Reframing the mammoth steppe: Insights from analysis of isotopic niches

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Highlights

1. Herbivores across the mammoth steppe had broadly homogenous isotopic niches.
2. Some species shifted their niche in response to environmental conditions.
3. Overlap between species' isotopic niches suggests functional redundancy.
4. Functional redundancy made the mammoth steppe a highly resilient ecosystem.

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Abstract

Woolly mammoth (*Mammuthus primigenius*), horse (*Equus* spp.) and bison (*Bison* spp.) coexisted with a variety of mammalian megafauna across the Pleistocene mammoth steppe – a megacontinental ecosystem that spanned northern Eurasia and northwestern North America. Previous research has suggested that highly conserved niches with minimal niche overlap allowed high levels of species diversity on the mammoth steppe. Here we evaluate previously published and some new collagen carbon and nitrogen isotope data (δ^{13}C, δ^{15}N) for mammoth steppe megaherbivores using Stable Isotope Bayesian Ellipses in R (SIBER) and linear regression models to determine isotopic niches for individual species during broad time intervals (pre-, during and post-Last Glacial Maximum (LGM)) at multiple geographic regions across the mammoth steppe. Individual species maintained relatively consistent isotopic niche positions at different geographic locations and during different times. Diet and habitat niches for any given species appear to have been similar across the mammoth steppe. Between some regions and times, however, species' isotopic niches changed, suggesting adaptation to local climatic conditions and/or changes in the nitrogen isotope patterns at the base of the food web. Isotopic niche overlap, including at the level of core niche overlap (>60 % overlap), was observed in at

least one time and region for most species. This overlap suggests high levels of functional redundancy in the ecosystem, whereby one species could fulfil another's ecological role in the latter's absence. Despite spatial and temporal environmental variation, species' adaptability and functional redundancy within the ecosystem would have made the mammoth steppe a highly resilient ecosystem.

1. Introduction

1.1. The Pleistocene mammoth steppe

1.1.1. Ecological characteristics

The mammoth steppe was the largest continuous ecosystem on Earth during the Pleistocene. It formed around 460 kyr BP (Kahlke, 2014; Kahlke and Lacombat, 2008) and extended from northwestern Canada (Yukon), Alaska and northern Asia to western Europe (Bocherens, 2003; Guthrie, 1982, 1984, 1990). This ecosystem was characterized by megaherbivores such as woolly mammoth (*Mammuthus primigenius*), horse (*Equus* spp.) and bison (*Bison* spp.) (Guthrie, 1968; Mann et al., 2013; Markova et al., 2015; Mol et al., 2006; Zimov et al., 2012) and herb-steppe-tundra flora (Bocherens, 2003; Guthrie, 1982, 1990, 2001). This diversity and association of megafaunal and floral elements do not occur in modern high-latitude ecosystems (Guthrie, 1982, 1990, 2001). Some researchers consider the mammoth steppe to have had animal and plant productivity similar to the modern African savannah (Zimov et al., 2012). Whether the mammoth steppe was unique to cold intervals of the Pleistocene and the mammoth steppe fauna were constrained to refugia during interglacials, at which times species such as the mastodon emigrated to the region (Zazula et al., 2014), is unknown. Likewise, it is unknown if the basic character of the mammoth steppe persisted through time with increases in floral and faunal diversity during interglacials as the boundaries of the mammoth steppe moved (Kahlke, 2014; Kahlke and Lacombat, 2008). Understanding how this ecosystem persisted through climatic changes is vital to reconstructing Pleistocene ecology, and to assessing risk factors for modern ecosystems facing significant changes from climate and anthropogenic activities (Barnosky et al., 2017; Dietl et al., 2015). To make this evaluation, we used tools from modern ecological studies to assess the adaptability of individual species from the mammoth steppe and the resilience of the ecosystem as a whole.

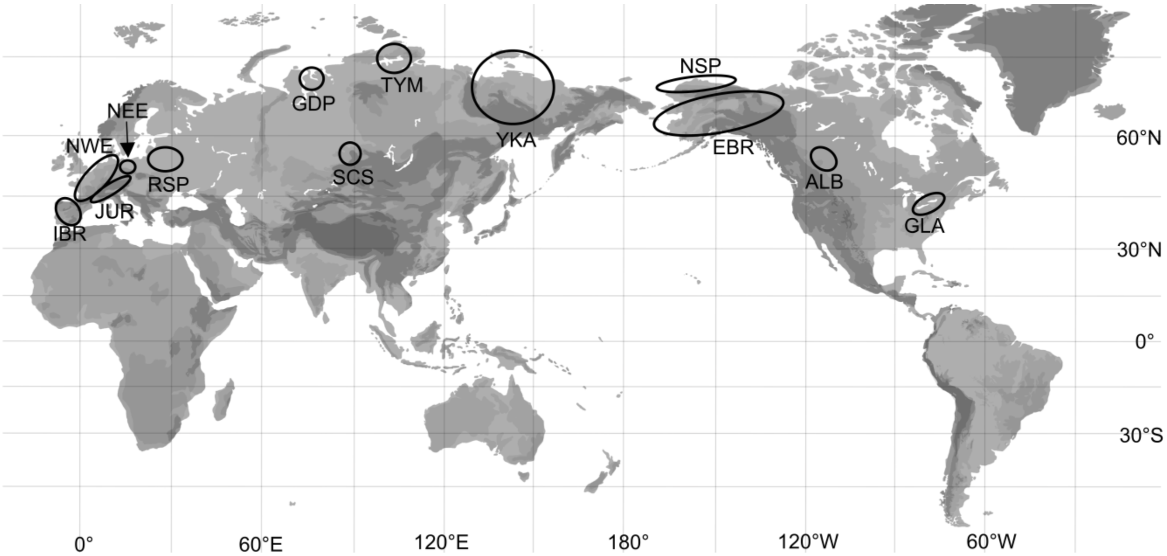

Figure 1. Regions examined in this study. Darker shades represent higher elevations. From left to right, regions are: Iberian Peninsula (IBR), Jura mountains (JUR), northwestern Europe (NWE), northeastern Europe (NEE), Russian plain (RSP), Gydan Peninsula (GDP), south central Siberia (SCS), Taymyr Peninsula (TYM), Yakutia (YKA), eastern Beringia (EBR), North Slope Alaska (NSP), Alberta (ALB) and Great Lakes Area (GLA).

Pollen, plant macrofossil and ancient DNA studies suggest that the mammoth steppe was a highly productive herb-steppe-tundra environment, dominated by grasses, sedges, forbs and herbaceous species, with some shrubs such as willow also present. There is little evidence for trees during stadials; however the region contained forests during interstadial and interglacial times (Binney et al., 2017; Blinnikov et al., 2011; Burns, 1991; Goetcheus and Birks, 2001; Guthrie, 1990, 1982; Castaños et al., 2014; Huntley et al., 2013; Mandryk, 1996; Muhs et al., 2001; Schweger et al., 2011; Strong and Hills, 2005; Willerslev et al., 2014; Zazula et al., 2011; Zimov et al., 2012). Plant species were unevenly distributed across the mammoth steppe due to local effects such as topography, drainage and latitude, and thus formed a "vegetational mosaic" (Guthrie, 1982). Nonetheless, similar vegetation characteristics were present at broad scales at different mammoth steppe sites, particularly prior to the Last Glacial Maximum (pre-LGM; Willerslev et al., 2014), and during the LGM (Binney et al., 2017). Megafauna may have encouraged rapid plant growth by fertilizing with feces and urine, and trampling and grazing, all of which can promote faster-growing flora (Blinnikov et al., 2011; Guthrie, 1982; Willerslev et al., 2014; Zimov et al., 2012).

Several other areas may have contained similar floral and faunal elements as the originally defined mammoth steppe during parts of the Pleistocene (Guthrie, 1982). Alberta is not traditionally considered part of the ecosystem but has been reconstructed to have been cold and arid, with herb-steppe-tundra flora during the periods where it was not glaciated. Alberta also contained similar fauna, including the woolly mammoth, as traditionally defined mammoth steppe regions (Burns, 1991, 2010; Burns and Young, 1994; Heintzman et al., 2016; Jass et al., 2011; Jass and Barrón-Ortiz, 2017; Kahlke, 2015; Mandryk, 1996). Further, the southernmost woolly mammoth remains in Europe occurred on the Iberian peninsula where mammoths lived during periods of dry, steppe conditions and in association with other mammoth steppe herbivores (Álvarez-Lao and García, 2011; García-Alix et al., 2012; Kahlke, 2015). Such areas are consistent with current definitions of the mammoth steppe during those times. Thousands of kilometers southeast of the mammoth steppe, reaching through Ontario and Quebec to the periglacial environment on the edge of the Laurentide Ice Sheet (LIS), there are also sites where post-LGM Pleistocene woolly mammoth, horse and bison remains have been found (Harington, 2003; Kahlke, 2015). These remains occur in areas previously determined to be mesic, forested landscapes, though the mammoths may have selected for more steppe-like environments within this habitat and/or inhabited the area during the initial stages of deglaciation, before forests were established (Metcalfe et al., 2013; Metcalfe and Longstaffe, 2014; Saunders et al., 2010). Unequivocal mammoth remains have not been found from earlier in the Pleistocene in the Great Lakes area (Harington, 1990). The boundaries of mammoth skeletal remains, linked to time periods during the Pleistocene, were mapped by Kahlke (2015). Here, we consider Alberta, Great Lakes and Iberian Peninsula populations populations within the context of the other regions examined, while acknowledging this difference in floral elements at times. As well, we rely on pre-existing woolly mammoth identification based on paleontological evidence, while acknowledging that interbreeding occurred between Columbian and woolly mammoths (Enk et al., 2011).

The majority of mammoth steppe species (e.g., mammoth, horse, bison, muskox (*Ovibos* sp.), caribou (*Rangifer tarandus*), saiga antelope (*Saiga tatarica*)), were able to cross the Bering Land Bridge between Eurasia and North America during stadials, when reduced sea levels created a terrestrial connection between Eurasia and North America (Bocherens, 2015; Guthrie, 1968, 2001; Mann et al., 2013; Mol et al., 2006; Shapiro et al., 2004; Zimov et al., 2012). Not all megafauna, however, were represented at all locations or all times across the mammoth steppe. The woolly rhinoceros (*Coelodonta antiquitatis*) and cave bear (*Ursus spelaeus, Ursus ingressus* and *U. kudarensis*) were significant species in Eurasia but have not been found in North America (Kahlke, 2014; Knapp, 2019; Stuart and Lister, 2011). Elk (*Cervus elaphus*) was present in

Europe throughout the Pleistocene but did not migrate to North America until ~13,000 ^{14}C years BP, likely responding to warmer and wetter conditions in post-LGM North America (Guthrie, 2006; Meiri et al., 2014). Fossils of American mastodon (*Mammut americanum*), for which no finite radiocarbon dates were measured in eastern Beringia (Zazula et al., 2014), are common in North America but they are not found in Eurasia (Guthrie, 2001). This likely reflects submergence of the Bering Land Bridge during interglacial periods when mastodon was likely present in the Arctic (Zazula et al., 2014). Vegetation differences are also observed over the late Pleistocene, with woodlands becoming more prevalent in parts of the mammoth steppe during warmer periods (Binney et al., 2017; Castaños et al., 2014; Schweger et al., 2011). A change from herb-steppe-tundra to bogs, wetlands and forests occurred post-LGM, as the climate shifted to warmer and wetter conditions. Fewer floral species were present at each site and there was less similarity of plant species among sites in post-LGM than during the pre-LGM (Barnosky et al., 2004; Binney et al., 2017; Edwards et al., 2001; Guthrie, 1982, 2001, 2006; Willerslev et al., 2014).

Multiple species extinctions occurred during the Pleistocene. For example, the cave bear has not been documented in post-LGM northwestern Europe, and likely went extinct at the beginning of the LGM (Baca et al., 2016; Knapp, 2019; Mackiewicz et al., 2017; Münzel et al., 2011; Terlato et al., 2018). A combination of human activity with increased climatic stressors was implicated in its extinction (Fortes et al., 2016; Knapp, 2019; Mackiewicz et al., 2017; Terlato et al., 2018). Despite extinctions and extirpations leading to a reduction in species richness in Europe during the LGM, species richness partially recovered post-LGM (Puzachenko and Markova, 2019). The majority of the extinction and extirpation events occurred during the terminal Pleistocene. In

North America alone, 35 genera of animals were extirpated, and 29 of those went extinct globally (Faith and Surovell, 2009), including the majority of the megaherbivore and megacarnivore species on the mammoth steppe. The exact timings of the extinctions are not resolved for all species (Broughton and Weitzel, 2018; Faith and Surovell, 2009; Guthrie, 2006; Gill et al., 2009). It is widely considered that human hunting, climate change or a combination of these factors led to the megafauna extinctions, though an extraterrestial impact has also been posited (Barnosky et al., 2004; Broughton and Weitzel, 2018; Cooper et al., 2015; Koch and Barnosky, 2006).

The extent that human hunting versus climate change was responsible for the megafauna extinctions may have varied between regions and between species (Barnosky et al., 2004; Broughton and Weitzel, 2018; Cooper et al., 2015; Koch and Barnosky, 2006). In North America, high species richness of mammoth steppe fauna may have made that ecosystem particularly vulnerable to disruption by human hunting (Pires et al., 2015). As well, many extinctions were considered to be approximately synchronous with Clovis habitation in North America (Faith and Surovell, 2009; Guthrie, 2006), though there is mounting evidence for pre-Clovis occupation of the Americas (e.g., Bourgeon et al., 2017; Halligan et al., 2016; Waters et al., 2011). The population reductions and environmental stress experienced by multiple species of North American megafauna, however, indicate that they may have already been in decline prior to arrival of clearly established populations of humans in North America (Faith, 2011; Guthrie, 2003; Shapiro et al., 2004; Zazula et al., 2014, 2017).

In Eurasia, *Homo sapiens sapiens* and their predecessors coexisted with Pleistocene megafaunal species for ~2 million years (Barnosky et al., 2004; Koch and Barnosky, 2006), and humans may have prefered habitats with warm-adapted species rather than the cold-adapted species that characterize the mammoth steppe (Carotenuto et al., 2018). As well, extinctions and extirpations were staggered over millennia among species (Stuart and Lister, 2011). Expanding forests and increased precipitation causing deeper snow cover during the terminal Pleistocene would have put increased stress on mammoth steppe grazers. Climate, rather than human hunting, is therefore generally considered the likely driving factor of the Eurasian Pleistocene extinctions (Barnosky et al., 2004; Carotenuto et al., 2018; Řičánková et al., 2018). Alternatively, a wave of human migration post-LGM may have triggered a set of European extinctions (Haynes, 2018).

