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Adapt or die—Response of large herbivores to environmental changes in Europe during the Holocene

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Adapt or die - response of large herbivores to environmental changes in Europe during the Holocene

Running head: Holocene foraging ecology of large herbivores

Primary Research Articles

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ABSTRACT

Climate warming and human landscape transformation during the Holocene resulted in environmental changes for wild animals. The last remnants of the European Pleistocene megafauna that survived into the Holocene were particularly vulnerable to changes in habitat. To track the response of habitat use and foraging of large herbivores to natural and anthropogenic changes in environmental conditions during the Holocene, we investigated carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope composition in bone collagen of moose (*Alces alces*), European bison (*Bison bonasus*) and aurochs (*Bos primigenius*) in Central and Eastern Europe. We found strong variations in isotope compositions in the studied species throughout the Holocene and diverse responses to changing environmental conditions. All three species showed significant changes in their δ^{13}C values reflecting a shift of foraging habitats from more open in the Early and pre-Neolithic Holocene to more forest during the Neolithic and Late Holocene. This shift was strongest in European bison, suggesting higher plasticity, more limited in moose, and the least in aurochs. Significant increases of δ^{15}N values in European bison and moose are evidence of a diet change towards more grazing, but may also reflect increased nitrogen in soils following deglaciation and global temperature increases. Among the factors explaining the observed isotope variations were time (age of samples), longitude and elevation in European bison, and time, longitude and forest cover in aurochs. None of the analyzed factors explained isotope variations in moose. Our results demonstrate the strong influence of natural (forest expansion) and anthropogenic (deforestation and human pressure) changes on the foraging ecology of large herbivores, with forests playing a major role as a refugial habitat since the Neolithic, particularly for European

bison and aurochs. We propose that high flexibility in foraging strategy was the key for survival of large herbivores in the changing environmental conditions of the Holocene.

INTRODUCTION

The Holocene has been an epoch of highly dynamic environmental changes (Roberts *et al.*, 2018). Warming of the climate since the Pleistocene/Holocene transition and Late Weichselian Glacial retreat in Europe resulted in forest expansion during the Early Holocene, with maximum forest cover established by around 8200 cal yrs BP. Early Holocene (11,650 - 8200 cal yrs BP) (Walker *et al.*, 2012) tree migration and forest expansion was followed by human expansion and the development of agriculture during the Neolithic (between 7000 to 2600 cal yrs BP, although dates for the Neolithic vary slightly in different regions of Central and Eastern Europe) (Puhe & Ulrich, 2001). The start of the Neolithic resulted in demographic explosion and increasing human pressure on the environment (Gignoux *et al.*, 2011, Shennan *et al.*, 2013), leading to progressive deforestation of the continent (Kaplan *et al.*, 2009, Roberts *et al.*, 2018). The transformation of Europe's landscapes from a nature-dominated to a more human-dominated state has been long and complex (Fyfe et al. 2015, Roberts et al. 2018). It created dynamic habitat conditions and strongly limited access to preferred habitats for wild animals, and influenced their distribution, densities, fitness or food habits, and in the worst cases led to population extirpations or species extinctions (Crees *et al.*, 2016, Pavelková Řičánková *et al.*, 2015, Rosvold *et al.*, 2013).

The majority of the abundant Pleistocene megafauna in Europe became extinct before the start of the Holocene (Elias & Schreve, 2007, Pacher & Stuart, 2009, Stuart, 1991). The major patterns of postglacial changes in Palearctic mammalian diversity were not extinctions but rather radical shifts of species distribution ranges and retreat northwards or eastwards (Pavelková Řičánková *et al.*, 2015). Few species of large European mammals survived the

Pleistocene/Holocene transition, and inhabited the European continent during the subsequent millennia (Benecke, 2005, Pavelková Řičánková *et al.*, 2015, Schmölcke & Zachos, 2005). These species were exposed to several processes related to climate and habitat change, as well as increasing human pressure (Hofman-Kamińska *et al.*, 2018b, Rosvold *et al.*, 2013). Two species, European bison (*Bison bonasus*) and moose (*Alces alces*), survived until present (moose) or were restored in the wild from captive survivors after extirpation at the beginning of the 20th century (European bison). Aurochs (*Bos primigenius*), widely distributed in Europe during the Pleistocene, survived into the Holocene but finally became extinct during the early 17th century (Van Vuure, 2005).

The feeding habits of these large herbivores have been detected by stable isotope analysis in the Pleistocene/Holocene transition and at the beginning of the Holocene (12,000±600 - 10,022±229 cal yrs BP) (Bocherens *et al.*, 2015). These feeding habits ranged from grazing in aurochs, to mixed-feeding in European bison, and to browsing in moose, reflecting feeding types determined by digestive system classification (Hofmann, 1989) and probably represent the natural feeding behaviour of these species. Changes in the diet patterns of these large herbivores have been identified by dental microwear textural analysis (DMTA) (Hofman-Kamińska *et al.*, 2018b) and may indicate behavioural changes in response to environmental changes, as well as different periods of favorable conditions during the Holocene in Europe. Forested areas, favorable for browsers such as moose, but marginal for grazers such as aurochs and European bison, might have created refugia from increasing human pressure during the mid-Holocene and promoted the survival of these latter species in forest habitats, but in circumstances of lowered fitness and population densities. This may have led to increased stochasticity and population fragmentations, and local extinctions (Cromsigt *et al.*, 2012, Kerley *et al.*, 2012). Opening of forest habitats would have created more optimal foraging conditions for grazers, less for browsers, but might have exposed them to increased human pressure and had similar effects (reduced fitness, population fragmentation and local extinction). Large mammals are particularly vulnerable to environmental changes and habitat fragmentations and exposed to risk of extirpation or extinction due to their body size, lower densities, larger spatial requirements, and disproportional exploitation by humans, particularly more specialized species that have a lower capacity for adaptation (Cardillo *et al.*, 2005, Keinath *et al.*, 2017). Did they adapt to the limits set by their morphological characteristics and foraging plasticity or not? What processes promoted their survival or led to their disappearance as habitat structure changed? Reconstruction of foraging habitats and dietary behavior may shed light on how large herbivores coped with changing environmental conditions.

Stable carbon and nitrogen isotopic ratios are increasingly used as environmental and dietary indicators for modern as well as for fossil herbivores (Bocherens *et al.*, 2009, Bocherens *et al.*, 2015, Britton *et al.*, 2012, Drucker *et al.*, 2003, Drucker *et al.*, 2010, García *et al.*, 2009, Gąsiorowski *et al.*, 2014, Gron & Rowley-Conwy, 2017, Hofman-Kamińska *et al.*, 2018a, Jürgensen *et al.*, 2017, Noe-Nygaard *et al.*, 2005, Šturm *et al.*, 2017). In this study we used stable carbon and nitrogen isotope compositions from radiocarbon dated bone samples as proxies for foraging habitats and diet of European bison, moose and aurochs throughout the Holocene in Europe. By studying the foraging ecology of three European large herbivore species over millennial timescales during the Holocene we aimed to: (1) identify habitat preferences and diets before and after the Neolithic environmental transformations; (2) analyze the response of the largest remaining Pleistocene megafauna in Europe to the major environmental changes of the Holocene (from increasing tree cover during the Early and pre-Neolithic Holocene to increasing habitat openness during the Neolithic and subsequent time periods); and (3) identify factors influencing their patterns of habitat use and diet. We hypothesized that forest expansion in the early Holocene forced large herbivores, especially those primarily adapted to grazing (aurochs and European bison) into forests as refugial habitats, to shift their pattern of habitat use, resulting in stable isotopic signatures change. Subsequently, increasing human pressure did not allow large herbivores to return to more open habitats, despite the creation of open habitats resulting from the deforestation of Europe in the Late Holocene.

