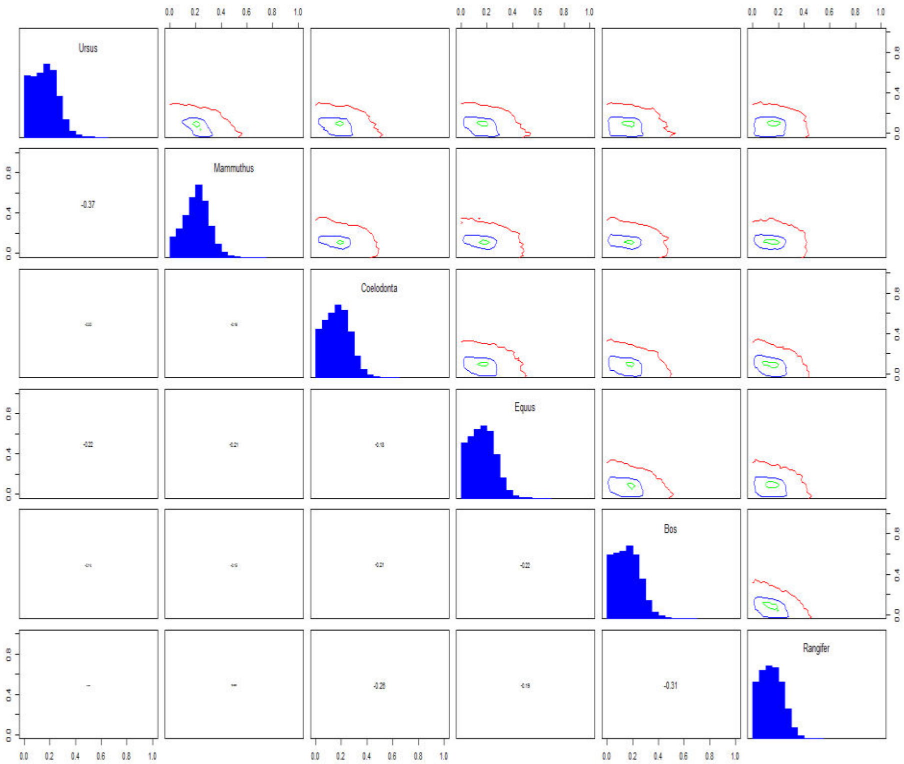
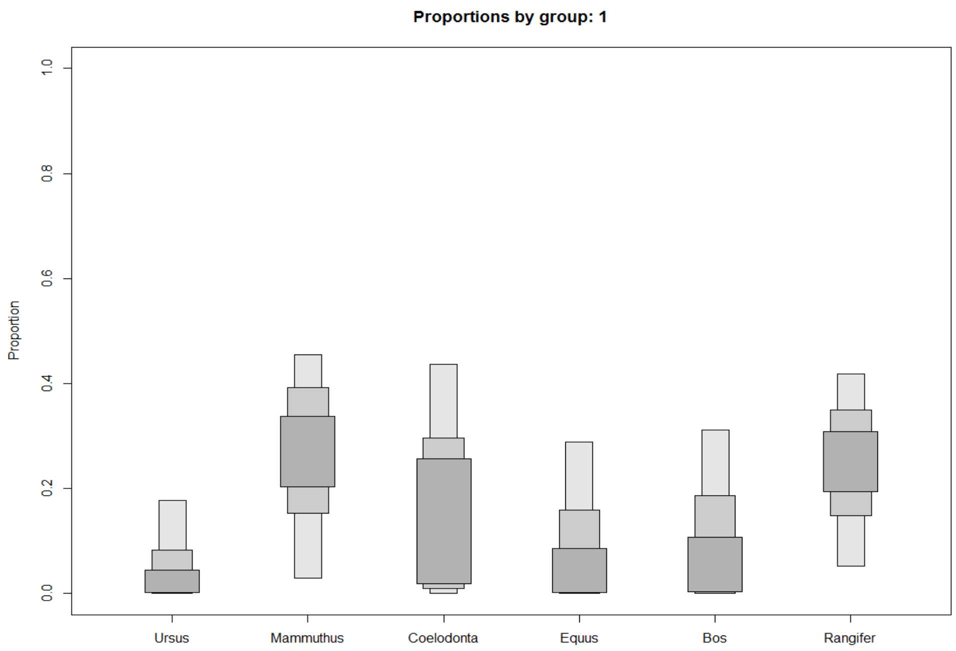

Matrix plot of proportions

S5 Proportion, proportion density and matrix plot of Tibia III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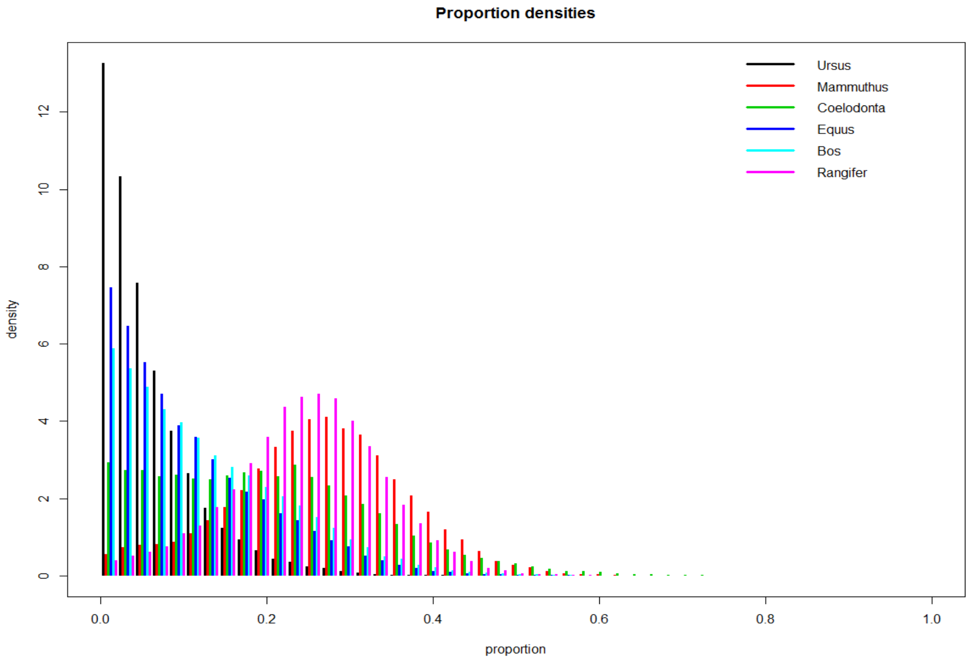
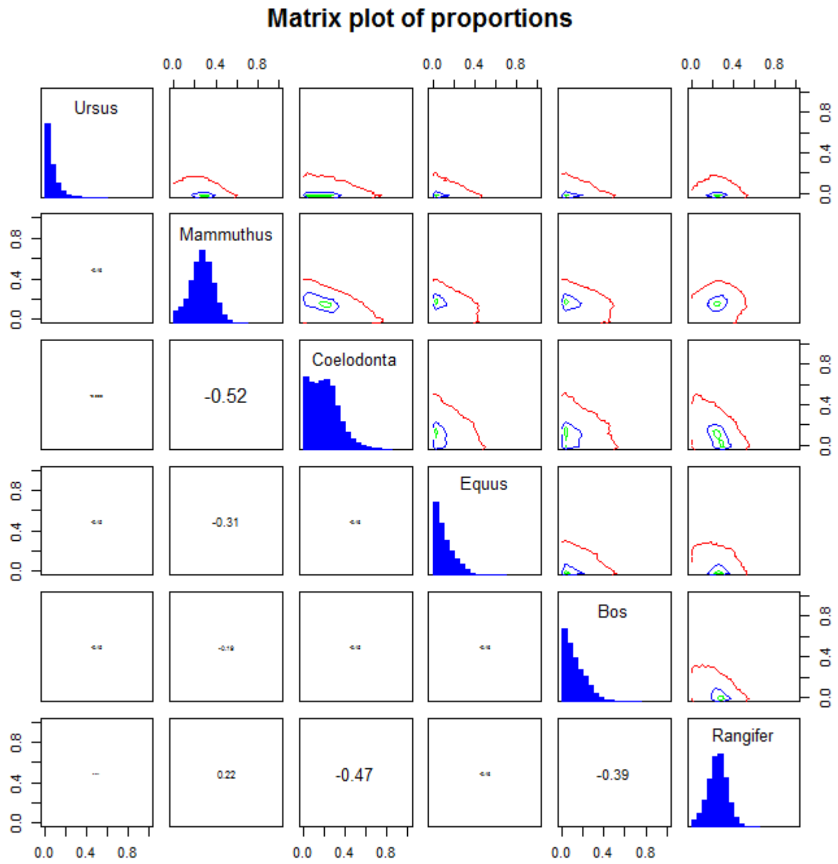
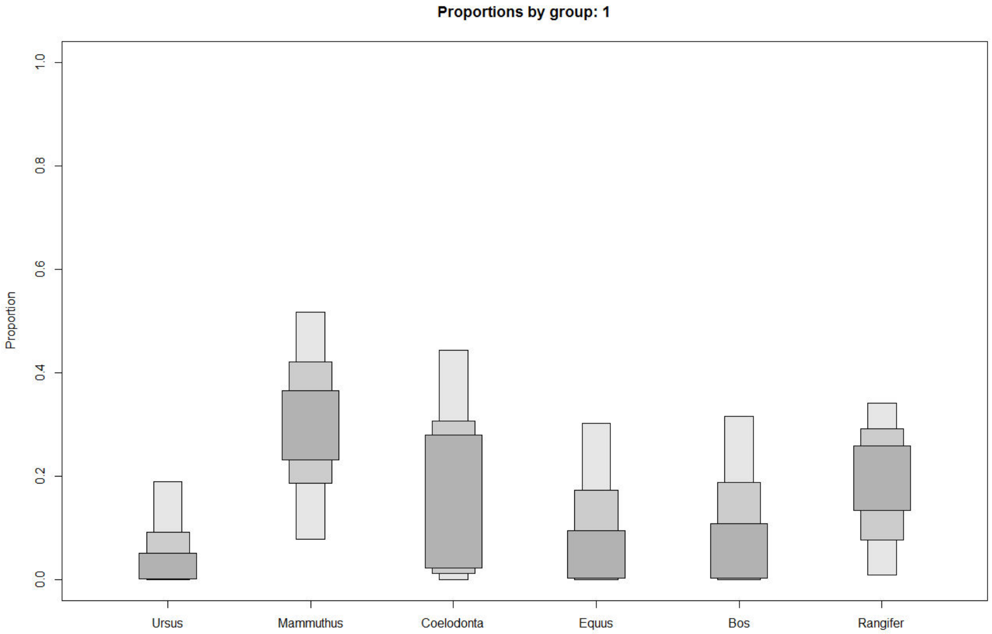
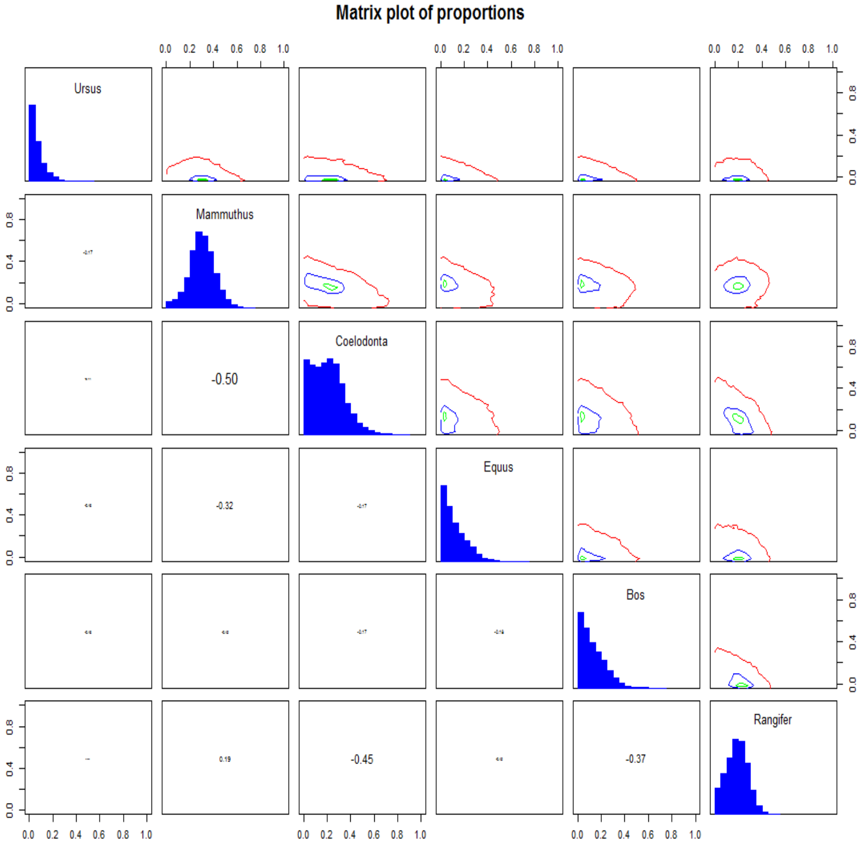
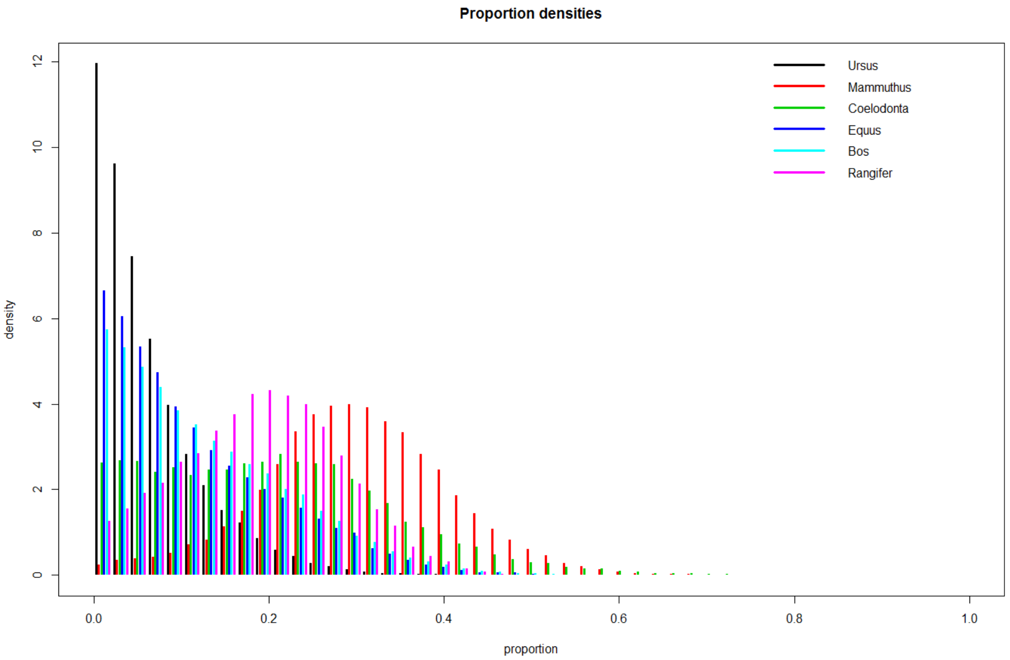

Proportion densities


Matrix plot of proportions

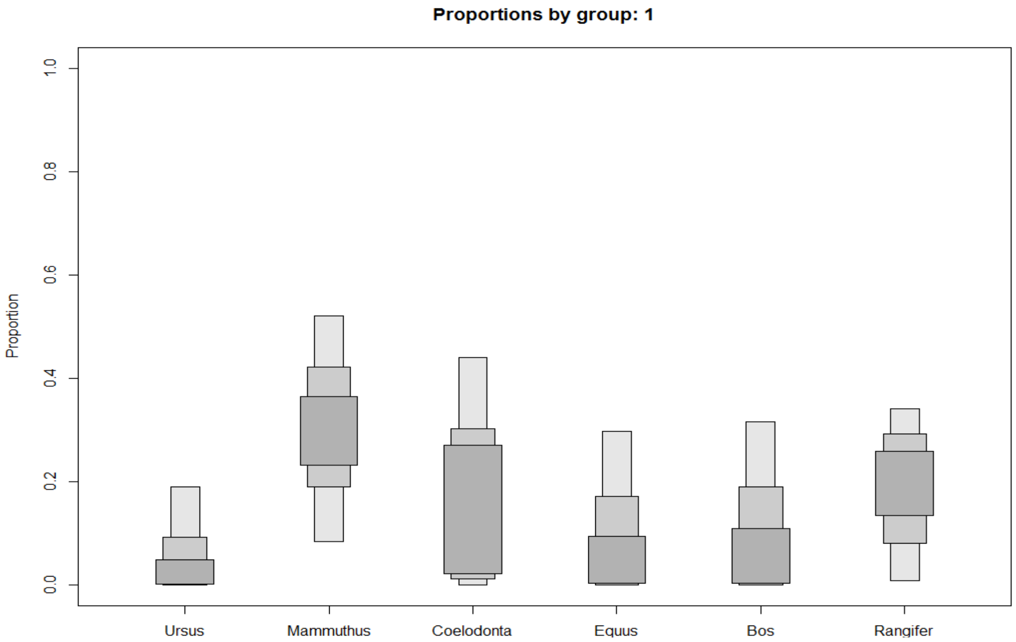
S6 Proportion, Proportion density and matrix plot of Tibia IV







S7 Proportion, proportion density and matrix plot of Tibia V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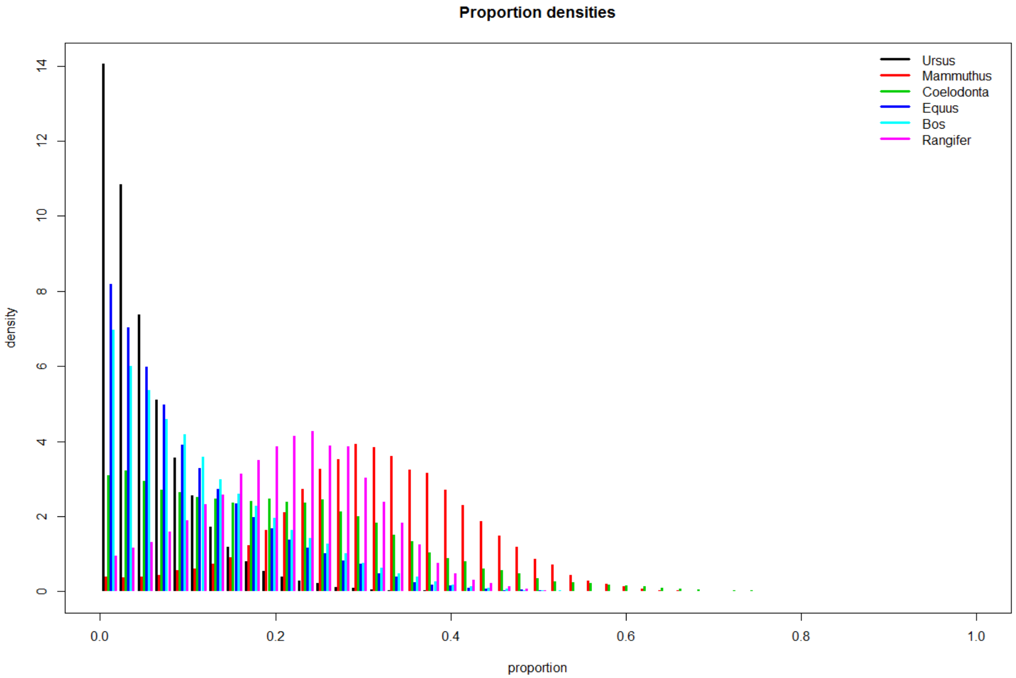
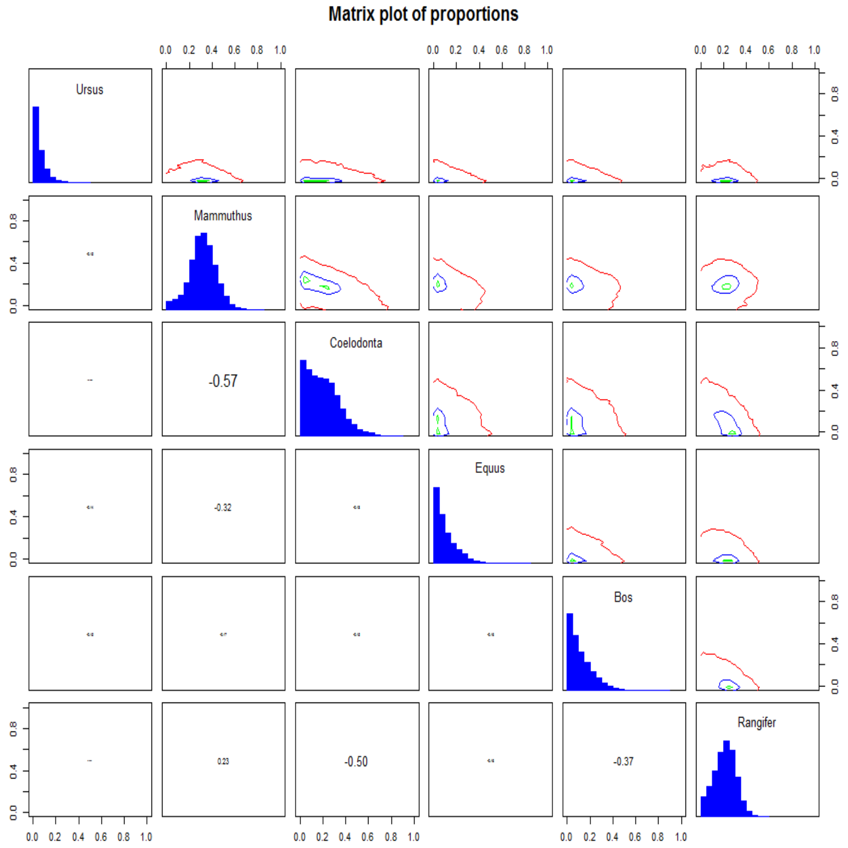
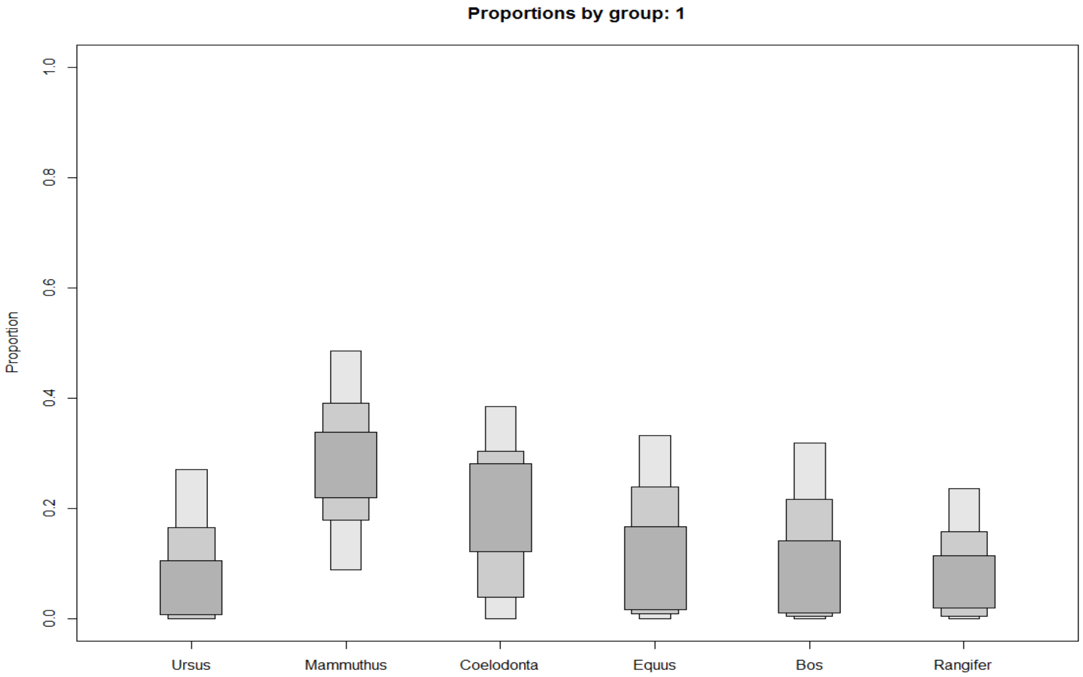

