**Strontium isotope analysis reveals prehistoric mobility patterns in the southeastern Baltic area**

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**Abstract**

We measured 87Sr/86Sr for all available human remains (*n* = 40) dating from the Mesolithic to the Bronze Age (ca. 6400-800 cal BC) in Lithuania. In addition, local baselines of archaeological fauna from the same area were constructed. We identified significant and systematic offsets between 87Sr/86Sr values of modern soils and animals and archaeological animals due to currently unknown reasons. By comparing 87Sr/86Sr human intra-tooth variation with the local baselines we identified 13 non-local individuals, accounting for 25-50% of the analysed population. We found no differences in the frequency of local vs. nonlocals between male and female hunter-gatherers. Six Mesolithic-Subneolithic individuals with 87Sr/86Sr values >0.7200 may have come from southern Finland and/or Karelia. Two Mesolithic-Subneolithic individuals from the Donkalnis cemetery with 87Sr/86Sr values <0.7120 likely came from the Lithuanian Baltic coast. These data demonstrate coastal-inland mobility of up to 85 km, which is also supported by archaeological evidence. The standard deviation in the intra-tooth 87Sr/86Sr indicates that mobility did not increase with the adoption of pottery technology at ca. 5000 cal BC but rather slowly decreased during the Neolithic and Bronze Age periods. We interpret this as a result of the introduction and subsequent intensification of farming. The least mobile way of life was practised by Subneolithic coastal communities during the 4th millennium cal BC, although 87Sr/86Sr do not exclude that they migrated along the coastline.

**Keywords**

Strontium isotope analysis, migration, mobility, southeastern Baltic, Stone Age, Bronze Age

**I. Introduction**

Recently, ancient DNA (aDNA) research has demonstrated that large-scale and long-distance human migrations took place throughout many European regions at the onset of and during the Neolithic and the Bronze Age (Allentoft et al. 2015; Haak et al. 2015; Mathieson et al. 2018; Olalde et al. 2018; Saag et al. 2021). The aDNA studies show that human mobility and migration were among the main agents for many cultural and economic changes throughout prehistory. Moreover, throughout the southeastern Baltic area, multiple and extensive, and in some cases sudden, economic and cultural changes took place during the Stone and Bronze Ages. Subneolithic Porous Ware ceramic was, in many areas, replaced by Neolithic Globular Amphora, Rzucewo, and Corded Ware ceramics during the period from ca. 3200-2800 cal BC (Piličiauskas 2018; Rimantienė 1989, 2002). Simultaneously, animal husbandry was incorporated into a mixed-type of economy in which wild resources continued to be exploited alongside domesticated species (Piličiauskas et al. 2020; Robson et al. 2019). At ca. 1300 cal BC barley cultivation commenced throughout the region (Piličiauskas et al. 2021), which was later supplemented by millet cultivation at ca. 1000 cal BC (Antanaitis-Jacobs et al. 2002; Piličiauskas et al. in prep.). At ca. 700 cal BC a wide range of plants were cultivated at the same time as farming intensified, at least in some coastal areas of Lithuania (Minkevičius et al. 2020).

In addition to genetics, mobility patterns can be identified via 87Sr/86Sr analysis. Strontium isotope analysis has, during more than three decades, proved itself as a useful tool for assessing human and animal mobility in the past (Ericson 1985; Gregoricka 2013; Knudson et al. 2012; Price et al. 1994; Shaw et al. 2010). The essence of the method lies in the ability of living organisms to incorporate strontium, as a substitute to calcium, into their tissues including highly durable tooth enamel. Strontium has four isotopes of which 87Sr is radiogenic, and forms from 87Rb, with a half-life of 49.23 billion years. The strontium ratio (87Sr/86Sr) varies according to geology, with older rocks having higher 87Sr/86Sr ratios. The biologically available strontium retains the 87Sr/86Sr ratio throughout its incorporation from soil to plants to humans, because these isotopes do not fractionate in the same way as the lighter isotopes of carbon and nitrogen. As tooth enamel does not remodel after its final mineralisation, it maintains the 87Sr/86Sr ratio that was recorded during the formation of the tooth. By analysing the 87Sr/86Sr values in human tooth enamel and through comparison with the 87Sr/86Sr ratio of the bioavailable strontium of fauna, flora, water and soils, it is possible to establish whether a person had been feeding on local resources during tooth formation (Bentley 2006; Holt et al. 2021; Montgomery 2010; Szostek et al. 2015). This enables us to trace the first generation of immigrants but only when there is a difference between the bioavailable strontium values at the place of birth/childhood and death. Moreover, by high-resolution micro-sampling of a single tooth, intra-tooth 87Sr/86Sr variation may be recorded, which reflects a chronological sequence (see e.g. Balasse 2002, 2003), that can provide further insights in how humans or animals moved during tooth enamel mineralisation (e.g. Boethius et al. 2021; Glykou et al. 2018; Lazzerini et al. 2021). However, in order to use 87Sr/86Sr in mobility studies it is essential to know the bioavailable 87Sr/86Sr across large areas. Presently very few 87Sr/86Sr measurements have been reported from Eastern Europe, compared to the numerous studies that have been carried out in Western, Central and Northern Europe (e.g. Bataille et al. 2020; Bentley and Knipper 2005; Blank et al. 2021; Borić and Price 2013; Fraser et al. 2018; Frei et al. 2019; Lahtinen et al. 2021; Price et al. 1994; Szczepanek et al. 2018). For instance, we were unable to find any bioavailable 87Sr/86Sr data for Belarus. For Lithuania, only data of modern grazing and agricultural soils was available prior to our study (Hoogewerff et al. 2019). For northeast Poland, 87Sr/86Sr of natural mineral waters has been published (Voerkelius et al. 2010). For Latvia, 87Sr/86Sr measurements on three snail shells (Price et al. 2020), seven domestic animals and 19 human bone samples are known (Petersone-Gordina et al. 2022), whilst from northwest Russia a 87Sr/86Sr baseline for the Staraya Ladoga area was recently published (Price et al. 2020). In Estonia, 87Sr/86Sr analysis has been applied in order to trace the origins of Bronze and Viking Age communities (Oras et al. 2016; Price et al. 2020).