MATERIALS AND METHODS

Sample collection and age determination

A total of 295 bone samples, including 121 European bison, 91 aurochs and 83 moose originating from 14 European countries were collected from paleontological, zoological and private collections (Table S1) in Central and Eastern Europe (Figure 1). We validated the species identification (especially for European bison and aurochs bones) (Gee, 1993), by comparing characteristic morphological features using modern European bison and moose bones from zoological collection of the Mammal Research Institute PAS in Białowieża and other well identified historical specimens as reference material. Additionally, we included into the analysis published stable carbon isotopic data for 69 specimens (19 moose, 5 European bison and 45 aurochs) and stable nitrogen isotopic data for 36 specimens (12 moose, 5 European bison and 19 aurochs) available in the literature (Antanaitis-Jacobs *et al.*, 2009, Bocherens *et al.*, 2015, Fornander *et al.*, 2008, Gravlund *et al.*, 2012, Jessen *et al.*, 2015, Lidén *et al.*, 2004, Linderholm *et al.*, 2014, Noe-Nygaard *et al.*, 2005). In total, 364 large herbivore bone samples and literature records were used in the study (Figure 1).

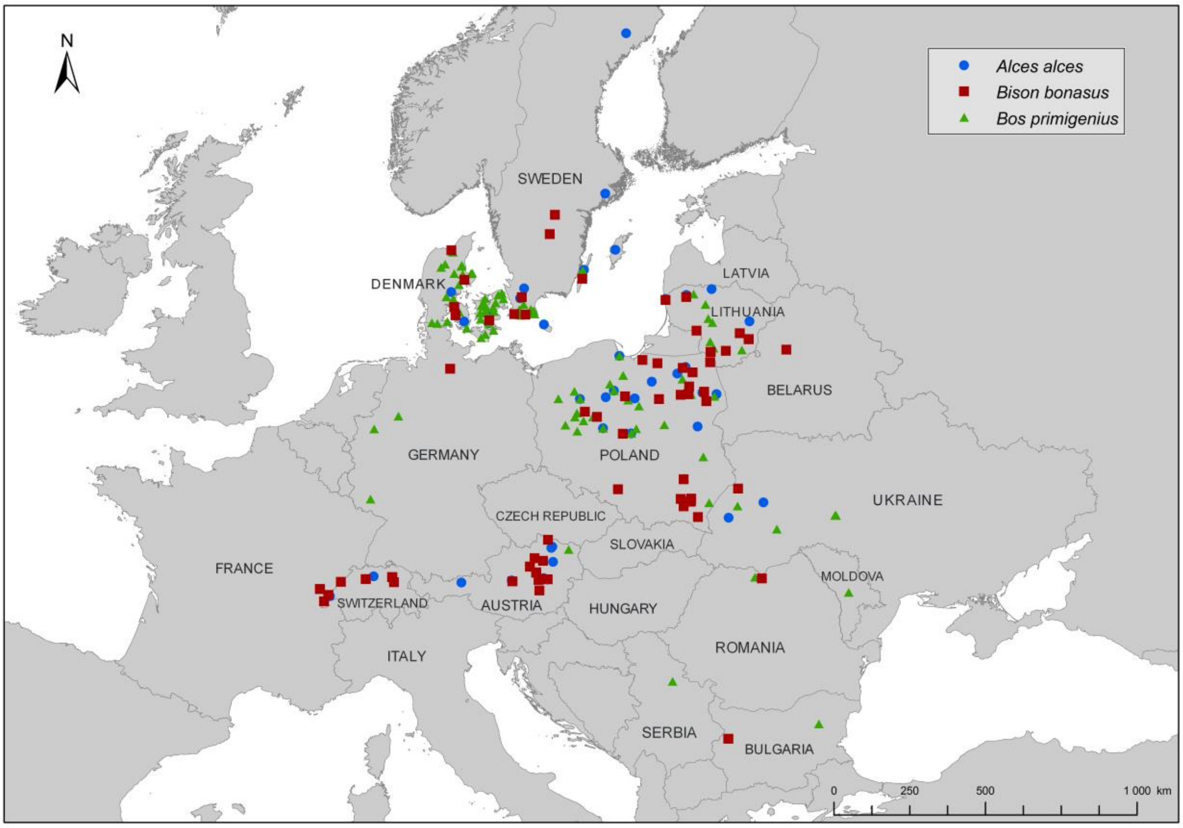

Figure 1. Distribution of localities with specimens of moose (*Alces alces*) (blue circles), European bison (*Bison bonasus*) (red squares) and aurochs (*Bos primigenius*) (green triangles) in the Holocene.

Age determinations of the bone samples were based on radiocarbon dating from the literature or museum data, or derived from archeological context. For 94 specimens without any, or uncertain, age determination we performed direct radiocarbon dating at the Laboratory of Ion Beam Physics, Eidgenössische Technische Hochschule Zürich, Switzerland (Swiss Federal Institute of Technology Zürich) (ETH). All radiocarbon dates were calibrated to BP dates with 1σ (95.4%) probability using the IntCal13 calibration curve in OxCal v4.2 (Reimer *et al.*, 2013). In total 186 bone samples were ^{14}C dated, another 178 had a well identified archeological context, in most of cases confirmed by additional radiocarbon dates performed for this study.

This study is unique in incorporating the analysis of an unprecedented number of European bison (*Bison bonasus*) bone material (126), (distributed widely across the European continent), a species with a very poorly studied Holocene history. Additionally, we provide a very large number of new ^{14}C radiocarbon dated bones for this species (59). Before this study only 32 radiocarbon dated European bison specimens were published (Blant & Wenger, 2010, Bocherens *et al.*, 2015, Ekström, 1993, Herrmann *et al.*, 2010, Hofman-Kamińska *et al.*, 2018b, Soubrier *et al.*, 2016, Spitzenberger, 2002, Węcek *et al.*, 2016).

Collagen extraction and stable isotope analysis

Small pieces of compact bone (0.7 g) were cleaned with acetone and distilled water in an ultrasound bath in order to remove dust and potential glue remains, before being crushed to a powder and sieved to obtain a grain size no larger than 0.7 mm. Collagen for the isotopic measurements was prepared according to the protocol described by Bocherens et al. (Bocherens *et al.*, 1997).

The elemental and isotopic measurements were performed at the Department of Geosciences at the University of Tübingen (Germany) using an elemental analyzer NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. The isotopic ratios were expressed using the "δ" (delta) value as follows: $\delta^{13}C = [(^{13}C/^{12}C)_{sample} / (^{13}C/^{12}C)_{reference} - 1] \times 1000(‰)$, $\delta^{15}N = [(^{15}N/^{14}N)_{sample} / (^{15}N/^{14}N)_{reference} - 1] \times 1000(‰)$. The internationally defined standards were V-PDB for $\delta^{13}C$ values and atmospheric nitrogen (AIR) for $\delta^{15}N$ values. Samples of collagen were normalized to $\delta^{13}C$ values of USGS24 ($\delta^{13}C$ = -16.00‰) and to $\delta^{15}N$ values of IAEA 305A ($\delta^{15}N$ = 39.80‰). The reproducibility was ±0.1‰ for $\delta^{13}C$ and ±0.2‰

for δ^{15}N measurements based on multiple analysis of purified collagen from modern bones (n > 175).

The reliability of the isotopic signatures of the collagen extracts was addressed using their chemical composition. Only high quality extracts with %C, %N, and C/N similar to those of collagen extracted from fresh bone were used for isotopic measurements. Therefore, only collagen extracts that had atomic C/N ratios with $2.9 \leq C/N \leq 3.6$ (DeNiro, 1985), %C > 8% and %N > 3% were taken for the analysis (Ambrose, 1990).

δ^{13}C and δ^{15}N variables

In European temperate and boreal ecosystems, woody and herbaceous plants follow the C_3 photosynthetic pathway and have δ^{13}C values ranging from -35‰ to -20‰ (Dawson *et al.*, 2002). The fraction of the vegetation that is C_4 is less than 0.1 and concentrates mostly in southern Europe (Still *et al.*, 2003). Plants growing under the canopy of densely forested environments exhibit lower δ^{13}C values in comparison to plants from open conditions (Bonafini *et al.*, 2013, Broadmeadow *et al.*, 1992, Gebauer & Schulze, 1991, Van der Merwe & Medina, 1991). Such a depletion in δ^{13}C is reflected in the bone collagen of forest-dwelling herbivores in boreal and temperate forests (Drucker & Bocherens, 2009, Drucker *et al.*, 2008), with a tentative threshold δ^{13}C value for foraging under dense canopy forest at -22‰, meaning that herbivores with such collagen δ^{13}C values have been foraging essentially under a dense canopy cover (Drucker *et al.*, 2008). Recent studies conducted on modern European bison and moose confirm that with increasing percentage of forest cover, stable carbon isotope concentration in collagen of large herbivores decreases (Hofman-Kamińska *et al.*, 2018a). It confirms also that stable carbon isotopes in herbivore collagen, which is continuously replaced through the whole animal's life by the incorporation of new atoms of carbon deriving from the diet, reflects foraging in densely forested *versus* open landscape conditions. Such patterns allow us to reconstruct the foraging habitats of large herbivores in the past on the basis of $\delta^{13}C$ values.