Proportion densities


Matrix plot of proportions

S8 Proportion, proportion density and matrix plot of Tibia VI



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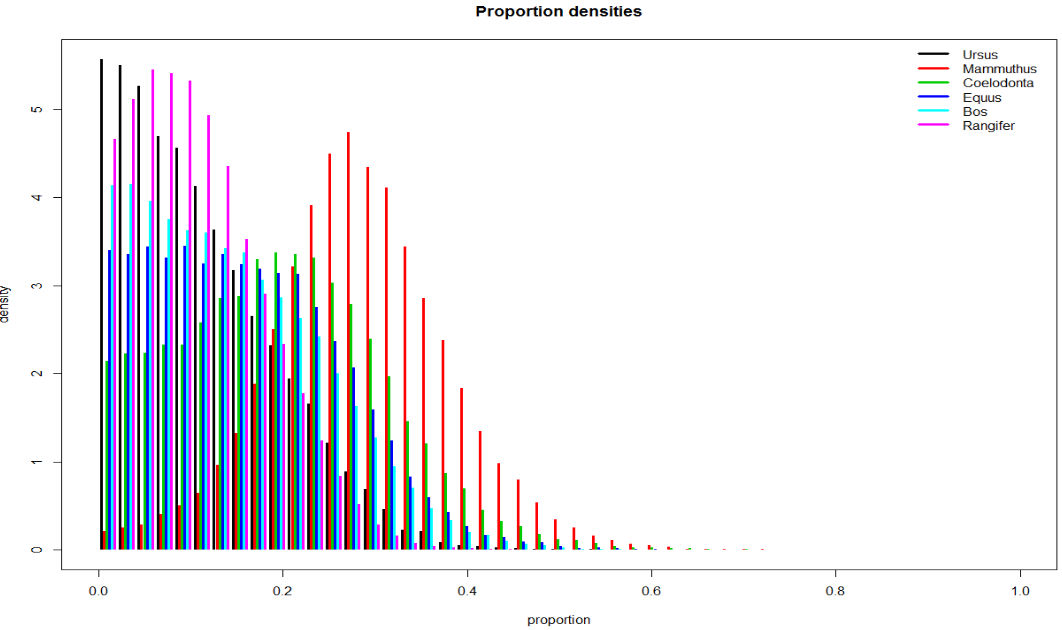
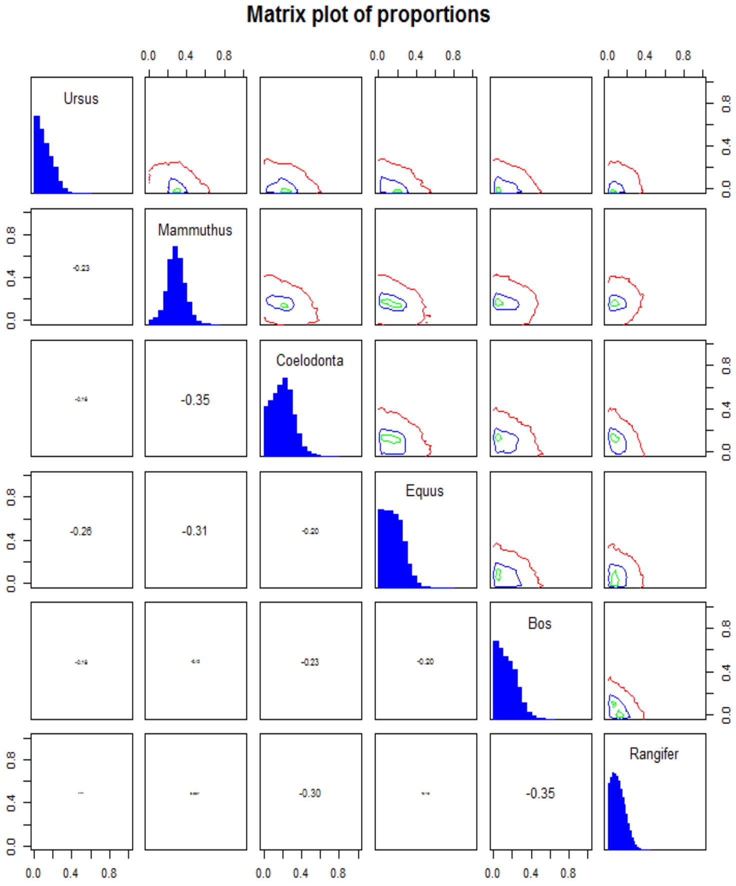
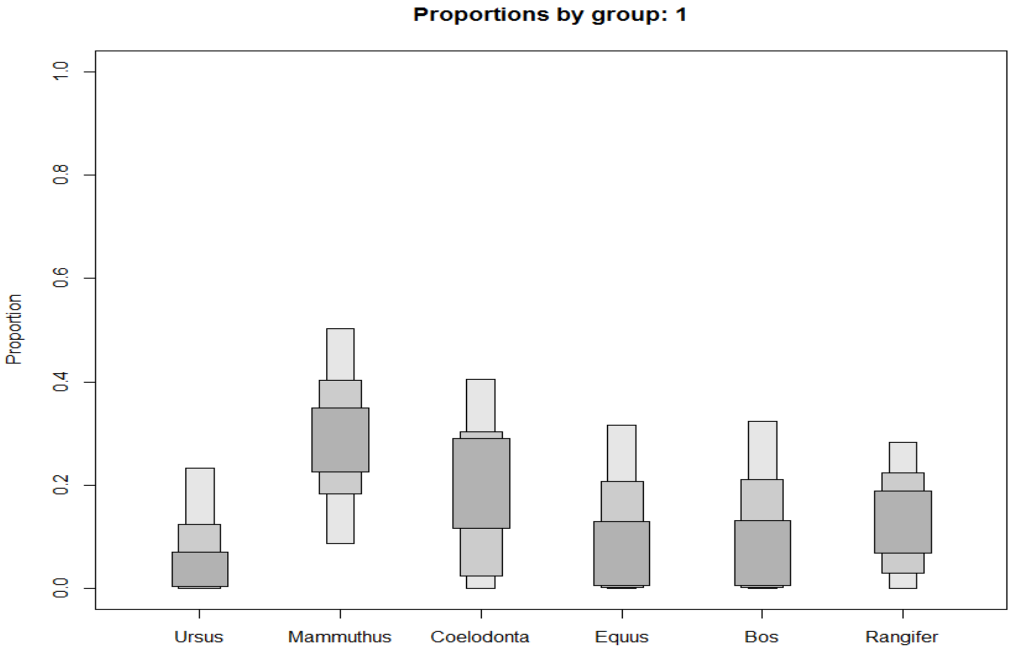


Proportion densities



Matrix plot of proportions

S9 Proportion, proportion density and matrix plot of Spy I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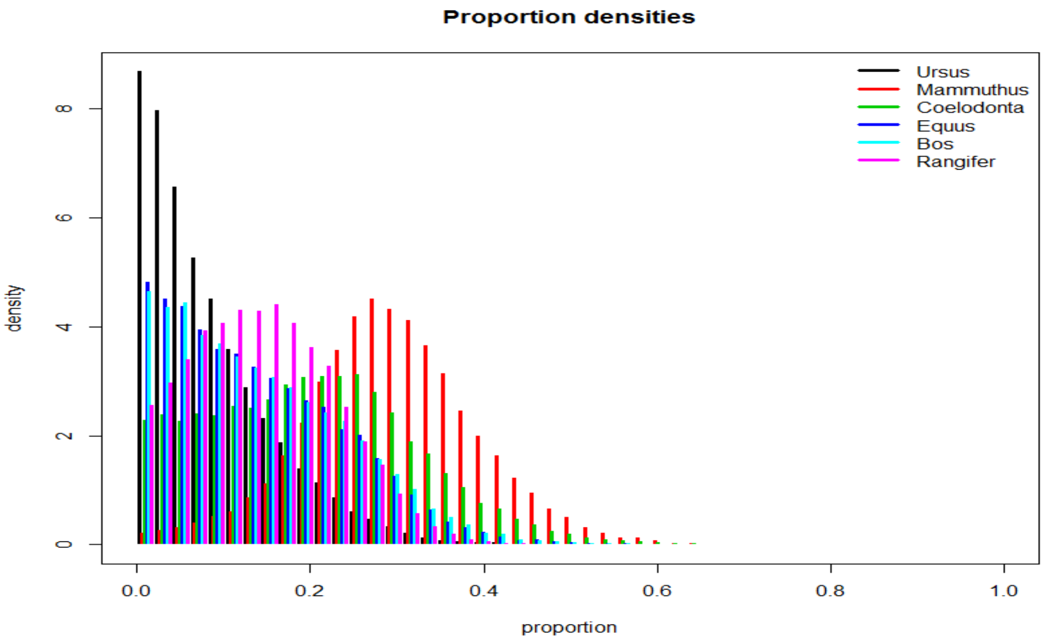
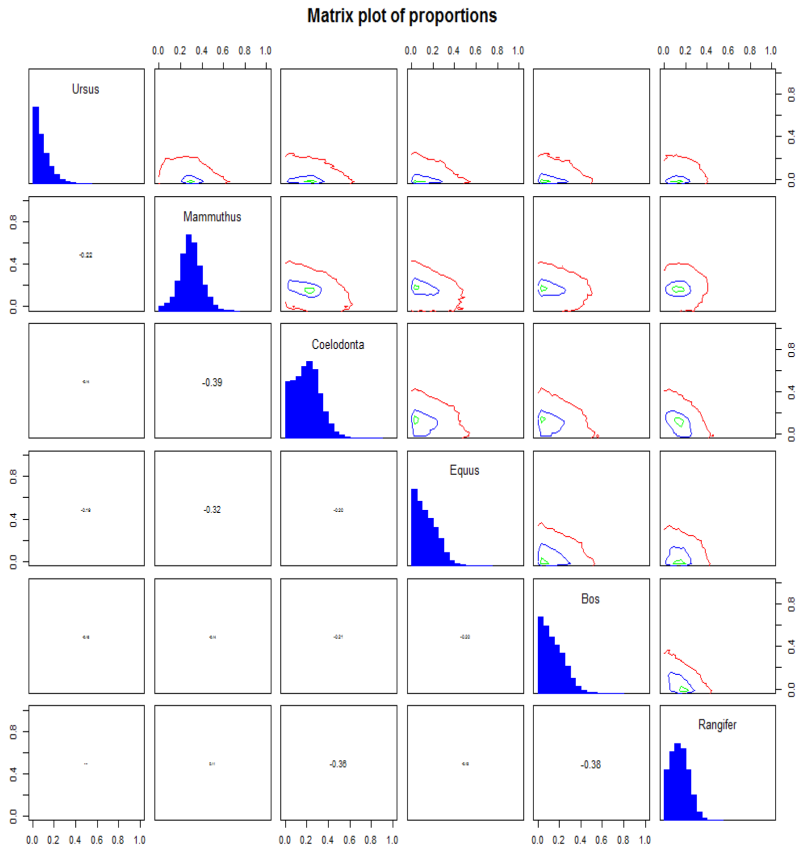
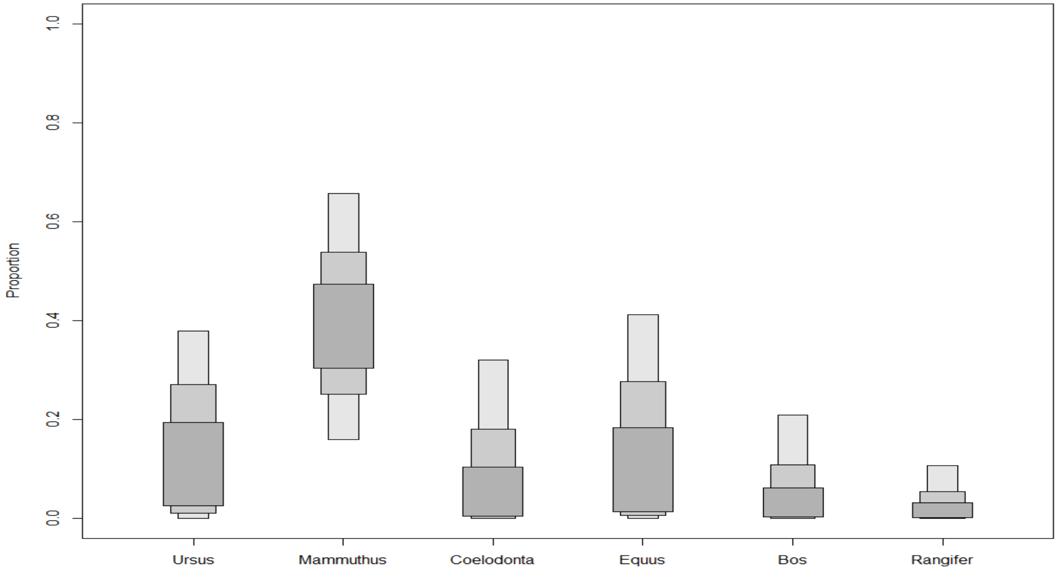

