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Tracing nuanced dietary patterns on the Great Hungarian Plain: Carbon and nitrogen isotopic analysis of Bronze and Iron Age populations

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Abstract

The Great Hungarian Plain (GHP) served as a geographic funnel for population mobility throughout prehistory. Genomic and isotopic research demonstrates non-linear genetic turnover and technological shifts between the Copper and Iron Ages of the GHP, which influenced the dietary strategies of numerous cultures that intermixed and overlapped through time. Given the complexities of these prehistoric cultural and demographic processes, this study aims to improve our understanding of diachronic and culture-specific dietary signatures. Here we report on stable carbon and nitrogen isotope values from 75 individuals from twenty sites in the GHP dating to a ~ 3000-year time span between the Early Bronze and Early Iron Ages. The samples broadly indicate a terrestrial C_3 diet with nuanced differences amongst cultures, suggesting exogenous influences that manifested in subsistence strategies. Compared to the Iron Age, the Bronze Age samples have slightly elevated $\delta^{15}N$ values implying higher reliance on protein. Interestingly, carbon values typical of C_4 vegetation indicate the consumption of millet, or a grain with comparable $\delta^{13}C$ values during the Middle Bronze Age. Overall, our results suggest a gradual transition in dietary patterns from the Early Bronze to Early Iron Age, demonstrating a relationship between subsistence and time periods, congruent with the archaeological record.

Introduction

Agriculture, a pivotal development in our prehistoric biocultural trajectory, spread from the Near East and north-western Anatolia, reaching the Carpathian Basin around the end of the 7th millennium BCE[1]. Located centrally and comprising the majority of this large basin, the Great Hungarian Plain (GHP) forms a lowland confluence connecting the Balkans, Pontic Steppe, and Central Europe[2,3]. The GHP acted as a geographic funnel for population movement whereby new people and their ideas and ways of life, including subsistence strategies, entered Europe from the east and south; as such, it functioned as a region of major cultural and technological transition throughout prehistory[4,5]. It is thus a crucial region for identifying and investigating dietary trends between prehistoric time periods and cultures. Here we report on stable carbon and nitrogen isotope values from 75 individuals from twenty sites in the GHP (Fig. 1) dating to a ~ 3000-year transect between the Early Bronze and Early Iron Ages (Table 1) to ascertain dietary associations with cultural transitions, not only between the Bronze and Iron Ages, but also within these periods and their cultures.

Stable Isotopes

The application of isotopes to prehistoric dietary analyses is complex as many factors affect the values obtained from samples[6,7,8,9,10]. In brief, organisms incorporate carbon and nitrogen from diet material. For carbon, most plants fall under one of two categories (C_3 and C_4) based on their photosynthetic pathway, which makes it possible to distinguish general plant groups. C_3 plants, which include temperate grasses and domesticated cereals from terrestrial ecosystems, exhibit carbon isotope values ($^{13}C/^{12}C$ ratio or $\delta^{13}C$) from − 38 parts per mil (‰) to -22‰, with a mean of -26.5‰[11,12,13]. C_4 plants, such as maize, sorghum, and millet, exhibit higher $\delta^{13}C$ values, ranging between − 21‰ and − 9‰, with a mean of -12.5‰[11, 14, 15]. Dietary nitrogen ($^{15}N/^{14}N$ ratio or $\delta^{15}N$) is incorporated via protein at a stepwise factor of about + 3‰ to 5‰[16,17,18]. Plants in some terrestrial ecosystems can range between − 15‰ to -10‰[19]; however, aquatic resources—including freshwater—can exhibit comparatively ^{15}N-enriched values due to the relative complexity of the foodweb[20,21]. Moreover, both nitrogen and carbon isotope values are affected by climate[22,23,24], soil conditions[25,26], elevation[27], water stress[28,29], health of the individual[30,31,32], and breastfeeding[9]. Lastly, milk consumption, not unlike breastfeeding, augments $\delta^{15}N$ values much like that seen in other dietary trophic level increases[33].

Cultural and dietary context

Animal husbandry, primarily of cattle, was the predominant subsistence practice during the Middle Copper Age of people migrating to the Carpathian Basin from the Eastern Steppe[34,35,36]. The contemporaneous cultures of the Late Copper Age, including the Baden, Vučedol, and Coţofeni, continued the tradition of animal husbandry and land cultivation[36,37,38]. A transformation from the ‘monolithic’ Baden culture to more varied and smaller regional Bronze Age communities was shaped either by internal developments or foreign influences, including population movement, of, for example, the Yamnaya, who arrived from the east during the Transitional Period (~ 2800-2,600 BCE)[39,40,41]. This was followed by the expansion of the Bell Beaker who migrated from the west (~ 2,500 BCE)[37,42], and was accompanied by several independent cultures (e.g., Makó-Kosihy-Caka, Nagyrév, Somogyvár-Vinkovici), all practicing intensive cereal cultivation and animal husbandry[43]. However, only small groups settled along Danube River routes[39,40,41].

The transition from the Early Bronze to Middle Bronze Age is marked by the development of the more sedentary Hatvan, Otomani/Ottomány, and Füzesabony cultures, all of whom occupied tells[37,40,42,44,45,46]. These groups and others coexisted for centuries, although not necessarily peacefully, until the end of the Middle Bronze Age[38,47]. The Füzesabony were partly contemporaneous with and subsequent to the Hatvan, with no indications that upon their arrival they usurped the former culture[46]. The Otomani-Füzesabony is associated with increased socio-political and metallurgical complexity in the Carpathian Basin, as evidenced by tell sites, communal cemeteries, and advanced trade networks[48]. By this point the plow had been introduced[49], with communities cultivating cereals like wheat and barley, vegetables and fruits, and likely fodder crops to feed cattle, pig, goat, sheep, and horses[37,50].