$\delta^{15}N$ values differ between plant types. Non-mycorrhizal plants such as graminoids, forbs and clubmosses exhibit higher $\delta^{15}N$ values than ectomycorrhizal and ericoid plants, such as trees and shrubs (Ben-David *et al.*, 2001, Craine *et al.*, 2009, Emmerton *et al.*, 2001, Hobbie *et al.*, 2005, Kristensen *et al.*, 2011, Schulze *et al.*, 1994). Intermediate values of $\delta^{15}N$ are found in mosses (Craine *et al.*, 2009, McLeman, 2006, Michelsen *et al.*, 1998, Michelsen *et al.*, 1996). These results allow us to reconstruct diet type based on stable nitrogen isotope compositions, even if it is not possible to provide a threshold $\delta^{15}N$ value for bone collagen of grazers versus browsers due to the impact of local environmental factors, but in a given context, grazers typically exhibit higher $\delta^{15}N$ values than browsers (Bocherens, 2003, Bocherens, 2015). It has been shown that the $\delta^{15}N$ values in plants decline with increasing elevation (Huber *et al.*, 2007, Sah & Brumme, 2003, Sparks & Ehleringer, 1997). This is probably connected with lower mineralization and lower net nitrification rates induced by more abundant rainfall and lower temperatures at higher elevation (Liu & Wang, 2010).

Forest cover and spatial data

We extracted total tree cover (hereafter described as forest cover), deciduous tree cover and needle-leaf tree cover , values for each bone specimen from the published dataset of (Fyfe *et al.*, 2015) using the geographic coordinates of herbivore bones, and their calibrated age. This generated data that described that nature of vegetation for the location and time period of every sample. The estimates of forest cover in Fyfe *et al*. (2015) were generated using data from the European Pollen Database (Fyfe *et al.*, 2009, Leydet, 2007–2018). Pollen data from individual site records were aggregated into contiguous 200-year long time windows between 18,000 and 0 yrs BP using the chronologies in (Giesecke *et al.*, 2014) and transformed from pollen proportions to % land cover classes (LCCs) using the pseudobiomization approach (Fyfe *et al.*, 2010). The resulting values were interpolated to produce the spatially-continuous estimates of forest cover at 20 km resolution for each time window using a thin-plate spline with elevation as a co-variate (Fyfe *et al.*, 2015).

The elevation for each specimen was extracted from the global raster data grids from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) in ArcGIS 10.5.0 using spatial analysis tools (ESRI, 2017). We used median 7.5 arc-seconds resolution, which has a root mean square error (RMSE) range between 29 and 32 meters (Danielson & Gesch, 2011).

Statistical analysis

In order to obtain the age of radiocarbon dated samples for statistical analyzes, we calculated an average between the lower and higher calibrated age range. We applied the same procedure to determine the average age for specimens dated archaeologically, e. g. for a specimen dated between 16-17th century, we assumed the age of 400 cal years BP. First, we tested differences in δ^{13}C and δ^{15}N between moose, European bison and aurochs for the whole of the Holocene with ANOVA. The normality of the variables' distribution was tested with Shapiro-Wilk test. To check homogeneity of variance assumption, Brown-Forsythe and Levene tests were performed for each period. When ANOVAs showed statistically significant differences, post hoc comparisons were performed using Tukey's HSD test for unequal N. To test whether Neolithic agriculture impacted δ^{13}C and δ^{15}N of large herbivores, we divided the Holocene specimens according to the criteria of Neolithization (the timing of the Neolithic varies across our sites in Europe but is broadly between 7000 and 2600 cal yrs BP). The Early and pre-Neolithic Holocene specimens included those from regions where Mesolithic cultures (between 12,000 and 6000 cal yrs BP) still occurred according to regional studies and

Neolithic and Late Holocene specimens from locations in space and time where Neolithic and later agriculture was established (Antanaitis-Jacobs *et al.*, 2009, Deak *et al.*, 2018, Puhe & Ulrich, 2001). We explored changes in δ^{13}C and δ^{15}N variables between the two periods for each of the species separately. In the next step we performed one-way ANOVA to study differences in δ^{13}C and δ^{15}N between European bison, moose and aurochs in each of the two periods.

We ran separate models for each of the two stable isotopes for each of the three species to investigate factors influencing δ^{13}C and δ^{15}N in bone collagen (in total 6 models). Due to the high correlation ($R > 0.5$), from the whole set of available explanatory variables: percentage of the total forest cover, percentage of deciduous forest, percentage of needle-leaf forest, age, longitude, latitude and elevation we excluded percentage of deciduous forest (highly correlated with percentage of the total forest cover; R from 0.74 to 0.81 in different species) and latitude (highly correlated with elevation; R from 0.75 to 0.81 in different species). Percentage forest cover was not available for all our specimens, due to the lack of pollen data for the oldest specimens, or absence of precise dating of faunal material, therefore for modeling we used only records with complete datasets (among 69 records from the literature we used only 22 complete datasets). Due to the large discrepancy of scale ranges (6-29° in longitude vs. 0-12000 cal yrs BP in time), we standardized our explanatory variables in R to have a mean of 0 and a sd of 0.5 using function standardize.y (Gelman & Hill, 2007). We then ran multiple linear regression models with single isotope abundance as the response variable. The Akaike Information Criterion (AIC) with the second-order correction for a small sample size (AICc) was used for model ranking. We did not find a singular best model within any of the models run, so we applied model averaging where cumulative weights of subsets of models did not exceed 0.95. We looked at full model averaging to identify factors significantly affecting δ^{13}C and δ^{15}N variables. The normality and homoscedasticity in the distribution of final model residuals was tested by inspection of the quantile–quantile distribution plot and model residuals against fitted values (estimated responses) plot. We checked all models for spatial autocorrelation. Semi-variograms showed no spatial autocorrelation in model residuals (Zuur *et al.*, 2009). Multiple regression models were completed in R (version 3.4.4) (R-Core-Team, 2016). Model ranking was done using the package MuMIn (Bartoń, 2015). All ANOVAs were performed in Statistica (version 9.1) (StatSoft, 2010).

RESULTS

Stable isotope signatures of large herbivores during the Holocene

At the scale of the whole Holocene, the three species of large herbivores differ in their δ^{13}C values ($F = 5.43$, $p = 0.005$, $N = 364$). Aurochs (-22.5±1.0‰) and moose (-22.4±0.9‰) have significantly higher mean δ^{13}C values than European bison (-22.8±1.1‰) ($p = 0.04$ and $p = 0.01$, respectively). All three species significantly differ in their δ^{15}N values ($F = 45.04$, $p < 0.0001$, $N = 332$). Moose are characterized by the lowest (+4.0±1.1‰), European bison by intermediate (+4.9±1.1‰) and aurochs by the highest (+5.5±1.2‰) δ^{15}N values ($p < 0.0001$, $p < 0.0001$and $p < 0.0001$, respectively) (Figure 2).