Proportion densities

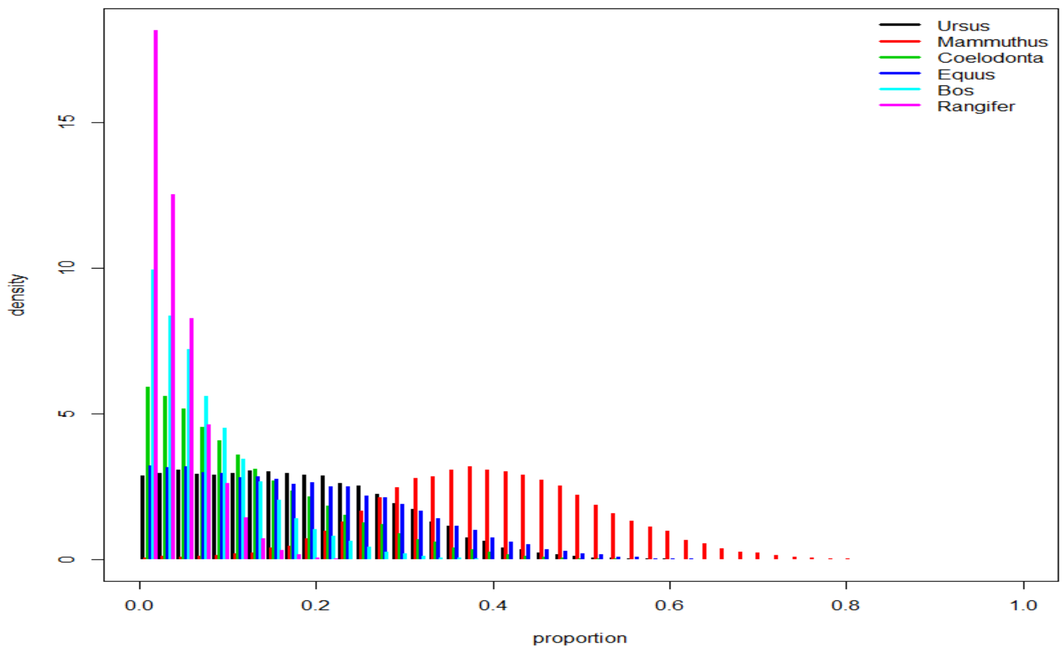

Matrix plot of proportions

S10 Proportion, proportion density and matrix plot of Spy II

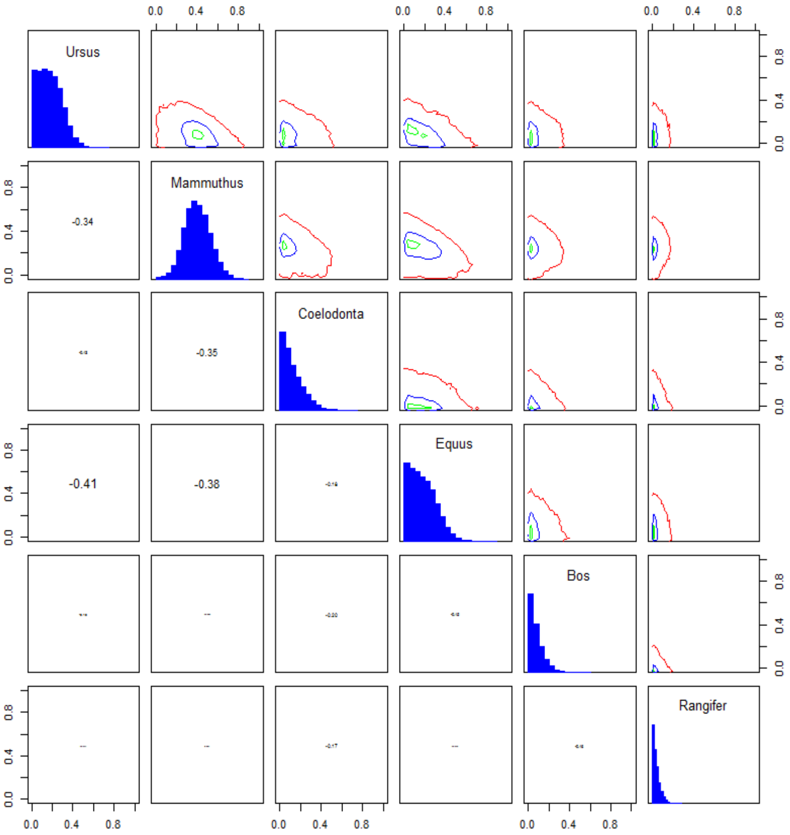
Proportions by group: 1



Proportion densities

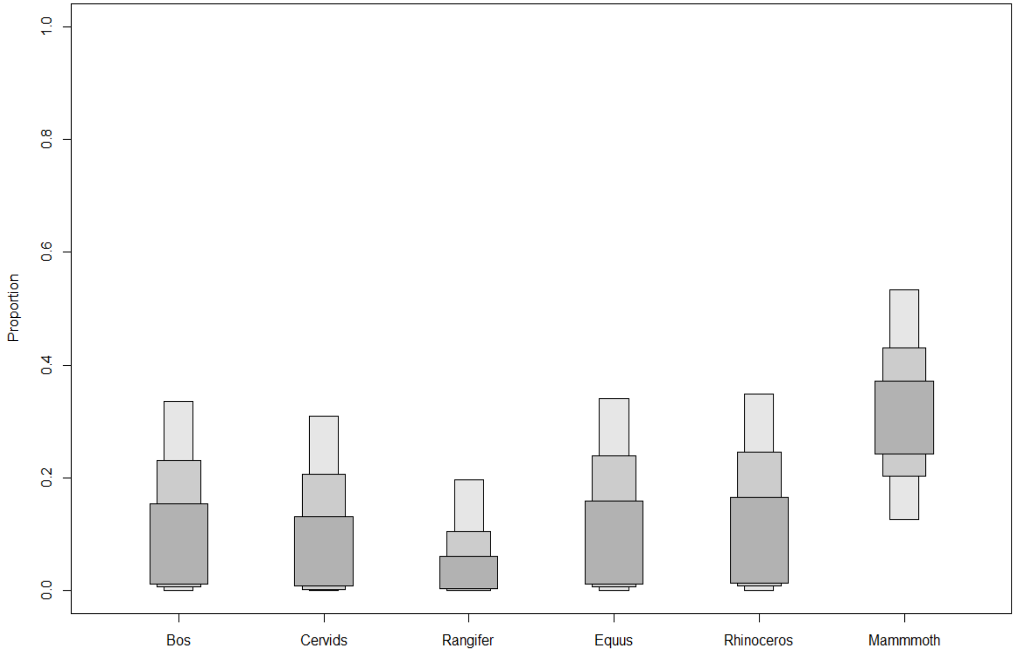


Matrix plot of proportions

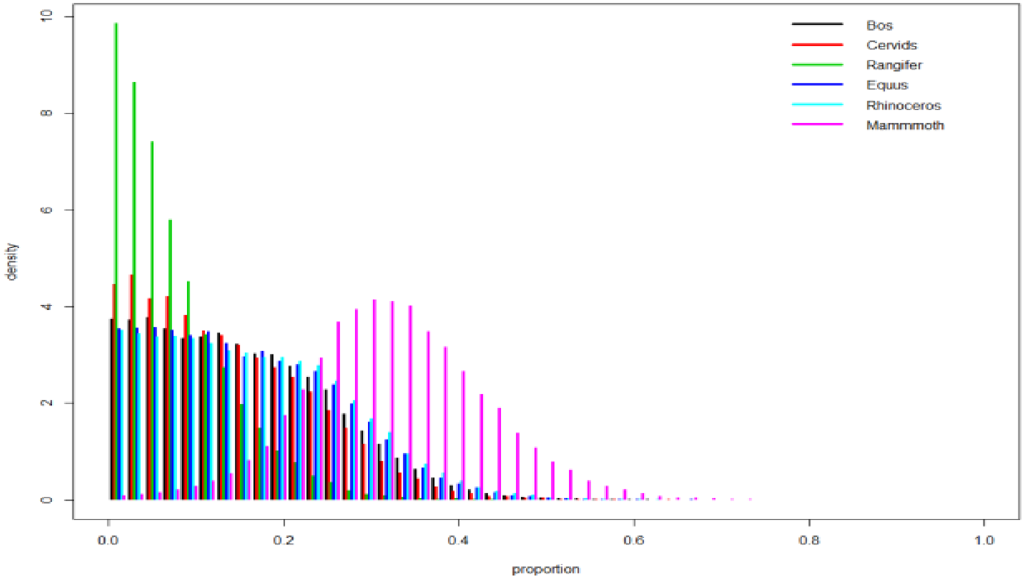


S11 Proportion, proportion density and matrix plot of Saint-Césaire Neandertal

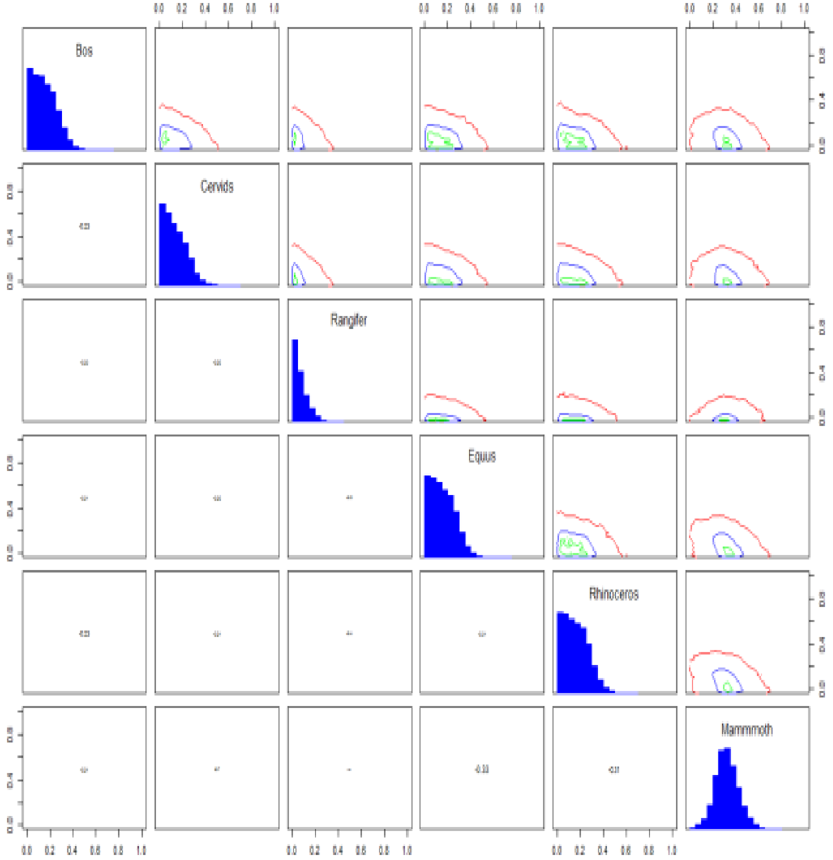
Proportions by group: 1



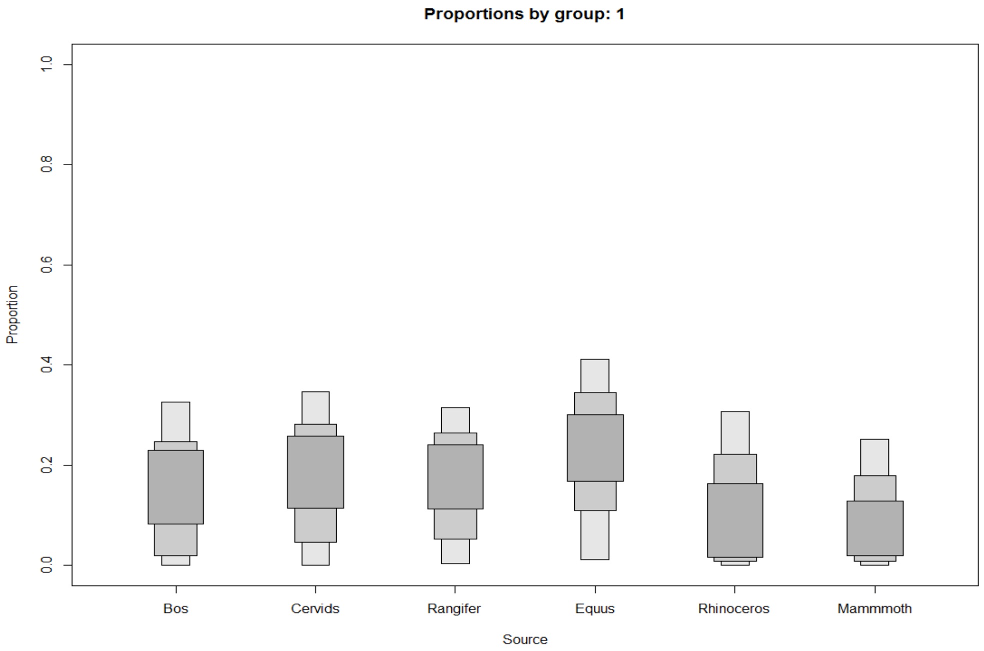
Proportion densities

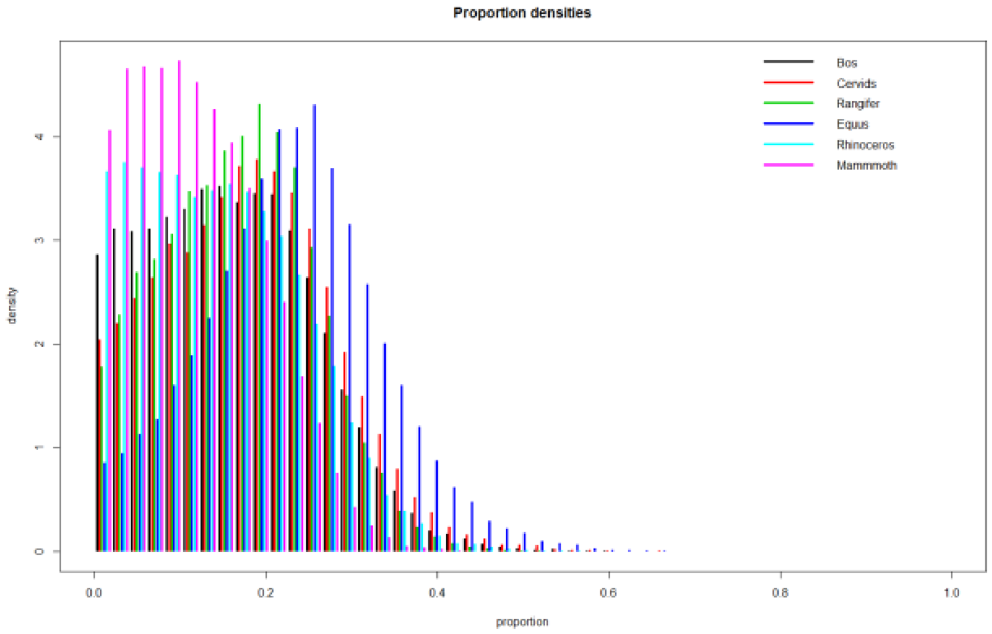


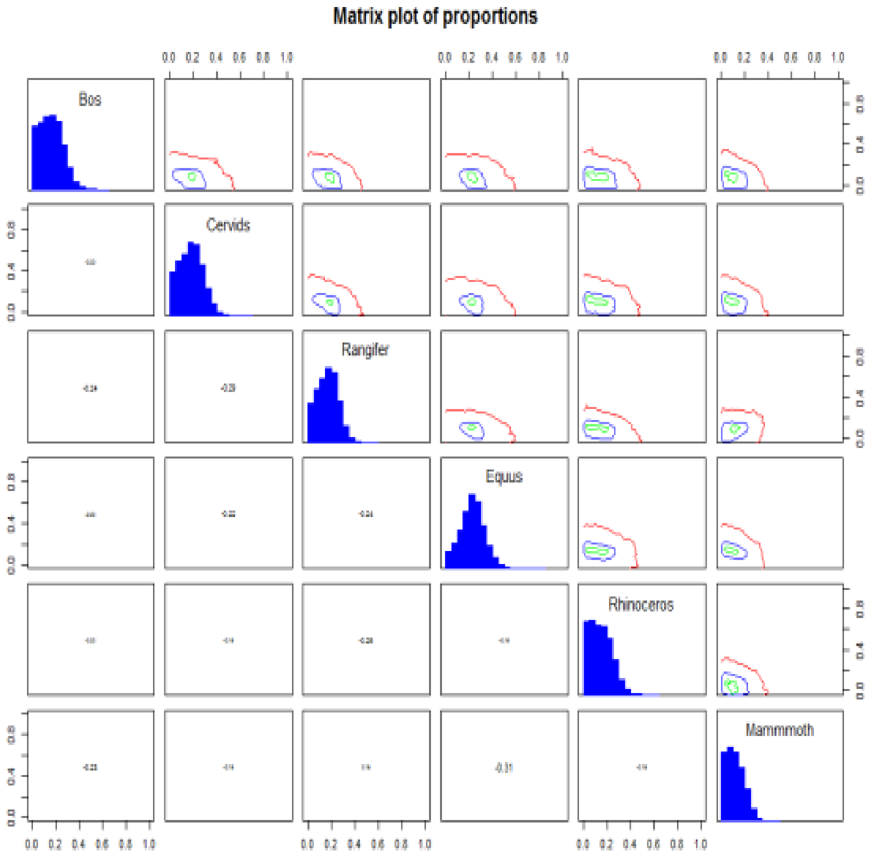
Matrix plot of proportions



S12 Proportion, proportion density and matrix plot of Saint-Césaire hyena







Different landscape use but no dietary change between early modern humans and last Neandertals in NW-Europe

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1. Introduction

Neandertals went extinct approximately 40,000 years ago (Higham et al., 2014). This coincided with the appearance of anatomically modern humans (AMH) in areas occupied by them before (Hublin, 2015; Nigst et al., 2014). In the current research theoretical scenarios attempt to explain the Neandertal downfall and the modern human rise. In general there are two different approaches recognizable. First one which argues in terms of potential species inherent features like biological and cultural/behavioral differences (Banks et al., 2008; Conard and Bolus, 2003; Finlayson et al., 2004; Fu et al., 2015; Hublin, 2012; Krause et al., 2010; Sanchez-Quinto and Lalueza-Fox, 2015). For others external causes precipitated the fall of Neandertals and the expansion of the modern humans. Climatic cold events like Heinrich events (d'Errico and Sánchez Goñi, 2003; Müller et al., 2011; Tzedakis et al., 2007) or mega volcanic ash dispersal like the eruption in the Phlegrean Field producing the Campanian Ignimbrite (CI)/Y-5 tephra (Fitzsimmons et al., 2013) and/or an inversion of the magnetic field (the Laschamp- and Mono lake geomagnetic event) and the extreme connected increased detrimental sun radiation (Valet and Valladas, 2010).

During last 5-10 years more and more details of ancestral relationships between AMH and Neandertals turned out. It seems to be reasonable to regard at least the last Neandertals and Pleistocene AMH as very closely related. Both (sub-?) species were able to interbreed and to have fertile progenies (Fu et al., 2015) during the second half of the Late Pleistocene at least in Eastern Europe. The genetic relationships among different Late Pleistocene hominid populations or (sub-?) species are obviously quite complex (Krause et al., 2010; Sanchez-Quinto and Lalueza-Fox, 2015) and can optimally characterized through a description of high-coverage genomes from as many Pleistocene humans as possible with the latest “next-generation” sequencing technologies.

Anyhow, the situation in Central and West Europe is probably more distinct, than e.g. in Asia or the Near East. This part of the continent had a long-separated hominid evolution that may have lasted more than 400,000 years, the substitute hominids where the Neandertals (Hublin, 2015). The AMH originated in Africa (Hershkovitz et al., 2015) and arrived through the Levant in Europe around 40,000 years ago while Neandertals began to become extinct at the same time (Higham et al., 2014).

The success of the one hominid group over the other has to be explained and especially ecological aspects like diet, mobility and territory range can provide empirical information about potential differences or commonalities between the last Neandertals and the first AMH in Europe. A different ecology has to be regarded as one potential reason for the success of the one (sub-?) species over the other.

If we can precise the ecological roles of both hominid groups in the mammoth steppe ecosystem of Belgium during the second half of the Late Pleistocene we may better understand the disappearance of one of them. An essential ecological aspect is the diet respectively the associated dietary and spatial organization strategies and the related cognitive and cultural characteristics. Several approaches were conducted to reconstruct Pleistocene hominid dietary ecology, e.g. zooarchaeology (Germonpré et al., 2014; Yravedra-Sainz de los Terreros et al., 2015), dental microwear patterns (Fiorenza, 2015; Harvati et al., 2013), tooth calculus analysis (Hardy et al., 2012; Henry et al., 2014), lithic use-wear and residue analysis (Hardy et al., 2008; Hardy and Moncel, 2011) as well as the investigation of stable isotopes of bone and dentin collagen and the one of the carbonate fraction (Bocherens and Drucker, 2006; Bocherens et al., 2015a; Bocherens et al., 2005b; Ecker et al., 2013; Hallin et al., 2012; Richards et al., 2008; Wißing et al., 2015b).

Here we present and discuss the stable carbon and nitrogen composition of two modern humans as well as from some Neandertal individuals from Goyet and Spy as dietary proxy. Also the sulfur isotopic values of these AMHs and Neandertals and associated faunal material were investigated to attain potential insights into the spatial behavior of hominids and fauna.

In terms of the investigation of ecological aspects the stable isotope approach is a quite prevalent tool in the late Pleistocene context (Bocherens, 2015; Naito et al., 2014; Stevens et al., 2014; Wißing et al., 2015a; Wißing et al., 2015b), since the stable isotope composition of collagen directly reflects the isotopic signature of the consumed protein part of the diet of the most recent years of an individual. Consequently we can estimate ecological behavior on an individual's long term scale, in contrast to other methods providing insights more as a snapshot or short/middle term time range (e.g. tooth wear analysis, residue analysis on stone tools, investigation of the species composition of the faunal assemblage at the site).

In former studies the isotopic evidence indicates that in all cases Neandertals were top predators with a special preference on large herbivores (e.g. Bocherens 2009; Wißing et al., 2015b). In contrast to dietary strategies of these very late Neandertals it has been assumed that early modern humans had a wider range of diet including aquatic (marine and freshwater) resources (Pettitt et al., 2003; Richards et al., 2005; Richards et al., 2001; Richards and Trinkaus, 2009). It has been argued, that especially the isotopic values of early modern humans exhibited a wider range of isotopic values which corresponds to the intake of marine and freshwater resources. But an essential aspect to compare both hominids directly is the lack of AMH remains close in time and space to the last Neandertals. Unquestionable AMH directly dated from the early Upper Paleolithic (UP) (36-28.5 ka BP) across Europe are very rare. Most of the specimens were discovered in Eastern Europe, Russia or at the periphery of the geographically Europe. So far only around one dozen sites in total provided human remains directly dated between 40-28.5 ka BP (see e.g. Higham et al., 2011). This situation significantly changes in the following middle Upper Paleolithic industry contexts across Europe (i.e. the Gravettian, Pavlovian, Périgordien IV-VI). On top of this circumstance comes that only eight directly dated human specimens have been analysed for stable carbon and nitrogen isotopic composition, even if it would have been possible since the collagen preservation was obviously given for all of them (Table S1). Relevant for the comparison of ecological aspects of both hominids through the investigation of stable isotopes is not only the closeness in time, but also the spatial aspect in comparison to each other relevant, since the isotopic baseline is, beneath other proxies, essentially impacted by both criteria. All early AMH were found at sites, where late Neandertal fossil could not be discovered. This is from now on different with the site Goyet which yielded both, very early modern human fossils and very late Neandertal bone remains. Both hominid types are represented through several individuals which additionally makes the site unique and suitable to test hypotheses of similarities of differences in the ecology between early AMH and late Neandertals in Europe.

2. Material and methods

2.1. 1.The “Troisième caverne” of Goyet

The “Troisième caverne” of Goyet is located within a limestone massif above the Samson river, a tributary of the Meuse River in the Mozet Commune in the Walloon Region in Belgium (Fig. 1). Almost the entire cave was excavated by Edouard Dupont in 1868 (Dupont, 1872). The stratigraphy described is very simplistic, following the state of the art at this time. Not only an ongoing dating program demonstrated that each of the five “layers” contains material from different periods, also former studies demonstrated this (Germonpré, 1997; Germonpré and Sablin, 2001; Stevens et al., 2009) anyhow the site yielded an very extensive occupation from the Middle and Upper Paleolithic periods (Flas, 2011; Germonpré, 1997; Germonpré and Sablin, 2001; Otte and Noiret, 2007; Pirson et al., 2012).

2.1.2. Spy

The Spy cave is roughly 25km westwards of the Goyet and one of the most famous Neandertal sites since the discovery of two almost complete Neandertal individuals in 1886 (Toussaint and Pirson, 2006). The stratigraphic attribution of the faunal remains does not follow modern standards; therefore all remains integrated in this study are directly dated.

2.1.3. Scladina

Scladina cave is around 15km NW of Goyet and was discovered in 1971. The site is still under investigation. All remains considered in this study came from complex 1A and have an age around 40,000 and 37,000 ka BP (Bonjean et al., 2009; Pirson et al., 2012)). No human remains were found in this complex, which age is similar to Spy and Goyet, but a rich and diverse mammal fauna yielded well-preserved collagen that was analysed for carbon and nitrogen isotopic composition (Bocherens et al. 1997, 2011).

2.2 Skeletal material

“Troisième caverne” of Goyet

The Goyet cave yielded a broad spectrum of Pleistocene AMH remains and late Neandertals (Rougier et al., 2013) (Rougier et al., submitted).

Most of the Neandertal remains and all the AMH remains are directly dated (Posth et al., 2016; Rougier et al in prep.; Wißing et al., 2015b). All remains dated clearly older the LGM. In this time range the ^{14}C-method is close to the limit of the possibility to detect carbon 14 and therefore yielding absolute dates. The small amount of the radiogenic isotope makes the method very sensitive for any contamination with modern carbon, or any potential irregularity in the pretreatment procedure of the bone/collagen; beside that the calibration of remains from this age is connected with several difficulties as well (Higham, 2011; Muscheler et al., 2014; Wood et al., 2010; Wood et al., 2013).Being aware of these circumstances the dating could processed on valid collagen and provides a concrete timeframe for both types of hominids:

The two AMH individuals date approximately between 29,370 (GrA-59685) and 30,880 (GrA-46175) ^{14}C uncal. BP; the uncalibrated C^{14} ages of the Neandertals approximately span between 36,590 (GrA-54024) and 41,200 C^{14} yr BP (GrA-46173) (Tab. 1 & fig.2) (Rougier et al in prep.) with the exception of one Neandertal specimen 2878-2D, dateing unexpectedly young, 32,190 (GrA-54028) C^{14} yr BP. This might be possible due to undetected contamination caused through varnishing. The 2878-2D tooth was part of the samples identified as human by E. Dupont and although we can not rule out that it was varnished like several other human remains detected while excavating the site. All recently detected human remains are not varnished. We consider this date as not valid and exclude it for discussion. What matter at this point is the fact, that we are facing in Goyet clearly with two groups of hominids, which are separated chronologically.

Beside the morphological attribution (Rougier et al., submitted)(Rougier et al., in prep.) mtDNA analysis confirmed the attribution of Neandertals and the presented AMH remains to their specific type of hominid (Rougier et al., accepted; Posth et al., 2016).

The majority of the Neandertal remains have been analysed for stable carbon and nitrogen isotopic composition in another study (Wißing et al., 2015b). Here we present stable carbon nitrogen and sulfur isotopic data of the two oldest AMH individuals from the site, represented by two adults (Q116-1 and Q376-3) as well as additionally six Neandertal remains investigated for carbon and nitrogen collagen isotopic. The sulfur isotopic results of all Neandertals and AMHs are part of this study (Tab. 1).