Although there was profound cultural diversification during the Early Bronze and Middle Bronze Ages, by the Late Bronze Age cultures appear to homogenize over large geographic regions, much like that which occurred between the Late Neolithic and Early Copper Age, as manifested in the reduction of local cultural expression. The emergence of several cultures, including the Piliny/Kyjatice in the northern mountain range, and Gáva east of the Tisza, likely resulted from interregional contacts between groups occupying different ecological zones, resulting in increased trade and information flow[51]. This is further supported by the spread and increased cultivation of millet[52,53].

Late Bronze Age villages were seemingly abandoned, and new traditions and material culture appeared in the eastern parts of the Carpathian Basin at the beginning of the Iron Age (~ 900/800 BCE), namely on the central and southern part of the GHP, in the Northern Mountain Range, and in Transylvania. The Early Iron Age of the GHP is largely underrepresented in the archaeological record, perhaps because the cultures of this period, in particular the pre-Scythian (Mezőcsát), who mainly occupied the central and northern parts of the GHP[54,55], were nomadic stockbreeders of gregarious animals (e.g., cattle, sheep, horse) unlike their more sedentary predecessors[54,56]. The Scythian (Vekerzug in the GHP) culture subsequently emerged and continued into the Middle Iron Age. Excavations of Vekerzug settlements indicate that agriculture and animal husbandry were practised along with highly developed iron metallurgy and ceramic manufacture[54,57]. Various other Middle Iron Age cultures occupied this region until the end of the 5th century BCE, when the Celts began their conquests and interrupted development of local cultures, not just in the Tisza region, but throughout the Carpathian Basin[54,58].

Table 1
Summary of the prehistoric time periods and their associated cultures and subsistence practices in the GHP.

Adapted from Gamarra et al. (2018).

Time Period	Date Range	Associated Sampled Cultures	Subsistence Practices
Early Bronze Age	2,600 to 2,000/1,900 BCE	Nyírség, Proto-Nagyrév, Bell Beaker, Hatvan	Intensive crop cultivation (barley, wheat, legumes) and animal husbandry
Middle Bronze Age	2,000/1,900 to 1,450/1,400 BCE	Füzesabony, Otomani/Ottomány	Intensive crop cultivation (barley, einkorn, emmer, legumes, rye, legumes) and animal husbandry
Late Bronze Age	1,450/1,400 to 800/ 900 BCE	Piliny/Kyjatice, pre-Gáva, Gáva	Intensive crop cultivation (einkorn, emmer, barley, legumes); common millet as staple crop
Early Iron Age	800/900 to 650 BCE	Pre-Scythian (Mezőcsát), Scythian (Vekerzug)	Pastoral/semi- nomadism/transhuman pastoralism; stockbreeding; crop cultivation
Middle Iron Age	650 to 450 BCE	Scythian (Vekerzug)	Pastoral/semi-nomadism/transhuman pastoralism; stockbreeding; crop cultivation

Previous archaeochemistry of the Great Hungarian Plain

To assess links between diet and cultural shifts on the GHP, stable isotope and ancient DNA (aDNA) research has been conducted on samples from the Neolithic through Iron Age[43,59,60,61,62]. Previous carbon and nitrogen stable isotope analyses of human and faunal osteological samples from this region have focused primarily on Neolithic and Copper Age populations, reporting a shift in subsistence strategies during the Late Neolithic and Copper Age towards increased consumption of animal protein compared to the previous subperiods[59,63,64,65,66]. Gamba et al.[60] analysed the genomes of thirteen GHP individuals dating to between the Early Neolithic and Early Iron Age; the Bronze and Iron Age samples provided evidence for genomic turnover that contrasted the genetic continuity observed during the Neolithic and Copper Age. Allentoft et al.'s[43] study of Eurasian genomes reported dynamic migrations during the Bronze Age, as well as the rise of the allele that confers the lactase gene, while de Barros Damgaard et al.[67] found that Scythian groups were genetically comprised of Late Bronze Age herders, farmers, and hunter-gatherers. Comparing carbon and nitrogen isotopic values with aDNA results from GHP samples, Gamarra et al.[59] found no associations between dietary, cultural, and genetic shifts from the Early Neolithic to Iron Age; however, Bronze and Iron Age individuals exhibited a diet higher in C_4 plants typical of agriculture compared to those from the Neolithic and Copper Age.

Genetic turnover and technological shifts between the Copper and Iron Ages were thus non-linear, influencing the dietary strategies of numerous distinct cultures that intermixed and overlapped through time. Owing to the complexities of these prehistoric cultural and demographic processes, the present study thus aims to improve our understanding of diachronic and culture-specific dietary signatures as revealed by the archaeology and stable isotopes, both between and within chronological periods and cultures. To accomplish this aim we analyze stable carbon and nitrogen isotope values from 75 individuals dating to between the Early Bronze and Early Iron Ages (Fig. 1). Specifically, we ask the following questions: 1) Can nuanced diet changes across millennia be detected? 2) If changes are detected, what do they imply regarding prehistoric trans-Carpathian communication and trade?

Results

Isotopic, palaeodemographic, and statistical information for each sample are provided in the Supplementary Material (S1). Figure 2 illustrates the range of the stable carbon and nitrogen isotopic results of samples from this study coupled with data of Gamarra et al.[59] and McCall[70]. The range of $\delta^{13}C$ values for the entire dataset is -21.2‰ to -14.8‰ (mean = -18.3‰ ± 1.6‰ (1σ)). The $\delta^{15}N$ value range for the entire dataset is + 8.3‰ to 12.9‰ (mean = + 10.5‰ ± 0.9‰ (1σ)). Overall, most samples indicate a terrestrial C_3 diet with nuanced statistical differences between certain groups, suggesting external influences that manifested in the diet. This is in keeping with what is known about food practices at the time and is also congruent with previous isotopic analyses[35,59].