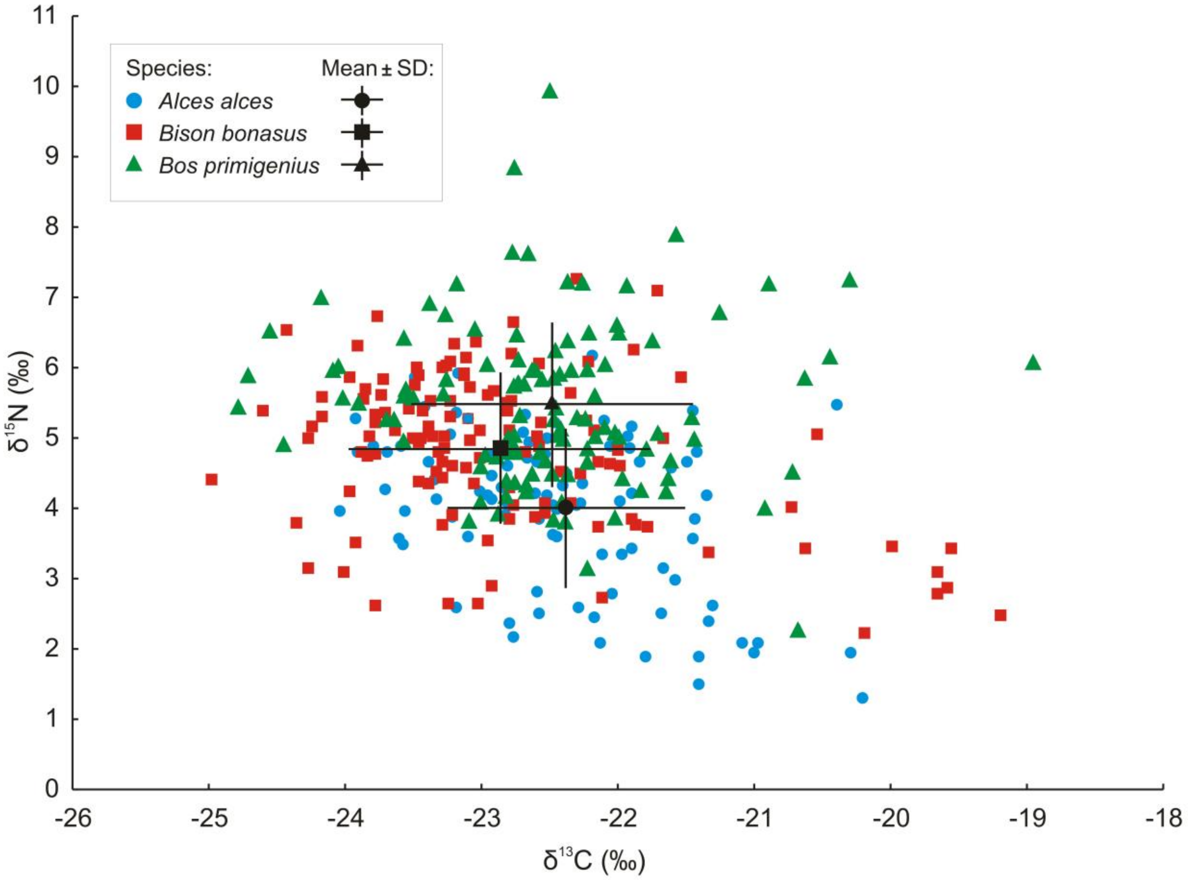

Figure 2. Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope signatures of moose (*Alces alces*) (blue circles), European bison (*Bison bonasus*) (red squares) and aurochs (*Bos primigenius*) (green triangles) with mean values and standard deviations.

We find that moose, European bison and aurochs samples have significantly higher mean δ^{13}C values in the Early and pre-Neolithic Holocene in comparison to the Neolithic and Late Holocene ($p = 0.0002$, $N = 97$; $p < 0.0001$, $N = 126$; $p = 0.003$, $N = 126$; respectively) (Figure 3). European bison and moose have significantly higher mean δ^{15}N values in the Neolithic and Late Holocene ($p = 0.0006$, $N = 97$; $p < 0.0001$, $N = 126$; respectively) compared to the Early and pre-Neolithic Holocene. Aurochs do not differ in mean δ^{15}N between those two periods ($p = 0.06$, $N = 100$) (Figure 3).

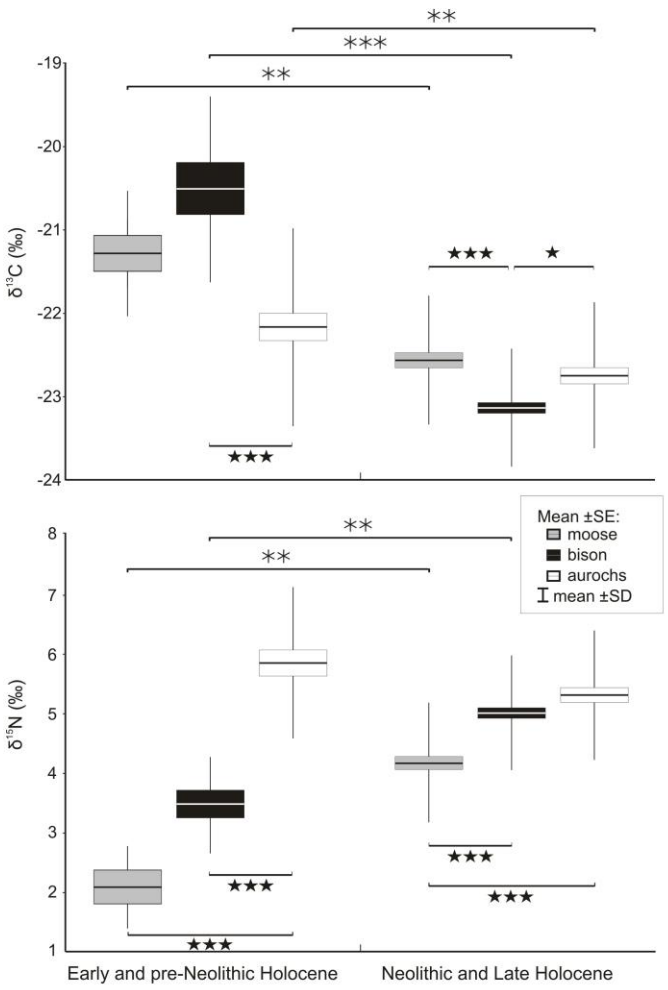

Figure 3. Differences in stable carbon δ^{13}C and nitrogen δ^{15}N isotope signatures between moose, European bison and aurochs in the Early and pre-Neolithic and in the Neolithic and Late Holocene sample groups and changes in δ^{13}C and δ^{15}N between the two periods. Asterisks indicate significant differences for each species between the two periods ** - for p = 0.001, ***- for p < = 0.0001, (pairwise differences for Tukey's HSD test for unequal N) and significant changes in δ^{13}C and δ^{15}N between three species in each of the period ★- for p = 0.01, ★★★- for p < = 0.0001.

The analysis of variance we use to explore differences in δ^{13}C and δ^{15}N values between European bison, moose and aurochs shows significant differences in both δ^{13}C ($F = 12.70$, $p < 0.0001$, $N = 79$; $F = 14.10$, $p < 0.0001$, $N = 270$, in the Early and pre-Neolithic and the

Neolithic and Late Holocene respectively) and in δ^{15}N values (F = 42. 50, $p < 0.0001$, N = 53; F = 28.86, $p < 0.0001$, N = 263, in the Early and pre-Neolithic Holocene and the Neolithic and Late Holocene respectively) in each of the period (Figure 3). During the Early and pre-Neolithic Holocene significantly lower mean δ^{13}C values are found in aurochs (-22.2±1.2‰) than in European bison (-20.6±1.1‰,) (p = 0.001) (Figure 3). Moose has an intermediate mean δ^{13}C value (-21.3±0.8‰). In the Neolithic and Late Holocene, the mean δ^{13}C value recorded in European bison (-23.1±0.7‰), is significantly lower than in moose (-22.6±0.8‰, $p < 0.0001$) and aurochs (-22.8±0.9‰, p = 0.007). In the Early and pre-Neolithic Holocene, the highest mean δ^{15}N value registered in aurochs (+5.8±1.2‰) is significantly different than in European bison (+3.5±0.9‰) (p = 0.0001) and moose (+2.1±0.7‰) (p = 0.0001) (Figure 3). In the Neolithic and Late Holocene, the lowest mean δ^{15}N registered in moose (+4.2±1.0‰) significantly differs from those in European bison (+5.0±1.0‰) ($p < 0.0001$) and aurochs (+5.3±1.1‰) ($p < 0.0001$) (Figure 3).