Due to the lack of research in our study area, we made a first attempt to trace mobility in the southeastern Baltic area during the Stone and Bronze Ages using 87Sr/86Sr analysis. Furthermore, our aim was to compare mobility patterns throughout the region from the Late Mesolithic to the Bronze Age. In this study we present 87Sr/86Sr data for all available human remains in Lithuania (*n* = 40) originating from 10 archaeological sites, dating from ca. 6400-800 cal BC. In contrast with previous mobility studies, which largely employed thermal ionisation mass spectrometry (TIMS), we widely applied laser ablation-multi collector-inductively coupled plasma-mass spectrometry (LA-MC-ICP-MS) in order to trace human mobility during the formation of tooth enamel. Based on archaeological animal tooth enamel 87Sr/86Sr ratios, local strontium ratio baselines were constructed for seven regions. For this, 68 archaeological faunal teeth enamel samples were analysed and the results were combined with an additional 40 archaeological faunal measurements reported by Piličiauskienė et al. (2022). In addition, we measured 87Sr/86Sr ratios in four modern rodents and leaves from 12 modern trees; the results cautioned us about the use of modern samples and allowed us to evaluate the extent and coverage of the sea spray effect on the Baltic coast. In doing so, we identified non-local individuals, in some cases discussed their possible places of origin, evaluated the numbers of non-locals and mobility during the Stone and Bronze Ages, and discussed mobility patterns connected to major economic and cultural transitions.