Temporal variability

The $\delta^{13}C$ and $\delta^{15}N$ results per each period and subperiod are summarized in Table 2. There is an overall statistical difference for the $\delta^{13}C$ values between the Bronze and Iron Ages (Mann-Whitney U: U = 900.500; $p = 0.001$; Fig. 3a); the Early Bronze, Middle Bronze, Late Bronze, and Early Iron Ages also exhibit significant statistical differences (Kruskal-Wallis: $X^2 = 31.122$, $p < 0.001$; Fig. 4a). As the Kruskal-Wallis test ($p < 0.001$) indicated differences between the Early Bronze, Middle Bronze, Late Bronze, and Early Iron

Ages, pairwise tests were employed, revealing a significant difference between the Early Bronze and Middle Bronze Ages compared with the Late Bronze and Early Iron Ages (Supplementary Material S2).

Similarly, for $\delta^{15}N$ values, there is an overall statistical difference between the Bronze and Iron Ages (independent samples t-test $t_{73} = 3.369$, $p = 0.001$; Fig. 3b). The Tukey's post hoc analysis, performed after a significant ANOVA ($F_{(3,68)} = 4.250$, $p = 0.008$) result, identified differences between the Late Bronze and Early Iron Ages, and differences among the Early Bronze, Middle Bronze, and Late Bronze Ages with the one-way ANOVA test ($F_{(3, 68)}$, $p = 0.008$; Fig. 4b). Furthermore, there is a negative correlation (-0.418, $p < 0.001$) across the Early Bronze, Middle Bronze, Late Bronze, and Early Iron Ages when comparing mean $\delta^{13}C$ and $\delta^{15}N$ values, seen when the increase in overall $\delta^{13}C$ values results in a decrease in $\delta^{15}N$ values.

Table 2

Summary of human $\delta^{13}C$ and $\delta^{15}N$ results of sample by period and subperiod with ‰ range, mean, and SD (± 1σ).

Period/Subperiod	**n**	**$\delta^{13}C$ range (‰)**	**Mean**	**SD**	**$\delta^{15}N$ range (‰)**	**Mean**	**SD**
Bronze Age	50	−21.2 to −14.8	−18.7	1.5	8.9 to 12.9	10.7	0.9
Iron Age	25	−20.5 to −14.9	−17.5	1.2	8.3 to 12.4	10.0	0.9
Early Bronze Age	9	−20.3 to −19.7	−20.0	0.2	9.3 to 12.9	10.7	1.2
Middle Bronze Age	18	−21.1 to −16.7	−19.4	1.3	8.9 to 12.2	10.7	0.9
Late Bronze Age	22	−19.9 to −14.8	−17.7	1.3	9.8 to 12.9	10.9	0.8
Early Iron Age	23	−20.5 to −14.8	−17.5	1.2	8.3 to 12.4	10.0	0.9

Cultural variability

The ranges for $\delta^{13}C$ and $\delta^{15}N$ values by culture are listed in Table 3; the $\delta^{13}C$ and $\delta^{15}N$ results are detailed in Fig. 5. For the inter-culture comparison ($n = 66$) there is an overall statistical difference between $\delta^{13}C$ values (Kruskal—Wallis: $X^2 = 25.159$, $p < 0.001$) with the Füzesabony found to be significantly different from the Gáva and Scythian (Fig. 5a). Similarly, the Proto-Nagyrév compared with the Gáva, Piliny/Kyjatice, pre-Scythian, and Scythian also demonstrate a notable difference in $\delta^{13}C$ values. The comparison of $\delta^{15}N$ values revealed an overall statistical difference between cultures ($F_{(5,60)} = 4.860$, $p = 0.001$; Fig. 5b). However, Scythian is the only culture with consistent differences for $\delta^{15}N$ values compared to the Füzesabony, Proto-Nagyrév, and Piliny/Kyjatice cultures (Tukey's test; Supplementary Material S2).

Table 3

Summary of human $\delta^{13}C$ and $\delta^{15}N$ results by culture with ‰ range, mean, and SD (± 1σ).

Cultures	Time Period(s)	n	$\delta^{13}C$ range (‰)	Mean	SD	$\delta^{15}N$ range (‰)	Mean	SD
Nyírség	Early Bronze Age	1	-20.2	N/A	N/A	9.3	N/A	N/A
Proto-Nagyrév	Early Bronze Age	4	-19.8 to -19.7	-19.8	0.1	10.6 to 12.9	11.7	0.9
Bell Beaker	Early Bronze Age	2	-20.3 to -20.2	-20.2	N/A	9.3 to 9.8	9.5	N/A
Hatvan	Early Bronze Age	1	-19.9	N/A	N/A	10.7	N/A	N/A
Hatvan or Füzesabony	Early Bronze Age /Middle Bronze Age	6	-21.0 to -17.2	-18.6	1.6	9.4 to 11.3	10.0	0.7
Füzesabony	Middle Bronze Age	18	-21.1 to -16.7	-19.4	1.3	8.9 to 12.2	10.7	0.9
Otomani/ Ottomány	Middle Bronze Age	1	-20.1	N/A	N/A	9.2	N/A	N/A
Piliny or Piliny/Kyjatice	Late Bronze Age	14	-19.8 to -16.1	-18.0	1.0	10.1 to 12.8	11.1	0.6
pre-Gáva or Gáva	Late Bronze Age, Early Iron Age	8	-18.0 to -14.8	-16.7	1.2	9.8 to 12.9	10.7	1.0
Pre-Scythian (Mezőcsát)	Early Iron Age	4	-18.1 to -14.8	-16.8	1.3	10.4 to 11.0	10.8	0.2
Scythian (Vekerzug)	Early Iron Age	19	-20.5 to -15.6	-17.7	1.1	8.3 to 12.4	9.8	0.9

Discussion

In the present study inhabitants of the GHP have been shown to exhibit a variety of carbon and nitrogen isotope ratios that suggest variability in dietary patterns throughout the 3000-year transect from the Early Bronze to Early Iron Age. As will be discussed, this variability may be linked in certain circumstances to Transcarpathian trade networks and/or migration, or cultural heterogeneity.