Factors influencing δ^{13}C and δ^{15}N values in large herbivores

The percentage total forest cover for moose, European bison and aurochs locations shows a similar temporal pattern with increase in the Early Holocene until the start of the Neolithic and then decreasing throughout the Late Holocene (Figure 4).

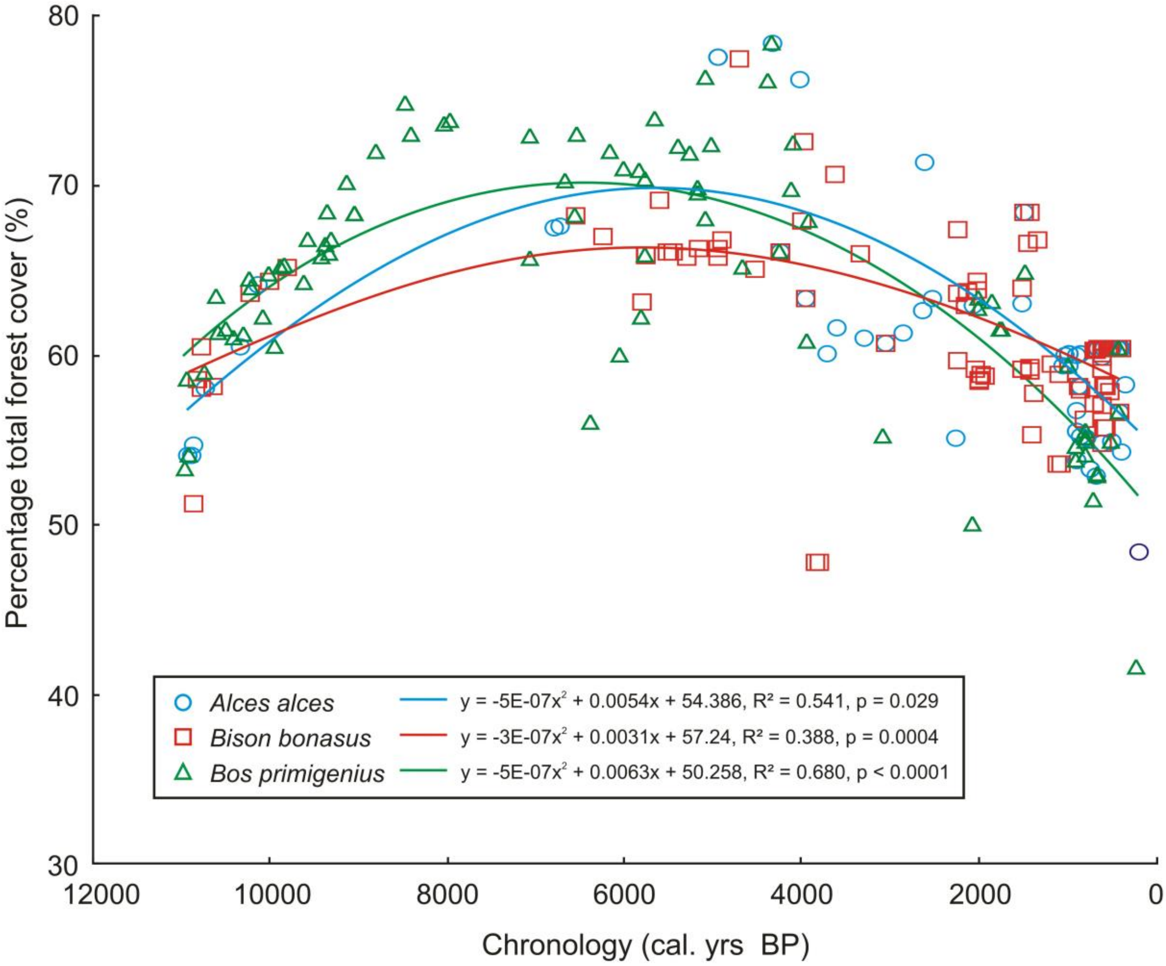

Figure 4. Percentage total forest cover in the Holocene for moose (*Alces alces*) (circles), European bison (*Bison bonasus*) (squares) and aurochs (*Bos primigenius*) (triangles) bone locations.

The δ^{13}C and δ^{15}N values in bones of large herbivores show some fluctuations throughout the Holocene with the pattern differing between the three species (Figure 5).

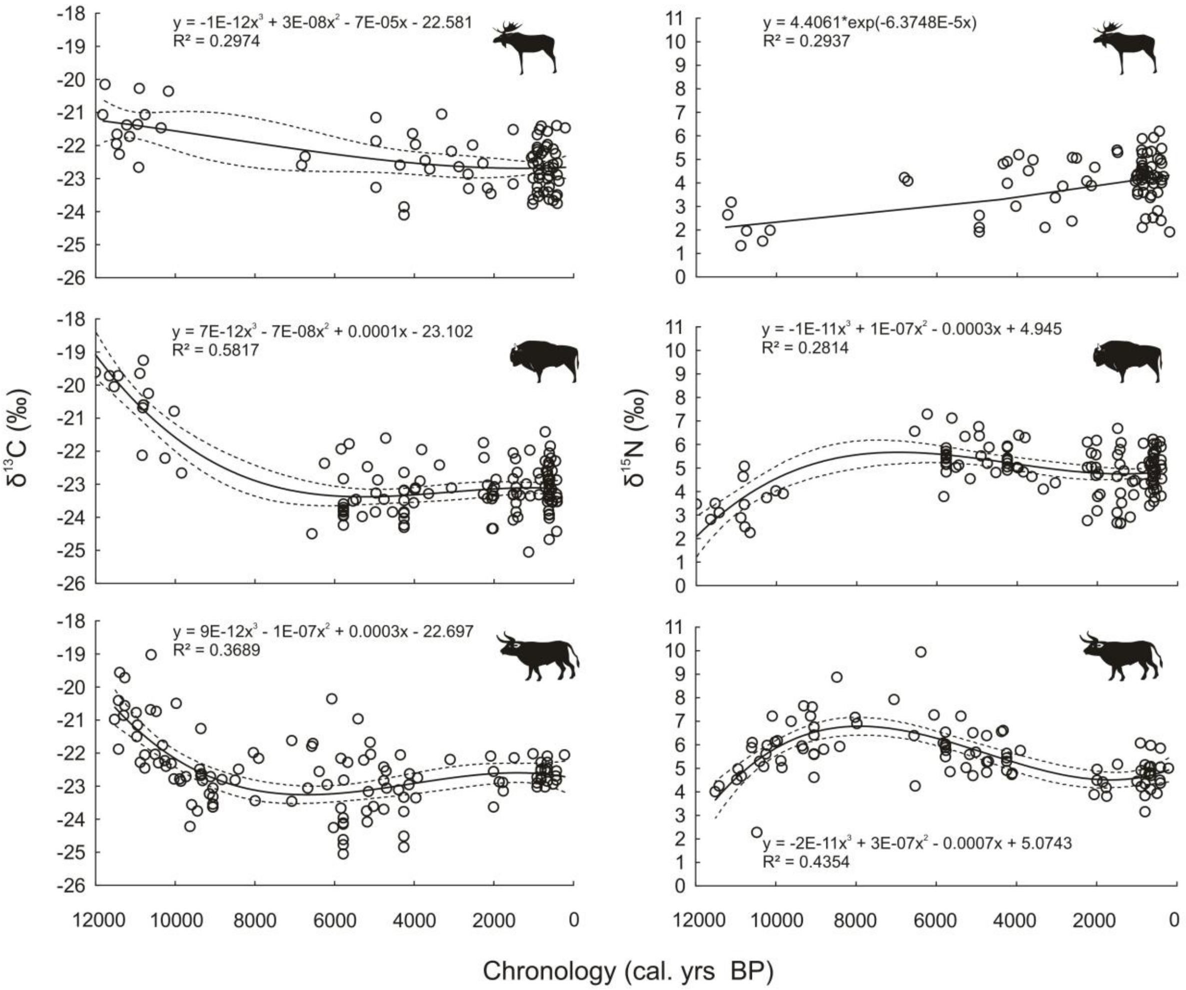

Figure 5. Chronological changes in stable carbon δ^{13}C and nitrogen δ^{15}N isotope signatures of moose, European bison and aurochs during the Holocene. The solid lines represent estimated regression lines and the dotted lines 0.95 confidence intervals.