1.1.2. Niche separation and functional redundancy

Niche separation, or *resource partioning*, is commonly used to explain species richness of the mammoth steppe, whereby diversity is maintained through lack of competition between species for resources (Graham and Lundelius, 1984; Guthrie, 1982, 1984). Dietary niche differences could have resulted from partitioning of habitats or forage (Guthrie, 1982), though the exact mechanisms of niche separation are not fully understood, and may have varied regionally (Bocherens, 2003; García-Vázquez et al., 2018; Guthrie, 2001). The niche feeding hypothesis was supported by an early isotopic metastudy of mammoth steppe herbivores (Bocherens, 2003) and is now commonly accepted in mammoth steppe literature. The same concept is explored in African ecological literature, for example, to explain how grazers of similar sizes coexist (Bonyongo and Harris, 2007; Codron et al., 2008; Cromsigt and Olff, 2006; Kartzinel et al., 2015; Kleynhans et al., 2011).

The concept of *functional redundancy* is commonly used in conservation ecology to assess the potential responses of ecosystem to the loss of specific species (Cadotte et al., 2011; Mori et al., 2013; Naeem, 2008; Sundstrom et al., 2012). Extinction of a keystone species with no functional redundancy would destabilize the entire ecosystem. In some cases, however, species are lost whose niche can be filled by other species. For example, during a temperature-induced perturbation of a coral reef, large herbivores compensated for the loss of small herbivores (Nash et al., 2016). Different tree species went extinct in Europe and in North America as a result of Pleistocene and Holocene climate change. However, gymnosperms retained similar levels of functional diversity on the two continents, indicating that species loss does not necessarily lead to loss of ecosystem functioning (Liebergesell et al., 2016).

The concepts of *niche separation* and *functional redundancy* can be considered opposed to each other (e.g., Resetarits and Chalcraft, 2007), as species with distinct diets cannot replace each other's niche. However, they can be complementary ideas (Sundstrom et al., 2012; Wardwell et al., 2008). Species may overlap in some response variables while remaining distinct in others (e.g., as this study principally considers dietary niche, overlap of some dietary items but not all). There have been several studies of competitive exclusion in the African savannah, the ecosystem most commonly compared to the mammoth steppe. African herbivores feed from a range of overlapping plant species and plant parts, although no two species utilize identical niches (Arsenault and Owen-Smith, 2008; Hansen et al., 1985; Kartzinel et al., 2015; Prins et al., 2006). African savannah herbivores exhibit lower dietary and niche separation during seasons of high plant productivity and greater niche separation during the low productivity dry season (Bukombe et al., 2017; Kleynhans et al., 2011; Prins et al., 2006). Experimental removal studies of herbivores in the African savannah did not observe complete functional redundancy between species, but there was functional redundancy for some response variables, such as vegetation height (Goheen et al., 2013; Pringle et al., 2014; van der Plas et al., 2016).

A large number of new isotopic studies have been published since 2003, when the concept of isotopic niche separation on the mammoth steppe was first examined by Bocherens (Bocherens, 2003; further data sets include e.g., Bocherens et al., 2011a, b, 2014a, b; Fox-Dobbs et al., 2008; Iacumin et al., 2010; Mann et al., 2013; Metcalfe et al., 2013, 2016; Raghavan et al., 2014; Stevens et al., 2009; Szpak et al., 2010). Here, we add new measurements from eastern Beringia and Alberta, Canada that augment the already vastly enlarged data set published over the past sixteen years. As well, recent mathematical approaches have allowed us to make more sophisticated assessments of isotopic niche (Jackson et al., 2011; Layman et al., 2007).

We use stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope compositions of bone, tooth and tusk collagen of megaherbivores to investigate the ecology of the mammoth steppe faunal community and mechanisms of herbivore coexistence. Archeological and paleontological studies use isotopic niche as a proxy for investigating diet and habitat (e.g., Lanoë et al., 2017; Szpak et al., 2014), two key components of a species' ecological niche. Isotopic niche is typically assessed by combining the carbon and nitrogen isotope compositions of a preserved tissue from a species (typically collagen) to determine the area of isotopic space bounded by these parameters (Jackson et al., 2011; Layman et al., 2007). This approach allowed us to reconstruct typical ecological niches during the late Pleistocene, as well as to assess variation between the pre-LGM, LGM and post-LGM prior to the extinctions. This allowed us to test if strict niche-feeding, functional redundancy, and/or a mixture of the two mechanisms are consistent with the isotopic data.

Knowing the extent of niche feeding on the mammoth steppe is critical to understanding the resilience of the mammoth steppe – to what extent the mammoth steppe floral and faunal species could persist in the face of anthropological and climatic changes. If mammoth steppe species were habitat or forage specialists with narrow niches, each species would have been at greater risk of extinction if those habitats or plant species were lost during climatic change (Slatyer et al., 2013). The entire ecosystem would also have been less resilient to the loss of any species (e.g., from human hunting) because of reduced functional redundancy (Malhi et al., 2016; Peterson et al., 1998; Pires et al., 2015; Rosenfeld, 2002; Wellnitz and Poff, 2001). In the absence of perturbations, however, an ecosystem with highly defined niches would have promoted more efficient use of resources, and thus increased ecosystem function (Mason et al., 2005).

Underlying the comparison of isotopic niches in our study is an unavoidable need to 'lump together' both regions (Fig. 1; Iberian Peninsula (IBR), Jura mountains (JUR), northwestern Europe (NWE), northeastern Europe (NEE), Russian plain (RSP), Gydan Peninsula (GDP), south central Siberia (SCS), Taymyr Peninsula (TYM), Yakutia (YKA), eastern Beringia (EBR), North Slope Alaska (NSP), Alberta (ALB) and Great Lakes Area (GLA)) and time bins (non-finite (INF); pre-LGM; LGM; post-LGM) because of low sample sizes. Previous studies of the mammoth steppe have used similar groupings, but there are no consistent methods for defining geographic or temporal units. Spatially, study areas have been as small as a single cave (e.g., Fizet et al., 1995), or as large as the entire mammoth steppe (e.g., Bocherens, 2003). Between the two extremes, other studies analyzed isotopic niche at varying geographic scales on the basis of different barriers, such as between continents or mountains (Bocherens et al., 2011a; Drucker et al., 2003b; Rabanus-Wallace et al., 2017; Raghavan et al., 2014; Richards and Hedges, 2003; Stevens et al., 2014). When considering what localities and areas should be grouped, we recognize that megafauna would have been able to travel between large areas and may have been migratory in some cases (e.g., Mann et al., 2015). In our study, we grouped species over large geographic regions to compare differences in isotopic niche between populations that we expected to have experienced substantial climatic differences (e.g., Alberta, eastern Beringia and the North Slope of Alaska; see Fig. 1).

There was a substantial climatic shift between the pre-LGM and post-LGM (i.e. the LGM) that was accompanied by substantial floral and faunal changes (Binney et al., 2017; Fox-Dobbs et al., 2008; Jass et al., 2011; Willerslev et al., 2014). A significant portion of previous work has used the LGM as the major defining temporal unit within the late Pleistocene (e.g., Bocherens et al., 2011a; Fox-Dobbs et al., 2008; García-Vázquez et al., 2018; Willerslev et al., 2014; Yeakel et al., 2013). Here, we use the boundaries suggested by Hughes and Gibbard (2015) for the global LGM of 27,540 to 23,340 cal BP, defining time prior to that as pre-LGM and after as post-LGM. We used a time boundary of 45,000 ^{14}C BP (van der Plicht and Palstra, 2016) for the pre-LGM and defined as non-finite (INF) older ages in which climate conditions cannot be assessed. The exact timing of the LGM varied between ice sheets (e.g., Monegato et al., 2017), leading to some uncertainty in this approach. While we can assess broad-scale patterns between species, regions and time bins despite this uncertainty in timing, analysis of isotopic niche overlap requires consistent conditions at the base of the food web. Therefore, where sample sizes permitted, we additionally examined niche overlap using the INTIMATE event stratigraphy of the Greenland ice-core records to define the time bins (Rasmussen et al., 2014). A similar dual temporal approach – combining broad scale and more narrowly defined temporal windows – has been applied previously (Jürgensen et al., 2017). More detailed geographic and temporal information is provided in the dataset, as well as some data for Holocene fauna (Supplementary Table 1).

1.2. Stable isotopes

1.2.1 Stable carbon and nitrogen isotopes in plants and collagen

Three categories of plants have distinct mechanisms of carbon fixation, and thus distinct δ^{13}C: C_3 ($\bar{x} = -27$ ‰), C_4 ($\bar{x} = -13$ ‰), and CAM (~ –27 to –11 ‰; modern averages from Koch, 2007; Marshall et al., 2007; O'Leary, 1988). The high latitude environments considered here are dominated by C_3 plants, and as yet, no Pleistocene C_4 vegetation has been reported from these sites (Blinnikov et al., 2011). Hence, this paper focuses on the isotopic compositions of C_3 plants.

The δ^{13}C of a plant depends on the δ^{13}C of atmospheric CO_2, the mechanism of CO_2 uptake, and the plant's access to water and water-use efficiency (Farquhar, 1989; Marshall et al., 2007). In modern tundra environments, plants have a general pattern of δ^{13}C: shrub < herb < fungi < lichen (Fig. 2a; Barnett, 1994; Ben-David et al., 2001; Drucker et al., 2010; Kristensen et al., 2011; Munizzi, 2017), and this pattern appears to hold in non-tundra environments, including steppes (Chen et al., 2005; Kohn, 2010; Song et al., 2008; Toft et al., 1989). Herbs include forbs and sedges, and annual and perennial grasses (Tahmasebi et al., 2017). Any changes in the δ^{13}C of atmospheric CO_2 over time should affect all plants equally, and thus not change the general pattern. The ranges overlap considerably among species (Barnett, 1994), and one study found no difference in average $\delta^{13}C$ between herbs and shrubs (Tahmasebi et al., 2017), likely because environmental differences between habitats and/or microhabitats of plants had a greater effect on $\delta^{13}C$ than plant type in that study. Plant parts may also have distinct $\delta^{13}C$ (Heaton, 1999), though consistent variation was not observed in high latitude plants (Tahmasebi et al., 2017), and variation within tundra plant parts was less than variation between species (Munizzi, 2017).

Plants in more arid environments have higher $\delta^{13}C$ than those in more mesic environments (Diefendorf et al., 2010; Ehleringer et al., 1987; Ehleringer and Cooper, 1988; Farquhar, 1989; Kohn, 2010; Tieszen, 1991; Wooller et al., 2007). Higher elevation, higher mean annual temperature and lower latitudes also correlate with higher plant $\delta^{13}C$ (Kohn, 2010). Temperature and altitude effects are disputed (Heaton, 1999; Kohn, 2011; Stevens et al., 2006) but several studies have found a positive relationship between C_3 plant $\delta^{13}C$ and temperature (Lipp et al., 1991; Schleser et al., 1999; Wang et al., 2013). Plants growing beneath a dense canopy cover typically have lower $\delta^{13}C$ than plants growing in an open environment, likely because of recycling of organic matter and/or lower light levels affecting leaf processes in forested environments (Bonafini et al., 2013; Drucker et al., 2008). Some researchers have suggested that plants had higher $\delta^{13}C$ during periods of lower atmospheric pCO_2, and vice versa (Schubert and Jahren, 2015), but this has not been consistently observed (Bocherens, 2003; Richards and Hedges, 2003; Stevens and Hedges, 2004). Saline conditions, such as in coastal environments, can lead to an increase in plant $\delta^{13}C$ (Sykes et al., 2011; Wooller et al., 2007), as can higher levels of nutrients such as nitrogen or phosphorus (Heaton, 1999; Tieszen, 1991; Toft et al., 1989).

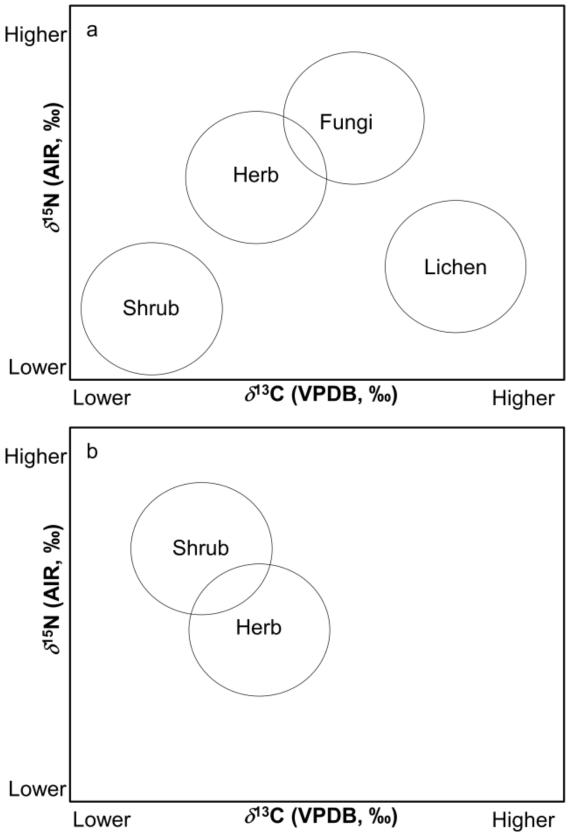

Figure 2. Conceptual diagram illustrating the relative carbon and nitrogen isotope compositions of (a) common modern tundra vegetation (Barnett, 1994; Ben-David et al., 2001; Drucker et al., 2010; Finstad and Kielland, 2011; Karlsson et al., 2000; Kristensen et al., 2011; Munizzi, 2017; Nadelhoffer et al., 1996), and (b) modern steppe vegetation (Chen et al., 2005; Song et al., 2008; Wu and Huang, 2010; Zhou et al., 2016). The δ^{15}N and δ^{13}C of fungi and lichens were not measured in steppes. Values of δ^{15}N are measured relative to the international standard AIR, and δ^{13}C is measured relative to the international standard VPDB.

The $\delta^{15}N$ of an ecosystem is related in part to the degree of nitrogen cycling, and thus the quantity of nitrogen loss. More arid ecosystems tend to exhibit greater nitrogen cycling and greater loss of nitrogen, predominately as ^{14}N. As a result, plants and soils in arid ecosystems typically have higher $\delta^{15}N$ than cooler, more mesic ecosystems (Ambrose, 1991; Amundson et al., 2003; Heaton, 1987; Stevens et al., 2008; Stevens and Hedges, 2004). Ecosystems affected by significant quantities of sea spray can also show an increase in $\delta^{15}N$ (Sykes et al., 2011). Other effects can also play an ecosystem-level role, for example, the increase in plant $\delta^{15}N$ associated with fertilization by dung (Szpak et al., 2012).