**II. Materials and Methods**

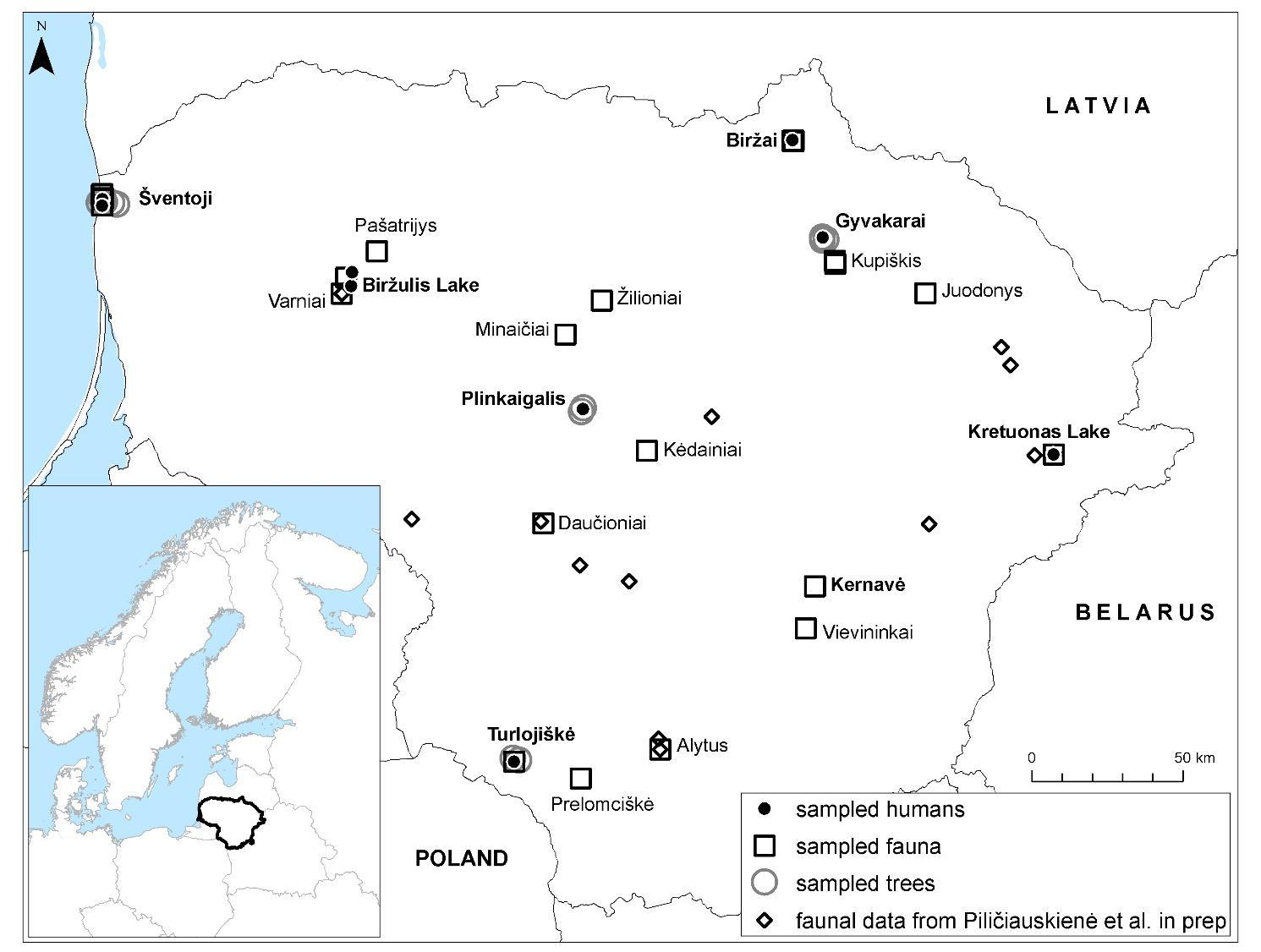
**II.1. Human remains**

We sampled all available non cremated human remains (*n* = 40) dating to the Stone and Bronze Ages, which contained teeth recovered from Lithuania. They were stored at the Faculty of Medicine, Vilnius University. We preferentially sampled the M1 (22/40) and M2 (11/40) in humans, although M3 (2/40), P1 (2/40) and P2 (2/40) were also sampled in cases when M1 and M2 were absent. In one case (i.e. Šventoji 43), a deciduous tooth (dm1) was analysed. The majority of the analysed individuals (26/40) have been directly 14C dated while the remainder were dated by contextual 14C dates. New 14C dates, acquired during the IZOMOB project, will be published separately (Simčenka et al. in prep). The dates of the studied individuals cover a long time span, ranging from the Late Mesolithic to the Late Bronze Age, ca. 6400-800 cal BC (Table 1).

The human remains in this study are mainly from inland Lithuanian Mesolithic-Neolithic cemeteries (Donkalnis (*n* = 11), Spiginas (*n* = 2), and Kretuonas 1B (*n* = 5)), Corded Ware Culture (hereafter CWC) single graves (Gyvakarai (*n* = 1), Biržai (*n* = 1), and Plinkaigalis (*n* = 2)), from refuse layers of Subneolithic-Neolithic dwelling sites (Šventoji 23 (*n* = 5), Šventoji 43 (*n* = 2), Kretuonas 1C (*n* = 3), and Kretuonas 1/1A (*n* = 4)), as well as from a single Late Bronze Age sacrificial site (Turlojiškė (*n* = 4)) (Table 1; Fig. 1). Turlojiškė is a wetland site that was used for depositing 20-45 years old male individuals. Two of the five preserved skulls demonstrate that the individuals suffered blunt force trauma, which was likely their cause of death due to a lack of healing. Furthermore, only parts of the skeletons were deposited in the boggy lake and two lacked skulls (Merkevičius 2012). For many of the other sites, extensive stable isotope analysis and radiocarbon dating has been performed previously (see Piličiauskas et al. 2011, 2017a and references therein). The only exception is the Šventoji 43 Subneolithic settlement which contained loose human teeth. This site has been investigated and published recently (Piličiauskas et al. 2019).