$\delta^{13}C$ values

In the present study samples from both the Bronze and Iron Ages largely fall within $\delta^{13}C$ values typical of consumers of C_3 plants, with a gradual increase in values through time concomitant with the archaeological evidence for the introduction of C4 plants, such as millet. It is posited that millet began as a crop of limited economic importance that was gradually incorporated into subsistence strategies from the Middle to Late Bronze Age[53]. While the AMS ^{14}C results of Filipović et al.[71] challenge this, our data continue to point to its slower incorporation, at least in the GHP. The Late Bronze Age Piliny/Kyjatice samples are the first to exhibit, as a whole, less negative $\delta^{13}C$ values, indicating a more substantial shift away from C_3 plants or aquatic resources to C_4 plants, in keeping with the archaeological record of increased millet consumption at this time. This trend is also observed among the Early Iron Age pre-Scythian (Mezőcsát) samples. The Iron Age samples, in general, exhibit $\delta^{13}C$ values suggestive of an increase in C_4 plants, though remain proportionally more C_3-based. However, the Early Iron Age Scythian samples display greater variability, with the reappearance of more negative $\delta^{13}C$ values, indicating some individuals consumed a mix of C_3 and C_4 cereals. This is potentially associated with increased sedentism, while others were to a greater extent pastoralist, relying more heavily on C_3 plants[72,73]. In our dataset only one human sample (HUNG155) accounts for any $\delta^{13}C$ signature (-20.5‰) representing a heavy reliance on C_3 plants during the Early Iron Age. This individual also exhibits the highest $\delta^{15}N$ value (12.5‰), significantly higher than other adult individuals, indicating another factor may have resulted in this enrichment. While inflammatory illness (e.g., tuberculosis) could account for this elevation, which in turn may be associated with the depleted $\delta^{13}C$ values[32], the identification of disease or infection was not possible due to poor skeletal preservation. Alternatively, this individual may have been engaged in pastoral nomadism[73,74]. HUNG155 derives from the Kesznyéten-Szérűskert cemetery, which yielded inhumed remains in a variety of burial positions, indicative perhaps, of both a diverse community and funerary rites.

Although the Scythians have historically been portrayed as an almost exclusively nomadic-pastoralist warrior class, isotopic and archaeological data from Iron Age sites in East-Central Europe, Eurasia, and the GHP point to a more complex scenario. The limited archaeological evidence for Early Iron Age sites in the GHP provides corroboration for nomadic pastoralism; however, finds from settlements in the GHP indicate that some Scythian communities engaged in a mixed agro-pastoralist economy[54,57]. Research at Scythian sites outside the Carpathian Basin yielded archaeobotanical evidence for floodplain cereal cultivation of broomcorn millet and hulled barley in Ukraine[75], and that of wheat, barley, millet and rye in central Asia[76] and Russia[77]. Macrofossils of six-row barley and millet were recovered at Rákoskeresztúr-Újmajor in the Alföld[78]. Additionally, pollen records dating to the Hungarian Early Iron Age allude to both the intensification of pastoralism and the continued importance of a mixed farming regime[56]. Recent isotopic evidence for cereal consumption in Scythian populations has also been reported for sites in Siberia and East Central Europe. The urban Bel’sk (Ukraine) population was found to generally be composed of more sedentary agro-pastoralists who focused on millet cultivation[72,73]. Lastly, it was posited that millet and C_3 cereals may have composed a significant proportion of the diets of two Scythian communities of the Minusinsk and Tuva basins (Siberia), but that consumption of animals foddered on C_3 plants would isotopically mask their contribution[79]. To establish whether this is associated with increased sedentism requires further strontium isotope analysis. Carbon and nitrogen isotopes of Early and Middle Iron Age Scythian populations from a dataset derived from diverse cemeteries will also help to identify potentially heterogenous lifeways within and between Iron Age cultures

Millet consumption in the Middle Bronze Age

Although there is scattered evidence that broomcorn millet was present in Europe (including present-day Hungary) from the Early Neolithic[52,66,80], direct radiocarbon dating of millet grains from sites in Central and Eastern Europe has disputed its importance in the diet or as a foddering source prior to the Bronze Age[81]. Despite the radiocarbon dating of millet to ~ 1600 – 1400 BCE from the site of Fajsz 18 (Hungary)[82], it is virtually undocumented archaeologically until the Late Bronze Age in the GHP[49,52]. Interestingly, our data indicate that the consumption of millet, or a grain with comparable $\delta^{13}C$ values, may have already begun in the Middle Bronze Age. More specifically, the Middle Bronze Age Füzesabony yielded variable $\delta^{13}C$ values that span both traditional terrestrial C_3 and C_4 ranges. Our results are supported by other recent isotopic, radiocarbon, and archaeobotanical findings. For example, millet grains have been identified in Middle Bronze Age contexts in Moldova from where it may have spread west up the Danube into the GHP along with other trade items[71,82]. In an isotopic analysis of the contemporaneous Trzciniec culture of Lesser Poland[83], it was posited that broomcorn millet may have been introduced to the region through cultural interaction with or migration of the Otomani-Füzesabony (and/or Tumulus) culture, as suggested by the exchange of culturally diagnostic prestige objects (e.g., beads, pins, amber, maces, ceramics[48,84,85,86]). Additionally, broomcorn millet was dated to the Middle Bronze Age at Maszkowice (Poland) where the authors note ceramic and metal artefacts are similar to those recovered in the south Tisza valley within the Otomani-Füzesabony tradition[71].