Plants take up nitrogen in several forms (e.g., amino acids, nitrate, ammonium) (Amundson et al., 2003; Craine et al., 2009, 2015a; Hobbie and Högberg, 2012; Nadelhoffer et al., 1996), from varying soil depths, and with or without mycorrhizal associations (Barnett, 1994; Craine et al., 2015a; Handley and Raven, 1992; Hobbie and Högberg, 2012; Nadelhoffer et al., 1996). Patterns of $\delta^{15}N$ between plant type are variable among environments (Craine et al., 2015a; Hobbie and Högberg, 2012). In high latitude tundra, however, nitrogen availability to plants is usually limited, and the following general pattern of nitrogen isotope compositions among species is reported in numerous modern tundra studies: shrub < lichen < herb < fungi (Fig. 2a; Ben-David et al., 2001; Drucker et al., 2010; Finstad and Kielland, 2011; Karlsson et al., 2000; Kristensen et al., 2011; Munizzi, 2017; Nadelhoffer et al., 1996). Overlap is common between plant types (Barnett, 1994; Munizzi, 2017). Values of $\delta^{15}N$ vary seasonally, with shrubs and graminoids being most distinct from each other during the summer and showing more overlap early and late in the growing season (Karlsson et al., 2000; Tahmasebi et al., 2017). Between plant-type variation is greater than within-plant variation (Munizzi, 2017). This $\delta^{15}N$ pattern of plant species, however, may not always apply to modern steppe environments; for example, shrubs had higher δ^{15}N than grasses in some Chinese steppe plants (Fig. 2b; Wu and Huang, 2010; Zhou et al., 2016).

The mammoth steppe had both steppe and tundra characteristics, with proportions varying over time and between regions (Binney et al., 2017; Elias and Crocker, 2008; Goetcheus and Birks, 2001; Guthrie, 2001; Zazula et al., 2011, 2003). The patterns likely vary between the steppe and tundra, depending on the dominant environmental controls (e.g., moisture levels, nitrogen availability, permafrost depth) and specific aspects of the nitrogen cycle. Further investigation of the δ^{15}N of plants from steppe and from transitional environments is needed, as well as studies of seasonal variations in plants from these environments.

The isotopic composition of an animal's bone, tooth or tusk collagen derives from the isotopic composition of the digestible portion of its diet (D. Codron et al., 2011). Because of metabolic effects, an animal's collagen typically has a higher carbon isotope composition than the dietary materials from which it formed. Large herbivore collagen is typically enriched in δ^{13}C by ~5 ‰ from diet (Bocherens and Drucker, 2003; Drucker et al., 2008; Kelly, 2000). Collagen δ^{13}C can also reflect metabolic effects specific to an animal's physiology. An animal suffering from winter starvation may utilize its fat reserves, which potentially could cause a lowering of δ^{13}C in its tissues, including collagen (Szpak et al., 2010). Fernández-Mosquera et al. (2001) found no change in cave bear δ^{13}C associated with colder sites, where greater lipid use might have been expected. However, hibernation signals in cave bear δ^{13}C resulting from lipid use have been suggested in other studies (Bocherens, 2015, 2018; Pérez-Rama et al., 2011). Ruminant species produce and release large quantities of methane, which has low $\delta^{13}C$. Loss of this methane may leave the remaining dietary carbon enriched in ^{13}C, which may be passed on to tissues such as bioapatite (Hedges, 2003) and potentially collagen as well. This could make their $\delta^{13}C$ higher than non-ruminant species (Britton et al., 2012). Body mass can also affect bioapatite $\delta^{13}C$, with larger animals having greater ^{13}C enrichment, though this effect has not been tested in collagen (Tejada-Lara et al., 2018).

The $\delta^{15}N$ of animal collagen reflects its diet plus 3 to 5 ‰ (Bocherens and Drucker, 2003; Bocherens, 2015). Physiological effects can also cause an increase in collagen $\delta^{15}N$. For example, a nursing individual consumes tissue from its mother, and so tissues from nursing animals have $\delta^{15}N$ one trophic level higher than their mother (Fogel et al., 1989; Metcalfe et al., 2010). Extreme nutritional stress may also cause an animal to recycle its own tissues, causing an increase in $\delta^{15}N$ (Hobson et al., 1993; Kelly, 2000; Kempster et al., 2007; Koch, 2007; Mosbacher et al., 2016; Polischuk et al., 2011), though some dispute this effect as animals under dietary stress may limit collagen remodelling (Bocherens, 2015). Hibernation in cave bears may have also led to tissue recycling and thus increased $\delta^{15}N$ (Bocherens, 2015, 2018; Pérez-Rama et al., 2011).

1.2.2 Isotopic niche

When considering a species at a single trophic level, combined evaluation of its carbon and nitrogen isotope compositions allows definition of an "isotopic niche". The isotopic niche can be defined to include the total area in isotopic space on a biplot of $\delta^{15}N$ versus $\delta^{13}C$ (measured in ‰) containing all measurements for a species (total area; TA; Layman et al., 2007), or it can be defined as the core (40 %) of the isotopic compositions of the species on such a biplot (standard ellipse area corrected for small sample size; SEA$_c$; Jackson et al., 2011). Either method provides a distinctly shaped and sized isotopic niche for each species. The isotopic niche depicts a subset of a group's ecological niche by describing the sum of the dietary, environmental and physiological factors that in combination affect the placement and size of the group's isotopic compositions (Bearhop et al., 2004; Hammerschlag-Peyer et al., 2011; Layman et al., 2012). Isotopic niche can be compared among groups. The extent of isotopic niche overlap can provide information about whether species use similar dietary and/or habitat resources, or feed from distinct isotopic niches (Hammerschlag-Peyer et al., 2011), thus providing insight into interactions between species.

Stable Isotope Bayesian Ellipses in R (SIBER) is one of the mathematical programs that can be used to perform this analysis (Jackson et al., 2011; Parnell et al., 2010). There are two main factors that can decrease the power of SIBER isotopic niche metrics. First, since the TA includes the total area covered within a group, adding additional samples to a group can increase the size of that group, but can never decrease it. This means that the isotopic niche for a group containing a large number of analyzed specimens has the potential to appear larger than one containing a small number of specimens (Jackson et al., 2011). Such an outcome is of particular concern in palaeoecology, where samples sets are commonly small (<30) and the size of sample sets from different groups can vary. These metrics should also be viewed with caution when comparing groups containing fewer than 10-30 individuals each (Jackson et al., 2011; Syväranta et al., 2013). Groups containing smaller numbers of samples remain interpretable, but the test is less powerful than for ecological data meeting these conditions.

Several studies have paired SIBER analysis with the more traditional niche analysis method of gut contents analysis (e.g., Layman and Allgeier, 2012; Staudinger et al., 2014). SIBER analysis of niche overlap has been used to assess overlap between invasive and native species (e.g., Hill et al., 2015; Jackson and Britton, 2013), and to compare the extent of dietary overlap of coexisting age classes (e.g., Staudinger et al., 2014) or species (e.g., Saporiti et al., 2014; Yurkowski et al., 2016) in both modern and paleontological contexts. Yurkowski et al. (2016) supported their SIBER analysis with linear modelling. SIBER metrics have also been used to assess ecosystem niche changes over time in historical and archeological contexts (e.g., Drago et al., 2017; Saporiti et al., 2014), and to examine archeological herbivore life-histories (Szpak et al., 2014). Lanoë et al. (2017) used isotopic niche to examine the Pleistocene/Holocene transition in eastern Beringia and Dantas et al. (2017) used it to examine Pleistocene Brazilian megaherbivores. No single metric perfectly quantifies niche overlap as niche separation occurs over numerous axes via numerous mechanisms. Isotopic niche analysis, however, is particularly valuable as it provides a linked signal between the forage species consumed and the habitat and environmental conditions at the site. It remains, however, that variations in species physiology and overlap in plant isotopic compositions could affect the isotopic overlap determined by SIBER analysis.

Previous work has generally examined the relative carbon and nitrogen isotope compositions of several megaherbivores at single mammoth steppe sites, or of fewer species at multiple sites (e.g., Bocherens et al., 1994a, b, 2011b, 2014a; Drucker et al., 2003a, b; Fizet et al., 1995; Fox-Dobbs et al., 2008; Iacumin et al., 2010; Kuitems et al., 2019; Lanoë et al., 2017; Mann et al., 2013; Metcalfe et al., 2013, 2016; Raghavan et al., 2014; Stevens et al., 2009; Szpak et al., 2010), either for a single point in time or over several time intervals. Our study extends that approach to a comparison of much of the available δ^{13}C and δ^{15}N data (and the associated ecological niche) across multiple species, times and sites for the entirety of the mammoth steppe throughout the late Pleistocene (Supplementary Table 1). Previous work has generally focused on the relative isotopic position in δ^{15}N-δ^{13}C space across species, site or time to determine variability in δ^{13}C or δ^{15}N. Our study expands on existing literature to consider isotopic niche overlap and relative position and to seek isotopic patterns that extend across multiple criteria.

2. Methods

2.1 Sampling

Stable isotope compositions of megaherbivore bone collagen and plants, and accompanying radiocarbon dates, were primarily compiled from available literature (1636 stable isotope measurements) and secondarily combined with new isotope and radiocarbon measurements (137 stable isotope measurements; 20 radiocarbon dates) (Supplementary Table 1; analytical methods in Appendix A). This compilation is not exhaustive, but we consider it to be representative of available information. Preservation of primary collagen isotopic compositions was evaluated when other information provided made this possible (i.e., collagen yield ≥ 1 %, C (wt %) ≥ 13 %, N (wt %) ≥ 4.8 %, atomic C/N ratio between 2.9-3.6) (Ambrose, 1990; DeNiro, 1985). Data that did not meet these criteria were rejected. If a specimen was not clearly identified at the generic level (e.g., *Bos* vs. *Bison*), the isotopic results were also excluded from the compilation. Isotopic results for teeth were excluded unless the samples were adult mammoth teeth or bison third molars, as the isotopic compositions of these elements reflect adult rather than juvenile diets (Balasse et al., 1999; Metcalfe et al., 2010). Isotopic data for antler were excluded as this tissue reflects seasonal and/or physiological signals (Finstad and Kielland, 2011; Miller et al., 2014; Stevens and O'Connell, 2016). When multiple data were available for a given sample as the result of radiocarbon measurements, we accepted the stable isotope results associated with the oldest date for collagen that had undergone ultrafiltration. Cave bears were included in this analysis, as they are commonly reconstructed as herbivores (e.g., Bocherens, 2018; Bocherens et al., 2006, 2014a; Krajcarz et al., 2016; Naito et al., 2016b), though this status is disputed by some (e.g., Jones and DeSantis, 2016; Peigné et al., 2009). Table 1 summarizes the number of samples considered organized by species, region and time interval, respectively.

Table 1. Number of megafauna samples by species, region and time bin.

		No.
Species	Aurochs (BOS)	1
	Bison (BSN)	138
	Camel (CAM)	1
	Caribou (CRB)	294
	Chamois (CHM)	3
	Cave bear (CVB)	121
	Elk (ELK)	242
	Horse (HRS)	348
	Irish elk (IRS)	1
	Ibex/wild goat (IBS)	3
	Helmeted muskox (HMK)	11
	Woolly mammoth (MTH)	250
	Mastodon (MTD)	57
	Muskox (MSK)	167
	Moose (MOS)	25
	Sagia antelope (SGA)	76
	Dall sheep (SHP)	20
	Roe deer (ROE)	1
	Woolly rhinoceros (RNO)	14
Region	Alberta (ALB)	70
	Eastern Beringia (EBR)	270
	Gydan Peninsula (GDP)	1
	Great Lakes Area (GLA)	25
	Iberian Peninsula (IBR)	236
	Near the Jura mountains (JUR)	187
	North eastern Europe (NEE)	19
	North Slope Alaska (NSP)	336

	North Western Europe (NWE)	382
	Russian Plain (RSP)	34
	South central Siberia (SCS)	41
	Taymyr Peninsula (TYM)	78
	Wrangel Island (WGI)	1
	Yakutia (YKA)	93
Time	>45,000 ^{14}C BP (INF)	281
	27,540+ cal BP (PRE)	493
	27,540 to 23,340 cal BP (LGM)	43
	23.340 to 11,700 cal BP (PST)	571
	11,700- cal BP (HCL)	84
	Not determined (NDT)	301

Based on previous work (e.g., Kuitems et al., 2019; Iacumin et al., 2000; Raghavan et al., 2014; Richards and Hedges, 2003) and geographic boundaries, samples were divided into ten regions (Fig. 1): Iberian peninsula (IBR), Jura mountains (JUR), northwestern Europe (NWE), northeastern Europe (NEE), Russian plain (RSP), Gydan Peninsula (GDP), south central Siberia (SCS), Taymyr Peninsula (TYM), Yakutia (YKA), eastern Beringia (EBR), North Slope Alaska, Alberta (ALB) and Great Lakes Area (GLA). The data were sorted into four time-bins: (1) non-finite (INF), (2) pre-LGM, (3) LGM, and (4) post-LGM, using the age-brackets suggested in previous work (Hughes and Gibbard, 2015). Additionally, interstadials and stadials were considered separately where sample sizes permitted. Samples were classified as “not determined” (NDT) when not dated, if insufficient information was given to classify the date, or if the calibrated date range included multiple time bins. Dates were calibrated using http://www.calpal-online.de/ following the method of García-Vázquez et al. (2018), and the 68 % range was used to assess the range of calibrated dates for a radiocarbon-dated specimen. Specimens for which the range of calibrated dates fell within the pre-LGM, LGM or post-LGM time bins were assigned to each bin (Time 2 in Supplementary Table 1). Specimens were additionally placed in time bins based on physical context (e.g., Bocherens et al., 2011a; Drucker et al., 2003a), or prior knowledge of the species at the site (e.g., Guthrie, 2006; Zazula et al., 2014). Where known, direct radiocarbon dates for samples, or the layer from which they were collected, are provided in Supplementary Table 1. As climate conditions cannot be associated with INF specimens, these data were treated with caution and were not used in modeling. The same method was used to assign specimens to Greenland stages (Time 3 in Supplementary Table 1). As yet, there are insufficient samples within regions and species to use only direct dates for mathematical analysis of ecological niche. Also, assessing changes from overly small time windows risks misidentifying wide isotopic ranges caused by generalist diets as changes in baseline isotopic compositions, particularly for areas such as Alberta or south central Siberia peninsula where data are limited. Better temporal resolution should be possible in the future as more studies combine acquisition of chronology and stable isotope data.

Data were compiled from the literature for modern, high latitude plants using studies that analyzed multiple growth forms (Barnett, 1994; Milligan, 2008; Tahmasebi et al., 2017; Wang and Wooller, 2006) (Table 2; Supplementary Table 2). Data points were removed if they were considered outliers in the original study, or if they were listed as roots. Modern plant δ^{13}C was corrected for the Suess effect to remove the biasing effect of modern atmosphere CO_2 δ^{13}C following the method of Tahmasebi et al. (2018) and Long et al. (2005).

Table 2. Number of modern, high latitude plant samples compiled from the literature.