The Goyet faunal remains integrated in this study (N=57) have a clear pre-Last Glacial Maximum (LGM) age between around 25,000 and 42,000 years ago, this was either confirmed by direct ^{14}C dates of the remains, by the species composition itself and/or through an ecological approach (Bocherens et al., 2011a; Stuart, 2015) (Tab.2). The carbon and nitrogen stable isotopes of the faunal remains have been published by Bocherens et al. (2011a). All δ^{34}S faunal values (N=24) are part of this study and are gained on the collagen the δ^{13}C and δ^{15}N values have been measured on as well.

Spy:

The Neandertal remains from individual Spy I and II have been investigated for carbon and nitrogen stable isotopic composition by Bocherens et al. (2013). Here we present the carbon and nitrogen isotopic composition of the Spy child (Spy IV), discovered some years ago while examining the collection (Crevecoeur et al., 2010). Additionally we present the sulfur isotopic composition of the individuals Spy I and Spy VI (Spy 94a and Spy 646a). The remains of individual Spy I date approximately 35,810 C^{14} yr BP (GrA-32623) and the ones from individual Spy II 33,940 C^{14} yr BP (GrA-32630) (Semal et al., 2013). The individual Spy VI (Spy 646a) dates approximately 32,970 C^{14} yr BP (GrA-32627) (Crevecoeur et al., 2010).

We also discuss isotopic carbon and nitrogen values of directly dated faunal remains (N = 8) from the Spy cave (Semal et al., 2013; Semal et al., 2009), the stable isotopic composition was published by Bocherens et al. (2013) and Wißing et al. (2015b) (Tab. 2). All measurements have been performed on the same collagen.

Scladina:

The stratified remains from this site came from complex 1A which has an age of 37,300 (GrA-32633) and 43,150 (GrA-32581) C^{14} yr BP (Pirson et al., 2012). All specimens (N = 38) and their carbon and nitrogen values considered here are published by Bocherens et al. (1997). All results for δ^{34}S are part of this study. The δ^{34}S was measured on the same collagen the carbon and nitrogen stable isotopes have been measured on.

2.3. Interpreting isotopic values of Pleistocene hominids

The stable carbon and nitrogen and sulfur isotope approach is an adequate tool to investigate ecological aspects within the mammoth steppe ecosystem these Pleistocene hominids were part of (Bocherens, 2015; Bocherens et al., 2015a; Nehlich, 2015; Szpak et al., 2010; Trinkaus et al., 2009; Wißing et al., 2015a; Wißing et al., 2015b; Yeakel et al., 2013). In the mammoth steppe ecosystem the stable carbon and nitrogen isotope analysis provides insides in the general character of the ecosystem or specific microhabitats (e.g. open vs. close landscape) (Drucker et al., 2008); the ecological niche (MacFadden and Shockey, 1997); estimation the role of grass/forbs versus trees/shrubs in herbivore diet (Drucker et al., 2010); the contribution of animal protein in omnivore diet (Hobson et al., 2000), and the relative amount of different prey species in omnivorous and carnivorous species diet (Bocherens, 2015; Bocherens et al., 2015b; Wißing et al., 2015b).

The question of any potential dietary differences between AMH and Neandertals became essential in the discussion about Neandertal extinction (Bocherens and Drucker, 2006; Richards et al., 2001; Trinkaus et al., 2009).

If we assume AMH would have had a broader dietary background than the Neandertals we expect significant difference of the carbon and nitrogen isotopic composition and the other way around. An increase amount of aquatic resources in AMH diet would result in clearly higher δ^{15}N than the Neandertals. In contrast not varying isotopic values would indicate an ecological behavior similar in terms of subsidence.

Sulfur stable isotopic values (δ^{34}S) in collagen can be used to distinguish between marine and terrestrial resource exploitation. Terrestrial animal in general yield average δ^{34}S values between 5 and 10‰, while marine organisms end up in average values around 20‰. In freshwater resources δ^{34}S are highly variable e.g. in riverine ecosystems δ^{34}S fall mostly in between -5 and +15‰, with local exceptions connected with local extreme values caused by small scale geographic geochemical processes of sulphate reduction or sulphide oxidation (Nehlich, 2015; Peterson and Fry, 1987).

In the Late Pleistocene mammoth steppe ecosystem context the sulfur isotopic composition has the potential to receive information about individual’s spatial behavior, since plants at the bottom of the foodweb receive their sulfur from the local geological bedrock and pass it through the foodweb (Drucker et al., 2015; Nehlich, 2015). A geologically distinguishable hunting area for the preferred prey would consequently result in a different δ^{34}S composition of the hominids. Here we can test if the catchment area of the two Neandertal groups in Spy and Goyet are different to each other and different to the early AMH from Goyet. Finally, through the δ^{34}S collagen composition we can test the potential variability within one hominid group of a given site.

2.4. Methods

Collagen preparation and isotopic analysis of Goyet human remains

Bone sampling followed standard procedure and has been described in Wißing et al. (2015b). A preliminary determination of the potential collagen preservation (nitrogen content in whole bone) was performed following (Bocherens et al., 2005a; Iacumin et al., 1997; Iacumin et al., 1996). Collagen extraction was done following (Longin, 1971) as described in (Bocherens et al., 1997). These measurements were performed with a Vario EL III elemental analyser (Elementar) (mean standard error 0.02 %, 0.05 %, and 0.03 % for %C, %N and %S, respectively). Isotopic measurements were prossessed at the Geochemical unit of the Department of Geosciences at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. Collagen preservation is given and follows general criteria considered for the chemical integrity of this protein (DeNiro, 1985). The isotopic ratios are expressed using the "δ" (delta)value as follows: $\delta^{13}C = [(^{13}C/^{12}C)sample/(^{13}C/^{12}C)reference - 1] \times 1000$ ‰ , $\delta^{15}N = [(^{15}N/^{14}N)sample/(^{15}N/^{14}N)reference - 1] \times 1000$ ‰ and $\delta^{34}S = [(^{34}S/^{32}S)sample/(^{34}S/^{32}S)reference - 1] \times 1000$ ‰. The standard for $\delta^{13}C$ is the internationally defined marine carbonate V-PDB. For $\delta^{15}N$ the atmospheric nitrogen (AIR) is used. $\delta^{34}S$ samples were calibrated relative to international standards NBS 123, NBS 127, IAEA-S-1 and IAEA-S-3. Analytical error based on laboratory standards is ± 0.1 ‰ for $\delta^{13}C$ values, ± 0.2 ‰ for $\delta^{15}N$ results and ±0.4‰ for $\delta^{34}S$ measurements.

$\delta^{34}S$ values which the atomic C/S_{coll} and N/S_{coll} ratios were in the range of 300 to 900 and 100 to 300, respectively, can be considered to be valid for our purpose (Bocherens et al., 2011b; Nehlich, 2015; Nehlich and Richards, 2009). Recent mammal collagen contains sulfur from 0.14 up to 0.33% (Bocherens et al., 2011b), this fits with the theoretical range of 0.14 to 0.29% based on DNA and amino acid sequences (Nehlich and Richards, 2009). Samples only with sulfur content in collagen between 0.13 and 0.24% were considered in this study.

Statistical methods

Cluster analysis

To identify any potential pattern of individual distribution of individual herbivorous and carnivorous specimens based on their $\delta^{13}C$ and $\delta^{15}N$ values we performed a cluster analysis using the Ward's minimum variance method with the software SAS JMP version 10.0 (Fig. 5-6). To provide insights into the isotopic variation within and among species we did a canonical discriminate analysis with the same software (Fig. 4).

Bayesian mixing model

Through this approach we can essentially estimate the consumption of animal protein by the AMH while the impact of plant protein is in general underestimated. The reason for this is a non-linear isotopic correlation between the most extreme end points of a pure vegetarian and a pure carnivorous feeding behavior. Even a very small amount of meat increases significantly the $\delta^{15}N$ values of bone collagen, for example an amount up to 50% plant food results in $\delta^{15}N$ values that are not lower 1 standard deviation of the collagen of a pure carnivorous species (Bocherens, 2009). Therefore we consider that the whole diet could include a reasonable amount of plant food with low δ^{15}N values. A tool to investigate the potential plant consumption is the analysis of stable nitrogen isotopes in single aminoacids. Naito et al. (2016) performed this kind of analysis on Spy Neandertal remains (Naito et al., 2016). For this reason we provide data rather on the relative protein source of the different prey species not absolute values. The method itself is characterized by at least three special features: uncertainties can be incorporated (standard derivation) into input data and the TEF (trophic enrichment factor). Second, the method provides not only a range of probability of a protein source proportion, but also the proportion densities in terms of probability; for example is a higher amount of a given source statistically more probable than a lower one, within the whole probability range for this source or not. Third: The software tool provides diagnostic matrix plots in which the statistical dependences between different protein sources are summarized. Dependences have either a negative or positive character. The SIAR software is taking into account these correlations among sources/prey species, which end up in an increasing probability range. In correspondence to previous works (Bocherens and Drucker, 2003; Bocherens et al., 2015a; Fox-Dobbs et al., 2007) we estimated a Tropic Enrichment Factor (TEF) of +1.1 ± 0.2 ‰ and +3.8 ±1.1 ‰ for δ^{13}C and δ^{15}N values, respectively.

As only precondition we assumed that most of the prey is provided by the large herbivorous guild.

mtDNA

The AMH remains presented in this study were analysed for mtDNA. These analysis confirmed there species attribution (Posth et al. 2016). Eight Neandertal samples (Q56-1, Q57-1, Q57-2, Q57-3, Q305-4, Q305-7, Q55-4, Q374a-1) processed for mtDNA analysis proved their attribution to Neandertals (Rougier et al. accepted). In al cases a morphological study supports the species attribution

3. Results

Chemical preservation of bones and collagen

For all analyzed samples the collagen preservation fulfilled the conditions for reliable biogenic stable carbon and nitrogen isotopic values. The detailed chemical characteristics are summarized in table 1. The carbon content in collagen ranged between 29.5% (Q48-1) and 45.6% (Q116-1). The nitrogen content in collagen ranges from 10.1% (Q48.1) to 16.3% (Q116-1). The C/N ration in collagen is between 3.3 and 3.4.

The conditions for sulfur stable isotopic values mentioned above were not fulfilled for all specimens. In all of these cases the % sulfur in collagen was above the accepted maximum of 0.26%, based on comparison with collagen extracted from fresh bones. This was the case for Neandertal specimens: Q48-1, Q119-2, Q305-7, Q376-9, and Q376-25.

Isotopic results

$\delta^{15}N$ and $\delta^{13}C$

We analyzed the $\delta^{15}N$ and $\delta^{13}C$ stable isotope composition of two AMH individuals (Q116-1 and Q376-3). The $\delta^{13}C$ values -19.1‰ yielded individual Q116 and -18.8‰ Q376-3. The $\delta^{15}N$ values are 10.9‰ for Q116-1 and 11.4‰ for Q376-3 (Table 1). The six Goyet-Neandertal specimens analyzed for their $\delta^{15}N$ and $\delta^{13}C$ stable isotope composition yielded $\delta^{13}C$ values between 19.0‰ and 19.7‰ (mean=-19.3‰) and $\delta^{15}N$ values between 11.3‰ and 12.5‰ (mean= 11.8‰). The Spy 646a (Spy IV) individual yielded a $\delta^{13}C$ value of 19.8‰ and a $\delta^{15}N$ value of 12.5‰.

$\delta^{34}S$

The $\delta^{34}S$ values for the analyzed Goyet AMHs are 8.6‰ (Q116-1) and 4.4‰ (Q376-3). The values for the Goyet Neandertals (N=11) span between 7.5‰ (Q305-4) and 11.6‰ (Q376-20) with a mean of 10.2‰. The $\delta^{34}S$ values for the Spy Neandertals are 3.6‰ for Spy 94a (Spy I) and 2.6‰ for Spy 646a (Spy IV). The faunal $\delta^{34}S$ values from Goyet (N=27) span between -7.2 and 8.4‰ (mean 1.2‰/SD 4.1‰). The faunal $\delta^{34}S$ values from Scladina (N=23) range from -17.0‰ up to 11.8‰ (mean 2.4‰/SD 5.8‰). The $\delta^{34}S$ values from Spy horse provided a value of 5.5‰ (sample IV2A 4207).

4. Discussion

4.1. Dietary ecology of the hominids

Preconditions

For the reconstruction of ecological niches through the investigation of stable isotopes some preconditions must be fulfilled. Beside aspects of chemical integrity of the collagen the sample

choice is essential. For our purpose as many as possible herbivorous, omnivorous and carnivorous mammal species had to be integrated into the study to integrate the hominids into an ecological context. A contextualizing of a given species is obligatory. Beside this it is important to compare specimens which are as close as possible in time and space, since there are changes in the isotopic baseline through time and space (Bocherens et al., 2014; Stevens et al., 2008; Wißing et al., 2015a; Yeakel et al., 2013). Therefore we increased our dataset with remains from Scladina layer 1A and Spy. We could not detect a chronological shift of the isotopic baseline between roughly 30,000 and 40,000 years in Belgium. The ecological niches of all participants beside for the AMH has been investigated and described in detail through the carbon and nitrogen stable isotopic composition (Wißing et al., 2015b).
Dietary habits, strategies and needs are a relevant aspect of the ecological niche a given species is occupying. Differences among species of the herbivore guild appear due to a special preference for a certain kind of plant food. This is reflected and memorized in the isotopic composition of the bone collagen, since the isotopic compositions of plants are bequeathed from one trophic level to the next one. The same principle is true for the carnivorous and omnivorous guild as well. Different predator species in general relay on different prey animals (Bocherens, 2015) to avoid or keep to a minimum the direct competition with other representants of the same guild. The characteristic isotopic signal for a given herbivore is directly reflected in the isotopic composition of the predator (considering the trophic enrichment factor) relaying on this species.

4.1.2. 2D-scatter plot ($\delta^{13}C$ versus $\delta^{15}N$)

Neandertals

In this study Neandertals from Spy and Goyet are considered. Apparently this hominid occupies a specific isospace, no other non-hominid predator is interfering with (fig. 3). The Neandertals from both sites yielded the highest nitrogen (average $\delta^{15}N$ = 11.5 ‰) and relatively high carbon isotopic values (average $\delta^{13}C$ = -19.2 ‰) in the whole ecosystem. The isospace occupied by Neandertals can be described as limited in expansion since the standard deviations (0.47‰ for $\delta^{15}N$ and for $\delta^{13}C$ 0.28 ‰) is relatively small. The individual differences in diet are only minor and are smaller to each other than to other species. The isospace is typically for so far all analyzed late Neandertals and is dued to a special preference on megaherbivores like mammoth (Wißing et al., 2015b).

Modern humans

The two analyzed individuals fall into the isospace occupied by the Neandertals. The δ^{13}C values are slightly higher and the average values may indicate an increasing meaning of reindeer for the modern humans in contrast to Neandertals, a detailed discussion of their dietary aspects are discussed below. Most manifesting at this point is the similarity of isotopic values of both hominid species (Fig.3). The ecological placement of the AMH in the faunal context visualized in the 2D-scatter plot shows high similarities between both types of hominids.

4.1.3. Discriminant analysis

Here we present the spatial distances or overlaps for each isospace to another (Fig.4) from a statistical perspective based on stable carbon and nitrogen isotopic composition. The relative positioning of the different isospaces is the essential information here. In figure 4 each species is represented through two circles. The inner areas contain roughly 50% of the points for a given species; the outer corresponds to a 95% confidence limit for the mean.
Herbivores and carnivores are again clearly spatially separated, with no overlap. Within the herbivorous guild the most specific isospaces are the ones occupied by mammoth, reindeer and cave bear (Fig. 4). Each of these species forms an endpoint of the ecological space the herbivores in total occupied. They form a triangle in which the other herbivores (rhinoceroses, bovids and horses) are in. The rhinoceroses, the bovids and the horses occupied distinct isospaces, but they overlapped partly to each other. The horses and the bovids overlap only very limited, while the rhinoceros is swaying into the isospaces of both species in equal shares; even roughly half of the rhinoceros isospace is shared with the bovids and horses (Fig. 4).

Among the carnivorous/omnivorous species we emphasize the attention on the hominids as an intensive debate about general meaning of large predators in Pleistocene ecosystem was done elsewhere (Van Valkenburgh et al., 2015) and from an isotopic point of in detail as well (Bocherens, 2015).

Visualized are the two Neandertal groups from Spy) and Goyet as well as the AMH from. The hominids in general are the predator the feweset interfering with other potential animal competitor. There is only a very minor overlapping with the hyena and AMH as well as the Spy Neandertals. The hominids occupied the most distinct ecological niche in terms of isospace within the carnivorous guild. While debating within the hominids group, most important is the circumstance that the Spy Neandertals, the ones from Goyet and the AMH are overlapping intensively to each other. This overlapping pattern is the most extensive one in this ecosystem. The Spy Neandertals share half of their isospace with the one from Goyet and the other way around. The Goyet Neandertal isospace is close to complete within the isospace occupied by the Goyet AMH. The Goyet Neandertals and AMHs from Goyet are more similar to each other in terms of isospace, than the Spy Neandertals to the ones from Goyet (Fig. 4).

4.1.4. *Cluster Analysis: Niche Deviation (hominids)*

A cluster analysis based on carbon and nitrogen stable isotopic composition of the herbivorous and carnivorous individuals was already performed and discussed in detail in Wißing et al. (2015b). In S1 the herbivorous species are presented in S2 the carnivorous species one.A striking feature can be recognized in carnivore cluster (S2): The first brench-off in the diagram divides the hominids (except one from Spy) from the rest of the carnivorous species. All carnivorous animals are closer to each other, than to Neandertals and AMH. The early brench–off of the hominids demonstrate that within the carnivorous guild the hominids played a very similar, most distinct role. The hominids are represented in a straight homogeneous cluster, consisting only of Neandertal and AMH remains. No other species are represented within this cluster. Both types of hominids cluster plot intermixed to each other. The differences among Neandertals and AMH are smaller than the variability among the Goyet and Spy Neandertals.

4.1.5. Reconstruction of hominid prey preference

For the two AMH specimen the possible relative proportions of consumed prey species were calculated using a Bayesian method (SIAR V4, Stable Isotope Analysis-package in R)(Parnell et al., 2010; The-R-CoreTeam, 2013) (Figure 5-10). The dietary reconstruction of the Neandertals has been analysed through this approach in another study (Wißing et al. 2015b). Since the additionally analysed Neandertal remains presented in this study yielded carbon and nitrogen stable isotopic composition very similar to the previously discussed ones we focus on the dietary reconstruction of the AMH.
Specimen Q116-1 and Q376-1

In figures 5 and 8 the dietary contribution of six prey species to these individuals were estimated by the SIAR Bayesian model based on the δ^{13}C and δ^{15}N values. For the violin plots (Fig. 5 + 8) the black boxes and whiskers show median with 1st and 3rd quartiles and ranges with 1.5 times length of the interquartile range above the 3rd quartile or below the 1st quartile, respectively. The shaded area indicates Karnel density plot of the probability density of prey proportions. Both individuals yielded very similar results, so we don’t discuss them separately.

The two most important prey species are the reindeer and the mammoth. Both species constitute roughly 25% of the protein source each. The rhinoceros provides around 15 and 20%, the bovids and horses roughly 10% of the diet. Cavebear played a very minor role, this species contributed max. around 5% to the protein intake.

These relative quantitative indications are associated with some statistical information which are relevant for their interpreting: In figure 6 and 9 we presented the proportion densities plots for each potential prey of these individuals. On the x-axis the proportion is given, while on the y-axis the density/probability is provided. The density for cave bear is the highest at the lowest proportion and decreases exponentially. This means a lower amount of cave bear has a much higher probability than a higher one. The same is true for the horses and the bovids, but much less extreme than for the cave bear. The rhinoceros (for specimen Q116-1), mammoth and reindeer have a bell shaped distribution of proportion vs. density. This implies that the highest probability for a specific amount is at a given value, a higher or a lower proportion is less probable. (Fig. 6 and 9).

To have a more comprehensive understanding about statistical dependences between each potential prey to all other ones we did a diagnostic matrix plot (Fig. 7 and 10). These plots show the correlations, positive or negative ones, among the different dietary sources. And is one of the biggest advantages SIAR can provide in contrast to most other tools. The higher correlations in general are, the more increased is the probability range for the potential prey. For both individuals the three highest correlations are negative ones, between the mammoth and the rhinoceros, between the rhinoceros and the reindeer and between the bovids and the reindeer. The negative correlation among mammoth and rhinoceros implies a higher amount of mammoth would need a lower amount of rhinoceros or an increasing amount of rhinoceros followed by a lower quantity of mammoth. This correlation is a very intensive one for both individuals. If we additionally consider the negative correlation between rhinoceros and reindeer we see that a lower amount of rhinoceros would imply a higher amount of reindeer and mammoth, since there are negative correlation between rhinoceros and mammoth and rhinoceros and reindeer. Finally it is hard to precise the range of probability for these species, this is dued to the above mentioned correlations. Anyhow the general trends are explicit; the most and less important prey species can be described through this analysis.