A web of long-standing, long-distance trans-Carpathian exchange and communication networks appear to have often followed rivers and their tributaries that connected the GHP north via the Vistula, Elbe and Oder rivers towards the Baltic and North seas, east via the Tisza into Lesser Poland and Ukraine, and south via the Sava, Morava, and Vardar rivers towards the Aegean[39]. The northward dispersal of millet from the GHP potentially progressed through such "communication corridors", together with the exchange of cultural objects and information[48]. Lastly, it must be noted that the elevated $\delta^{13}C$ values of this period may also, at least in part, result from consumption of livestock that had been grazed on C_4 plants[83]. However, this is a less parsimonious explanation given that previous cultures from the same region ought then to also exhibit elevated $\delta^{13}C$ values if they or their livestock consumed wild C_4-enriched plants[79]. Moreover, $\delta^{13}C$ values of fauna (− 21.8‰ to − 19.4‰ with a mean value of − 20.6‰ ±0.6‰ (1σ)) previously obtained from the GHP are consistent with terrestrial C_3 environment ranges[59,61].

Establishing whether millet was adopted by the Füzesabony through trade (e.g. as part of a network package from other areas), or by migrants directly introducing this crop to the local GHP population, requires additional genetic data along with strontium and oxygen isotope approaches. Moreover, analysis of other Middle Bronze Age cultures from the GHP, including the Tumulus, is needed to address whether millet consumption gradually intensified from the Middle Bronze Age onwards, as suggested by our results, or if, as posited by Filipović et al.[71], it became an important crop from the outset.

$\delta^{15}N$ values

Both the Bronze and Iron Age samples exhibit less variable $\delta^{15}N$ values than previous periods[59]. Subtle changes between subperiods until the Early Iron Age point to a gradual shift from a more terrestrially omnivorous diet, potentially with a low trophic level aquatic resource influence. The slightly higher $\delta^{15}N$ values of the Bronze Age than Early Iron Age samples indicate greater reliance on protein in the former period. Additionally, the Early Iron Age Scythian samples were consistently different to many other cultures for $\delta^{15}N$ values; their significantly lower (mean = 9.8‰) values suggest either less animal protein or lower trophic level protein, perhaps due to a focus on agriculture and away from aquatic resources entirely. The Scythians also differed considerably from the Late Bronze Age Piliny/Kyjatice, the latter of which lived between mountains. This geographic restriction may have resulted in dietary constraints.

Lastly, it must be noted that manuring affects the $\delta^{15}N$ values of crops and their consumers[87,88,89] with cattle manure altering values by + 2 to 8‰, and pig manure by + 15 to 20‰[90]. Given humans, who consume mainly herbivorous animal protein, have an expected $\delta^{15}N$ range of + 8.5‰ to 12.5‰, those consuming manured cereals in a mixed plant- and animal-based diet should exhibit a concentrated range between + 6‰ to 9‰[35,88,91]. Accordingly, our study shows that $\delta^{15}N$ values progressively decrease from the Early Bronze to the Iron Age, with a stabilization of values that are likely due to manured crop consumption. The vast majority of Early Iron Age Scythian samples fall within the manured crop consumption range, suggesting a subsistence strategy of some animal protein intake combined with manured crops[35,65,87,88,91]. This indicates more uniform agricultural practices that resulted in more homogenized isotopic values.

Conclusions

The isotopic data presented here indicate a gradual shift in subsistence strategies from the Early Bronze to the Early Iron Age in the GHP, with evidence for subtle variation between distinct cultures within epochs. In keeping with previous findings, near exclusive consumption of C_3 plants remains characteristic of the Early Bronze Age. The enriched $\delta^{13}C$ ratios of the Füzesabony, indicative of C_4 plant consumption, corroborate the growing isotopic and archaeobotanical evidence for the introduction of millet during the

Middle Bronze Age in the Carpathian Basin and Eurasia at large. $\delta^{13}C$ values continue to rise into the Late Bronze (Piliny/Kyjatice and (pre)Gáva) and Early Iron Ages (pre-Scythian/Mezőcsát), but are more variable for the Early Iron Age Scythians, who furthermore demonstrate relatively depleted $\delta^{15}N$ values in comparison to both Early Bronze Age populations and the pre-Scythians.

Potential links between the Füzesabony and the introduction of millet, to contemporaneous Middle Bronze Age cultures of Lesser Poland and Ukraine, have been posited[7]and corroborated with the archaeological evidence for complex trans-Carpathian communication and trade networks at this time. Further investigations will clarify whether millet was introduced by migrants or as part of a trade network activities.

Despite scarce evidence for Scythian settlements in the GHP or Eurasian steppe, recent archaeobotanical and stable isotope findings challenge the perception of Scythian societies as defined exclusively by pastoral nomadism, instead depicting a more complex scenario in which certain groups were nomadic herders while others engaged in mixed farming, potentially also occupying more settled communities. The isotopic profile of our Scythian sample, with $\delta^{13}C$ values that span both traditional terrestrial C_3 and C_4 ranges and a reduction in $\delta^{15}N$ values, suggest an agro-pastoralist economy.

The previously undetected nuanced differences we report here between the isotopic signatures of distinct cultures, and throughout the Early Bronze to Early Iron Age, demonstrate that dietary evolution remains as complex and nonlinear as the cultural processes, and economic strategies with which it is entangled. The continued amalgamation of research that includes both multi-isotopic and archaeological approaches will help shed further light on local and trans-Carpathian subsistence and trade. Lastly, due to the fact that we cover a wide range of cultures throughout a large time frame, some sample sizes are small. Future studies should build upon our results with larger datasets to provide an even higher resolution analysis of the detected trends.

Materials And Methods

Stable carbon and nitrogen isotope analyses were conducted on bone and tooth samples from 75 human individuals spanning the Early Bronze to the Early Iron Age from the GHP micro region and the adjacent Northern Mountain Range (Supplementary Material, S1). When possible, material was assessed for palaeopathological data.