The average model shows that none of the analysed factors significantly affected δ^{13}C and δ^{15}N stable isotope abundances in moose (Table S2,Table S3). For European bison, the ranges of R^2 of competing models used in averaging were between 0.3988 - 0.4235 and the average model shows significant effect of age and longitude on δ^{13}C stable carbon isotope signatures (Table S2, Table S3). The δ^{13}C values decrease in time in the first half of the Holocene, then stabilize during the following period, and increase with longitude (Table S3, Figure 6). The ranges of R^2 of competing models used in averaging were between 0.3720 -

0.3793 and the average model indicates that δ^{15}N values in European bison are significantly affected by age and elevation (Table S2, Table S3). The δ^{15}N concentration increases through time in the first half of the Holocene, then slightly decreases (Figure 6). With increasing elevation, δ^{15}N values significantly decrease (Figure 6).

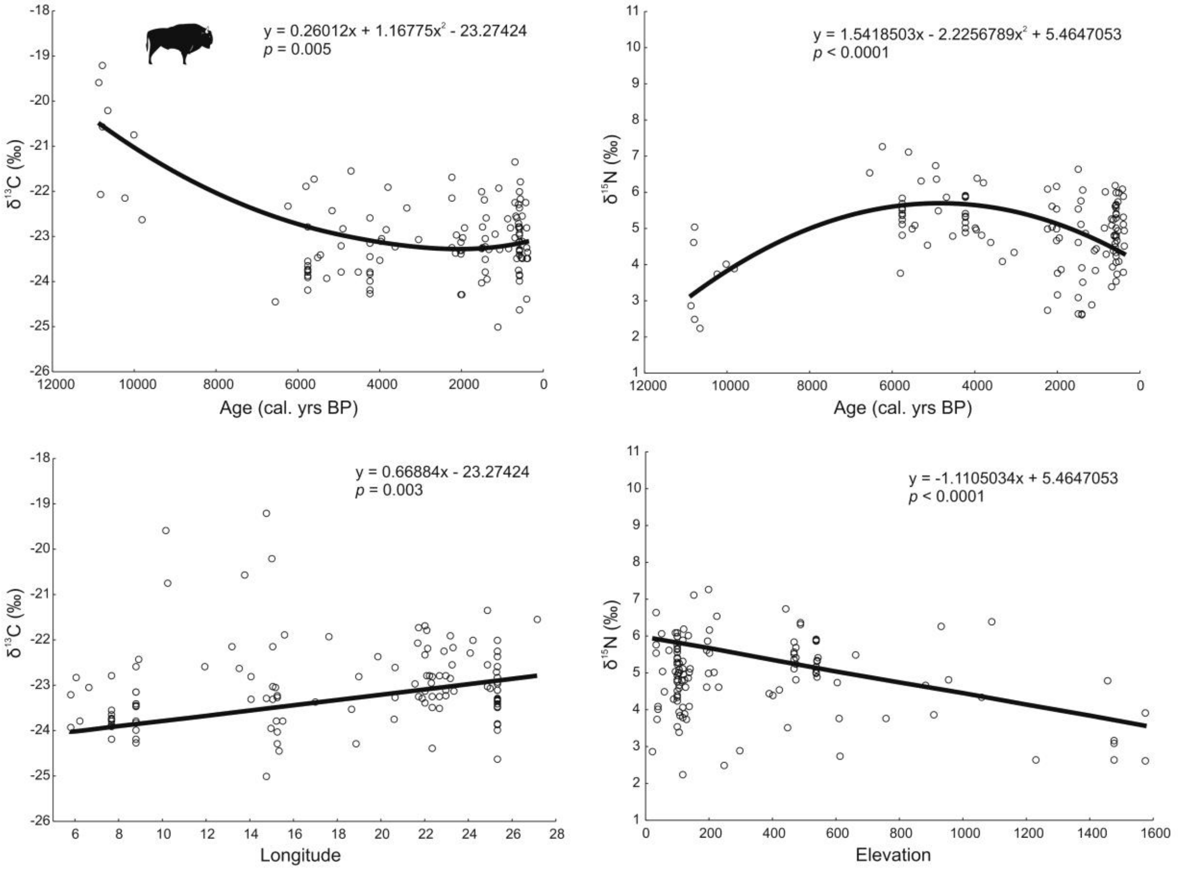

Figure 6. Influence of the age, longitude and elevation on stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope signatures of the European bison (*Bison bonasus*) in the Holocene.

The ranges of R^2 of competing models used in averaging were between 0.4273 - 0.4443 and the average model for aurochs shows significant effect of age, longitude and total forest cover on δ^{13}C values (Table S2, Table S3). The δ^{13}C values decrease through time and with increasing forest cover, and increase with increasing longitude, i.e. from West to East (Table S3, Figure 7). The ranges of R^2 of competing models used in averaging were between 0.4025 -

0.4174 and the average model shows a significant effect of age and longitude on δ^{15}N values in aurochs (Table S2, Table S3). The δ^{15}N values decrease in time, while increasing with longitude, therefore becoming higher from West to East (Figure 7).

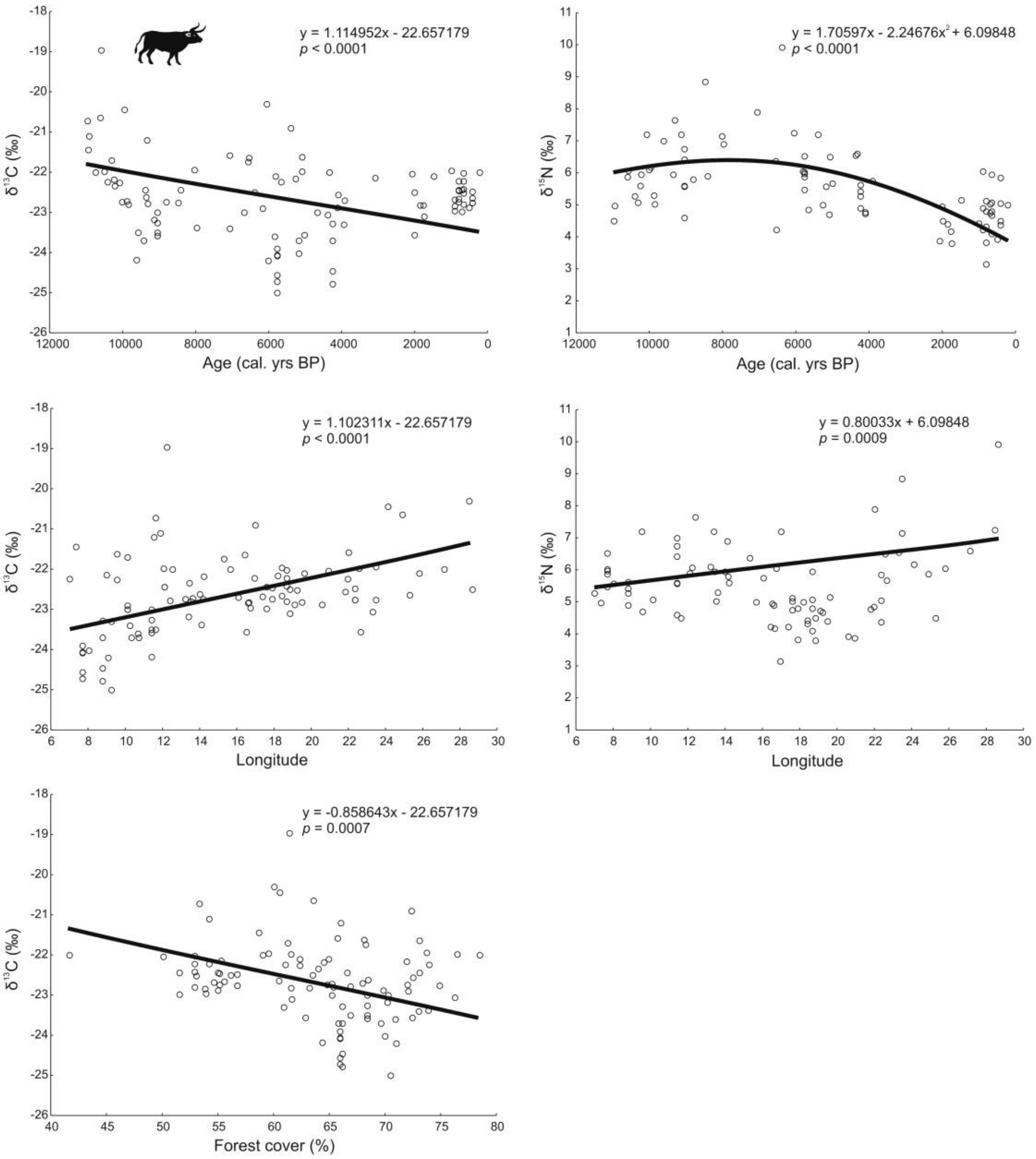

Figure 7. Influence of the age, longitude and forest cover on stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope signatures of aurochs (*Bos primigenius*) in the Holocene.