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **No.** | **Site name** | **Site type** | **Grave or Find No.** | **Sex** | **Age** | **Tooth** | **Period** | **Dating cal BC** | **References for chronology** |
| 1 | Biržai | Single grave |  | Male | 30-35 | M1 (26) | Neolithic | 2570-2350 | Piličiauskas et al. 2017a |
| 2 | Donkalnis | Cemetery | 1 | Female | 18-20 | M1 (26) | Subneolithic | 3520-3140 | Butrimas 2019 |
| 3 | Donkalnis | Cemetery | 3 | Female | 25-30 | M3 (28) | Subneolithic | 4730-4530 | Antanaitis-Jacobs et al. 2009 |
| 4 | Donkalnis | Cemetery | 5 | Unknown | 5-9 | M1 (26) | Mesolithic | 6060-5900 | Piličiauskas et al. 2017a |
| 5 | Donkalnis | Cemetery | 6 | Female | >30 | M2 (37) | Subneolithic | 4720-4530 | Piličiauskas et al. 2017a |
| 6 | Donkalnis | Cemetery | 7 | Male | ~50 | P2 (25) | Subneolithic | 3520-3370 | Simčenka et al. in prep |
| 7 | Donkalnis | Cemetery | I | Male | >30 | M2 (47) | Subneolithic | 4710-4505 | Simčenka et al. in prep |
| 8 | Donkalnis | Cemetery | III | Male | 20-30 | M1 (36) | Subneolithic | 4650-4400 | Simčenka et al. in prep |
| 9 | Donkalnis | Cemetery | IV | Unknown | adult | M1 (36) | Subneolithic | 4780-4560 | Simčenka et al. in prep |
| 10 | Donkalnis | Cemetery | V | Unknown | 20-30 | M1 (26) | Mesolithic | 5315-5060 | Simčenka et al. in prep |
| 11 | Donkalnis | Cemetery | VI | Unknown | 6-8 | M1 (26) | Subneolithic | 4450-4270 | Simčenka et al. in prep |
| 12 | Donkalnis | Cemetery | 2 | Male | 20-25 | M1 (36) | Mesolithic | 6060-5915 | Butrimas 2019 |
| 13 | Gyvakarai | Single grave | I402 | Male | 35-45 | M2 (27) | Neolithic | 2620-2470 | Piličiauskas et al. 2017a |
| 14 | Kretuonas 1 | Settlement | pl2:O94:sl.s | Unknown |  | M1 (16) | Subneolithic-Neolithic | 4750-1800 | Girininkas and Daugnora 2015; Simčenka et al. in prep |
| 15 | Kretuonas 1 | Settlement | pl2:R94:sl.s | Unknown |  | M1 (46) | Subneolithic-Neolithic | 4750-1800 | Girininkas and Daugnora 2015; Simčenka et al. in prep |
| 16 | Kretuonas 1 | Settlement | I404H | Unknown |  | M2 (27) | Subneolithic-Neolithic | 4750-1800 | Girininkas and Daugnora 2015; Simčenka et al. in prep |
| 17 | Kretuonas 1A | Settlement | B2:88-89 | Male | 20-30 | M2 (37) | Subneolithic-Neolithic | 4750-1800 | Girininkas and Daugnora 2015; Simčenka et al. in prep |
| 18 | Kretuonas 1B | Cemetery | 1 | Female | 20-25 | M1 (16) | Subneolithic | 4460-3820 | Antanaitis-Jacobs et al. 2009 |
| 19 | Kretuonas 1B | Cemetery | 2 | Unknown | 14-16 | M1 (36) | Subneolithic | 4550-3820 | Piličiauskas et al. 2017a |
| 20 | Kretuonas 1B | Cemetery | 5 | Male | 25-30 | M1 (36) | Subneolithic | 4450-4340 | Piličiauskas et al. 2017a |
| 21 | Kretuonas 1B | Cemetery? | 5242 (4?) | Unknown | ? | M2 (47) | Subneolithic | 4550-3820 | Piličiauskas et al. 2017a |
| 22 | Kretuonas 1B | Cemetery? | 5502 (6?) | Unknown | ? | M1 (16) | Subneolithic | 4550-3820 | Piličiauskas et al. 2017a |
| 23 | Kretuonas 1C | Settlement | 2a | Male | 20-30 | M1 (46) | Neolithic | 2200-1800 | Girininkas and Daugnora 2015 |
| 24 | Kretuonas 1C | Settlement | Č102 | Unknown |  | M2 (47) | Neolithic | 2200-1800 | Girininkas and Daugnora 2015 |
| 25 | Kretuonas 1C | Settlement | C100 | Unknown |  | M1 (46) | Neolithic | 2200-1800 | Girininkas and Daugnora 2015 |
| 26 | Plinkaigalis | Cemetery | 241 | Female | 50-55 | P1 (44) | Neolithic | 2860-2410 | Antanaitis-Jacobs et al. 2009 |
| 27 | Plinkaigalis | Cemetery | 242 | Female | >40 | M2 (17) | Neolithic | 3260-2630 | Antanaitis-Jacobs et al. 2009 |
| 28 | Spiginas | Cemetery | 2 | Male | ~50 | M2 (47) | Neolithic | 2130-1750 | Piličiauskas et al. 2017a |
| 29 | Spiginas | Cemetery | 4 | Female | 30-35 | M1 (46) | Mesolithic | 6440-6230 | Butrimas et al. 1985 |
| 30 | Šventoji 23 | Settlement | 1 | Male | 25-35 | M3 (48) | Subneolithic | 3500-3120 | Piličiauskas et al. 2017b |
| 31 | Šventoji 23 | Settlement | 2 | Male | 25-35 | P1 (24) | Subneolithic | 3640-3380 | Piličiauskas et al. 2017b |
| 32 | Šventoji 23 | Settlement | 3 | Unknown | 7-11 | M2 (37) | Subneolithic | 3635-3380 | Piličiauskas et al. 2017b |
| 33 | Šventoji 23 | Settlement | 4 | Unknown | 20-30 | M1 (46) | Subneolithic | 3640-3120 | Piličiauskas et al. 2017b |
| 34 | Šventoji 23 | Settlement | 5 | Unknown | 13-18 | P2 (15) | Subneolithic | 3640-3120 | Piličiauskas et al. 2017b |
| 35 | Šventoji 43 | Settlement | P1 L27/6 | Unknown | 5-7 | M1 (46) | Subneolithic | 3900-3650 | Piličiauskas et al. 2019 |
| 36 | Šventoji 43 | Settlement | P2 Q33/5 | Unknown | 5-10 | dm1 (84) | Subneolithic | 3900-3650 | Piličiauskas et al. 2019 |
| 37 | Turlojiškė | Wetland deposits | 2 (II-3) | Male | 25-30 | M1 (16) | Late Bronze Age | 1015-797 | Mittnik et al. 2018 |
| 38 | Turlojiškė | Wetland deposits | 3 (96-III-2) | Male | 35-45 | M2 (16) | Late Bronze Age | 928-810 | Piličiauskas et al. 2017a |
| 39 | Turlojiškė | Wetland deposits | 4 (98-II-10) | Male | 20-25 | M1 (46) | Late Bronze Age | 1001-825 | Simčenka et al. in prep |
| 40 | Turlojiškė | Wetland deposits | 6 (99-II-7) | Male | 20-25 | M1 (16) | Late Bronze Age | 916-806 | Simčenka et al. in prep |