4.1.6. Comparison of Neandertals and AMH prey preference in Goyet and Spy

The isotopic values for the Neandertals (Wißing et al., 2015b) and the AMH in Goyet are relatively close to each other (Fig. 4, Tab. 1). Furthermore it has been discussed why the relative meaning of the different prey species are more robust than the absolute values. Based on the dietary reconstructions of single Neandertal individuals from Goyet and Spy (Wißing et al., 2015b) and the one of the two AMH individuals presented here, a table is summarizing the relative meaning of each prey for each individual (Tab. 3). The table contains also the relative amount of different prey species for the cave lion, hyena, wolf and brown bear based on another study (Wißing et al., 2015b) to complete the carnivorous guild and to highlight the specific role of both hominids again. Ranking is based on the SIAR diet reconstruction models and goes from number 1 up to 5, while 1 means the most preferred prey and 5 the less one. This is in correspondence to the six main herbivorous prey species in this context. If two or more prey species yielded very similar ranking the same number is given. By comparison the different Neandertals individuals we see, the relative meanings of the different prey species are in most of the cases very similar. The most important species is the mammoth for all analysed Neandertals. For one individual (tibia III) the meaning of reindeer and mammoth is the same, both species occupied the first rank. The second most important prey species for the Neandertals is in general the rhinoceros. The third place is roughly shared between the horse and the bovids. Both species played a moderate role for these Neandertals. The meaning of the reindeer is bigger for the Neandertals individuals from Goyet than for the two adult individuals from Spy. Cave bear played the most unimportant role for all Neandertals beside the Spy II individual where this species may had a slightly more important role.

Most important here is the direct comparison with the two modern humans from Goyet: For both AMH individuals the mammoth and the reindeer are the most important prey species. The second most important species is the rhinoceros, followed by the bovids and the horse. The most dispensable prey species is the cave bear. Is becomes clear that the relative meaning of the different prey species is in general nearly the same for both species. Only the reindeer plays in average a more important role for the modern humans. The biggest herbivorous species played for both types of hominids the same major role. Both hominids had on a larger individual time scale a very similar subsistence strategy.

4.2. Aspects of habitat and mobility

4.2.1. Context

Differences on the one hand as well as site characteristic $\delta^{34}S$ isotopic compositions in the total range observed from Belgium Late Pleistocene sites have been observed in other similar ecosystems as well: In the Moravian Plain the site of Predmostí herbivore and carnivore collagen was investigated beside other stable isotopes for $\delta^{34}S$ isotopic composition (Bocherens et al., 2015b) (av. 2,25‰; N=14). At the Geißenklösterle in the Ach Valley (SW-Germany) mammoth, reindeer and horse remains with a very similar Late Pleistocene ecological background have been analysed for $\delta^{34}S$ (Drucker et al., 2015). At the Geißenklösterle beside one reindeer specimen (11.9‰ $\delta^{34}S$) the three species provided relatively low values between-2.2 and 3.6 $\delta^{34}S$ (av. 0.24‰; N=8; exclusive above mentioned reindeer). These values are likely to reflect results for animals dwelling in the surroundings of the site (Drucker et al., 2015). Another site with a similar ecological background than the Belgium ones is the loess site Ziegeleigrube Coenen, Germany around 150km east of Goyet. Here the $\delta^{34}S$ isotopic composition is slightly higher than in the Ach Valley in average (av. 3.6‰; N=15) for herbivorous and carnivorous species (Wißing et al., 2015a). This reflects the characteristic $\delta^{34}S$ signal in this area. The site with the highest $\delta^{34}S$ values for herbivorous species is Abri Pataud in Dordogne (SW-France) with an average of 10.3 ‰ (N=15) (Drucker et al., 2015). All together it is plausible to argue that each site/area has their own typical local characteristic $\delta^{34}S$ values like we will highlight for the Belgium sites as well. Further investigation is needed to test if there could be a general east west gradient in Europe with higher values in the west and lower ones in the east.

4.2.2. Faunal remains

It becomes visible in figure 11 that the majority of the faunal remains yielded $\delta^{34}S$ values roughly between -3‰ and 8.5‰ (av. 2.5‰, N=60) beside some cave bears from Scladina and Goyet as well as one Goyet reindeer with lower values. These specimens yielded sulfur values up to -17‰ for a cave bear from Scladina. The cave bears in general yielded clearly the lowest $\delta^{34}S$ values (av. -4.0‰) of all species. Among the faunal values, only a canid from Scladina and some reindeer tooth from Scladina yielded more positive values than the “main field” (grey background).

This indicates that there is another habitat in the range of these canid and reindeer with $\delta^{34}S$ values around 12‰ as well one with lower values corresponding to the reindeer from Goyet. In contrast to bone values $\delta^{34}S$ in dentin reflects the shorter time span of tooth formation; this is true for the tooth remains from reindeer specimens from Scladina with higher $\delta^{34}S$ composition. Unfortunately a direct comparison of $\delta^{34}S$ of dentin collagen values and bone collagen values of the same individual is not part of this study; potential difference could indicate intraindividual mobility aspects.

We consider the “main-field” seen in fig. 11 as the local sulfur signal of this area while we aware that the isotopic span is relatively wide, but since the geological bedrock in this area is quite divers (Azmy et al., 2009), we expect a wider range of sulfur isotopic compositions. Anyhow among the faunal

remains all specimens beside the ones discussed are within this range with grey background. The defined typical δ^{34}S range in this area is supported by the rel
atively centered position of the hyenas from Goyet and Scladina who had access to all available mammoth steppe fauna in this ecosystem (Wißing et al., 2015b).

4.2.3. Hominids

We investigated three different hominid groups: the Neandertals from Goyet, the ones from Spy and the modern humans from Goyet.

4.2.3.1. Neandertals

Spy Neandertal: The two analysed individuals yielded δ^{34}S values of 3.6 and 2.6‰. These individuals are centered in the field defined as local signature consequently both Spy Neandertals had their main drainage are in the surrounding ecosystem. Their values correspond to the ones obtained on carnivores like hyenas from Scladina and Goyet as well as the canids from Goyet as well.
Goyet Neandertals: The Goyet Neandertals yielded the highest δ^{34}S values for a well represented species in this ecosystem. No other species beside one canid and some reindeer tooth specimens from Scladina yielded similar values. It is relevant to point out that the whole Neandertals group consisting out of several individuals has relatively high and similar δ^{34}S values. Only one individual (Q305-4) yielded slightly lower δ^{34}S values (7.5‰). Interestingly enough this specimen also yielded the lowest δ^{15}N values of all hominids (10.7‰). Based on the δ^{34}S values, while considering the δ^{15}N and δ^{13}C, we assume an origin different from the local ecosystem. Of course we do not know where their catchment area was. It could be relatively nearby where the above mentioned reindeer and canid specimens grew up or maybe several hundred of kilometers away in SW France where a whole ecosystem with relatively high δ^{34}S could be detected. At least we can rule out an origin of this Neandertals from region with significant lower values like in the Ach Valley, the Moravian Plains or the Rhine area.

Summarized the Neandertals from Goyet where no locals in contrast to the ones from Spy. Interestingly the non-local Goyet Neandertal remains show evidence for cannibalism (Rougier et al., accepted). This is not the case for the local Spy Neandertals.

4.2.3.2. Modern humans

Both ancient AMH were analysed for $\delta^{34}S$. Both yielded values always lower the signal obtained on the Neandertals from Goyet (only Neandertals specimen Q 305-4, discussed above has slightly lower $\delta^{34}S$ than AMH individual Q116-1). AMH individual Q376-3 yielded values centered in the field defined as local signal. Specimen Q116-1 is on the edge of the local $\delta^{34}S$ signal. If we would hypothesize AMH had a higher intake of e.g. aquatic resources in their diet this could explain the different $\delta^{34}S$ values, but only in combination with higher $\delta^{15}N$ and/or $\delta^{13}C$ values between both types of hominids. The longer aquatic food chains would cause scenarios like this. The homogenous C/N stable isotopic composition between both species indicates that the most reasonable explanation is to assume there was a geographical/geological difference in origin of main prey between Neandertals and AMH, while they had a very similar prey spectrum in terms of species at the same time. It was the hunting ground which was different for the Goyet Neandertals and the Goyet AMH.

5. Conclusion

In this study results of $\delta^{15}N$ and $\delta^{13}C$ isotopic analysis of ancient modern humans and Neandertals from Goyet and Spy (both Belgium) were presented. We also provide $\delta^{34}S$ values obtained on Neandertals, the modern humans and on carnivorous and herbivorous mammal species of the same ecosystem from both sites.

Through the $\delta^{15}N$ and $\delta^{13}C$ investigation we demonstrated that early AMH and Neandertals occupied a very distinct ecological niche in terms of protein source. Among the omnivorous/carnivorous guild both types of hominids occupied the most specific ecological niche with nearly no overlap with other predators. The dietary differences between Neandertals of Goyet and Spy are more pronounced, than between the modern humans and the Neandertals from Goyet. Modern humans and Neandertals relied essentially on the same prey species. Our results support a purely terrestrial diet in an ecosystem with no recognizable differences from the stable isotopic point of view.

The study of $\delta^{34}S$ composition of faunal and hominid remains allowed concluding about hominid land-use strategies. In contrast to dietary similarities the landuse pattern was clearly different. The Goyet Neandertals do not reflect the local $\delta^{34}S$ signal obtained on a broad set of faunal remains, consequently they where no locals. Maybe this aspect regard some attention in the context of intensive cannibalism observed on the same remains. This is in contrast to the Neandertals from Spy who clearly fall into the local $\delta^{34}S$ range and were probably buried intentionally. The modern humans reflect for one individual clearly the local signal, while the other one is on the limit of the local signal.

This implicates the Goyet Neandertals and AMH had the same prey but a clearly different catchment area. The Goyet site is an excellent opportunity for the understanding of ecological characteristics of late Neandertals and early modern humans, since both hominids could be recovered from this site associated with a rich faunal assemblage and chemically well preserved bone material. These circumstances are unique and make the site a keysite for the understanding of the ecological behavior of the last Neandertals and early modern humans in Europe.

Figures

Tables

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Fig. 1

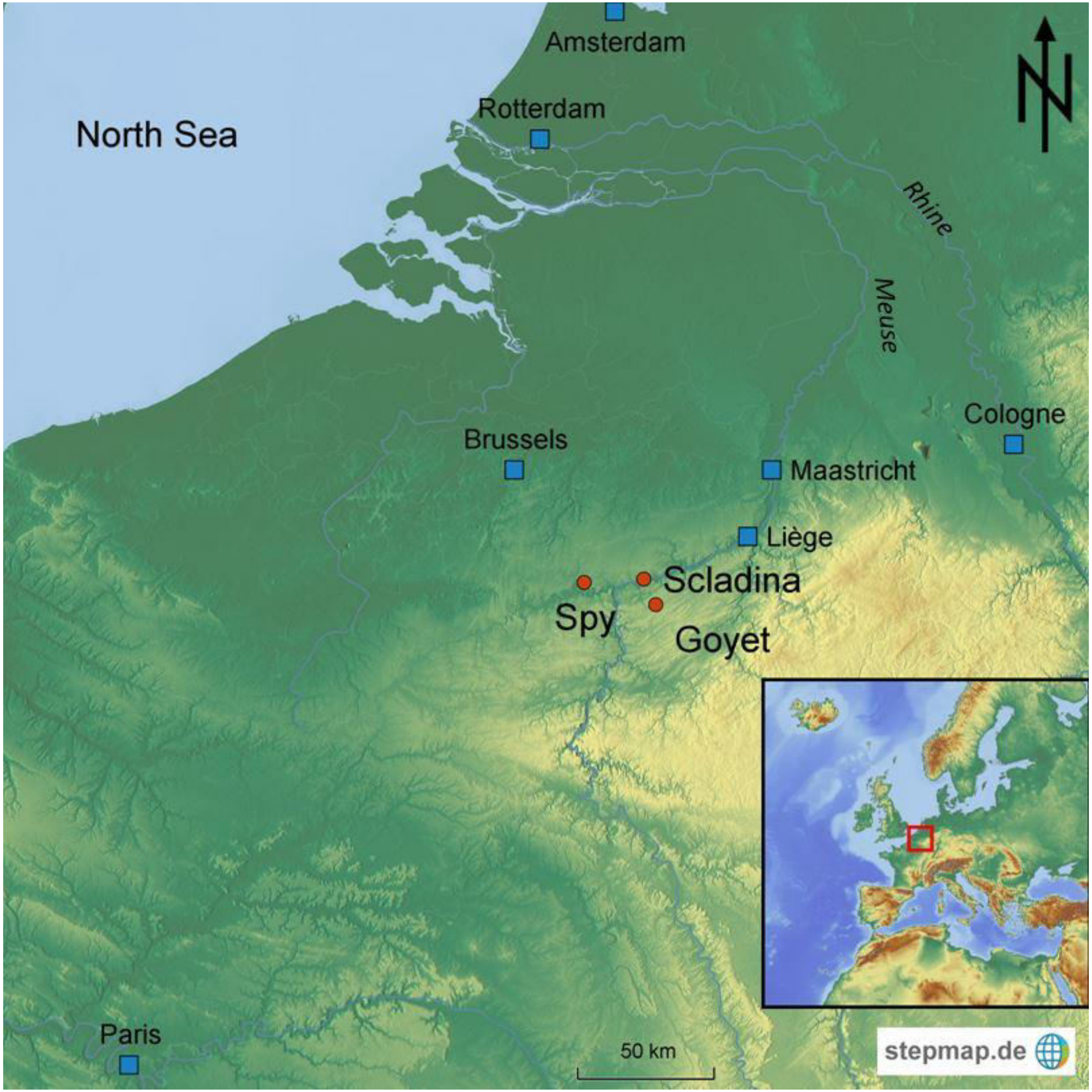
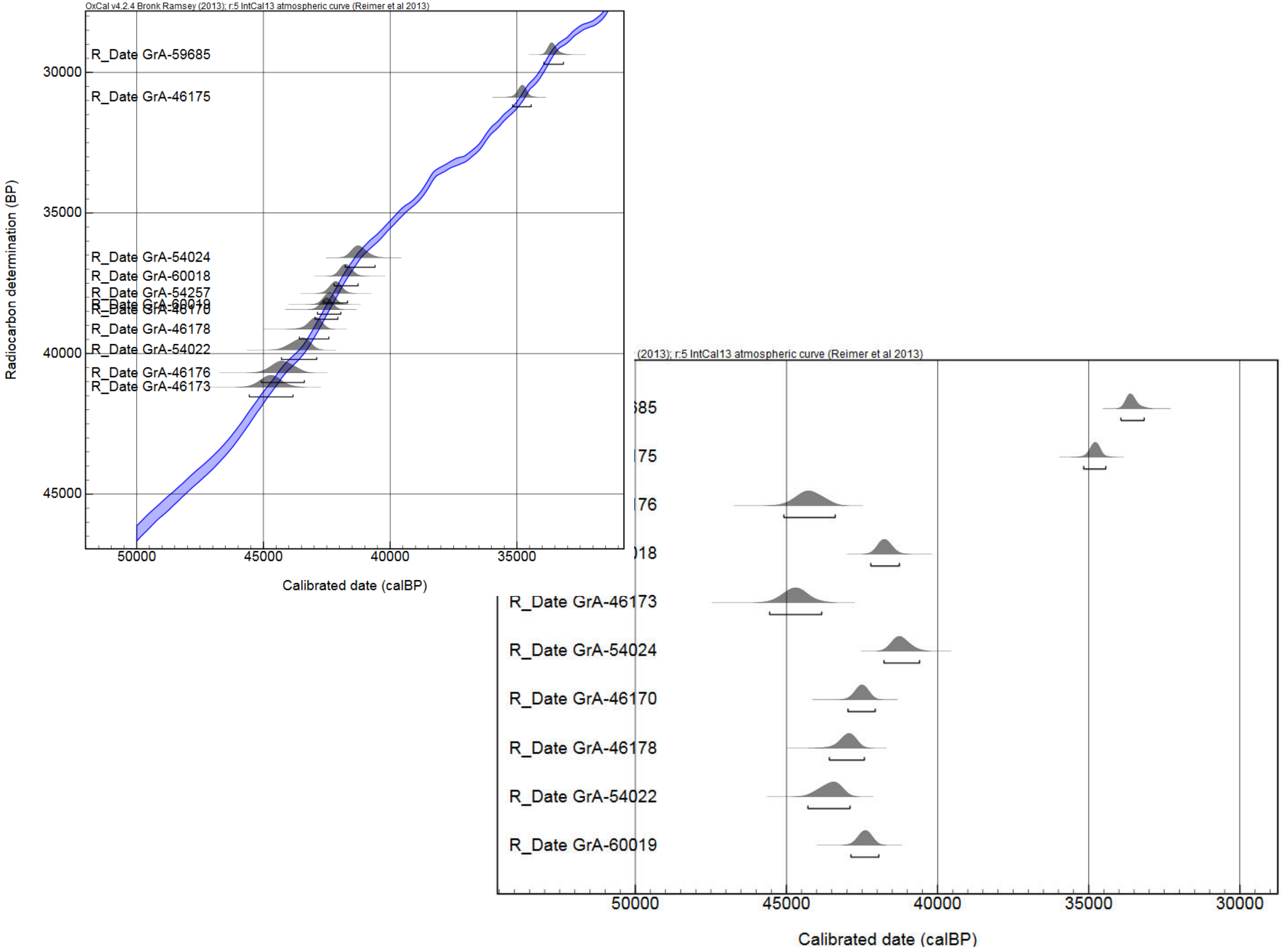

Amsterdam
Rotterdam
North Sea
Rhine
Meuse
Cologne
Brussels
Maastricht
Liège
Scladina
Spy
Goyet
Paris
50 km
stepmap.de

Fig. 2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R_Date GrA-46176
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30000
35000
40000
45000
Radiocarbon determination (BP)
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40000
35000
Calibrated date (calBP)
(2013); r:5 IntCal13 atmospheric curve (Reimer et al 2013)
685
175
176
018
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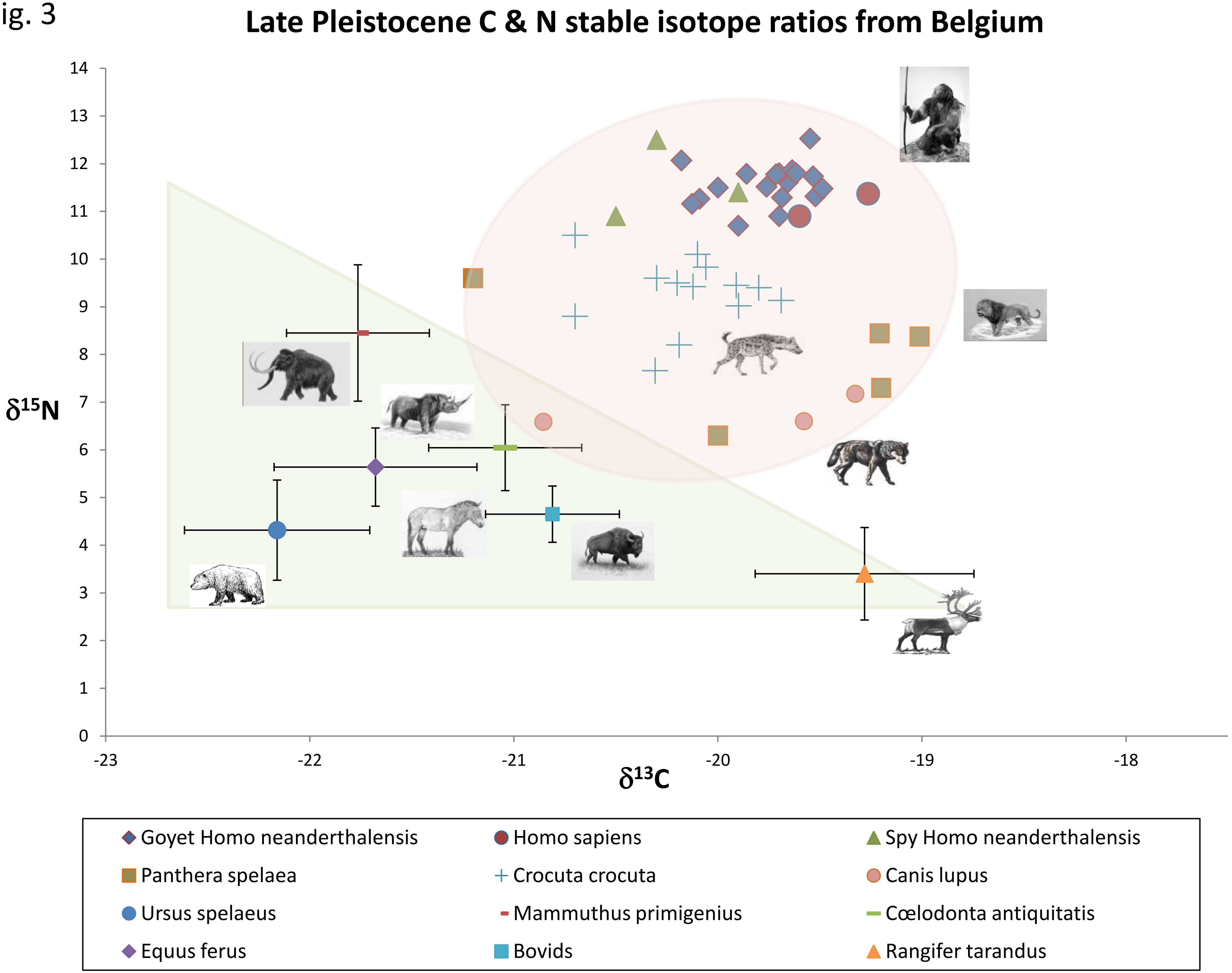
R_Date GrA-46170
R_Date GrA-46178
R_Date GrA-54022
R_Date GrA-60019
50000
45000
40000
35000
30000
Calibrated date (calBP)

Fig. 3



Late Pleistocene C & N stable isotope ratios from Belgium
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
δ15N
-23
-22
-21
-20
-19
-18
δ13C
◆ Goyet Homo neanderthalensis
● Homo sapiens
▲ Spy Homo neanderthalensis
■ Panthera spelaea
+ Crocuta crocuta
● Canis lupus
● Ursus spelaeus
- Mammuthus primigenius
- Cœlodonta antiquitatis
◆ Equus ferus
■ Bovids
▲ Rangifer tarandus