DISCUSSION

Stable isotope composition of large herbivores during the Holocene

Reconstruction of the habitat use and diet of large herbivores inhabiting Central and Eastern Europe has shown a wide variation of foraging habitats and diets of moose, European bison and aurochs throughout the Holocene. Comparing mean values of isotopic signatures in the scale of the whole Holocene, we found that moose and aurochs more often occupied open habitats and less forested areas, reflected in their higher mean δ^{13}C values, while European bison more often foraged in forested habitats. Differences among the diets of the three species are reflected in their δ^{15}N values and predict different foraging niches with moose being the most browsing, and aurochs the most grazing species (Hofmann, 1989).

The selection of early successional forests and tundra subalpine areas by moose before the forest maximum and later stream valley shrub habitats and forest gaps, which offer high availability of browse and cover, reflects the historical selection of relatively open habitats and woody diet of this large herbivore (Czernik *et al.*, 2013, Morow, 1976, Olsson *et al.*, 2011, Wam & Hjeljord, 2010b). Whilst the distribution range of moose strongly contracted eastward, the species did not experience extirpation in the wild and is now recolonizing its historical range (Niedziałkowska *et al.*, 2016a, Niedziałkowska *et al.*, 2016b, Schmölcke & Zachos, 2005).

According to δ^{15}N values, aurochs in the Holocene had more herbaceous plants in the diet than two other species. This is consistent with the previous stable isotope nitrogen analysis of bone collagen from Scandinavia and England confirming grazing of the aurochs, which is similar to cattle foraging behaviour (Lynch *et al.*, 2008, Noe-Nygaard *et al.*, 2005). Intermediate between the most grazing aurochs and the most browsing moose nitrogen isotope composition of European bison supports earlier findings on its mixed diet and plasticity in adaptation to utilize a wide range of forest habitats (Bocherens *et al.*, 2015, Hofman-Kamińska *et al.*, 2018a, Hofman-Kamińska *et al.*, 2018b, Kowalczyk *et al.*, 2011, Merceron *et al.*, 2014). This flexibility may result from the European bison's evolutionary adaptations to various food resources and habitats as reflected by genome analysis and gene selection (Gautier *et al.*, 2016).

Our data show that following deglaciation of northern Europe, in the earliest phase of the Holocene (between 11.6 - 10.5 ka cal yrs BP) moose, European bison and aurochs from Scandinavia and northern Europe occupied relatively more open habitats, which at that time were open tundra and shrubland with undeveloped forest (Björck *et al.*, 2002, Jessen *et al.*, 2015). Later, before the advent of the Neolithic, between 9.5 ka cal yrs BP and 7 ka cal yrs BP, aurochs stayed in more forested habitats, but no dated samples from European bison or moose are available during this period to draw comparisons with. Bones of aurochs originating from this highly forested Preboreal and Boreal period decreased mean δ^{13}C values to be the lowest among analyzed species in the Early and pre-Neolithic Holocene.

In the Early and pre-Neolithic Holocene, the diet of aurochs consisted of a relatively high fraction of grasses and forbs, as reflected by this species having the highest δ^{15}N values compared to both moose and European bison diet, which particularly in moose had relatively the highest levels of browse. European bison and moose living in the Early Holocene in more open tundra-like environments (steppe-tundra and forest-steppe with dwarf shrubs and trees such as willows, birches and pines) consumed more easily digestible leaves of shrubs and trees as indicated by nitrogen signatures (Bocherens *et al.*, 2015).

During the Neolithic and Late Holocene, the lower δ^{13}C values of European bison indicate that this species foraged most frequently in forested habitats, while moose and aurochs utilized this type of habitat less often. Moose exhibited the lowest δ^{15}N values of the three species in the Neolithic and Late Holocene, which suggests a diet with a relatively high fraction of browse, whilst European bison and aurochs consumed more herbaceous material. The lowest between the three species, but higher than expected δ^{15}N values in moose could be the effect of summer diet enriched with aquatic and herbaceous forage, which is observed in modern moose (Wam & Hjeljord, 2010a). In contrast to our findings, the dental microwear textural analysis (DMTA) showed that during the Late Holocene the diet of aurochs from northeastern Europe was mixed or browsing (Hofman-Kamińska *et al.*, 2018b). This is likely to be the effect of seasonality in the animal's diet, which is possible to detect through teeth microwear analysis (Percher *et al.*, 2018), therefore has a different chronological resolution than the reconstruction of the diet reflecting the whole life of the animal, which is given by the analysis of stable isotopes (Hedges *et al.*, 2007).

Stable isotopic compositions show a significant shift of foraging habitats from more open in the Early and pre-Neolithic Holocene to more forested in the Neolithic and Late Holocene specimens in all analyzed species. Such a pattern, already documented in red deer (*Cervus elaphus*) (Drucker *et al.*, 2003, Drucker *et al.*, 2008), is consistent with the changes in the forest cover as a result of vegetation succession in Europe in the Early Holocene, but it is not compatible with the reduction of the forest cover as a result of agricultural activities following the Neolithic and subsequent periods (Woodbridge *et al.*, 2018). Despite reductions in tree cover as a result of Neolithic development, the largest European ungulates continued to forage in forest. This has continued through the last 2000 yrs BP, when the scale of forest reduction was the largest (Kaplan *et al.*, 2009). This probably reflects avoidance of human pressure and the refugial character of forest habitats for large ungulates (Kerley *et al.*, 2012). Thus, aurochs and European bison, pre-adapted to open or mixed habitats (Bocherens *et al.*, 2015, Hall, 2008), became classical refugee species *sensu* Kerley et al. (2012) after the Neolithic and later transformation of European vegetation. This mechanism is similar to modern examples, where human impact results in a direct loss of habitats and an increase in avoidance behaviour of affected wildlife (Buuveibaatar *et al.*, 2016, Jiang *et al.*, 2007, Paton *et al.*, 2017). Modern moose in Scandinavia, as a hunted species, avoid human encounters by exploiting open habitats mostly during the night (Bjørneraas *et al.*, 2011). Conversely, a lack of persecution of modern European bison has resulted in increasing utilization of open habitats by populations that were introduced mainly to forests (Kowalczyk *et al.*, 2013).

Stable nitrogen isotope compositions of moose and European bison were lower in the Early and pre-Neolithic Holocene than in the Neolithic and Late Holocene. This may relate to shifts in the diet of these species from more browsing in the Early and pre-Neolithic Holocene to more grazing in the Neolithic and Late Holocene. However, the much lower δ^{15}N values in herbivore bones at the beginning of the Holocene in comparison to later periods, might also be connected with lower total available N (g/m^2) in the pioneer stages of soil formation in the glacier forefield, which increases exponentially along the soil developmental gradient (Göransson *et al.*, 2016). Reconstruction of diet based on dental microwear textural analysis (DMTA) showed that European moose had a browsing diet from the Neolithic period through to the Middle Ages. In the case of European bison, the same analysis showed the dominance of graminoids and forbs in the diet of this species living in the Neolithic subalpine region in Switzerland; however, by the Roman period and Middle Ages European bison from northeastern Europe had a mixed diet (Hofman-Kamińska *et al.*, 2018b), probably due to lower accessibility of open habitats. We show that aurochs was the only large herbivore that did not change its δ^{15}N values from Early and pre-Neolithic to Neolithic and Late Holocene. It seems that despite the change in environmental conditions and growth of total available N (g/m^2) in soils (Göransson *et al.*, 2016), δ^{15}N values in aurochs did not increase. Aurochs diet in the Neolithic and Late Holocene still had a relatively high fraction of graminoids and forbs (similarly to European bison), but due to lower availability of this plant groups in forest habitats, they had to incorporate some woody material into their diet. Thus, the limits set by ecological conditions of forest habitats (i.e. availability of preferred graze) were more profound for specialized grazers such as aurochs than for mixed feeders like European bison. Habitat specialists are more sensitive to environmental changes and vulnerable to extinction

(Keinath *et al.*, 2017). This suggests that environmental changes would have had a much stronger impact on aurochs than other species. The extirpation and final extinction in the 17th century of this widely distributed in the Late Pleistocene and Early Holocene species supports this assertion (Wright, 2013, Wright & Viner-Daniels, 2015).