*Table 1. Human teeth studied*



*Fig. 1. Locations of human, animal and plant samples analysed in this study*

**II.2. Faunal remains**

Modern day Lithuania is mainly covered by glacial deposits ( SI2). Since the variation of 87Sr/86Sr ratios in the bioavailable strontium, in the glacial deposits, was expected to be considerable and hard to predict, our strategy was to create 87Sr/86Sr baselines for every area from which human remains were sampled. In order to reconstruct the archaeological strontium isotope baselines and to avoid Sr “pollution” in modern water and soil, we only used archaeological faunal remains. Using fauna further enabled us to avoid extreme 87Sr/86Sr values, which are likely to be present in plants (Bentley 2006). Firstly, we identified zooarchaeological remains from the same sites from where we had sampled human remains. If absent, we identified animal bones from the nearest archaeological sites, most often situated up to 10 km from the human remains. We selected animals, especially small species with small home ranges, but this was not always possible. Therefore, many species of both wild and domestic taxa were incorporated into our study (Table 2). The chronology of the sampled animal remains was very wide, from the Subneolithic (e.g. Daktariškė 5) to the early modern period (e.g. Varniai). We decided to include animals predating the 19th century AD for the reconstruction of the local strontium baseline, since local fertilisers were in use until World War II. The only modern animal remains analysed in this study were the teeth of four small rodents from Minaičiai village.