Collagen extraction was performed at the University College Dublin Conway Institute (Dublin, Ireland) following a modified version of the Longin method[92], which can be found in detail elsewhere[93,94,95]. Each sample was weighed to ~ 0.6 mg and placed into a tin capsule. Several samples were processed twice to assure repeatability. All samples were within the acceptable range of two standard deviations of each other[59]. Samples were processed using a Thermo Finnigan DeltaPlus XL mass spectrometer. The accuracy and precision of the measurements, based on repeated measurements of two international laboratory standards USGS40 and USGS41, is ± 0.1‰ (1σ) for $\delta^{13}C$ and ± 0.1‰ (1σ) for $\delta^{15}N$. All carbon isotopic results are expressed as a delta (δ) value relative to Vienna Pee Dee Belemnite (VPDB), and all nitrogen isotopic results as a delta (δ) value relative to ambient air (AIR).

Samples were assessed for contamination based on carbon and nitrogen content or weight (%). Acceptable %C ranges for modern mammalian bone collagen are between 15.3% and 47%, and for %N between 5.5% and 17.3%; samples falling outside those ranges were deemed inappropriate for analysis[96]. Statistical analyses were performed to assess differences between time periods, demographic groups (i.e., age and sex), and cultures. Statistical analyses were not conducted on certain groups when the number of samples was too few to yield any meaningful analyses ($n \leq 4$). Each group was checked for normality using a Shapiro-Wilk test, and equality of variance with Levene's test, with a $p < 0.050$ as the statistical significance level. For pairwise comparisons among groups, t-tests (for normally distributed data), and Mann-Whitney U tests (for abnormally distributed data) were employed using $p < 0.050$ as the statistical significance level. When comparing multiple groups and to determine significant differences between them, one-way ANOVA and Kruskal-Wallis tests were employed for normally and abnormally distributed data, respectively. Post-hoc analyses were performed in cases of significance according to the normality of the data (Tukey's, Mann-Whitney U, and Bonferroni tests). Statistical data were generated using R (v. 3.6.3[97]) using the ggplot2[98] package to generate figures. All data generated and/or analysed for this study are included either in text or in the Supplementary Material (S1), including all of the statistical tests.

Declarations

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Author Contributions

AMC conceived of the study. AMC performed the isotopic lab work with the aid of BG. AMC performed the formal analyses with the aid of BG. JD, ZB, AC, PC, LD, AE, MH, AH, ÁK, JK, PK, KK, LS, ZKZ, and KS provided skeletal materials and/or interpreted archaeological or anthropological information. JD, KrKi, TS, and TH performed the osteological analyses. AMC, KSDC, and TS performed and created all statistical analyses and plots. RP and TH supervised the study. AMC wrote the manuscript with input from all co-authors.

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Competing interests: The authors declare no competing interests.

Ethics statement: All necessary permits were obtained for the described study, which complied with all relevant regulations and ethical approval (Herman Ottó Múzeum, Miskolc; Dobó István Castle Museum, Eger; Hungarian National Museum, Budapest; Déri Museum, Debrecen; Budapest History Museum - Aquincum Museum and Archaeological Park, Budapest; Damjanich János Museum, Szolnok).

Data availability: All data generated or analysed during this study are included in this published article [and its supplementary information files].