Factors influencing δ^{13}C and δ^{15}N values in large herbivores

Spatio-temporal analysis of stable isotopic ratios of large herbivores throughout the Holocene showed that European bison and aurochs responded to environmental changes, but to different extents with different factors explaining the observed variations. None of the factors considered here influenced δ^{13}C and δ^{15}N values in Holocene moose bones. Modern studies on moose showed that this species can inhabit a wide variety of habitat types including forests, open willow-birch shrublands bogs, and alder swamps (Gębczyńska & Raczyński, 1989, Olsson *et al.*, 2011) and might have a very diverse diet which can contain different types of woody material (e.g. shoots, bark, foliage and fallen leaves) as well as aquatic vegetation, grasses and forbs (Baskin & Danell, 2003, Shipley, 2010, Wam & Hjeljord, 2010b), which are characterized by variable nitrogen isotope content (Ben-David *et al.*, 2001, Drucker *et al.*, 2010). An additional factor not tested here that may have had a significant impact on habitat and food type selection (thus influencing the isotopic signatures) is seasonal partial migration of moose (Ball *et al.*, 2001). Lower responses of moose to Holocene environmental changes may also result from a preference for mosaic habitats as mentioned earlier, thus the environmental changes were to some extent beneficial for moose. A second factor is the adaptation and preference of moose to marshlands (Olsson *et al.*, 2011, Stephenson *et al.*, 2006), a habitat which was probably less impacted either by forest succession and human pressure, due to lower accessibility and suitability of these terrains for agriculture activities until drainage in the modern period.

Stable carbon and nitrogen isotope variability in European bison and aurochs are best explained by a model incorporating the time factor. Decreasing δ^{13}C values through time suggests the shift in the pattern of habitat use from open to more forested habitats. In European bison and aurochs the nonlinear increase of δ^{15}N through time from the beginning of the Holocene, reaching the maximum for European bison around 6 ka cal yrs BP and aurochs around 9 ka cal yrs BP, could be an effect of total growth available N (g/m^2) in soils that developed following glacial retreat (Göransson *et al.*, 2016). The second explanation behind this pattern could be changing mean annual temperature, increasing since the beginning of the Holocene up to 7800 cal yr BP (Davis *et al.*, 2003). The δ^{15}N in plants increases with increasing mean annual temperature (Amundson et al. 2003, Craine et al. 2009).

The positive relationship between δ^{13}C signatures of European bison and aurochs with longitude may indicate more natural pattern of habitat use in a gradient from the south-west to the north-east of the study area related to lower human impact caused by delayed, or less intensive, agricultural development, or lower suitability for cultivation and pasture (Davison *et al.*, 2006, Kaplan *et al.*, 2009). Thus, in the more forested northeastern Europe (Kaplan *et al.*, 2009), large ungulates utilized more open habitats, probably having more natural character (open river valleys, large forest gaps caused by disturbance events, such as insect outbreaks or windfalls), which influenced their stable isotope composition. Aurochs were associated with riverine flat-lands (Hall, 2008) and modern European bison restored to forest habitats, but show high preference to open habitats (Kjellander et al. in prep) with the lowest δ^{13}C values, reflecting utilization of mainly forest habitats at locations with forest cover above 70% (Hofman-Kamińska *et al.*, 2018a). The increase of δ^{15}N values with longitude suggests a greater contribution of grassy vegetation in the diet of aurochs from northeastern Europe, which confirms our presumptions based on δ^{13}C modeling that this species foraged in more natural open habitats in this region.

We find that with increasing elevation, δ^{15}N values in European bison decrease, reflecting lower δ^{15}N values in plants at higher elevations (Huber *et al.*, 2007, Sah & Brumme, 2003, Sparks & Ehleringer, 1997). A similar tendency has been found in the study on modern European bison from Poland, where European bison from the Carpathian Mountains have the lowest δ^{15}N among all studied European bison populations (Hofman-Kamińska *et al.*, 2018a). Such an effect has not been detected in aurochs as there is an insufficient range of elevation (Mannel *et al.*, 2007, Sah & Brumme, 2003) available for aurochs samples (0-536 m.a.s.l.), in contrast to European bison for which elevation varied from 32 to 1575 m.a.s.l.

Forest cover estimated for analyzed specimen locations shows a hump-shaped polynomial trajectory over time, consistent with changes of forest cover in Europe (Roberts *et al.*, 2018). It seems that pattern of habitat use by large herbivore reflected habitat structure shaped by natural and anthropogenic factors (Fyfe *et al.*, 2015). Thus, large herbivores adapted to the environmental changes of the Holocene, expressed some flexibility that promoted their survival in dynamic and often unsuitable conditions of Holocene Europe.

Our data show variable shifts in foraging habitats and diet of large herbivores throughout the Holocene in Central and Eastern Europe. These shifts were caused by forest expansion and then increasing human pressure related to the spread of Neolithic agriculture. European bison and aurochs changed from open habitat dwellers to become refugee species in forest habitats. This restriction to less optimal habitats use alongside intensified hunting probably led to lower population densities and reduced fitness of large herbivores, gradual fragmentation of their populations and to their disappearance from large parts of Europe. Moose is the species best adapted to mosaic habitats, and was thus probably less impacted by environmental changes as revealed by models in this study, or may have even benefited from both the expansion of forest and subsequent deforestation, creating more diverse habitats.

Some factors (age and longitude) influencing the observed shifts in large herbivore habitat use and diet were similar suggesting a unified pattern of these impacts. Some factors were different (forest cover in aurochs, elevation in European bison) or did not explain the observed variations, which indicate individual responses of each species related to their biology and plasticity. Adaptability of the last remnants of megafauna in Europe allowed them to survive through the entire Holocene (i.e. moose) or until the 17th century as in the case of aurochs (Van Vuure, 2005), or the beginning of the 20th century for European bison (Pucek, 1991). The two survivors that are recolonizing Europe through either natural expansion (moose) or targeted restoration programmes (European bison) are characterized by the highest adaptability to environmental conditions (Hofman-Kamińska *et al.*, 2018a).

Patterns analyzed at the European scale may differ regionally and involve factors not considered in this study. We aimed at a synthetic investigation of large herbivore response to environmental changes in the Holocene, which would not be possible at the regional scale due to limited number of specimens. We hope that our data increases broader understanding of animal adaptation to environmental changes and mechanisms of refugee species concept that is widespread in the modern world.

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AUTHORS' CONTRIBUTIONS

EH-K and RK designed the study; EH-K, HB, MP and TS conducted a query in museums; EH-K, HB, RK, WG, DM, MP, GP provided samples; HB and DGD performed stable isotope analyses; RMF and JW provided data and interpretation of forest cover; EH-K performed statistical analyses; EH-K performed graphical visualization; EH-K analyzed the results; EH-K and RK gave interpretations of results; EH-K and RK wrote the original draft, which was reviewed and edited by all co-authors.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

Supporting information:

Table S1. Description of specimen site, inventory number, storage institution, age, stable isotope data and environmental data.

Table S2. Model selection (based on the AICc criteria) for the considered linear models of moose, European bison and aurochs.

Table S3. Averaged parameter estimates for linear models of moose, European bison, and aurochs data.

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