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| --- | --- | --- | --- | --- |
| **No.** | **Site** | **Species** | **Dating** | **87Sr/86Sr** |
| 1 | Alytus | Beaver (*Castor fiber* L.) | Iron Age | 0.712512 |
| 2 | Alytus | Beaver (*Castor fiber* L.) | Iron Age | 0.713009 |
| 3 | Alytus | Roe deer (*Capreolus capreolus* L.) | Iron Age | 0.714884 |
| 4 | Biržai | Sheep (*Ovis aries* L.) | medieval | 0.716664 |
| 5 | Biržai | Sheep (*Ovis aries* L.) | medieval | 0.715811 |
| 6 | Biržai | Sheep (*Ovis aries* L.) | medieval | 0.715327 |
| 7 | Biržai | Pig (*Sus scrofa domesticus* L.) | medieval | 0.713332 |
| 8 | Biržai | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | medieval | 0.715223 |
| 9 | Biržai | Sheep (*Ovis aries* L.) | medieval | 0.714752 |
| 10 | Biržai | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | medieval | 0.715311 |
| 11 | Biržai | Pig (*Sus scrofa domesticus* L.) | medieval | 0.712829 |
| 12 | Biržai | Pig (*Sus scrofa domesticus* L.) | medieval | 0.712579 |
| 13 | Daktariškė 5 | Beaver (*Castor fiber* L.) | Subneolithic-EBA | 0.714841 |
| 14 | Daktariškė 5 | Goat (*Capra hircus* L.) | EBA | 0.714250 |
| 15 | Daktariškė 5 | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | EBA | 0.713485 |
| 16 | Daktariškė 5 | Beaver (*Castor fiber* L.) | Subneolithic-EBA | 0.713292 |
| 17 | Daktariškė 5 | Red deer (*Cervus elaphus* L.) | Subneolithic-EBA | 0.714950 |
| 18 | Daučioniai | Marten (*Martes martes* L.) | Iron Age | 0.714397 |
| 19 | Daučioniai | Pig (*Sus scrofa domesticus* L.) | Iron Age | 0.715258 |
| 20 | Juodonys | Pig (*Sus scrofa domesticus* L.) | LBA-Iron Age | 0.715664 |
| 21 | Juodonys | Pig (*Sus scrofa domesticus* L.) | LBA-Iron Age | 0.715380 |
| 22 | Kėdainiai | Pig (*Sus scrofa domesticus* L.) | medieval | 0.712175 |
| 23 | Kėdainiai | Cattle (*Bos taurus* L.) | medieval | 0.715965 |
| 24 | Kernavė | Small rodent | medieval | 0.714902 |
| 25 | Kernavė | Hare (*Lepus timidus*/L. *europaeus* P.) | medieval | 0.717023 |
| 26 | Kernavė | Beaver (*Castor fiber* L.) | medieval | 0.714411 |
| 27 | Kernavė | Small rodent | medieval | 0.714252 |
| 28 | Kernavė | Small rodent | medieval | 0.715429 |
| 29 | Kernavė | Hare (*Lepus timidus*/L. *europaeus* P.) | medieval | 0.716675 |
| 30 | Kernavė | Hare (*Lepus timidus*/L. *europaeus* P.) | medieval | 0.716236 |
| 31 | Kretuonas 1C | Beaver (*Castor fiber* L.) | Neolithic | 0.714215 |
| 32 | Kretuonas 1C | Marten (*Martes martes* L.) | Neolithic | 0.714270 |
| 33 | Kretuonas 1C | Marten (*Martes martes* L.) | Neolithic | 0.714248 |
| 34 | Kretuonas 1C | Beaver (*Castor fiber* L.) | Neolithic | 0.714769 |
| 35 | Kretuonas 1D | Beaver (*Castor fiber* L.) | Neolithic | 0.716665 |
| 36 | Kretuonas 1D | Roe deer (*Capreolus* *capreolus* L.) | Neolithic | 0.714617 |
| 37 | Kretuonas 1D | Roe deer (*Capreolus* *capreolus* L.) | Neolithic | 0.713601 |
| 38 | Kretuonas 1D | Marten (*Martes martes* L.) | Neolithic | 0.715623 |
| 39 | Kretuonas 1D | Beaver (*Castor fiber* L.) | Neolithic | 0.714069 |
| 40 | Kupiškis | Cattle (*Bos taurus* L.) | medieval | 0.718725 |
| 41 | Kupiškis | Cattle (*Bos taurus* L.) | medieval | 0.718586 |
| 42 | Kupiškis | Cattle (*Bos taurus* L.) | medieval | 0.717330 |
| 43 | Kupiškis | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | medieval | 0.717161 |
| 44 | Kupiškis | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | medieval | 0.717412 |
| 45 | Kupiškis hillfort | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | Iron Age | 0.717587 |
| 46 | Kupiškis hillfort | Pig (*Sus scrofa domesticus* L.) | Iron Age | 0.717082 |
| 47 | Minaičiai | Small rodent | Modern | 0.710317 |
| 48 | Minaičiai | Small rodent | Modern | 0.707845 |
| 49 | Minaičiai | Small rodent | Modern | 0.707411 |
| 50 | Minaičiai | Small rodent | Modern | 0.709168 |
| 51 | Pašatrijys | Marten (*Martes martes* L.) | Iron Age | 0.717884 |
| 52 | Pašatrijys | Beaver (*Castor fiber* L.) | Iron Age | 0.714339 |
| 53 | Prelomciškė | Sheep/goat (*Ovis aries* L./*Capra hircus* L.) | Iron Age | 0.713690 |
| 54 | Prelomciškė | Pig (*Sus scrofa domesticus* L.) | Iron Age | 0.713655 |
| 55 | Šventoji 2 | Beaver (*Castor fiber* L.) | Subneolithic | 0.713814 |
| 56 | Šventoji 23 | Beaver (*Castor fiber* L.) | Subneolithic | 0.709482 |
| 57 | Šventoji 26 | Beaver (*Castor fiber* L.) | Subneolithic | 0.714338 |
| 58 | Šventoji 3 | Dog (*Canis familiaris* L.) | Subneolithic | 0.710034 |
| 59 | Šventoji 4 | Beaver (*Castor fiber* L.) | Subneolithic | 0.709612 |
| 60 | Šventoji 4 | Dog (*Canis familiaris* L.) | Subneolithic | 0.709989 |
| 61 | Šventoji 4 | Roe deer (*Capreolus* *capreolus* L.) | Subneolithic | 0.711298 |
| 62 | Šventoji 43 | Fox (*Vulpes vulpes* L.) | Subneolithic | 0.713400 |
| 63 | Šventoji 43 | Roe deer (*Capreolus* *capreolus* L.) | Subneolithic | 0.714821 |
| 64 | Turlojiškė | Water vole (*Arvicola terrestris* L.) | LBA | 0.712793 |
| 65 | Turlojiškė | Water vole (*Arvicola terrestris* L.) | LBA | 0.714260 |
| 66 | Turlojiškė | Water vole (*Arvicola terrestris* L.) | LBA | 0.712696 |
| 67 | Turlojiškė | Water vole (*Arvicola terrestris* L.) | LBA | 0.712657 |
| 68 | Varniai | Pig (*Sus scrofa domesticus* L.) | Early Modern | 0.714592 |
| 69 | Varniai | Pig (*Sus scrofa domesticus* L.) | Early Modern | 0.716614 |
| 70 | Vievininkai | Small rodent | Early Modern | 0.714941 |
| 71 | Vievininkai | Small rodent | Early Modern | 0.716168 |
| 72 | Žilioniai | Cattle (*Bos taurus* L.) | Iron Age | 0.715472 |