Form	No.
Herb	305
Lichen	16
Moss	6
Fungi	3
Shrub	127

2.3. Statistical analysis

Variability in δ^{13}C and δ^{15}N among species, regions and time bins was assessed using linear models, Akaike Information Criterion (AIC; Barton, 2016; Calcagno, 2013; Lenth, 2016; Mazerolle, 2016) and confidence intervals (CIs) of parameter coefficients in R version 3.2.2 (R-Core-Team, 2012) using the R Studio interface version 0.99.484 (R-Studio-Team, 2015).This analysis was conducted separately for carbon and nitrogen isotopes. Details of model selection are provided in Appendix B.

Isotopic niche was determined using SIBER scripts from the SIAR package (Stable Isotope Analysis in R; Parnell and Jackson, 2013) in R version 3.1.1 (R-Core-Team, 2012) using the R Studio interface version 0.98.1083 (R-Studio-Team, 2015). The database was interrogated to make comparisons for (1) groups of species in a given region and time; (2) groups of regions at a given time and for a given species, and (3) times at a given region for given species. Fig. 3 presents examples of the mathematical treatments using the dataset of modern high latitude plants. Niche overlap was determined by calculating the proportion of the TA or SEA$_c$ overlap between two groups. Groups were considered to overlap if either metric showed overlap. The overlap was calculated by dividing the area of overlap by the area of one of the two groups, and this step was conducted twice, using the area of each group. Overlap less than 30 % was considered minimal. Overlap of 30 to 60 % was considered moderate and indicated resource sharing. Overlap greater than 60 % was considered high, as it indicated ecologically significant overlap in the core niche (Gebremedhin et al., 2016; Guzzo et al., 2013; Langton, 1982; Simpfendorfer et al., 2001). We examined whether there was variability in niche position of a species in different regions and at different times, as has been done to assess male versus female seal dietary changes over historical time bins (Drago et al., 2017). In many cases, 10 to 30 specimens were not available for each species from a region during a specific time. Isotope ranking of species, region and time bin was still performed when there were <10 specimens in some of the groups, but rankings were only considered to be robust if the same pattern was observed over multiple species, regions or times.

3. Results

3.1. Plant isotopic niche

The typical graphical outputs from SIBER used to assess niche overlap, including isotopic niche overlap using the total area (TA) and small-sample-size corrected ellipses (SEA_c), are shown in Fig. 3 for modern high latitude plants.

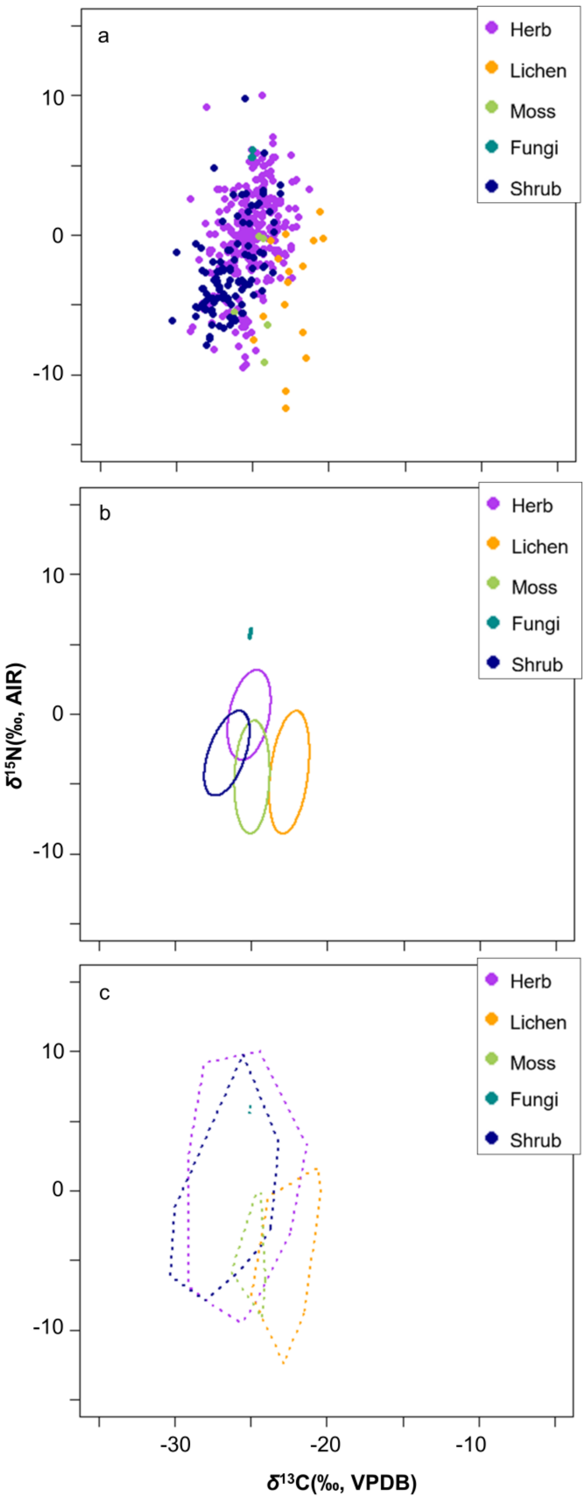

Figure 3. Graphs of δ^{15}N versus δ^{13}C for modern high latitude vegetation produced using SIBER. (a) Individual data. (b) Small-sample-size corrected ellipses (SEA$_c$) encompassing 40 % of the data for each growth form (c) Convex hulls encompassing the total area (TA) of all data for each

growth form. (c). Average $\delta^{13}C$ shrub < herb < fungi < moss < lichen. Average $\delta^{15}N$ moss < lichen < shrub < herb < fungi.

3.2. Herbivore modelling

The model with the best fit for the $\delta^{13}C$ data was:

$\delta^{13}C \sim 1 + \text{Species} + \text{Region} + \text{Time} + \text{Region:Species} + \text{Time:Species}$

Details of model validation are in Appendix B and Supplementary Table 3. The confidence intervals for 'Time' overlapped 0, indicating this was an uninformative parameter, and it was not considered further.

Two models had AIC*c* < 4, and thus both were considered valid fits for the $\delta^{15}N$ data:

1) $\delta^{15}N \sim \sim 1 + \text{Species} + \text{Region} + \text{Time} + \text{Region:Species} + \text{Time:Species} + \text{Time:Region} + \text{Region*Species*Time}$
2) $\delta^{15}N \sim \sim 1 + \text{Species} + \text{Region} + \text{Time} + \text{Region:Species} + \text{Time:Species} + \text{Time:Region}$

Details of model validation are provided in Appendix B and Supplementary Table 4. All parameters were considered informative.

3.3 Isotopic Ranking

'Species', 'Region:Species' and 'Time:Species' were all informative variables in the best fitting models for both $\delta^{13}C$ and $\delta^{15}N$. Therefore, the variation in species' $\delta^{13}C$ and $\delta^{15}N$ rankings were assessed. Qualitative results for the less commonly analysed species are provided in Appendix C. Regional analyses are provided in Appendix D, and time-analysis is provided in Appendix E.

General trends in δ^{13}C for the most common isotopically analysed megafaunal herbivores are evident across all regions and time bins. As “Species:Region:Time” was not an informative variable in the best model, all regions were considered together for a time group, and all times were considered together for a regional group. The typical pattern of δ^{13}C was mammoth and horse < bison & elk & rhino < muskox < caribou (Fig. 4; Supplementary Table 5). There are exceptions to this pattern in northeastern Europe and during the LGM. These may result from small sample sets that do not capture average isotopic signals.

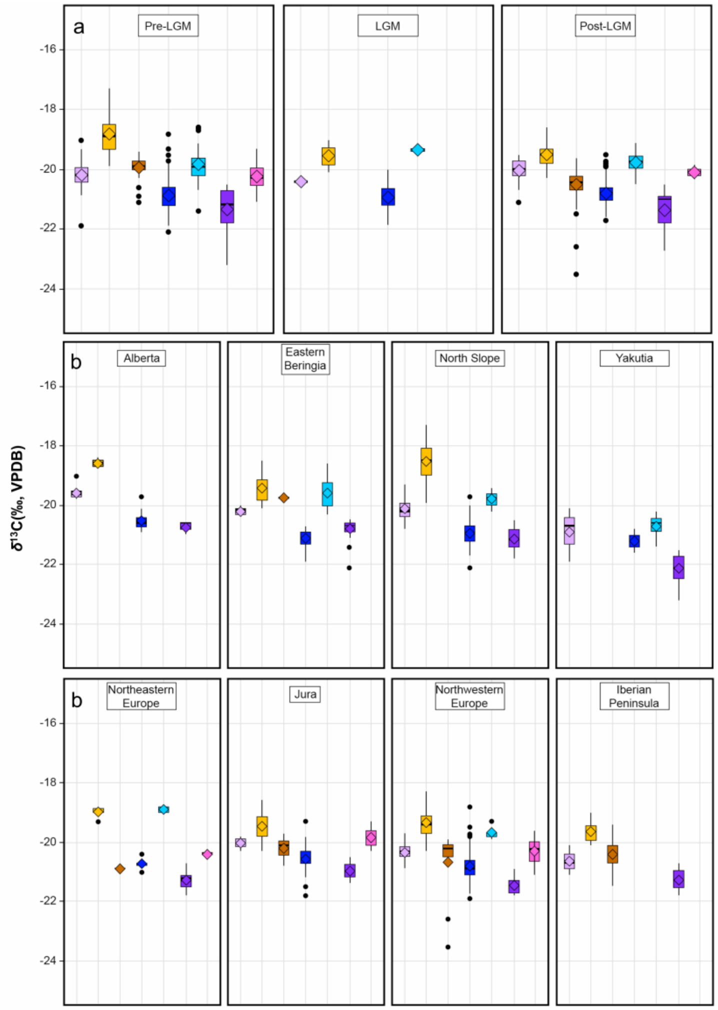

Figure 4. Box and whisker plots showing variation in δ^{13}C for the most commonly isotopically analysed megafaunal herbivores from (a) each region and (b) time bin (graphs cover two rows). The diamond represents the mean value, the horizontal line indicates the median value and boxes show the 25th and 75th percentiles. Whiskers show the largest value that extends no further from the outside of the box than 1.5 times the distance between the 25th and 75th percentiles. Data outside the whiskers are outliers. Lilac = bison, yellow = caribou, orange = elk, dark blue = horse, light blue = muskox, purple = mammoth, pink = rhinoceros.

As for δ^{13}C, a general pattern in δ^{15}N was observed across the mammoth steppe, though it varied slightly between time bins and regions (Fig. 5; Supplementary Table 5). Elk, bison and caribou had the lowest δ^{15}N, followed by muskox, rhinoceros and mammoth. In pre-LGM, elk < caribou < bison < muskox & rhinoceros < mammoth. In post-LGM, elk < bison < caribou < rhinoceros < mammoth & muskox. Horse δ^{15}N varied over time and between regions, from the lowest δ^{15}N in regions such as post-LGM Alberta and post-LGM JUR to the third highest δ^{15}N in pre-LGM JUR, overlapping rhinoceros and mammoth δ^{15}N (Fig. 5). The sample sizes for the LGM were too small to determine consistent patterns. Variations in the pattern included pre-LGM site NEE, where muskox had low δ^{15}N, post-LGM Alberta, where mammoth had low δ^{15}N, and post-LGM NWE, where elk had high δ^{15}N. The extent of the difference in δ^{15}N between species varied substantially between regions and times, as suggested by the fact that ‘Species:Region:Time’ was an informative variable in a top model.

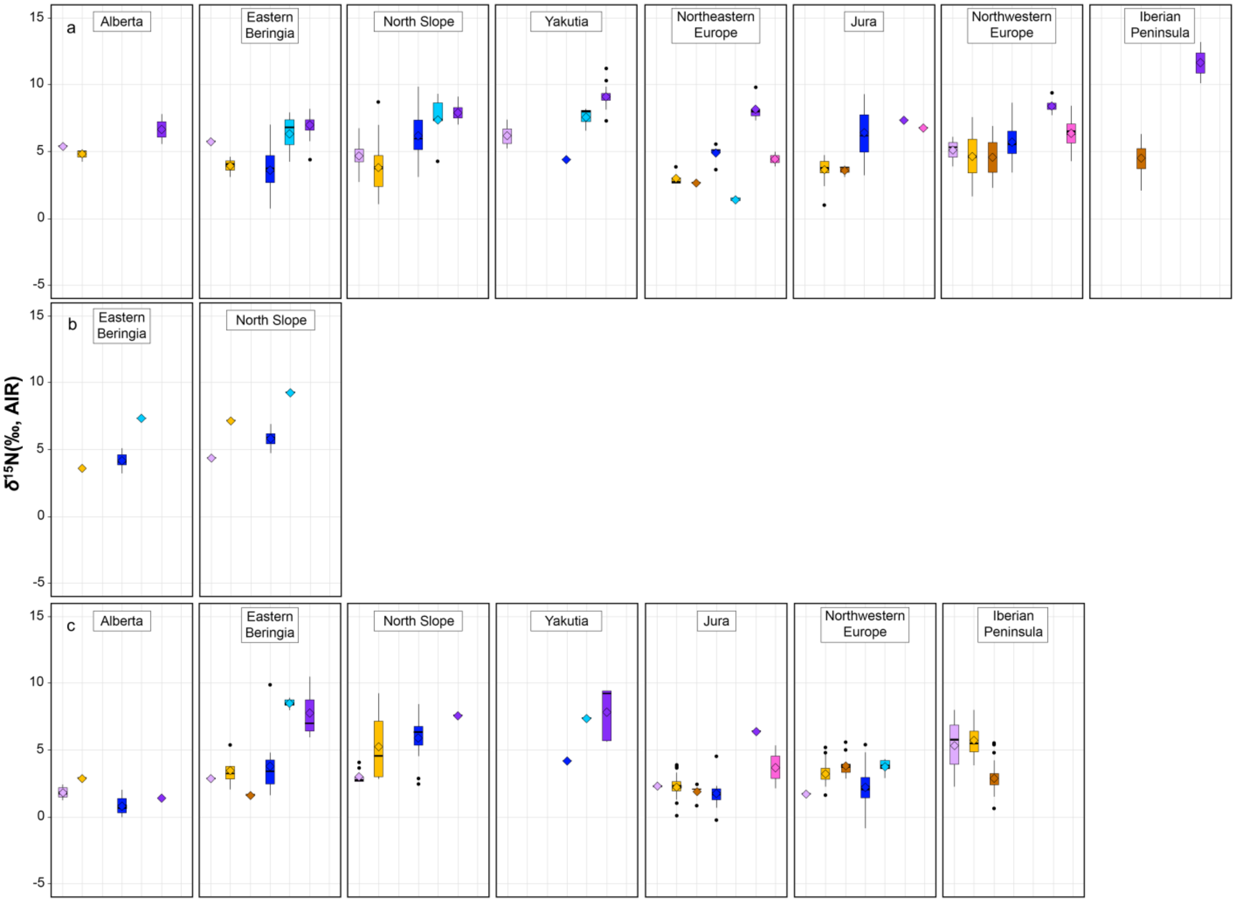

Figure 5. Box and whisker plots showing variability in δ^{15}N for the most common isotopically analysed megafaunal herbivores in each region during the (a) pre-LGM, (b) LGM, and (c) post-LGM time bins. The diamond represents the mean value, the line indicates the median value and boxes show the 25th and 75th percentiles. Whiskers show the largest value that extends no further from the outside of the box than 1.5 times the distance between the 25th and 75th percentiles. Data outside the whiskers are outliers. Lilac = bison, yellow = caribou, orange = elk, dark blue = horse, light blue = muskox, purple = mammoth, pink = rhinoceros.