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Figures

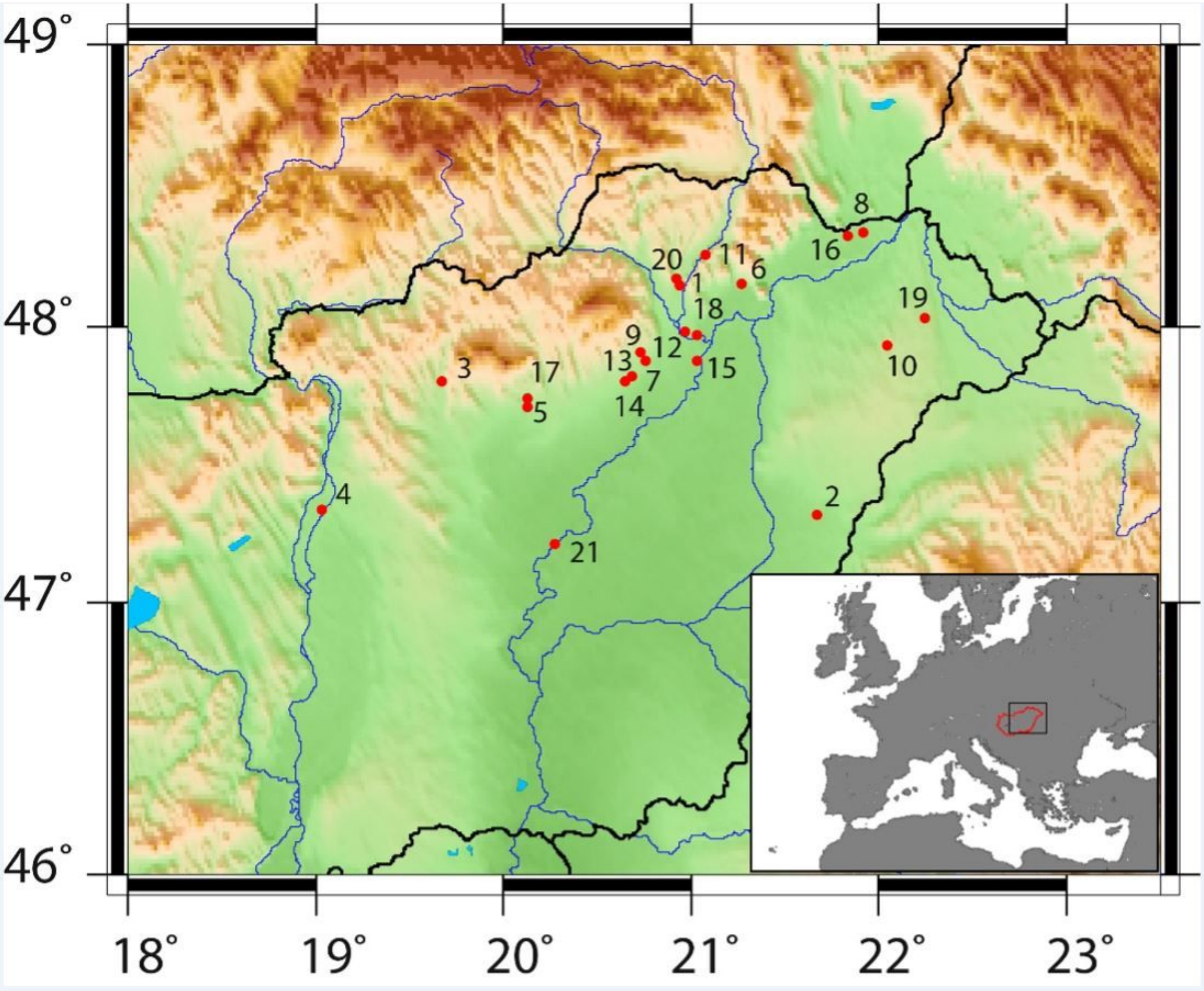

Figure 1

Map showing the location of sites. 1. Ongaújfalu-Állami gazdaság, 2. Konyár-Pocsaji műút, 3. Apc-Berekalja I, 4. Szigetszentmiklós-Üdülősor, 5. Kompolt-Kígyósér, 6. Mezőzombor-Községi temető, 7. Mezőkeresztes-Csincse-tanya, 8. Nagyrozvágy-Pap-domb, 9. Vatta-Dobogó, 10. Ófehértó-Almezői dűlő, 11. Felsődobsza, 12. Köröm-Kápolnadomb, 13. Mezőkeresztes, 14. Mezőkeresztes-Cet halom, 15. Oszlár-Nyárfaszög, 16. Pácin-Alsókenderszer, 17. Ludas-Varjú-dűlő, 18. Kesznyéten-Szérűskert, 19. Szikszó-Hell Ring, 20. Besenyszög Berek-ér partja. Generic Mapping Tools 4.5.13[68] and the topographic ETOPO dataset[69] were used to create this map.