*Table 2. 87Sr/86Sr measurements for animal teeth enamel via ID-TIMS. External precision (2σ) = 0.000013. EBA – Early Bronze Age, LBA – Late Bronze Age*

**II.3. Modern plants**

When very few animals or when only a single species (e.g. water vole from Turlojiškė) was available for analysis or when the faunal remains came from a fairly large distance (ca. 10-40 km) from the analysed human remains (e.g. Gyvakarai and Plinkaigalis), we sampled leaves of seven young modern trees (lime, ash, alder, and aspen). Furthermore, we decided to use modern tree leaves in order to investigate the sea spray effect on the Baltic coast and for this we sampled leaves from five trees (aspen and birch) growing 50 to 6000 metres from five sites along the modern coastline. Young trees between 1.5-3.0 m in height were chosen in order to avoid deep rooted systems. Close to each sampled tree, the subsoil lithology was recorded by a soil core sampler. Since Sr-rich and easily weatherable carbonates can highly contribute to 87Sr/86Sr in soil, the presence of carbonates in the subsoil was evaluated by reacting sediments from ca. 0.5 m in depth with drops of diluted (10%) hydrochloric acid (Table 3).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **No.** | **Sample** | **Site** | **Subsoil** | **Species, height** | **Lat.** | **Long.** | **87Sr/86Sr** |
| 1 | SV1 | Šventoji | Fine-medium sand, non-calcareous | Aspen (*Populus tremula*), 1.5 m | 55.9877 | 21.1665 | 0.716509 |
| 2 | SV2 | Šventoji | Fine sand, non-calcareous | Aspen (*Populus tremula*), 1.5 m | 55.9915 | 21.1384 | 0.712911 |
| 3 | SV3 | Šventoji | Gravelly sand, non-calcareous | Birch (*Betula pendula*), 2 m | 55.9925 | 21.1005 | 0.713778 |
| 4 | SV4 | Šventoji | Fine-medium sand, non-calcareous | Birch (*Betula pendula*), 3 m | 55.9950 | 21.0901 | 0.708499 |
| 5 | SV5 | Šventoji | Fine-medium sand, non-calcareous | Aspen (*Populus tremula*), 1.5 m | 55.9900 | 21.0727 | 0.710816 |
| 6 | TRL1 | Turlojiškė | Clay, calcareous | Lime (*Tilia cordata*), 2 m | 54.3690 | 23.2983 | 0.713153 |
| 7 | TRL2 | Turlojiškė | Till, non-calcareous | Lime (*Tilia cordata*), 1.5 m | 54.3633 | 23.3303 | 0.714883 |
| 8 | PLIN1 | Plinkaigalis | Deluvial loam, calcareous | Ash (*Fraxinus excelsior*), 2 m | 55.4131 | 23.6475 | 0.71598 |
| 9 | PLIN2 | Plinkaigalis | Till, calcareous | Ash (*Fraxinus excelsior*), 2 m | 55.4026 | 23.6378 | 0.712086 |
| 10 | GVK1 | Gyvakarai | Till, calcareous | Alder (*Alnus incana*), 1.5 m | 55.9184 | 24.9120 | 0.711082 |
| 11 | GVK2 | Gyvakarai | Gravelly sand, non-calcareous | Alder (*Alnus incana*), 3 m | 55.9096 | 24.9113 | 0.715833 |
| 12 | GVK3 | Gyvakarai | Till, non-calcareous | Aspen (*Populus tremula*), 2 m | 55.9119 | 24.9304 | 0.715114 |

*Table 3. 87Sr/86Sr measurements for modern tree leaves via ID-TIMSincluding species and subsoil descriptions. External precision (2σ) = 0.000013*

**II.4. Sources of bioavailable Sr**

The territory of Lithuania has experienced numerous glaciations, as such it is covered with a sequence of Quaternary deposits, mainly of glacial origin, the thicknesses of which reach more than 200 m in the highlands, but in places in the lowlands they are negligible (Aleksa 2007; Gorlach et al. 2015). In addition, in numerous river outcrops pre-Quaternary rocks are exposed. In many regions, the surface is covered by glacial till, while patches of glaciofluvial sand and gravel or fine glaciolacustrine sediments are also common. Larger areas of sandy outwash and clayey glaciolacustrine sediments are also present. Glacial deposits contain Precambrian igneous and metamorphic rocks, transported by ice sheets from Scandinavia and pre-Quaternary sedimentary rocks eroded by glaciers more locally, mostly including Silurian, Devonian, Permian or Cretaceous carbonates ( SI2). The proportion of Precambrian and carbonate rock components, however, varies. According to some estimates, deposits transported from Scandinavia may compose ca. 25% of the glacial till in Lithuania (Kudaba 1983).