The extent of the difference in δ^{15}N between species varies substantially between regions and times, as suggested by the fact that ‘Species:Region:Time’ is an informative variable. The variation in degree of change, however, is insufficient to disrupt the general δ^{15}N pattern (Fig. 6).

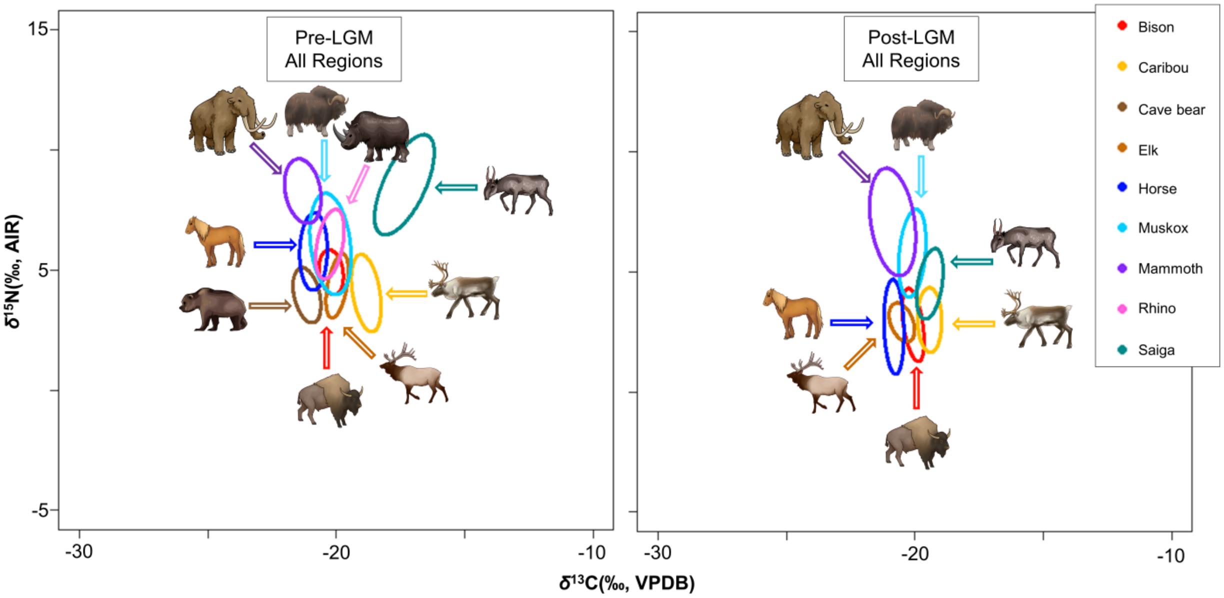

Figure 6. SEA$_c$ niche positions of the major megafaunal herbivores on the mammoth steppe. Regions were combined for SIBER analysis, making niche overlap and δ^{15}N niche position less reliable than separate regional analyses. A minimum of three data points were required for a species to be included.

3.4. Niche overlap

Niche overlap was assessed separately for each time and region for all species with at least three measured specimens (selected examples shown in Fig. 7; Supplementary Table 5). Six species had TA core niche overlap with another species for at least one time and region (bison, caribou, elk, horse, muskox and mammoth) while four species had SEA$_c$ core niche overlap (bison, caribou, elk and muskox). Conversely, three species were most likely to overlap into another species' core niche: caribou (bison and muskox), horse (bison, elk and mammoth) and sagia (caribou and muskox). Resource sharing, or moderate niche overlap, was additionally observed for the rhinoceros and cave bear. Analysis of Alberta prior to the LGM required combining INF and pre-LGM dates (Fig. 7); however, TA niche overlap observed between horse and mammoth was also observed in pre-LGM North Slope and post-LGM eastern Beringia as well as in combined INF & pre-LGM Alberta horse and mammoth.

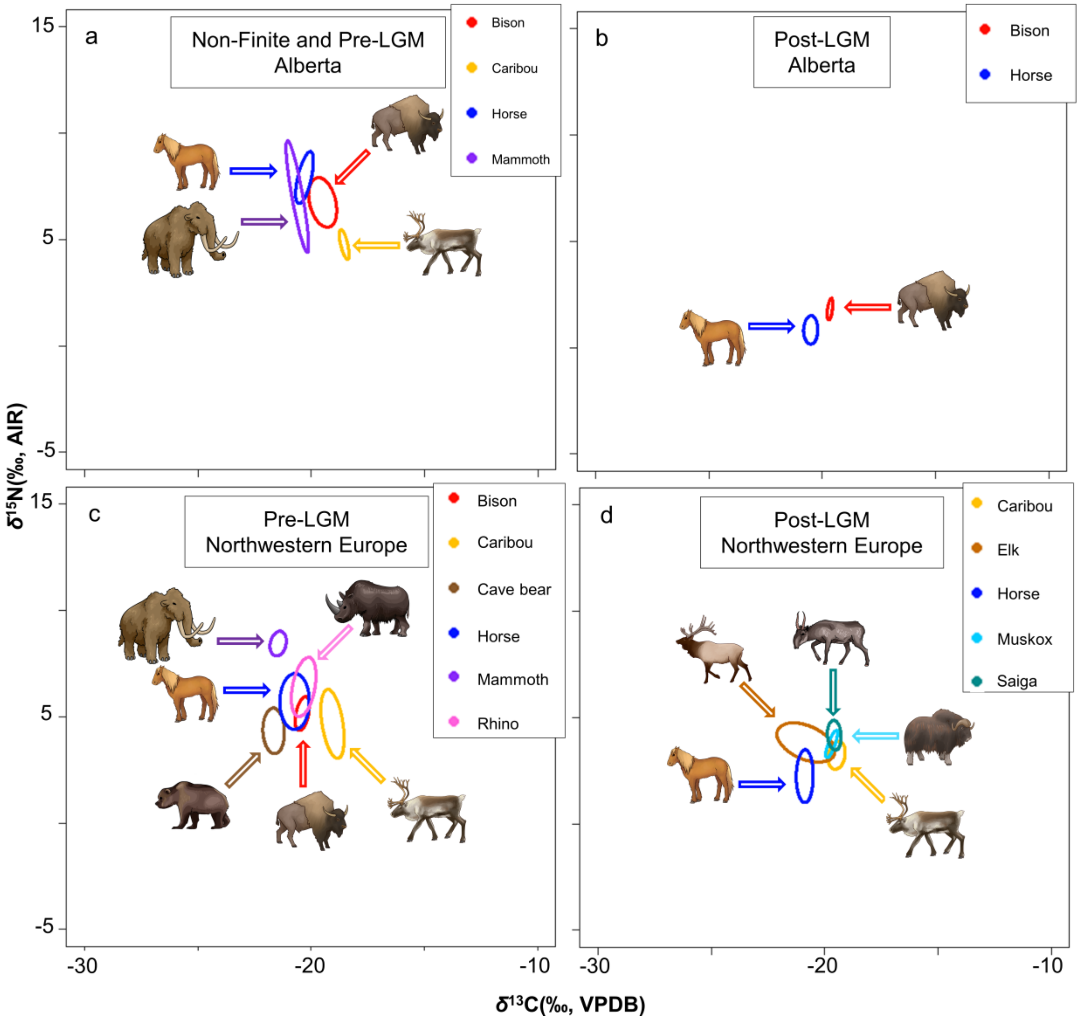

Figure 7. SEA$_c$ niche positions and overlaps of megafaunal herbivores from (a) INF and pre-LGM Alberta; (b) post-LGM Alberta; (c) pre-LGM northwestern Europe and (d) post-LGM

Europe. Pre-LGM northwestern Europe has SEA_c core niche overlap of bison with horse, and moderate niche overlap of bison with rhinoceros, horse with rhinoceros and rhinoceros with horse. Post-LGM northwestern Europe has SEA_c core niche overlap of muskox with saiga, and moderate niche overlap of muskox with elk and saiga with muskox.

In most cases, Greenland stadial and interstadial-based time bins did not have enough samples for quantitative analysis of niche overlap of multiple species. The one exception was NWE Greenland stadial 2.1 (14,692-22,900 cal BP), where the isotopic niche of three species (caribou, horse and saiga) was considered (Fig. 8a-c). Moderate TA niche overlap was observed between caribou and saiga. In several cases where insufficient datapoints exist to quantify niche overlap, qualitative overlap was still observed (Fig. 8d-f). Overlap was observed between elk/bison and elk/ibex in IBR Greenland stadial 2, between horse/mammoth in NSP Greenland stadial 2.1 and between bison/horse in NSP Greenland stadial 3 (23,340-27,540 cal BP).

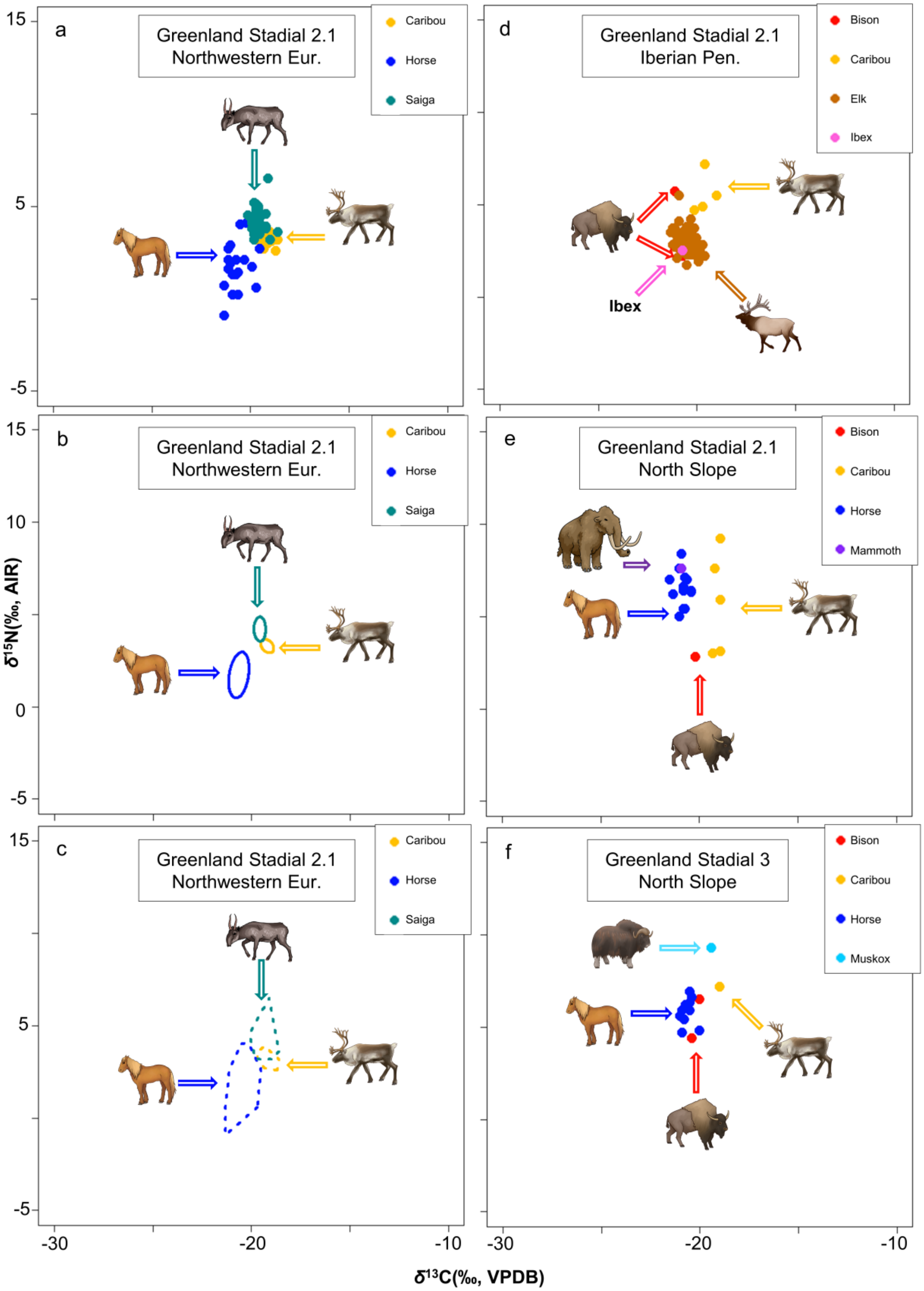

Figure 8. Niche positions and overlaps of megafaunal herbivores with time bins based on Greenland stadials and interstadials. (Left) Niche representations of Greenland stadial 2.1 northwestern Europe (a) Individual data points; (b) Small-sample-size corrected ellipses (SEA_c)

encompassing 40 % of the data and (c) Convex hulls encompassing the total area (TA). Northwestern Europe during Greenland stadial 2.1 had TA moderate niche overlap of caribou with saiga. (Right) Individual data points for multiple regions and times (d) Greenland stadial 2.1 Iberian Peninsula; (e) Greenland stadial 2.1 North Slope Alaska and (f) Greenland stadial 3 North Slope Alaska.

4. Discussion

4.1. Plants

The δ^{13}C pattern of plant growth forms observed in the SIBER results (Fig. 3) were consistent with the conceptual framework (Fig. 2). The patterns were generally the same for δ^{15}N, except that lichen had lower δ^{15}N than shrubs in the SIBER results. Further sampling of both plant types would help elucidate the causes of this variation. There was extensive overlap between plant growth forms (Fig. 3c). As herbivores consume large quantities of plant material, however, they can be considered to "average" the material they consume. When considering the core 40 % of each growth forms' isotopic niche, there is substantially less overlap (Fig. 3c), allowing for isotopic patterns to be passed to the consumer.