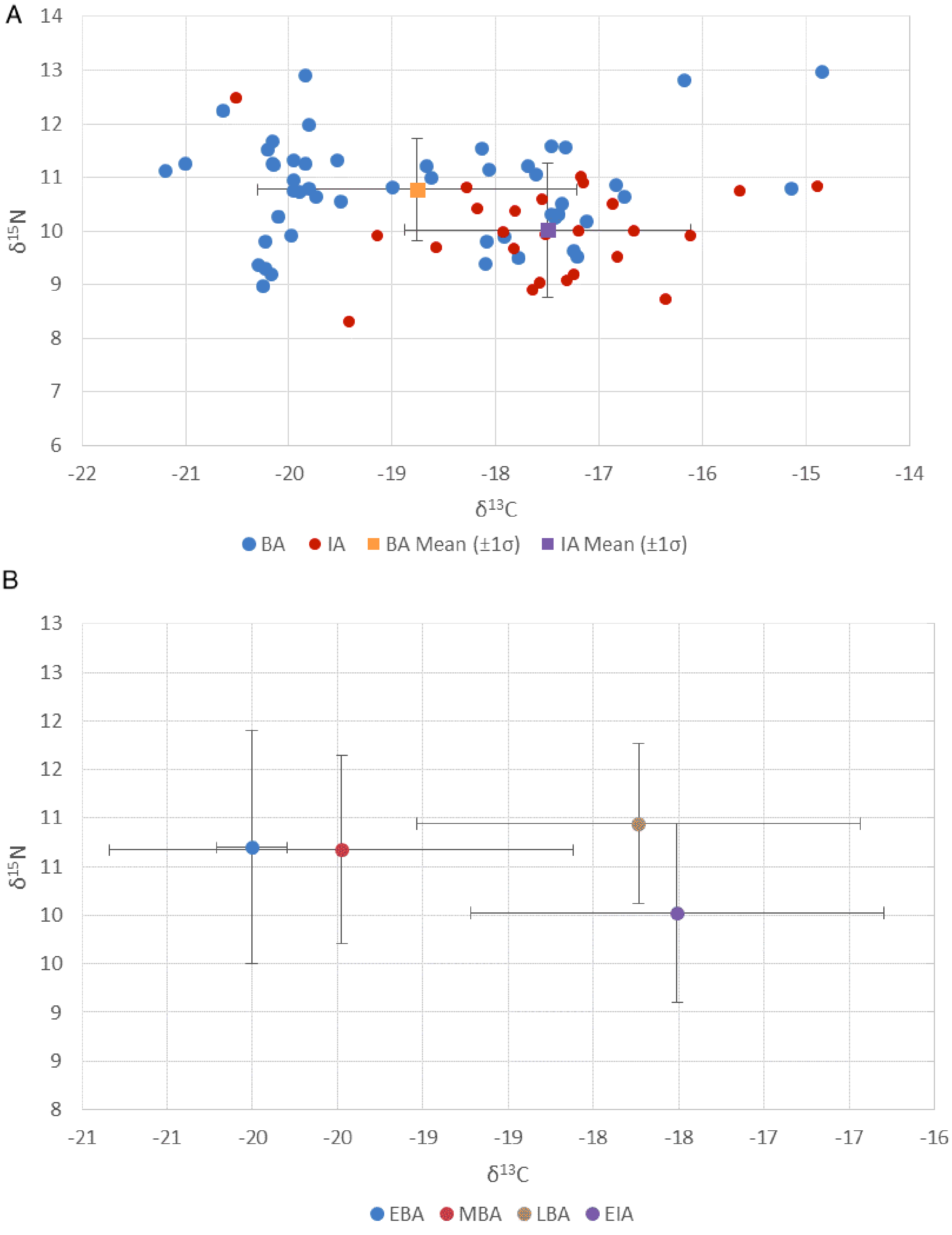

Figure 2

Scatterplots of human δ^{13}C and δ^{15}N values with mean δ^{13}C and δ^{15}N values (±1 σ) by period A) Bronze Age/BA (n=50) and Iron Age/IA (n=23) and subperiod B) Early Bronze Age/BA (n = 9), Middle Bronze Age/MBA (n =18), Late Bronze Age/LBA (n = 22), and Early Iron Age/EIA (n=23).

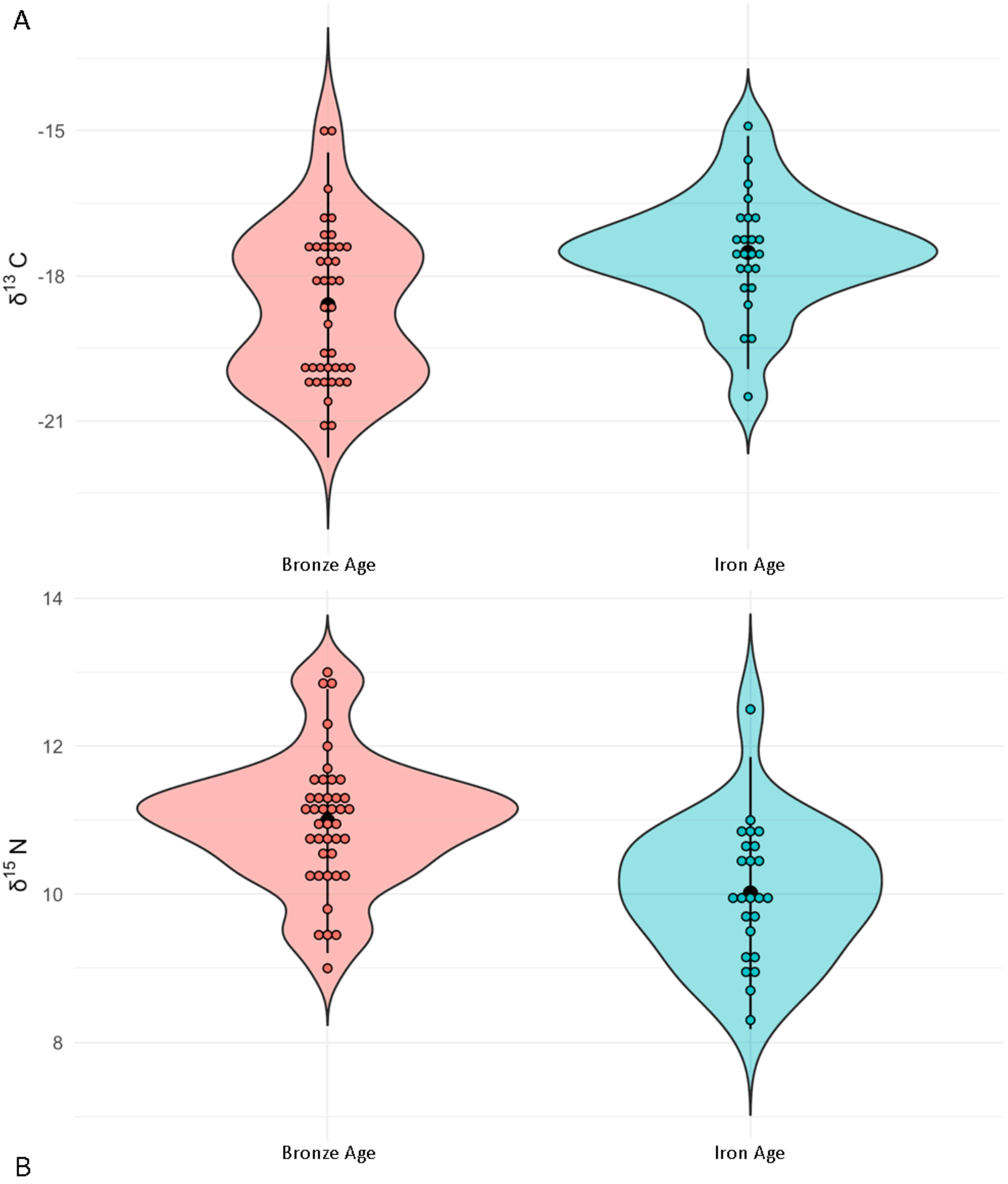

Figure 3

Violin plot of human A) δ^{13}C and B) δ^{15}N values by period: Bronze Age (n=50) and Iron Age (n=23). Center black dot represents mean; center black line represents distribution.

Figure 4

Violin plot of human A) $\delta^{13}C$ and B) $\delta^{15}N$ values by subperiod: Early Bronze Age (n=9), Middle Bronze Age (n=18), Late Bronze Age (n=22), and Early Iron Age (n=23). Center black dot represents mean; center black line represents distribution.

Figure 5

Violin plot of human $\delta^{13}C$ and $\delta^{15}N$ values by cultures listed in roughly chronological order: PN (Proto-Nagyrév, n =4), FZ (Füzesabony, n = 12), HFTZ (Hatvan or Füzesabony, n = 6), PLKY (Piliny or Piliny/Kyjatice, n = 14), PG (pre-Gáva or Gáva, n = 7), PS (Pre-Scythian/Mezőcsát, n = 4), and SA (Scythian/Vekerzug, n = 19). Center black dot represents mean; center black line represents distribution.

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