Fig. 4

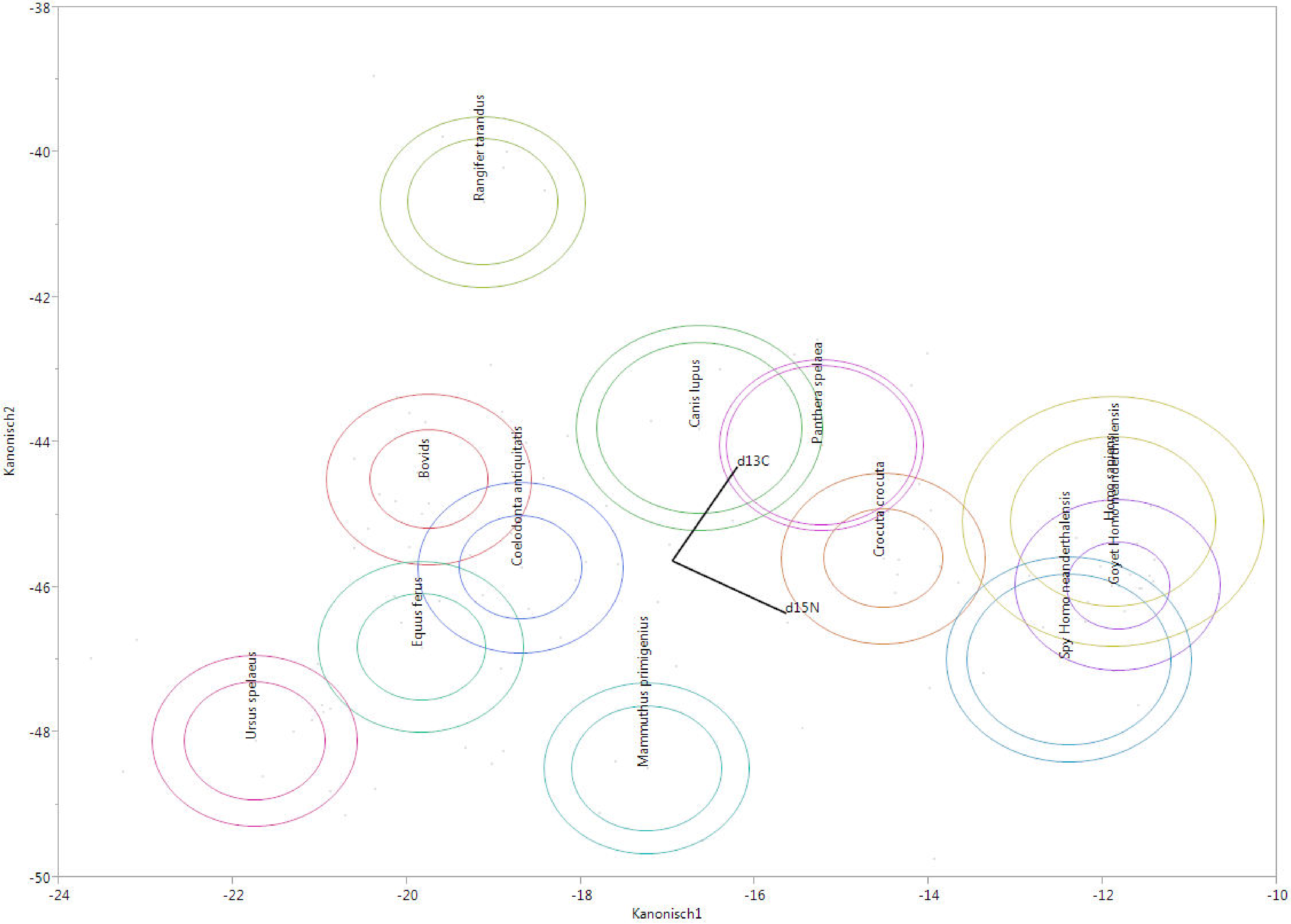

Rangifer tarandus
Canis lupus
Panthera spelaea
Bovids
Coelodonta antiquitatis
d13C
d15N
Crocuta crocuta
Homo sapiens
Goyet Homo neanderthalensis
Spy Homo neanderthalensis
Equus ferus
Ursus spelaeus
Mammuthus primigenius
Kanonisch2
-38
-40
-42
-44
-46
-48
-50
Kanonisch1
-24
-22
-20
-18
-16
-14
-12
-10

Fig. 5

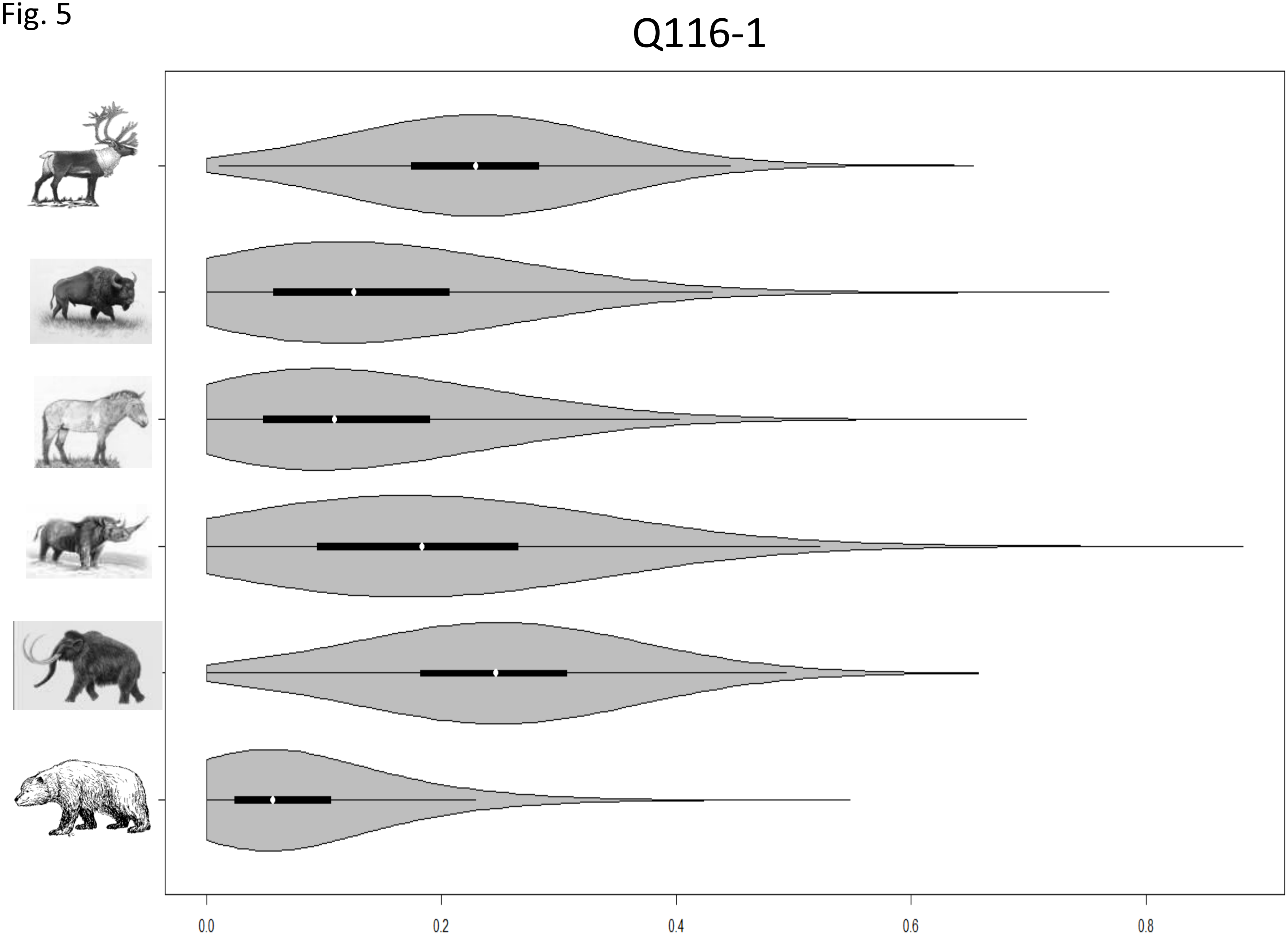


Fig. 6

Q116-1

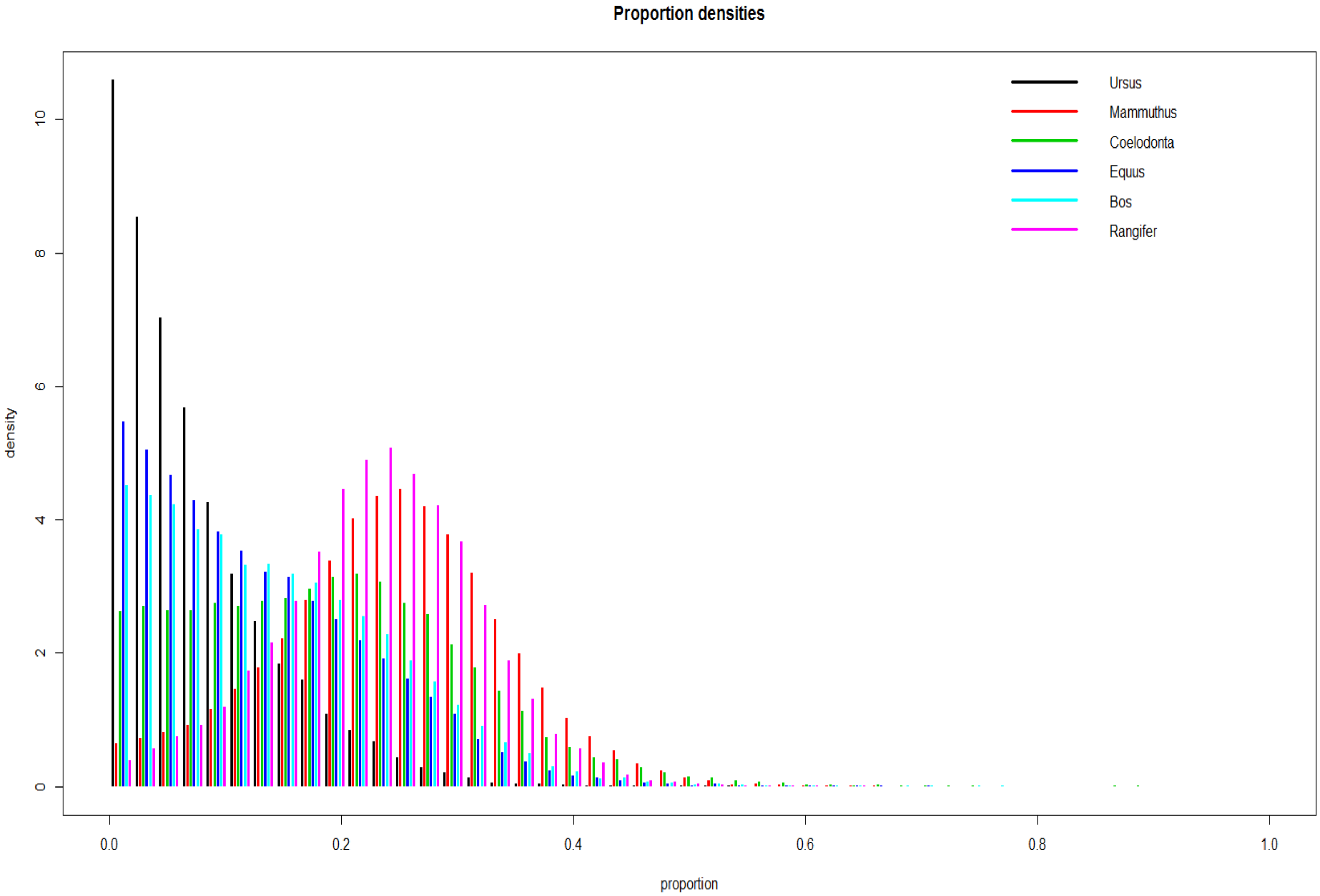
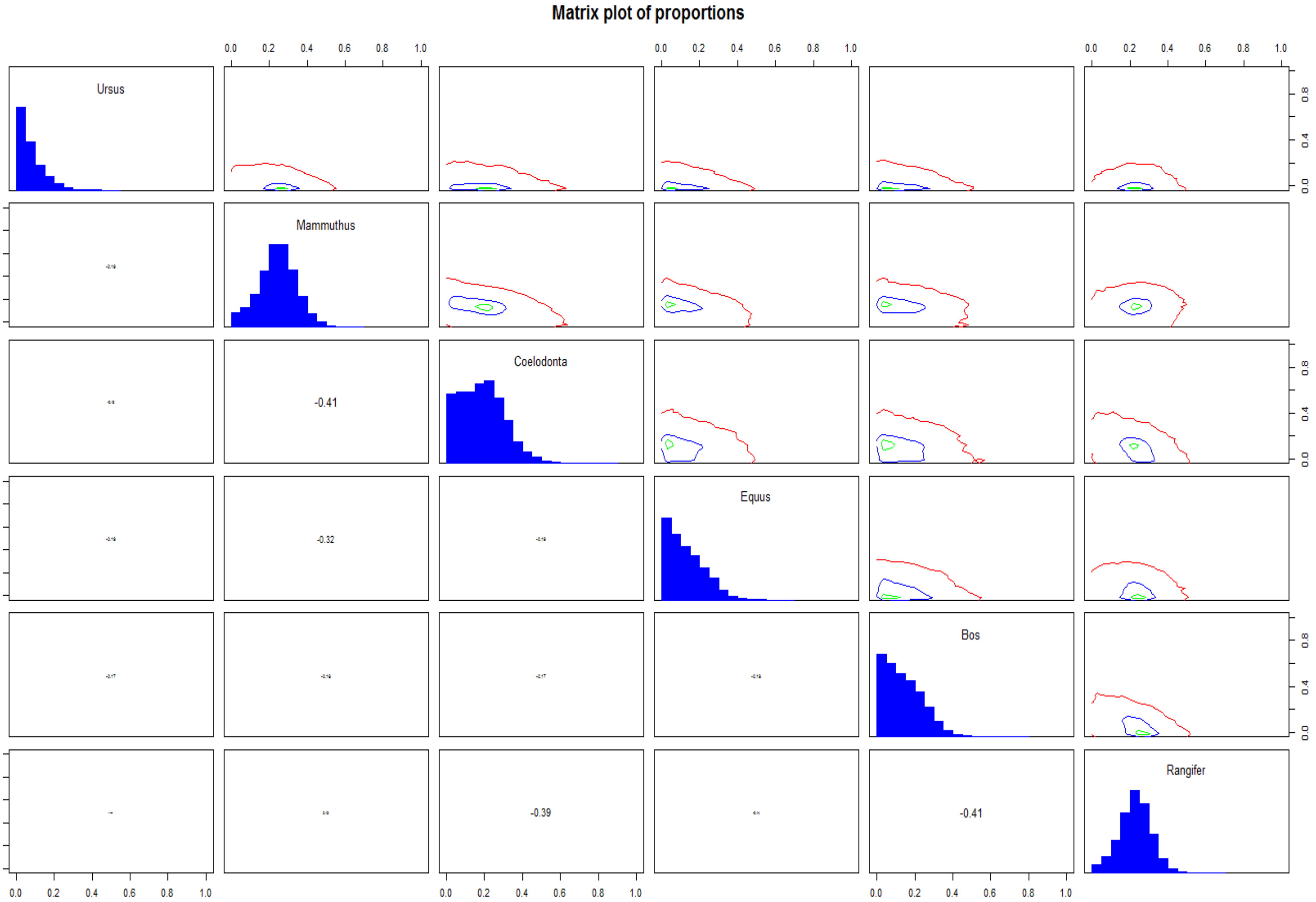

Proportion densities
Ursus
Mammuthus
Coelodonta
Equus
Bos
Rangifer
density
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
proportion

Fig. 7

Q116-1


Matrix plot of proportions
Ursus
Mammuthus
Coelodonta
Equus
Bos
Rangifer
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-0.32
-0.39
-0.41
0.0
0.2
0.4
0.6
0.8
1.0

Fig. 8

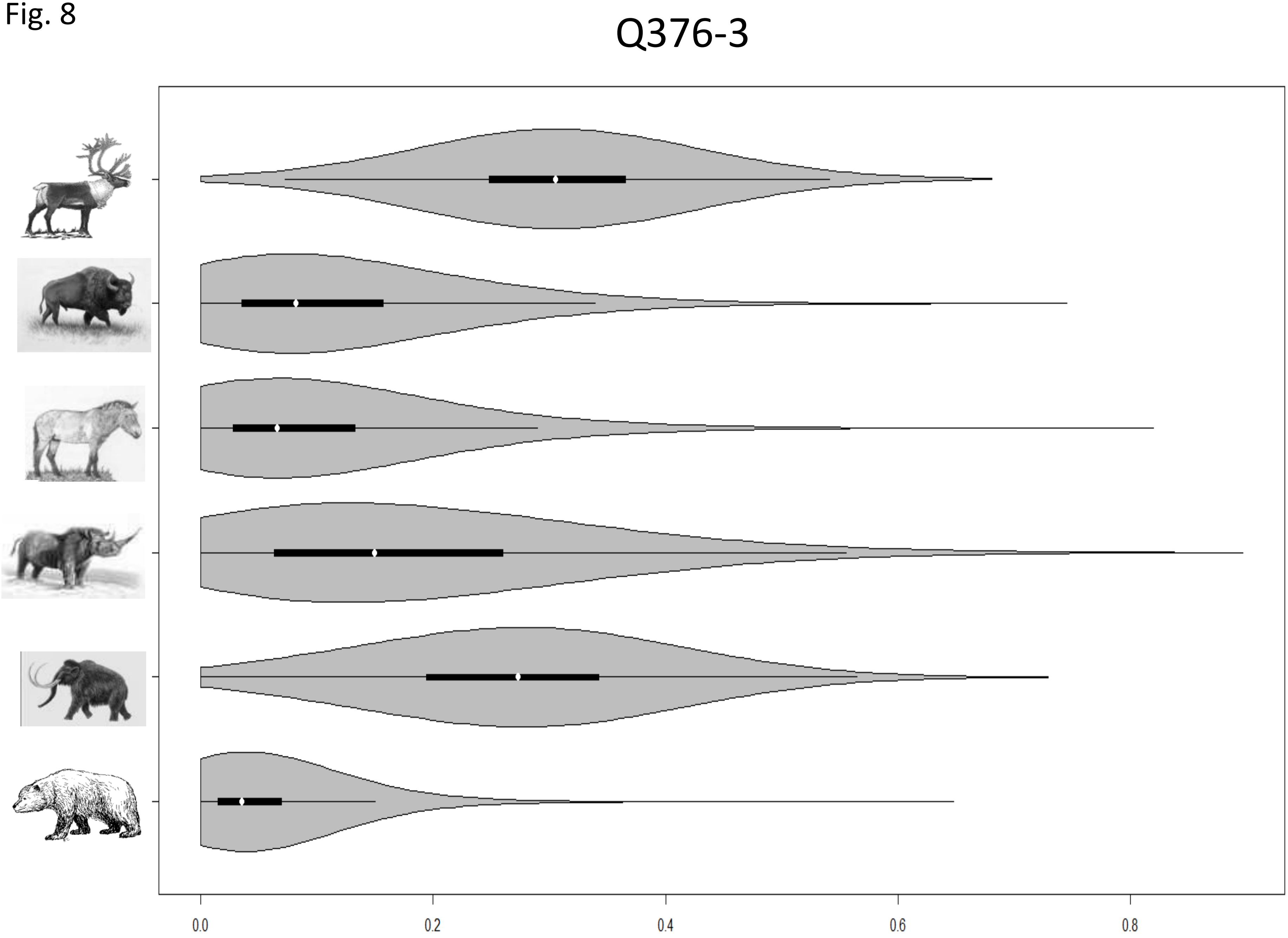


Fig. 9

Q376-3

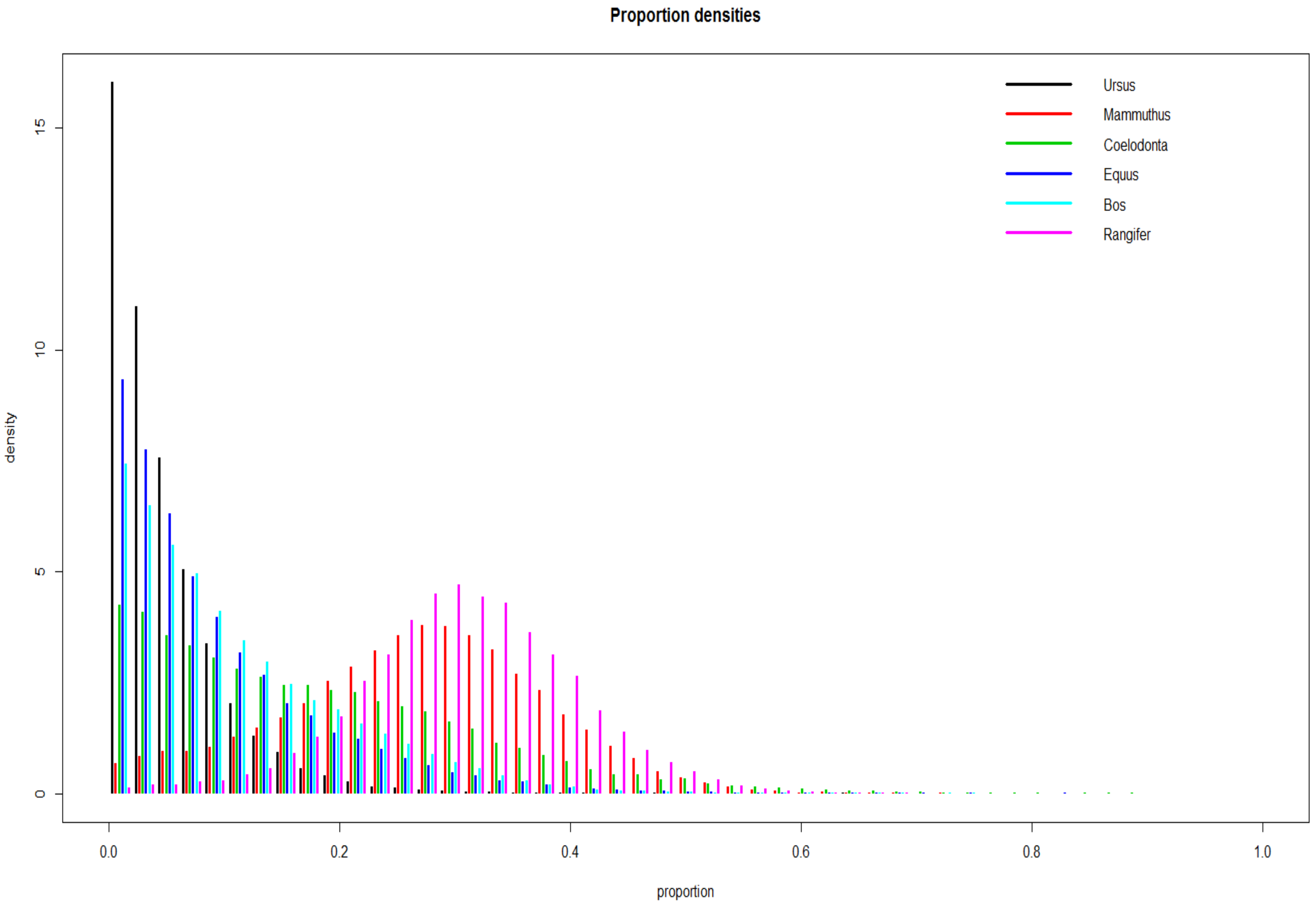

Proportion densities
density
0
5
10
15
proportion
0.0
0.2
0.4
0.6
0.8
1.0
Ursus
Mammuthus
Coelodonta
Equus
Bos
Rangifer