The δ^{13}C and δ^{15}N of steppe plants were reported in separate studies (Chen et al., 2005; Song et al., 2008; Toft et al., 1989; Wu and Huang, 2010; Zhou et al., 2016); however, as only averages and standard deviations were provided, isotopic niche cannot be assessed from these datasets. In these studies, average plant δ^{13}C ranged from ~ –25 to –23 ‰, and average plant δ^{15}N, from ~ –2 to +6 ‰. We caution against direct use of the plant isotopic compositions to calculate herbivore diets, in part because of the understudied nature of steppe plants' δ^{13}C and δ^{15}N. As well, the

$\delta^{15}N$ of steppe plants changed between a Pleistocene glacial event and the current Holocene interglacial (Tahmasebi et al., 2018). Without a better understanding of these dynamics, we prefer to consider patterns of differences in isotopic composition between plant functional groups rather than specific isotopic compositions.

4.2. Pleistocene herbivore niches

The consistency in the patterns of average carbon and nitrogen isotope compositions among species at various sites and times (Figs. 4-6; Supplementary Table 5) suggests that the herbivores' main dietary, physiological and habitat/environmental niches were conserved across the mammoth steppe through time and space. This general pattern agrees with previous reports (e.g., Bocherens, 2003, 2015), and highlights the value of a metastudy approach. The isotope positions of less commonly analyzed species from the mammoth steppe generally conform to expected patterns (Appendix C). Ruminant physiology (Hedges, 2003) or body-size differences (Tejada-Lara et al., 2018) may play a role in some of these patterns. For example, the non-ruminant horse and mammoth typically have the lowest $\delta^{13}C$ of coeval megaherbivores. The non-ruminant rhinoceros, however, commonly has higher $\delta^{13}C$ than bison or elk; Fig. 4; Supplementary Table 5). Likewise, if body size was the primary control, the $\delta^{13}C$ pattern would be expected to be horse < rhinoceros < elephant (Tejada-Lara et al., 2018) rather than mammoth & horse < rhinoceros. Hence, physiological processes are not sufficient on their own to explain mammoth steppe herbivore $\delta^{13}C$ patterns.

The consistently higher average $\delta^{15}N$ of mammoth reflects a distinct diet or habitat (Drucker et al., 2015; Naito et al., 2016a; Schwartz-Narbonne et al., 2015). Several hypotheses have been proposed to explain this feature, including consumption of forage in arid microhabitats (Bocherens, 2003; Iacumin et al., 2000; Kuitems et al., 2012), consumption of plants fertilized with dung (Metcalfe et al., 2013), and/or selection of specific plants or plant parts during forage (Kuitems et al., 2012; Metcalfe et al., 2013). Mammoth core niche overlaps with horse both pre- and post-LGM, suggesting that some horse also exploited this distinct niche, as has been previously observed in both the INF & pre-LGM and the post-LGM time bins (Drucker et al., 2015, 2018; Schwartz-Narbonne et al., 2015).

Multiple lines of evidence suggest that horse, bison and mammoth were primarily grazers (consumed grasses, forbs and sedges rather than tissues from shrubs or trees; Bocherens, 2003, 2015; Guthrie, 1990, 2001; Rivals et al., 2010, 2012, 2017). Similar diets for these three species are consistent with the core niche overlap of horse with both bison and mammoth. Rather than obligate grazing, however, some authors have suggested a degree of mixed-feeding (consumption of both graze and browse). Tooth wear analysis has suggested that mammoths from northwestern Europe and the Great Lakes area were mixed-feeders (Rivals et al., 2010; Saunders et al., 2010). Pleistocene bison also had the potential to incorporate browse into their diets, as their physiology allow them to raise their heads higher than extant *Bison bison* (Guthrie, 1990; McDonald, 1981). Plant material recovered from teeth also suggests that Pleistocene bison consumed some browse (Guthrie, 1990). Tooth mesowear and microwear studies likewise suggest that Pleistocene and early Holocene bison diets included a browse component; the proportion of browse varied by time and site, both on and off the mammoth steppe (Rivals et al., 2007, 2009, 2010; Rivals and Álvarez-Lao, 2018; Rivals and Lister, 2016; Rivals and Semprebon, 2011; Saarinen et al., 2016). Tooth wear studies similarly suggested that horses consumed varying amounts of browse in northwestern Europe and eastern Beringia, depending on site and time (Rivals et al., 2010, 2014; Rivals and Lister, 2016; Saarinen et al., 2016; Semprebon et al., 2016), as well as inhabiting environments with varying levels of forest (Saarinen et al., 2016). Studies of modern *Equus* and *Bison* also indicate incorporation of some browse into diets (Craine et al., 2015b; Gębczyńska et al., 1991; Guthrie, 1990; Hansen, 1976; Kaiser et al., 2013; Kowalczyk et al., 2011; Marshal et al., 2012; Painter and Ripple, 2012; Peden et al., 1974; Schulz and Kaiser, 2013; van den Berg et al., 2015;Waggoner and Hinkes, 1986; Xu et al., 2012). Many *Equus* populations are grazers that consume minimal browse (e.g., Hansen, 1976), but browse is a dominant food in some populations of wild/feral *Equus* species either yearly or seasonally (Marshal et al., 2012; Schulz and Kaiser, 2013; Xu et al., 2012). Similarly, modern bison are generally grazers (e.g., Peden et al., 1974) but some European and American populations consume high quantities of browse (Kowalczyk et al., 2011; Painter and Ripple, 2012; Waggoner and Hinkes, 1986). Bison respond to decreasing protein levels in graminoids by increasing shrubs and forbs in their diet; the proportion of shrubs and forbs in bison diets is therefore projected to increase in response to anthropogenic climate change (Craine et al., 2015b). Likewise, while mammoths are reconstructed here as grazers, modern elephants are mixed feeders (Ahrestani et al., 2012; J.B. Codron et al., 2011; Hansen et al., 1985).

Beyond the grazing versus browsing dichotomy, other dietary distinctions involve consumption of different plant parts and plant heights, and different plant species within the grazing or browsing niche. This can cause variation in δ^{13}C and δ^{15}N, as well as the protein content of forage (Codron et al., 2008; Tahmasebi et al., 2017), as has been observed for buffalo and zebra in the African savannah (Arsenault and Owen-Smith, 2008; Kleynhans et al., 2011). The high variability in horse δ^{15}N between regions and time (Fig. 5) may reflect one of these types of dietary selection. In the case of Alberta horse and bison, their relative δ^{15}N position varied with their representation (and hence inferred abundance) in the fossil record. During INF & pre-LGM times in Alberta, horse was more abundant and had higher δ^{15}N than bison, whereas the reverse occurred post-LGM (Fig. 7; Supplementary Table 5; population information from Jass et al., 2011). Post-LGM Alberta contained some boreal forest cover (Strong and Hills, 2005) and horse may have eaten from a more nutrient-poor browse niche, leading to a reduced population and lower δ^{15}N than bison. Horse had evidence of more stress post-LGM demonstrated by increased percentages of horse teeth with hypoplastic events. These may indicate more dietary stress in post-LGM horse than in pre-LGM horse, or bison from either time (Barrón-Ortiz et al., In Submission). Alternatively, the δ^{15}N of grasses relative to shrubs may have changed as the ecosystem type shifted. Future work that considers species range, diversity and population sizes (e.g., Lorenzen et al., 2011) should assess the niche position of species in relation to these variables.

Modern caribou eat both graze and browse, and consume lichen in winter where available (Bjørkvoll et al., 2009; Guthrie, 1990, 2001; Heggberget et al., 2002; Larter et al., 2002; Larter and Nagy, 1997; Rozenfeld et al., 2012). Plant material preserved in small enamel pits between the molar cusps of caribou teeth suggests winter feeding on lichens, and otherwise mixed-feeding (Guthrie, 2001). Such a diet may be responsible for the generally high δ^{13}C of Pleistocene caribou (Fig. 4. Bocherens, 2003, 2015; Bocherens et al., 1996, 2014b; Castaños et al., 2014; Fizet et al., 1995; Fox-Dobbs et al., 2008; Iacumin et al., 2000). The generally low δ^{15}N of caribou may relate to browse consumption. Caribou nitrogen isotope position is lower than bison during the pre-LGM and higher than bison post-LGM, suggesting either adaptable diets for caribou or ecosystem shifts between the tundra and steppe models (Fig. 2). An adaptable diet for caribou, with varying levels of browse and lichen consumption, is supported by tooth microwear studies of Pleistocene caribou from across the mammoth steppe and through time (Rivals and Álvarez-Lao, 2018; Rivals and Solounias, 2007; Rivals and Semprebon, 2017; Rivals et al., 2010; Saarinen et al., 2016).

Modern elk are opportunist mixed-feeders that live in both closed canopy forests and open habitats (Christianson and Creel, 2007; Dumont et al., 2005; Gebert and Verheyden-Tixier, 2008). This is consistent with tooth wear studies that suggest the Pleistocene elk was a mixed-feeder whose diet shifted over time and between regions (Rivals and Álvarez-Lao, 2018; Rivals and Lister, 2016; Rivals et al., 2009, 2017; Saarinen et al., 2016). Elk had typically low δ^{15}N, suggesting a primarily browse diet. The atypically high δ^{15}N in post-LGM northwestern Europe may have been a response to reduced browse intake (Castaños et al., 2014) or changes in δ^{15}N of the forage. Dietary competition between elk and caribou was previously suggested (Cupillard et al., 2015) but we did not observe moderate or core isotopic niche overlap between these species (Supplementary Table 5). Instead, elk had isotopic core niche overlap with bison and horse.

Reconstructed diets of Pleistocene muskox (*Ovibos*) indicate varying proportions of browse and graze (Guthrie, 2001; Mann et al., 2013; Raghavan et al., 2014). However, muskox regularly had high δ^{15}N, which would not be expected for a browser, as well as high δ^{13}C (Figs. 4-5; Supplementary Table 5). This could reflect an environmental difference, in which muskox consumed similar plants to the grazing bison but from a more arid microhabitat. Muskoxen are poorly adapted to foraging in deep snow (Ihl and Klein, 2001; Schaefer and Messier, 1995). Hence, they may have faced greater levels of winter starvation, leading to higher δ^{15}N (Mosbacher et al., 2016), though this would likely not have been recorded in their collagen (see Bocherens, 2015). The most parsimonious explanation involves both lichen consumption, as suggested for Pleistocene muskox as well as caribou (Bocherens, 2015; Bocherens et al., 2015; Fox-Dobbs et al., 2008), and sedge consumption, which is a common component of muskox winter diets (Ihl and Klein, 2001; Larter et al., 2002; Larter and Nagy, 1997; Mosbacher et al., 2016; Rozenfeld et al., 2012). Lichen consumption by muskoxen could explain their higher average δ^{13}C than bison (Fig. 3). As this forage is protein-poor, it may not have contributed substantially to muskox δ^{15}N (Drucker et al., 2001). Increased consumption of sedges, which generally have higher δ^{15}N than grasses and forbs in the modern tundra environment (Ben-David et al., 2001; Munizzi, 2017), could explain higher muskox δ^{15}N than bison or caribou. This explanation is consistent with the isotopic overlap in diet between muskox and caribou, and muskox and bison (Supplementary Table 5), as well as the dietary overlap between modern muskox and caribou (Larter and Nagy, 1997; Staaland and Olesen, 1992). Muskoxen additionally overlapped their core niche with sagia and had moderate niche overlap with elk. Notably, the only site where rhinoceros and muskox were measured together (pre-LGM northeastern Europe), rhinoceros had typically high δ^{15}N and muskox had shifted to atypically low δ^{15}N.

Multiple proxies have suggested that woolly rhinoceros were primarily grazers (Bocherens, 2003; Boeskorov, 2012; Kahlke and Lacombat, 2008; Rivals and Álvarez-Lao, 2018). Some teeth-wear and keratin isotopic studies, however, suggest some local and seasonal variation in degree of grazing and potential inclusion of browse (Rivals and Lister. 2016; Saarinen et al., 2016; Tiunov and Kirillova, 2010). Rhinoceros δ^{13}C was higher than other non-ruminants, and was similar to bison and elk, while rhinoceros δ^{15}N was typically high, similar to muskox (Figs. 4-5). Moderate niche overlap was observed with horse (Supplementary Table 5), consistent with both species as primarily herbivores. While niche overlap was not observed with muskox, this reflected an atypical shift in muskox δ^{15}N in pre-LGM northeastern Europe. The rhinoceros high δ^{15}N may reflect a similar diet to muskox, with some sedge consumption.

4.3. Functional redundancy and resource partitioning

We are not the first to suggest substantial Pleistocene functional redundancy. Pires et al. (2015) suggested a higher degree of functional redundancy on the Pleistocene mammoth steppe than in the modern African savannah network and Davis (2017) demonstrated that Pleistocene North America had more functional redundancy than present North America. Other studies have noted niche overlap and species dietary plasticity on the mammoth steppe based on isotopic analysis (Bocherens, 2018; Bocherens et al., 2015; Drucker et al., 2015, 2018; Fox-Dobbs et al., 2008; García-Vázquez et al., 2018; Münzel et al., 2016; Schwartz-Narbonne et al., 2015) and tooth wear studies (Rivals et al., 2010), albeit not describing this as functional redundancy. Pleistocene niche overlap also occurred outside the mammoth steppe (see Lanoë et al., 2017). The present work similarly found that at least one herbivore species overlapped the core niches of six mammoth steppe species: bison, caribou, elk, horse, mammoth, muskox (Supplementary Table 5). These findings are consistent with functional redundancy as the typical case across the mammoth steppe over time. They are also consistent with seasonal variation in the mechanism of herbivore coexistence, with more niche separation occurring in winter during times of low forage availability. Tooth wear studies have suggested seasonally-based resource partitioning (Rivals et al., 2009, 2017; Rivals and Lister, 2016), as has been observed for some modern African savannah species (Bukombe et al., 2017; Kleynhans et al., 2011; Prins et al., 2006) and suggested for some Brazilian Pleistocene megaherbivores (Dantas et al., 2017). It is possible that competitive exclusion occurred during winter periods of resource scarcity and that species had overlapping niches during the rest of the year. This could be tested by isotopic studies of tissues, such as hair, that retain seasonal signals.

Pleistocene extirpations and/or extinctions of single species can be considered natural deletion experiments (Liebergesell et al., 2016). We can use the outcome of those events to assess the resilience of the mammoth steppe. One such event was the extinction of the generally herbivorous cave bear during the pre-LGM (Knapp, 2019; Mackiewicz et al., 2017; Münzel et al., 2011; Terlato et al., 2018). Before the extinction of the cave bear, the brown bear was generally carnivorous in northwestern Europe (Münzel et al., 2011). After cave bear extinction, the brown bear adapted to fill their ecological niche, both by adopting a more herbivorous diet and by using cave dens (Münzel et al., 2011). On the Iberian peninsula, the brown bear isotopic niche did not appear to shift after the cave bear extinction (García-Vázquez et al., 2018). Elk δ^{13}C, however, shifted after cave bear extinction to occupy more of the cave bear's former niche (Supplementary Table 5; García-Vázquez et al., 2018). Niche breadth and overlap could be further examined in the modern ecology of Palearctic regions, which serve as refugia for remaining mammoth steppe herbivores (Řičánková et al., 2015).

High levels of species diversity can result from a number of factors, acting singly or in concert. While competitive exclusion is one such factor, intrinsic properties, such as region size, temperature and plant productivity can operate in the opposite direction, increasing diversity in an area (Kisel et al., 2011; Ricklefs, 2015). Top-down control of predation can also influence the structure of herbivore communities (Hopcraft et al., 2010, 2012), particularly in areas where rainfall and soil nutrient content provide high levels of plant productivity (Hopcraft et al., 2010). Vegetation-mediated predation risk is a factor controlling what niche space is used by savannah herbivores (Anderson et al., 2016; Barnier et al., 2014; Bukombe et al., 2017; Hopcraft et al., 2012; Sinclair, 1985). This can lead to habitat overlap between herbivore species as a predator-avoidance strategy (Sinclair, 1985), as well as to changes in herbivore diet (Barnier et al., 2014). In addition, the large body size of the mammoth steppe herbivores would have allowed them to survive on lower quantities of forage (Zhu et al., 2018), allowing a greater number of herbivores to survive in the environment. The mammoth steppe had high primary productivity and plant diversity (Guthrie, 2001; Willerslev et al., 2014; Zimov et al., 2012), as well as a diverse set of predators with the capacity to limit the megaherbivore population size (Van Valkenburgh et al., 2015). This combination is consistent with a range of controls on the ecosystem.

5. Conclusions

By the start of the Holocene, many megafauna species on the mammoth steppe were extinct or had been extirpated, and the ecosystem as a whole was lost. Loss of habitat or dietary niche has been suggested as a partial or entire cause of these extinctions (Barnosky et al., 2004; Koch and Barnosky, 2006; Shapiro et al., 2004; Řičánková et al., 2018; Puzachenko et al., 2017). Individual species' survival was attributed either to greater dietary flexibility (Raghavan et al.,

2014) or species' ability to track their habitats through changing climatic conditions, particularly by relocation (Pushkina et al., 2014; Řičánková et al., 2015).

By examining the changing isotopic position of species between regions and over time, our study found dietary flexibility in some species that survived the Pleistocene-Holocene transition, such as caribou and saiga. A lack of dietary flexibility, however, cannot explain all the Pleistocene mammoth steppe extirpations and extinctions. For example, we found substantial changes in the isotopic niche position of horse that suggest some dietary flexibility, yet this species suffered dramatic range reductions.

Rather than only considering individual species' responses to climate and floral changes, we can evaluate the response of the ecosystem as a whole. Our data are consistent with overlapping niches and therefore a degree of functional redundancy (Fig. 7 & 8; Supplementary Table 5). The mammoth steppe fits the model of a resilient system where, if one species was lost, other species could broaden their niche to fulfil ecosystem functions. This resilience would have been valuable in the case of either human hunting or climate change that disproportionately affected any individual species. In Europe, the mammoth steppe ecosystem coexisted with humans and proto-humans. While the ecosystem was in a constant state of flux from environmental changes during the Pleistocene, aspects of the ecosystem persisted. During the post-LGM period, however, this ecosystem faced the combined pressures of hunting by anatomically modern humans alongside rapid warming and increased moisture, rather than a simply one of these pressures (Broughton and Weitzel, 2018; Cooper et al., 2015; Rabanus-Wallace et al., 2017). This combination likely led to the extinction of many megafauna and the collapse of the mammoth steppe. The loss of this resilient ecosystem serves as a warning for modern ecologists, as more vulnerable ecosystems around the world are now facing combined threats from global warming and other anthropogenic effects.

Author contributions

R.S.N. conducted the isotopic analysis, literature search and wrote the initial manuscript; R.S.N. and F.J.L. conceived the study, conducted the sampling, interpreted the data and revised the manuscript. K.J.K. and R.S.N. conducted the mathematical analysis. K.A.H., P.D., C.J., G.Z., and J.Z.M. provided substantive comments on the manuscript. P.D., G.Z. and C.J. provided access to the samples. The research was supported by funding awarded to F.J.L. and R.S.N.

Competing financial interests

The authors declare no competing financial interests.

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Supplementary Tables

Supplementary Table 1. Sample data set including location, time, species, and isotopic compositions for Pleistocene megafauna.

Supplementary Table 2. Sample data set including location, time, species, and isotopic compositions for modern high-latitude plants.

Supplementary Table 3. Summary of AIC*c* results for models assessing δ^{13}C response.

Supplementary Table 4. Summary of AIC*c* results for models assessing δ^{15}N response.

Supplementary Table 5. Results of the SIBER mathematical analysis for groups from each region and time.

Appendices

Appendix A: Analytical methods

Appendix B: Model selection

Appendix C: Less commonly analysed species

Appendix D. Regional parameters

Appendix E. Temporal parameters

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Reframing the mammoth steppe: Insights from analysis of isotopic niches.

Appendices A-E

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Appendix A: Analytical methods

Collagen extraction for stable isotope analysis was performed at the Laboratory for Stable Isotope Science, The University of Western Ontario, London, Canada using a modified Longin (1971) method with minor alterations (Metcalfe et al., 2010). Samples were removed from specimens using a Dremel® cutting wheel and the exposed surfaces cleaned. Consolidant was removed from sample surfaces using a Dremel equipped with a burr attachment. Consolidant and its removal does not significantly affect collagen carbon and nitrogen isotope compositions (France et al., 2011). Samples were then crushed and treated with 0.25 M HCl at room temperature for 24 hours. This solution was then replaced by 0.5 M HCl held at room temperature; the acid was changed daily until the samples were gelatinized. After gelatinization, humic removal was performed at room temperature with a solution of 0.1 M NaOH for 20 minutes and repeated until the solution remained clear. The samples were then rinsed with water at room temperature until NaOH was removed completely. HCl was then used to adjust the pH to less than 3, and the collagen was solubilised at 90°C.

A Costech elemental combustion system (ECS 4010) attached to a Thermo-Scientific Delta V or to a Thermo-Scientific Delta^{plus} XL stable isotope ratio mass spectrometer (IRMS) operated in continuous-flow mode was used to measure the carbon and nitrogen isotope compositions. Two-point calibrations were used to relate the measured carbon and nitrogen isotope compositions to internationally accepted standards (VPDB for carbon, AIR for nitrogen). Values of δ^{13}C were calibrated to VPDB using NBS-22 (accepted value –30.0 ‰) and IAEA-CH-6 (accepted value –10.5 ‰) or USGS-40 (accepted value –26.4 ‰) and USGS-41 (accepted value +37.6 ‰). Values of δ^{15}N were calibrated to AIR using USGS-40 (accepted value –4.5 ‰) and either IAEA-N2 (accepted value +20.3 ‰) or USGS-41 (accepted value +47.6 ‰). The same standards were used to provide two-point calibration curves for sample carbon and nitrogen contents, using the following accepted values: NBS-22, C = 86.3 %; IAEA-CH-6, C = 42.1 %; USGS-40, C = 40.7%, N = 9.5 %; USGS-41, C = 40.7%, N = 9.5%; IAEA-N2, N = 21.5%. Accuracy and precision were assessed using an internal laboratory keratin standard (MP Biomedicals Inc., Catalogue No. 90211, Lot No. 9966H), which was included in all analytical sessions. For 92 measurements of this standard, δ^{13}C = –24.1 ± 0.1 ‰ (mean ± 1 SD; accepted value, –24.1 ‰), δ^{15}N = +6.3 ± 0.2 ‰ (accepted value, +6.4 ‰), C content = 48 ± 1 wt. % (accepted value, 46.8 wt. %), N content = 15 ± 1 wt. % (accepted value, 14.6 wt. %), and atomic C/N ratio = 3.7 ± 0.2 (accepted value, 3.7). Reproducibility of the isotopic data was evaluated for 31 samples. The standard deviation between values varied for δ^{13}C from 0.0 - 0.5 ‰, with an average difference of 0.1 ‰, and for δ^{15}N, from 0.0 - 0.2 ‰ (SD), with an average difference of 0.1 ‰.

New radiocarbon dates for previously undated specimens were obtained from the University of Arizona Accelerator Mass Spectrometry (AMS) Laboratory without ultrafiltration.

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Appendix B: Model selection

B.1. Methods

We considered a total of 18 models in our analyses with the most parameterized model including isotopic composition (δ^{13}C or δ^{15}N) as the dependent variable with interaction terms for species with region, species with time, and region with time, plus their singular terms as explanatory variables (Table B.1). Other models considered in the analysis included various combinations of those variables (Table B.1; Supplementary Tables 2-5). We assessed the normality and heteroscedasticity of the linear models with normal quantile-quantile plots and with residual-fitted value plots. Candidate models were first assessed using AIC values adjusted for small sample sizes (AIC*c*), and those with lowest ΔAIC*c* (0 to 4) were deemed to best fit the data. This analysis was conducted separately for carbon and nitrogen for all Pleistocene specimens falling into pre-LGM, LGM and post-LGM time bins. For the top models selected using AIC*c*, we then assessed the 85% confidence intervals (CI) of the coefficients for each parameter. Coefficients with 85% CIs that did not overlap 0 were considered informative (Arnold, 2010) and thus were retained in our analysis. Linear modeling was performed in R version 3.2.2 (R-Core-Team, 2012) using the R Studio interface version 0.99.484 (R-Studio-Team, 2015).

Table B.1. Candidate models used to assess differences in isotope (δ^{13}C, δ^{15}N) data for megaherbivores from the mammoth steppe.

No.	Model
1	Isotope (δ^{13}C or δ^{15}N) ~ 1 + Species + Region + Time + Region:Species + Time:Species + Time:Region
2	Isotope ~ 1 + Species + Region + Time + Region:Species + Time:Species
3	Isotope ~ 1 + Species + Region + Time + Region:Species + Time:Region
4	Isotope ~ 1 + Species + Region + Time + Time:Species + Time:Region
5	Isotope ~ 1 + Species + Region + Time + Region:Species
6	Isotope ~ 1 + Species + Region + Time + Time:Species

7	Isotope ~ 1 + Species + Region + Time + Time:Region
8	Isotope ~ 1 + Region + Time + Time:Region
9	Isotope ~ 1 + Species + Region + Region:Species
10	Isotope ~ 1 + Species + Time + Time:Species
11	Isotope ~ 1 + Species + Region + Time
12	Isotope ~ 1 + Species + Region
13	Isotope ~ 1 + Species + Time
14	Isotope ~ 1 + Region + Time
15	Isotope ~ 1 + Region
16	Isotope ~ 1 + Species
17	Isotope ~ 1 + Time
18	Isotope ~ 1
19	Isotope (δ^{13}C or δ^{15}N) ~ 1 + Species + Region + Time + Region:Species + Time:Species + Time:Region + Region*Species*Time

B.2. Results

B.2.1 Results for Carbon

Of the 18 models considered for the δ^{13}C data (Table B.1), only one model had ΔAIC*c* < 4. This model was the best fit both for all the dated Pleistocene samples (Supplementary Table 2), and for samples from the most data-rich groups (Supplementary Table 3). This model included ‘Species’, ‘Region’ and ‘Time’, and the interaction terms for ‘Region:Species’ and ‘Time:Species. The interaction terms indicate differences in δ^{13}C between species among regions and between species with time. There was no heteroscedastity and the residual and Q-Q plots were normal. Confidence intervals (CIs) of the parameters ‘Species’, ‘Region’, ‘Region:Species’ and ‘Time:Region’ did not overlap 0, indicating that they were informative terms. The CIs for ‘Time’ overlapped 0 for the model, indicating no overall differences in δ^{13}C between time bins; this parameter was therefore not considered further.

B.2.2 Results for Nitrogen

Of the 18 models considered for δ^{15}N (Table B.1), the most parameterized model and the second-most parameterized model had $\Delta AIC_c < 4$ (Supplementary Table 4). Both models included 'Species', 'Region' and 'Time', as well as the interaction terms 'Region:Species', 'Time:Species' and 'Time:Region', and one of the models included 'Region:Species:Time'. There was no heteroscedastity and the residuals were normal. All parameters were considered informative at the 85% confidence level (i.e. did not overlap 0) for the model that included all Pleistocene samples.

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Appendix C: Less commonly analysed species

C.1. Results

Nine species (camel (*Camelops hesternus*), cave bear (*Ursus spelaeus, Ursus ingressus* and *U. kudarensis*), helmeted muskox (*Bootherium bombifrons*; when not distinguished as 'helmeted muskox', this paper refers to *Ovibos* as muskox), ibex goat (*Capra pyrenaica*), moose (*Alces alces*), mastodon (*Mammut americanum*), roe deer (*Capreolus capreolus*), saiga antelope (*Saiga tatarica*) and sheep (*Ovis dalli*) infrequently had dated specimens with measured isotopic compositions (e.g. only at one site or in one time bin). While these species may have been common on the mammoth steppe, the lack of isotopic data for them means that only qualitative observations were possible. These observations are summarized in Table C.1.

Table C.1. Isotopic observations for less commonly analyzed species on the mammoth steppe.

Species	Times Present	Regions Present	Niche
Camel	Post-LGM	Alberta	Higher δ^{15}N and δ^{13}C than all except caribou
Cave bear	Pre-LGM	Jura, Iberian Peninsula, northwestern Europe	Overlapping niche with horse
Helmeted Muskox	Pre-LGM, Post-LGM	Alberta, eastern Beringia	Similar δ^{15}N to horse, lower than muskox, similar δ^{13}C to camel/muskox
Ibex goat	Pre-LGM, Post-LGM	Iberian Peninsula	Similar low δ^{15}N to elk, δ^{13}C varies between time bins (lowest or middle)
Mastodon	Post-LGM	Great Lakes area	Low δ^{15}N, similar δ^{13}C to mammoth
Moose	Post-LGM	Jura	Lower δ^{15}N than mammoth and rhinoceros, higher than caribou and bison. Similar δ^{13}C to bison, rhinoceros.
Roe deer	Pre-LGM	Northwestern Europe	Similar δ^{15}N and δ^{13}C to elk
Saiga	Pre-LGM, LGM, Post-LGM	Eastern Beringia, south-central Siberia, Russian plain, northwestern Europe	Overlapping niche with caribou and muskox
Sheep	LGM, post-LGM	Eastern Beringia	Ranges from lowest δ^{15}N to highest

C.2. Discussion

At present, only limited inferences can be made for these species by comparing their δ^{13}C and δ^{15}N position and niche overlap to coeval species (Table C.1), as follows.

Pleistocene camels were found across North America as far north as eastern Beringia (Zazula et al., 2011). Stable isotope and teeth-wear analyses suggest they were mixed feeders (Semprebon and Rivals, 2010; Yann et al., 2016). In post-LGM Alberta, both browse and graze forage would have been available. The relatively high camel δ^{15}N and δ^{13}C suggests they were likely consuming primarily graze, or were consuming another plant species with high δ^{15}N such as sedge.