Fig. 10

Q376-3

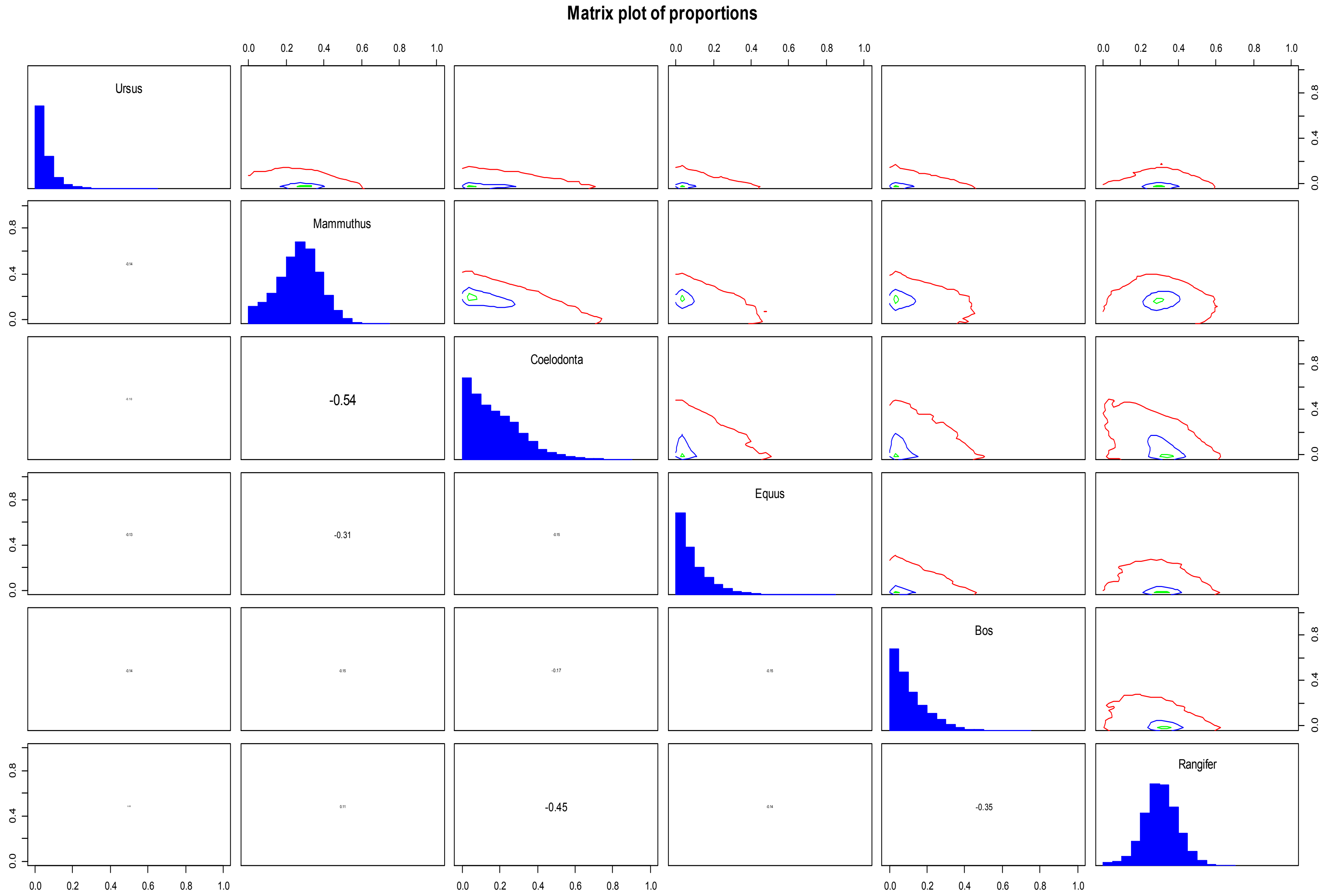
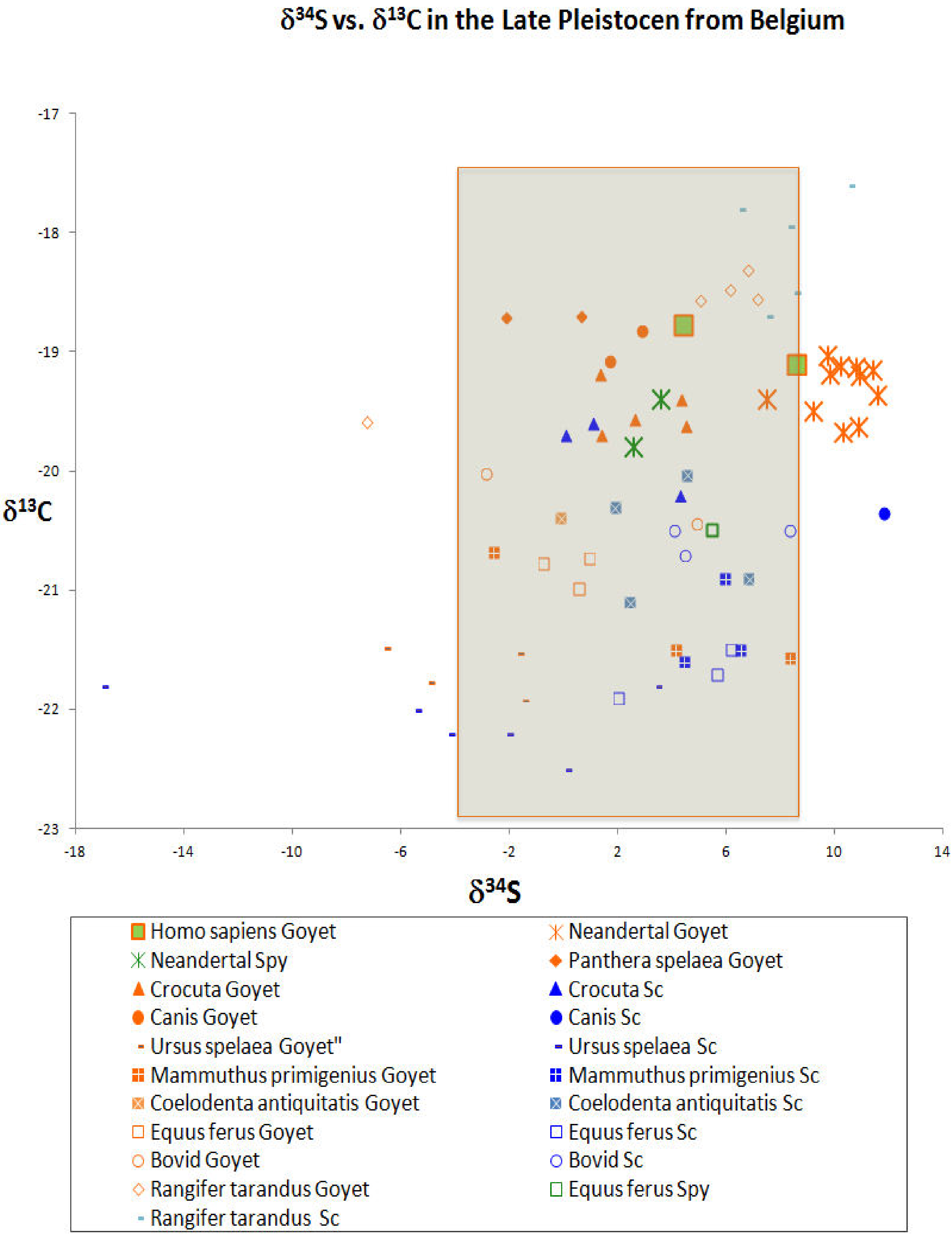
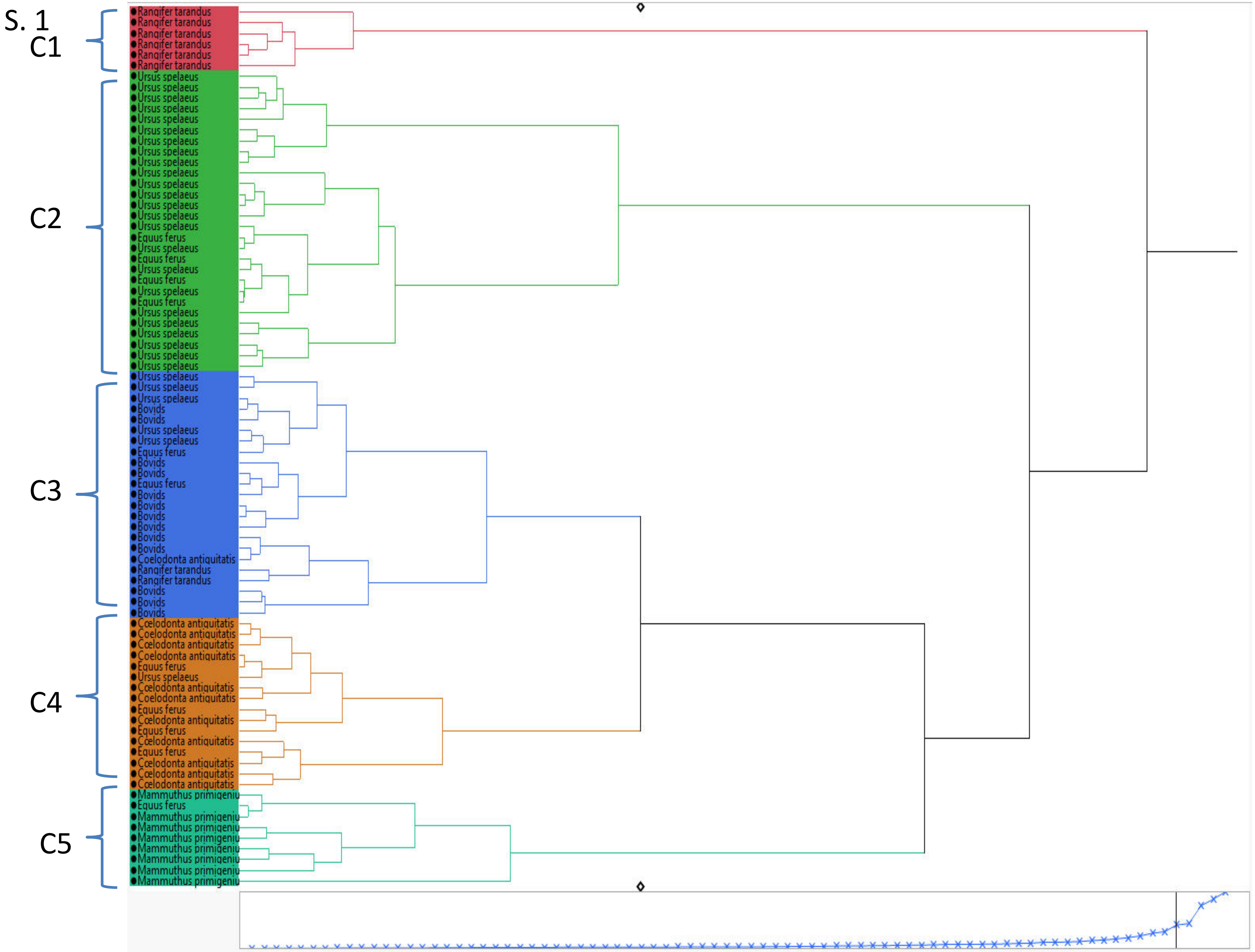

Matrix plot of proportions
Ursus
Mammuthus
Coelodonta
Equus
Bos
Rangifer
-0.14
-0.10
-0.54
-0.13
-0.31
-0.15
-0.14
-0.15
-0.17
-0.15
0.05
0.11
-0.45
-0.14
-0.35
0.0
0.2
0.4
0.6
0.8
1.0

Fig. 11


δ34S vs. δ13C in the Late Pleistocen from Belgium
δ13C
-17
-18
-19
-20
-21
-22
-23
δ34S
-18
-14
-10
-6
-2
2
6
10
14
Homo sapiens Goyet
Neandertal Spy
Crocuta Goyet
Canis Goyet
Ursus spelaea Goyet"
Mammuthus primigenius Goyet
Coelodenta antiquitatis Goyet
Equus ferus Goyet
Bovid Goyet
Rangifer tarandus Goyet
Rangifer tarandus Sc
Neandertal Goyet
Panthera spelaea Goyet
Crocuta Sc
Canis Sc
Ursus spelaea Sc
Mammuthus primigenius Sc
Coelodenta antiquitatis Sc
Equus ferus Sc
Bovid Sc
Equus ferus Spy


S. 1
C1
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
Rangifer tarandus
C2
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Equus ferus
Ursus spelaeus
Equus ferus
Ursus spelaeus
Equus ferus
Ursus spelaeus
Equus ferus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
C3
Ursus spelaeus
Ursus spelaeus
Ursus spelaeus
Bovids
Bovids
Ursus spelaeus
Ursus spelaeus
Equus ferus
Bovids
Bovids
Equus ferus
Bovids
Bovids
Bovids
Bovids
Bovids
Bovids
Coelodonta antiquitatis
Rangifer tarandus
Rangifer tarandus
Bovids
Bovids
Bovids
C4
Coelodonta antiquitatis
Coelodonta antiquitatis
Coelodonta antiquitatis
Coelodonta antiquitatis
Equus ferus
Ursus spelaeus
Coelodonta antiquitatis
Coelodonta antiquitatis
Equus ferus
Coelodonta antiquitatis
Equus ferus
Coelodonta antiquitatis
Equus ferus
Coelodonta antiquitatis
Coelodonta antiquitatis
Coelodonta antiquitatis
C5
Mammuthus primigeniu
Equus ferus
Mammuthus primigeniu
Mammuthus primigeniu
Mammuthus primigeniu
Mammuthus primigeniu
Mammuthus primigeniu
Mammuthus primigeniu
Mammuthus primigeniu

S.2

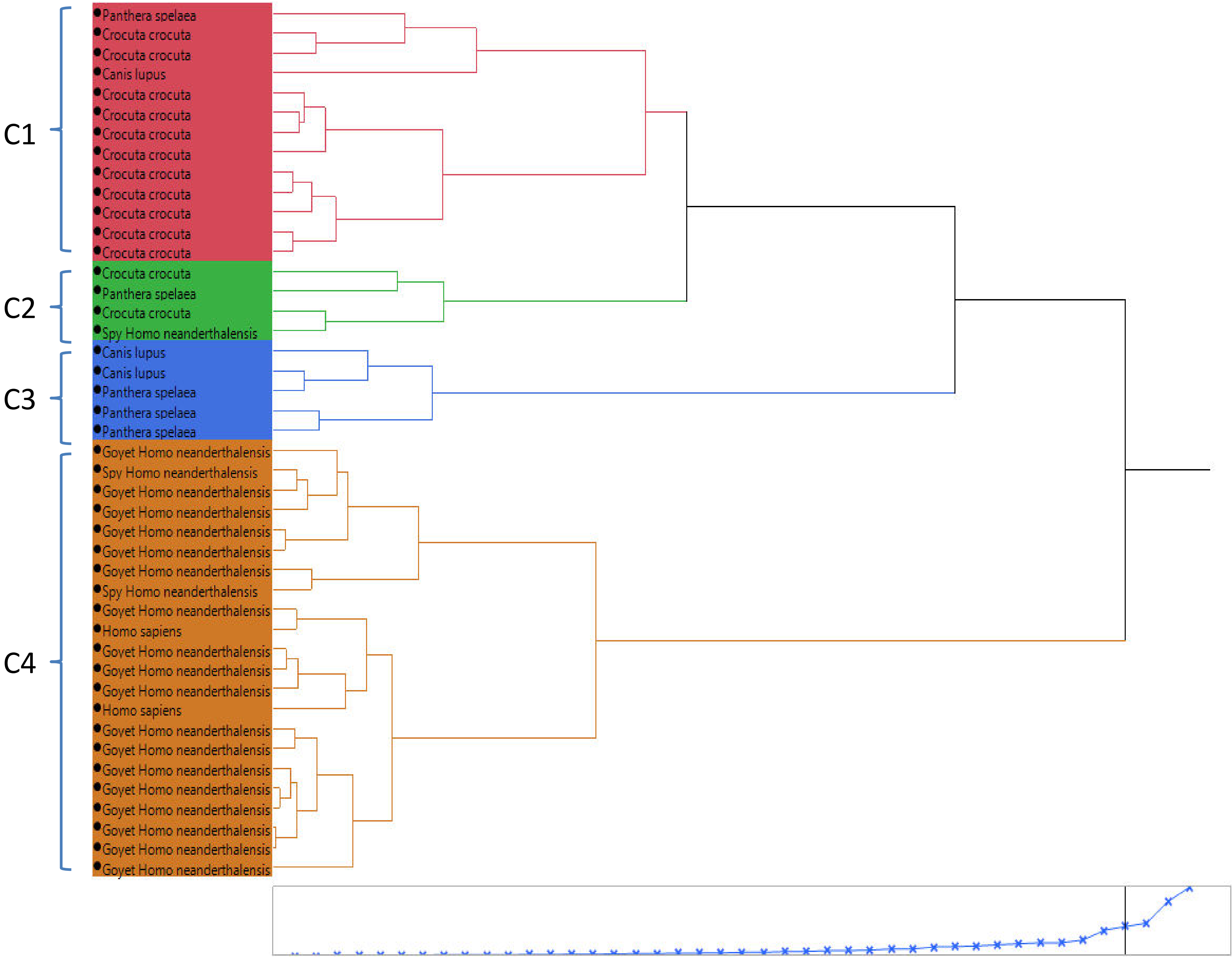

C1
Panthera spelaea
Crocuta crocuta
Crocuta crocuta
Canis lupus
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
Crocuta crocuta
C2
Crocuta crocuta
Panthera spelaea
Crocuta crocuta
Spy Homo neanderthalensis
C3
Canis lupus
Canis lupus
Panthera spelaea
Panthera spelaea
Panthera spelaea
C4
Goyet Homo neanderthalensis
Spy Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Spy Homo neanderthalensis
Goyet Homo neanderthalensis
Homo sapiens
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Homo sapiens
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis
Goyet Homo neanderthalensis

Table 3

Relative amount of different prey species

		Mammoth	Rhinoceros	Horse	Bovid	Reindeer	Cavebear
Cave lion		4	3	3	2	1	2
Hyena		1	1	1	1	1	2
Wolf		3	2	2	1	1	1
Brown Bear		3	2	2	2	2	1
Neandertal	Goyet (Tibia III)	1	2	3	3	1	4
	Goyet (Tibia IV)	1	2	3	3	2	4
	Goyet (Tibia V)	1	2	3	3	2	4
	Goyet (Tibia VI)	1	2	3	3	4	4
	Spy I	1	2	4	4	3	5
	Spy II	1	3	2	4	5	2
mod. Human	Q116-1	1	2	4	3	1	5
	Q376-3	1	2	4	3	1	5

Table 1 Human remains

ID	Species	Specimen	Dating ID	Date	%C_{coll}	%N_{coll}	C/N	$\delta^{13}C$	$\delta^{15}N$	%S coll (0.13-0.26)	atomic C/Scoll (300-900)	atomic N/Scoll (100-300)	δ^{34} S	References
Site: Goyet														
Q116-1	*Homo sapiens*	Lt humerus diaphysis frag.	GrA-46175	30,880 ± 170	45.6	16.3	3.3	19.1	10.9	0.14	867	266	8.64	1,6
Q376-3	*Homo sapiens*	Rt humerus diaphysis frag.	GrA-59685	29,370 +180 - 170	43.3	15.4	3.3	18.8	11.4	0.14	814	248	4.43	1,6
C5-1	*Homo neanderthalensis*	Parietal frag.	-	-	43.0	14.7	3.4	19.7	12.1	0.24	469	138	10.32	1,5
Q48-1	*Homo neanderthalensis*	Lt pubis frag.	-	-	29.5	10.1	3.4	19.6	11.3	2.1	37	11	11.5	1,5
Q53-4	*Homo neanderthalensis*	Rt humerus diaphysis frag. (humerus III)	GrA-54022	39,870 +400, - 350	42.9	15.1	3.3	19.0	11.7	0.19	603	182	9.72	1,2,5
Q55-1	*Homo neanderthalensis*	Lt clavicle frag.	GrA-54257	37,860 +350 - 310	36.9	12.9	3.3	19.2	11.3	0.19	522	157	9.80	1,2,5
Q55-4	*Homo neanderthalensis*	right tibia IV			39.6	14.0	3.3	19.2	11.6	0.24	443	134	11.41	1,2
Q56-1	*Homo neanderthalensis*	Rt femur diaphysis frag. (femur I)	GrA-46170	38,440 +340, - 300	45.4	15.5	3.4	19.5	11.5	0.15	807	236	9.22	1,2, 5
Q57-1	*Homo neanderthalensis*	Lt tibia diaphysis frag. (tibia II)	GrA-46173	41,200 +500, - 410	46.0	16.8	3.2	19.2	11.8	0.2	767	240	10.9	1,2, 5
Q57-2	*Homo neanderthalensis*	Rt femur diaphysis frag. (femur II)	GrA-54024	36,590 +300, - 270	42.7	15.0	3.3	19.1	11.9	0.23	496	149	10.78	1,2,5

Q57-3	*Homo neanderthalensis*	Rt tibia diaphysis frag. VI	GrA-60019	38.260 +350 - 310	43.8	15.4	3.3	19.6	11.2	0.17	693	209	10.88	1,2,5
Q 119-2	*Homo neanderthalensis*	rib frag.	-	-	38.9	13.8	3.3	19.3	11.5	0.45	228	69	11.90	1,5
Q305-4	*Homo neanderthalensis*	Lt tibia diaphysis frag. (tibia I)	GrA-46176	40,690 +480, - 400	47.1	16.7	3.3	19.4	10.7	0.16	785	239	7.50	1,2,5
Q305-7	*Homo neanderthalensis*	right tibia III	-	-	41.9	14.9	3.3	19.0	11.3	0.29	381	116	11.30	1,2,5
Q374a-1	*Homo neanderthalensis*	right tibia V	-	-	43.1	15.2	3.3	19.1	11.8	0.18	647	196	10.23	1,2,5
Q376-1	*Homo neanderthalensis*	Hand prox. phalanx 2-4	GrA-46178	39,140 +390, - 340	46.7	17.0	3.2	19.2	10.9					2,5
Q376-20	*Homo neanderthalensis*	Rt humerus diaphysis frag. (humerus II)	GrA-60018	37,250 +320 - 280	39.8	14.0	3.3	19.4	11.8	0.25	429	130	11.57	1,2,5
Q376-9	*Homo neanderthalensis*	Rib frag.	-	-	37.0	13.1	3.3	19.2	11.8	0.85	116	35	12.9	1,5
Q376-25	*Homo neanderthalensis*	Rib frag.	-	-	39.1	13.9	3.3	19.0	11.5	0.33	321	97	11.42	1,5
2878-2D	*Homo neanderthalensis*	Lower lt P4 (mandible 2878-8)	GrA-54028	32,190 +200, - 190	41.4	14.4	3.4	19.0	12.5					1,5
Site: Spy														
Spy 94a (Spy I)	*Homo neanderthalensis*	R M3, maxilla frag. attached	GrA-32623	35810 +260, - 240	43.7	15.2	3.4	19.4	11.4	0.16	728	217	3.60	1,3, 4
Spy 430a (Spy II)	*Homo neanderthalensis*	Right middle 3rd manual phalanx	GrA-32630	33940 +220, - 210	46.8	15.8	3.5	20.3	10.8					3, 4
Spy 92b (Spy II)		Incisor	GrA-32626	36,350 +310/- 280	47.1	16.7	3.3	19.8	10.9					3, 4

Spy 572a (Spy II)		Rt scapula	GrA-21546	31,810 +250/-250	41.5	14.4	3.4	19.8	11.0					3, 4
Spy II average					45.1	15.6	3.4	20.0	10.9					
Spy 646a (Neandertal child Spy IV)	*Homo neanderthalensis*	Right hemi-mandible	GrA-32627	32970 +200/-190	43.1	15.4	3.3	19.8	12.5	0.17	676	207	2.60	1, 7

References

1 = This study

2 = Wißing et al. 2015b

3 = Bocherens et al., 2013

4= Semal et al., 2013

5= Rougier et al., submitted

6= Rougier et al., in prep (AMH-Paper)

7= Crevecoeur et al., 2010

ID	Site	Species	Skeletal element	%Cc	%Nc	C/N	%Sc	C/Scoll	N/Scoll	δ^{34}S	δ^{13}C	δ^{15}N	^{14}C-Age	Reference date	Reference for stab. Isotopes
Goyet-A2-7	Goyet	*Panthera spelaea*	*phalanx*	41.3	15.3	3.1					-18.5	8.4			1
Goyet-A3-1	Goyet	*Panthera spelaea*	*astragalus*	44.7	15.5	3.4	0.19	626	185	-2.1	-18.7	8.4			1,5
Goyet-B5-1	Goyet	*Panthera spelaea*	*humerus R*	38.2	13.6	3.3	0.16	629	192	0.6	-18.7	7.3			1,5
Goyet-B5-2	Goyet	*Panthera spelaea*	*humerus R*	34.8	11.7	3.5					-20.7	9.6			1
Goyet-B5-4	Goyet	*Panthera spelaea*	*humerus R*	28.2	10.0	3.3					-19.5	6.3			1
Goyet-A1-6	Goyet	*Crocuta crocuta*	*2nd metacarpus*	41.4	15.2	3.2	0.17	649	204	1.4	-19.7	9.5			1,5
Goyet-A3-5	Goyet	*Crocuta crocuta*	*3rd metatarsus*	44.3	15.5	3.3	0.18	644	192	1.4	-19.2	9.1			1,5
Goyet-A3-6	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.2	15.5	3.2	0.19	612	189	4.5	-19.6	9.4			1,5
Goyet-A3-7	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.8	16.0	3.2	0.17	679	213	2.6	-19.6	9.8			1,5
Goyet-A3-8	Goyet	*Crocuta crocuta*	*3rd metatarsus*	43.5	15.8	3.2	0.17	696	216	4.3	-19.4	9.0			1,5
Goyet-B4-1	Goyet	*Crocuta crocuta*	*humerus*	41.9	15.0	3.3					-19.8	7.7			1
SC1800	Scladina	*Crocuta crocuta*	*phalanx I*	42.9	15.6	3.2	0.18	636	198	4.3	-20.2	8.8			2,5
SC1900	Scladina	*Crocuta crocuta*	*phalanx I*	42.6	15.6	3.2	0.16	710	223	1.1	-19.6	10.1			2,5
SC2000	Scladina	*Crocuta crocuta*	*phalanx I*	42.8	15.7	3.2	0.16	713	224	0.1	-19.7	8.2			2,5
SC2100	Scladina	*Crocuta crocuta*	*phalanx I*	42.9	15.6	3.2					-19.4	9.5			2
SC1700	Scladina	*Crocuta crocuta*	*mandible*	39.9	14.6	3.2					-19.8	9.6			2
SC2200	Scladina	*Crocuta crocuta*	*maxillary*	42.0	15.4	3.2					-19.3	9.4			2

IV2A 13534	Spy	*Crocuta crocuta*	*First molar*	42.0	14.2	3.4					-19.90	11.90	42750 +850/-650 (GrA-44547)	Semal 2013	4
Goyet-A3-3	Goyet	*Canis lupus*	*4th metatarsus*	43.5	15.6	3.3	0.18	644	198	1.7	-19.1	6.6			1,5
Goyet-A3-4	Goyet	*Canis lupus*	*4th metatarsus*	43.5	15.3	3.3	0.17	691	208	2.9	-18.8	7.2			1,5
SC30300	Scladina	*Canis lupus*	*Pisiform L*	42.5	14.4	3.4	0.16	709	206	11.8	-20.4	6.6			1,5
Goyet-A2-3	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.9	14.3	3.3					-22.1	4.5			1
Goyet-A2-4	Goyet	*Ursus spelaeus*	*3rd metacarpum*	44.3	15.3	3.4					-21.7	3.4			1
Goyet-A2-5	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.2	13.5	3.4					-21.6	3.1			1
Goyet-A2-6	Goyet	*Ursus spelaeus*	*3rd metacarpum*	38.7	13.3	3.4					-22.1	3.0			1
Goyet-A3-20	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.5	16.0	3.2	0.15	749	236	-5.0	-21.8	2.8			1,5
Goyet-A3-22	Goyet	*Ursus spelaeus*	*3rd metacarpum*	40.7	14.6	3.2	0.16	663	204	-6.6	-21.5	2.6			1,5
Goyet-A3-23	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.4	13.7	3.4	0.16	651	194	-1.5	-21.9	4.3			1,5
Goyet-A3-24	Goyet	*Ursus spelaeus*	*3rd metacarpum*	40.1	14.4	3.2	0.14	759	234	-1.7	-21.5	4.9			1,5
Goyet-A3-25	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	15.7	3.1					-21.4	3.1			1
Goyet-A3-26	Goyet	*Ursus spelaeus*	*3rd metacarpum*	38.8	13.4	3.4					-21.6	5.8			1
Goyet-A3-27	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.5	15.5	3.3					-21.5	4.6			1
Goyet-A3-28	Goyet	*Ursus spelaeus*	*3rd metacarpum*	36.8	13.4	3.2					-22.3	5.3			1
Goyet-B4-9	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	14.9	3.2					-21.3	3.5			1
Goyet-B4-10	Goyet	*Ursus spelaeus*	*3rd metacarpum*	37.9	13.7	3.2					-21.8	4.4			1
Goyet-B4-11	Goyet	*Ursus spelaeus*	*3rd metacarpum*	39.3	13.3	3.4					-20.9	4.4			1

Goyet-B4-12	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.7	15.8	3.2					-20.9	3.7	1
Goyet-B4-13	Goyet	*Ursus spelaeus*	*3rd metacarpum*	42.2	15.3	3.2					-21.0	4.8	1
Goyet-B4-14	Goyet	*Ursus spelaeus*	*3rd metacarpum*	42.0	14.9	3.3					-21.8	4.5	1
Goyet-B4-15	Goyet	*Ursus spelaeus*	*3rd metacarpum*	43.0	15.3	3.3					-21.0	4.6	1
Goyet-B4-16	Goyet	*Ursus spelaeus*	*3rd metacarpum*	36.4	14.5	2.9					-21.0	6.0	1
Goyet-B4-17	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.8	14.5	3.4					-20.8	3.9	1
Goyet-B4-32	Goyet	*Ursus spelaeus*	*radius*	40.7	14.8	3.2					-21.7	5.2	1
Goyet-B4-34	Goyet	*Ursus spelaeus*	*3rd metacarpum*	41.2	14.1	3.4	0.35	314	92		-22.0	2.7	1,5
SC3100	Scladina	*Ursus spelaeus*	*mandible*	40.9	14.8	3.2	0.15	727	226	0.1	-22.5	3.7	1,5
SC3200	Scladina	*Ursus spelaeus*	*mandible*	42.4	15.2	3.3					-22.1	5.7	1
SC3300	Scladina	*Ursus spelaeus*	*mandible*	43.3	15.8	3.2	0.16	709	222	-2.1	-22.2	6.0	1,5
SC3500	Scladina	*Ursus spelaeus*	*phalanx II*	44.0	16.0	3.2	0.16	731	228	3.4	-21.8	5.1	1,5
SC3600	Scladina	*Ursus spelaeus*	*phalanx II*	42.8	15.6	3.2	0.16	722	225	-17.0	-21.8	3.0	1,5
SC3700	Scladina	*Ursus spelaeus*	*phalanx II*	42.4	15.4	3.2	0.16	699	218	-5.4	-22.0	6.1	1,5
SC3800	Scladina	*Ursus spelaeus*	*phalanx II*	42.5	15.5	3.2	0.15	732	229	-4.2	-22.2	5.0	1,5
Goyet-A2-1	Goyet	*Mammuthus primigenius*	*long bone*	41.0	15.0	3.2	0.13	846	265	-2.6	-20.7	8.1	1,5
Goyet-A3-9	Goyet	*Mammuthus primigenius*	*long bone*	43.9	15.6	3.3	0.16	732	223	4.1	-21.5	7.0	15
Goyet-B4-2	Goyet	*Mammuthus primigenius*	*skull*	41.0	14.6	3.3	0.15	730	223	8.4	-21.6	6.7	1,5
SC600	Scladina	*Mammuthus primigenius*	*tooth fragment*	42.6	15.5	3.2	0.14	830	259	6.0	-20.9	8.4	2,5

SC700	Scladina	*Mammuthus primigenius*	*tooth fragment*	41.5	15.2	3.2	0.13	828	260	6.6	-21.5	9.4			2,5
SC800	Scladina	*Mammuthus primigenius*	*tooth fragment*	41.3	15.1	3.2	0.14	796	249	4.5	-21.6	8.3			2,5
Spy D3 19B 121 1474	Spy	*Mammuthus primigenius*	*Milk molar*	35.1	12.50	3.3					-21.1	11.6	42330 +550/-450 (GrA-32616)	Semal et al. 2009	3
IV2A 13549	Spy	*Mammuthus primigenius*	*Plate of molar*	37.7	13.8	3.2					-21.3	8.1	42950 +800/-650 (GrA-44548)	Semal et al. 2013	4
Goyet-A2-2	Goyet	*Coelodonta antiquitatis*	*unciforme*	43.8	16.2	3.2					-20.0	4.3			1
Goyet-A3-2	Goyet	*Coelodonta antiquitatis*	*scaphoide*	43.8	15.2	3.4	0.18	647	193	-0.1	-20.4	5.7			1,5
Goyet-B4-3	Goyet	*Coelodonta antiquitatis*	*1st metacarpum*	40.0	14.6	3.2					-20.8	5.9			1
SC30100	Scladina	*Coelodonta antiquitatis*	*metatarsal II R*	44.4	15.7	3.3					-21.1	5.5			1
SC900	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.6	15.5	3.2	0.13	874	273	6.9	-20.9	5.5			2,5
SC1000	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.1	15.4	3.2	0.13	872	274	1.9	-20.3	6.9			2,5
SC1100	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	42.2	15.2	3.2	0.14	822	254	4.6	-20.0	6.4			2,5
SC1200	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	41.2	15.0	3.2	0.14	806	251	2.5	-21.1	5.3			2,5
SC1300	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	41.8	15.2	3.2	0.12	900	281		-20.4	7.5			2,5
SC1400	Scladina	*Cœlodonta antiquitatis*	*lower P2 (R)*	43.1	15.7	3.2					-20.6	5.5			2
Spy 13637 Ulg	Spy	*Cœlodonta antiquitatis*	*Lower P3 or P4*	43.3	14.2	3.6					-20.8	6.8	25670 +130/-120 (GrA-37936)		4
Spy D2 Pal Plateau 4	Spy	*Cœlodonta antiquitatis*	*Milk molar*	40.4	14.4	3.3					-20.1	7.2	44350 +650/-500 (GrA-32613)	Semal et al. 2013	3
Goyet-A3-10	Goyet	*Equus ferus*	*ectocuneiform*	44.9	15.9	3.3	0.15	822	249	0.6	-21.0	5.1			1,5
Goyet-A3-11	Goyet	*Equus ferus*	*ectocuneiform*	41.9	15.4	3.2	0.14	800	252	1.0	-20.7	6.4			1,5
Goyet-A3-12	Goyet	*Equus ferus*	*ectocuneiform*	43.9	15.4	3.3	0.16	746	224	-0.7	-20.8	5.9			1,5
Goyet-B4-4	Goyet	*Equus ferus*	*tibia*	41.0	14.8	3.2					-20.5	6.6			1

SC28400	Scladina	*Equus ferus*	*upper P2 (L)*	33.6	12.9	3					-21.1	6.5			1
SC3900	Scladina	*Equus ferus*	*upper tooth (R)*	42.5	15.6	3.2	0.14	790	248	5.7	-21.7	5.2			2,5
SC4100	Scladina	*Equus ferus*	*upper tooth (R)*	42.6	15.8	3.1	0.13	908	289		-21.7	5.1			2,5
SC4200	Scladina	*Equus ferus*	*upper tooth (R)*	42.8	15.8	3.2	0.13	874	276	2.0	-21.9	5.0			2,5
SC4300	Scladina	*Equus ferus*	*upper tooth (R)*	39.9	14.5	3.2	0.14	781	244	6.2	-21.5	4.8			2,5
SC4400	Scladina	*Equus ferus*	*upper tooth (R)*	40.9	15.0	3.2	0.12	910	286		-21.6	7.0			2,5
IV2E 4207	Spy	*Equus ferus*	*Premolar / Molar*	35.6	14.2	2.9	0.15	633	216	5.5	-20.5	4.5	32810 +250/-230 (GrA-44576)	Semal et al. 2013	4,5
Goyet-B4-6	Goyet	*Bos primigenius*	*centrotarsus*	38.7	14.1	3.2					-20.0	3.8			1
Goyet-A3-13	Goyet	*Bison priscus*	*tibia*	40.9	14.6	3.3	0.16	687	209	-2.8	-20.0	4.1			1,5
Goyet-A3-14	Goyet	*Bison priscus*	*tibia*	41.4	14.6	3.3	0.15	725	219	4.9	-20.4	4.8			1,5
Goyet-B4-5	Goyet	*Bison priscus*	*centrotarsus*	40.9	14.7	3.2					-20.0	5.7			1
Goyet-B4-7	Goyet	*Bison priscus*	*centrotarsus*	38.8	14.1	3.2					-20.4	3.9			1
SC29000	Scladina	*Bison priscus*	*lower M3 (R)*	32.6	11.5	3.3					-20.8	4.4			1
SC29100	Scladina	*Bison priscus*	*lower P4 (L)*	32.1	12.8	2.9					-19.8	5.6			1
SC4500	Scladina	*Bos or Bison*	*lower P (R)*	41.7	15.2	3.2	0.15	764	239	4.1	-20.5	4.8			2,5
SC4700	Scladina	*Bos or Bison*	*lower P3 (R)*	42.7	15.7	3.2	0.14	806	254	8.4	-20.5	4.3			2,5
SC4800	Scladina	*Bos or Bison*	*lower M1(R)*	41.2	15.3	3.1					-19.9	5.3			2
SC4900	Scladina	*Bos or Bison*	*lower P3 (R)*	40.8	15.0	3.2	0.15	725	229	4.5	-20.7	4.4			2,5
SC28800	Scladina	*Bos primigenius*	*lower M3 (L)*	33.9	12.7	3.1					-20.7	4.9			1
SC28900	Scladina	*Bos primigenius*	*lower P4 (L)*	35.0	13.6	3.0					-20.3	4.5			1
Goyet-A3-15	Goyet	*Rangifer tarandus*	*astragalus*	42.3	15.5	3.2	0.17	667	209	7.2	-18.5	2.6			1,5

Goyet-A3-16	Goyet	*Rangifer tarandus*	*astragalus*	43.0	15.1	3.3	0.18	620	187	6.2	-18.5	3.3			1,5
Goyet-A3-17	Goyet	*Rangifer tarandus*	*astragalus*	43.4	15.3	3.3	0.14	803	242	5.1	-18.6	3.4			1,5
Goyet-A3-18	Goyet	*Rangifer tarandus*	*astragalus*	43.9	15.4	3.3	0.15	773	232	6.8	-18.3	3.1			1,5
Goyet-A3-19	Goyet	*Rangifer tarandus*	*astragalus*	44.1	15.2	3.4	0.15	787	232	-7.2	-19.6	4.5			1,5
Goyet-B4-8	Goyet	*Rangifer tarandus*	*centrotarsus*	41.1	14.9	3.2					-18.6	3.9			1
Spy 10640 Ulg	Spy	*Rangifer tarandus*	*First Phalanx*	43.4	14.4	3.5					-19.8	4.9	29040 +180/-160 (GrA-37934)	Semal et al. 2009	4
Spy 13071 Ulg	Spy	*Rangifer tarandus*	*Metacarpal*	35.6	14.1	2.9					-18.4	1.6	36920 +400/-350 (GrA-44546)	Semal et al. 2013	4
Spy D4 19B 121 1480	Spy	*Rangifer tarandus*	*Metacarpal*	39.3	17.4	2.60	0.14	735	279						5
SC29700	Scladina	*Rangifer tarandus*	*tooth*	37.5	12.4	3.5	0.2	625	178	8.3	-17.9	3.5			5
Sc 22400	Scladina	*Rangifer tarandus*	*P2-P4*	35.6	12.9	3.2	0.13	746	232	7.49	-18.7	3.1			5
Sc 22700	Scladina	*Rangifer tarandus*	*M2 inf*	38.8	14.2	3.2	0.14	761	239	8.49	-18.5	5.0			5
Sc 22800	Scladina	*Rangifer tarandus*	*M1 inf*	39.6	14.5	3.2	0.15	706	221	10.52	-17.6	3.6			5
Sc 22900	Scladina	*Rangifer tarandus*	*P4 sup*	39.7	14.6	3.2	0.15	696	219	6.48	-17.8	4.8			5
Sc 23000	Scladina	*Rangifer tarandus*	*M2 sup*	40.9	14.9	3.2	0.14	784	245	13.13	-16.7	7.2			5

1= Bocherens et al., 2011a

2=Bocherens et al., 1997

3= Bocherens et al., 2013

4= Wißing et al., 2015b

5= this study