Cave bear has an overlapping isotopic niche with horse, supporting the hypothesis of an herbivorous diet (e.g. Bocherens et al., 2006, 2014, 2018; Krajcarz et al., 2016). Hibernation may have caused increased δ^{15}N and decreased δ^{13}C (Bocherens, 2015, 2018; Pérez-Rama et al., 2011). It is not known, however, if this effect would have caused a sufficient isotopic shift to remove the niche overlap. When in direct competition with herbivorous brown bears, cave bears may have avoided competition by using niches from different altitudes (García-Vázquez et al., 2018).

The helmeted muskox has a lower δ^{15}N than *Ovibos* sp., potentially indicating some browse consumption, and suggesting distinct dietary strategies for the two genera.

Modern ibex are mixed feeders whose diet varies with altitude, season and population density. (Acevedo and Cassinello, 2009). Pleistocene ibex were similarly reconstructed as mixed feeders based on tooth-wear studies (Rivals and Álvarez-Lao, 2018; Rivals et al., 2017). The low δ^{15}N of ibex are similar to the mixed-feeding elk, and likely indicate some browse consumption. Their variable δ^{13}C over time may indicate feeding in both open environments and closed forest canopies.

A browsing dietary niche has been established for mastodon (Coltrain et al., 2004; Green et al., 2017; Haynes, 1991; Koch et al., 1998; Rivals et al., 2012; Zazula et al., 2014), consistent with its interglacial occupancy of regions considered at other times to be mammoth steppe. While trees were not present in all regions and times during the Pleistocene, woody shrubs were present during much of this time (e.g., Goetcheus and Birks, 2001; Höfle et al., 2000; Zazula et al., 2014). If mastodon were obligate browsers, that may explain why they were not found in most of the mammoth steppe regions after the last interglacial (Jass and Barrón-Ortiz, 2017; Zazula et al., 2014). A significant browse component in mastodon diet may also explain its low δ^{15}N (Coltrain et al., 2004; Koch et al., 1998; Metcalfe et al., 2013, 2016; Metcalfe and Longstaffe, 2014; Zazula et al., 2014). Additionally, the low mastodon δ^{15}N may reflect lower plant δ^{15}N baselines during warmer periods such as interglacials (Tahmasebi et al., 2018).

Modern moose are browse specialists that seasonally consume aquatic plants where available, as aquatic plants are high in protein (Ben-David et al., 2001; Kaiser et al., 2013; MacCracken et al., 1993; Wam and Hjeljord, 2010). Pleistocene moose tooth-wear is consistent with a browse diet (Saarinen et al., 2016). A diet including high δ^{15}N aquatic plants (Milligan, 2008) is consistent with their higher δ^{15}N relative to bison. Some modern bison and moose populations have similar δ^{15}N, but these bison populations likely fed on atypical forage (Hofman-Kamińska et al., 2018).

Modern and Pleistocene roe deer were browsers (Lovari et al., 2017; Rivals and Álvarez-Lao, 2018.) Modern roe deer typically prefer glades at the edges of forests rather than closed canopy forests (Lovari et al., 2017). The Pleistocene roe deer had similar isotopic compositions to the mixed-feeding Pleistocene elk.

Pleistocene saiga antelope may have had mixed-feeding diets with a winter portion of lichen, similar to caribou (Drucker and Henry-Gambier, 2005; Jürgensen et al., 2017), consistent with the overlapping isotopic niches of caribou and saiga. Modern saiga antelope consume a mixture of browse and graze (Kaiser et al., 2013), but are unable to thrive on a diet of pure graminoids (Abaturov and Dzapova, 2015). Pleistocene saiga, however, were suggested to have had substantial dietary flexibility and to have eaten from a wide dietary niche during the Pleistocene (Jürgensen et al., 2017), consistent with saiga overlapping their niche with the core niche of both caribou and muskox.

Modern Dall sheep are mixed-feeders with a flexible diet. Their Pleistocene population has been reconstructed as having been seasonal grazers (Rivals et al., 2010). Pleistocene Dall sheep have a wide range in δ^{15}N, potentially consistent with a mixed-feeding diet. Dall sheep survived the Terminal Pleistocene extinctions and currently occupy alpine habitats (Guthrie, 1982); their survival may have been aided by dietary flexibility. Some specimens considered as *O. dalli* here may have been classified as such, in part, based on geographic location. That species-level assignment requires further testing.

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Appendix D: Regional parameters

D.1. Results

The interaction term of ‘Species’ and ‘Region’ was informative in explaining variation in δ^{13}C whereas the interaction term of ‘Region’ with ‘Time’, and of all three parameters, ‘Region’, ‘Species’ and ‘Time’, were not. We therefore considered the pattern of δ^{13}C variation between regions with different species, but did not consider it with different time bins. For all common species except caribou (bison, elk, horse, muskox, mammoth and rhinoceros) δ^{13}C Yakutia < Northeastern Europe, Northwestern Europe & North Slope Alaska < Jura < Alberta (Fig D.1).

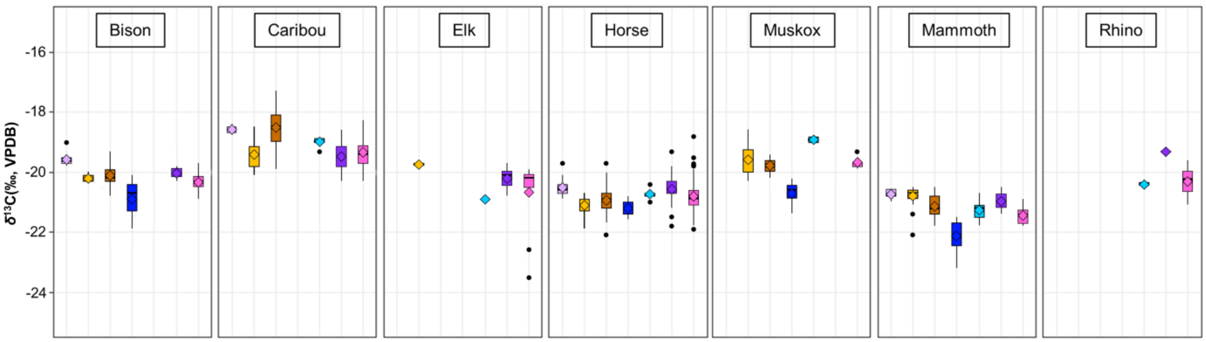

Figure D.1. Box and whisker plots showing variation – by region – in δ^{13}C aggregated across time bins for the most commonly analysed megafaunal herbivores for each region. Lilac = Alberta, yellow = eastern Beringia, orange = North Slope, dark blue = Yakutia, light blue = northeastern Europe, purple = Jura, pink = northwestern Europe. The diamond represents the mean value, the line indicates the median value and boxes show the 25th and 75th percentiles. Whiskers show the largest value that extends no further from the outside of the box than 1.5 times the distance between the 25th and 75th percentiles. Data outside the whiskers are outliers.

Although ‘Region’, ‘Region:Species’, ‘Time:Region’ and ‘Region:Species:Time’ were all considered informative parameters in the top δ^{15}N models as defined using AIC*c*, consistent regional patterns were difficult to observe (Fig. D.2). Only tentative patterns could be assigned. In the majority of cases, δ^{15}N of Alberta < eastern Beringia < Yakutia, and in the majority of cases northeastern Europe < Jura & northwestern Europe.

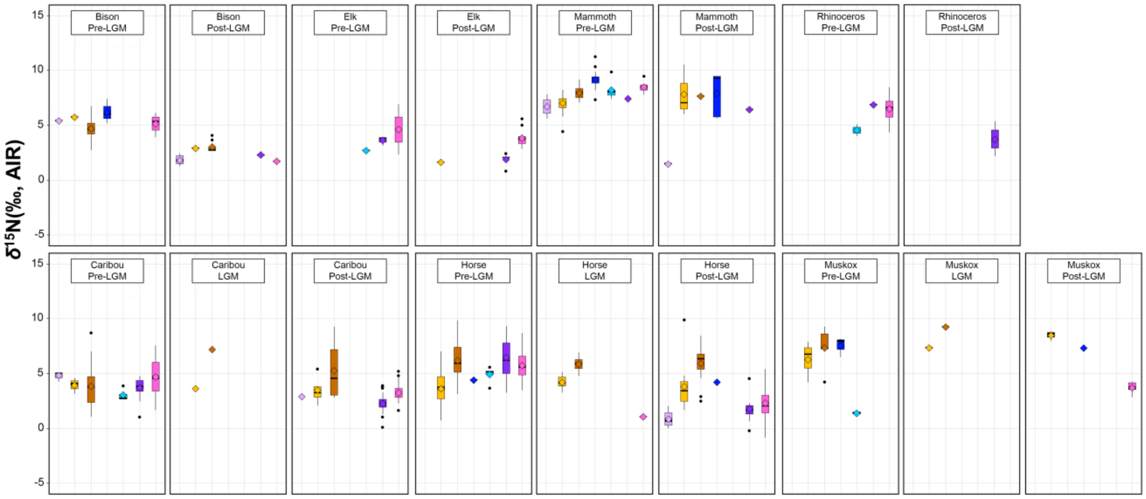

Figure D.2. Box and whisker plots showing variability in δ^{15}N for each region during each time bin. Lilac = Alberta, yellow = eastern Beringia, orange = North Slope, dark blue = Yakutia, light blue = northeastern Europe, purple = Jura, pink = northwestern Europe. The diamond represents the mean value, the line indicates the median value and boxes show the 25th and 75th percentiles. Whiskers show the largest value that extends no further from the outside of the box than 1.5 times the distance between the 25th and 75th percentiles. Data outside the whiskers are outliers.

D.2. Discussion

A number of mechanisms could explain the regional differences in δ^{13}C. Systematic variations in canopy cover could produce the observed distribution of δ^{13}C (Bonafini et al., 2013; Drucker et al., 2008). However, regions experienced differing levels of forest cover over time, and yet the δ^{13}C pattern generally held consistent (Binney et al., 2017). Altitude could play a role (Heaton, 1999; Kohn, 2011), particularly given the higher δ^{13}C of the Jura mountain region baseline, though it would not explain the higher δ^{13}C of Alberta. An aridity gradient is not a parsimonious explanation, as it should have affected both δ^{15}N and δ^{13}C (Amundson et al., 2003; Kohn, 2010), but there is no clear pattern in δ^{15}N between regions. Differences in light levels between regions at different latitudes are also unlikely to have played a role, as the δ^{13}C pattern does not correspond to latitude differences. Temperature may have played a role in the low average δ^{13}C in the Yakutia region. We conclude that the δ^{13}C pattern likely represents the interplay of several factors. Notably, caribou do not appear to follow the typical pattern between regions, suggesting an atypical response to changes between regions. This further complexity cautions against use of a single species or region to draw conclusions about isotopic patterns across the mammoth steppe.

A complex interplay of factors is likely involved in setting the δ^{15}N baseline of regions as well. The mammoth steppe contained a variable mosaic of plant types across its span (Blinnikov et al., 2011; Willerslev et al., 2014) and varied climatically within regions because of factors such as distance from a melting glacier and the maturity of the underlying soil (Drucker, 2012; Drucker et al., 2003, 2011; Stevens et al., 2008). More browse availability in some regions (e.g. Binney et al., 2017) could lead its mixed-feeders to have lower δ^{15}N, though a corresponding decrease in δ^{13}C would be expected to result from feeding in a dense canopy (Bonafini et al., 2013; Drucker et al., 2008). A lack of clear patterns in δ^{15}N could also result from shifts over time in a region's correspondence to the steppe or tundra model. Species responded to Pleistocene climatic changes with individualistic migration patterns and adaptations (Baca et al., 2017). As such, the considerable variability in the isotopic response of species to regional differences is perhaps unsurprising.

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Appendix E. Temporal parameters

E.1. Results

‘Time’ was not an informative parameter in the top linear model for δ^{13}C, and so the data was not assessed.

‘Time’, ‘Time:Species’, ‘Time:Region’ and ‘Region:Time:Species’ were all informative variables in top δ^{15}N models. The δ^{15}N of the post-LGM was lower than pre-LGM for virtually all species and regions (Fig. E.1). Exceptions to this pattern occurred for three species in eastern Beringia (horse, muskox and mammoth), for one species in North Slope Alaska (caribou) and one species in Taymyr Peninsula (mammoth). There was no apparent pattern to the change in δ^{15}N of a species or region during the LGM.

Figure E.1. Box and whisker plots showing variability in δ^{15}N for the most common regions during each time bin for each species. Purple = pre-LGM, blue = LGM, light blue = post-LGM. The diamond represents the mean value, the line indicates the median value and boxes show the 25th and 75th percentiles. Whiskers show the largest value that extends no further from the outside of the box than 1.5 times the distance between the 25th and 75th percentiles. Data outside the whiskers are outliers.

E.2. Discussion

Some previous work has detected patterns in the δ^{13}C variation of a species or a region over time, and related them to changes in pCO$_2$ and/or canopy cover (Noe-Nygaard et al., 2005; Raghavan et al., 2014; Richards and Hedges, 2003). We found no evidence for patterns in δ^{13}C over time that encompass most regions or species. This suggests that changes in δ^{13}C do not reflect a global phenomenon, such as changed pCO$_2$. Instead, they may reflect species' dietary shifts in response to changing conditions (e.g. after the extinction of the cave bear, the Iberian elk δ^{13}C shifts into the previously occupied niche; García-Vázquez et al., 2018), or changes in the forest extent and structure and thus the level of canopy cover (e.g. Binney et al., 2017; Strong and Hills, 2005; Willerslev et al., 2014).

Previous work on the changing δ^{15}N baseline of regions over time commonly focuses on narrow time windows and small regions. Using this approach, low δ^{15}N post-LGM was found to correspond to immature soils derived from a recently melted glacier (Drucker, 2012; Drucker et al., 2010, 2011; Stevens et al., 2008). This may also have played a role in the low post-LGM δ^{15}N that characterizes Alberta, as new soil formation would have been initiated in the wake of retreating glaciers. However, this can also be considered a global phenomenon relating to increased moisture levels post-LGM (Rabanus-Wallace et al., 2017). While average δ^{15}N changed over time, the magnitude or direction of change was not the same for all species or all regions. For example, a larger dataset of Taymyr peninsula and Yakutia mammoth do not show a decrease in δ^{15}N post-LGM in either region (Kuitems et al., 2019). This suggests that some species responded to the changing climatic conditions by varying their diet or that ecological shift varied between regions. There may be additional δ^{15}N baselines shifts between smaller climatic events, as observed within the pre-LGM in Europe (Bocherens et al., 2014). Future studies of additional regions over narrow time windows would be useful in further testing of this possibility.

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