It may be assumed that three sources contributed to the formation of the bioavailable Sr in Lithuania: (i) high radiogenic Sr from Precambrian rock debris transported from Scandinavia by the ice sheets, (ii) low radiogenic Sr from marine carbonates, and (iii) low radiogenic Sr from the Baltic Sea which may have been incorporated into living organisms via marine foods or may have been introduced into soils of the coastal zone via the sea spray effect. In central and northern Sweden, the Proterozoic igneous and metamorphic rocks have 87Sr/86Sr values between 0.7200 and 0.7400 as demonstrated from measurements of surface water and archaeological animals (Bäckström and Price 2016; Löfvendahl et al. 1990; Price et al. 2018). Since marine carbonate rocks inherit their 87Sr/86Sr from seawater, they also contain more Sr and weather faster than other rock types (Palmer and Edmond 1992). Cretaceous marine carbonates have low 87Sr/86Sr in the order of 0.7073-0.7078 (McArthur et al. 2001; Veizer et al. 1997), whereas Silurian, Ordovician, Devonian marine carbonate rocks have 87Sr/86Sr between 0.7078 and 0.7093 (Cramer et al. 2011; Diener et al. 1996; Edwards et al. 2015). Foods from marine environments have the same isotopic values as seawater. Although surface water near Gotland in the Baltic Sea yielded a 87Sr/86Sr value of 0.7093 (Andersson et al. 1992), values vary throughout the Baltic Sea due to the different catchment areas of all the rivers that enter it (Åberg and Wickman 1987; Löfvendahl et al. 1990). Significant consumption of marine fish or seals may shift consumers’ 87Sr/86Sr towards the value of seawater (see Eriksson et al. 2018; Lahtinen et al. 2021). However, due to the process of biopurification, marine dietary components contribute up to five times less Sr to the human diet compared to terrestrial ones (Fornander et al. 2015). Sea spray can have a similar effect on 87Sr/86Sr in humans since marine radiogenic Sr can then be mixed with the 87Sr/86Sr found in terrestrial settings. In a study by Snoeck (2014), a significant impact of the sea spray effect in 87Sr/86Sr values was reported from up to 200 metres from the coastline (see also Alonzi et al. 2020). Considering that most of the areas analysed in this study are located between 80 and 320 km away from the Baltic Sea and long-distance transport of large quantities of seafood is highly unlikely during the Stone and Bronze Ages, it may be assumed that a sea-derived Sr would only influence one of the areas in this study, Šventoji (Fig. 1).

**II.5. Regions studied**

For each of the seven study regions a Quaternary geological map with the locations of the sampled human, faunal and modern tree samples is given ( SI3). The first region, Šventoji, is located on the Baltic Sea coast in northwestern Lithuania. Here, Subneolithic dwellings and fishing sites are found on a sandy Littorina Sea terrace, on the banks as well as in the middle of the former lagoonal lake. Marine and Baltic Ice Lake sand and gravel cover large areas and stretch 5 km inland from the modern coastline. Further inland, glacial till rises to the surface ( SI3:A). The second region includes Biržulis Lake with the Donkalnis and Spiginas Stone Age cemeteries that are located on islands in the lake. The lake is situated in the Žemaičiai Upland and surrounded by morainic hills composed of till in the south and east, and with glaciofluvial landforms in the northwest (SI3: B). The third region includes the Plinkaigalis cemetery that is situated in the Middle Lithuanian Lowland, on the bank of the Šušvė River. It is surrounded by a rather extensive flat plain of glacial till with a narrow belt of an undulating surface stretching from south to north. However, large patches of glaciofluvial sand and gravel and fine proglacial lake sediments occur further to the west and south (SI3: C). The fourth region includes the Turlojiškė Bronze Age site and is situated in the Dzūkų Upland, in the middle of a former lake. The present-day peat bog is on a slightly undulated glaciofluvial and glaciolacustrine sediment surface, surrounded by ice-marginal hills composed of glacial till (SI3: D). The fifth, Biržai, is a city in northern Lithuania at the mouth of the Apaščia River at the human-made Širvėna Lake. The surroundings are part of the Pasvalys Plain with a surface mainly covered by glacial till. However, large patches of glaciolacustrine sand exist only 5-10 km to the north and northeast (SI3: E). The sixth region, Gyvakarai, is situated on the small Žvikė stream that flows through the Pasvalys Plain. Glacial till dominates the plain surface covered by patches of glaciofluvial and glaciolacustrine sediments (SI3: F). The seventh and final region, Kretuonas Lake, is situated on the border of a large glaciofluvial undulating plain to the west with a hilly ice-marginal landscape, mainly composed of glacial till, to the east. A rather large area to the southeast right beside the modern lake is covered by sand deposited in the proglacial lake of the last glaciation (SI3: G).

**II.6. Methods**

87Sr/86Sr analysis was carried at the Vegacenter at the Swedish Museum of Natural History in Stockholm by isotope dilution-thermal ionisation mass spectrometry (ID-TIMS) and laser ablation-multi collector-inductively coupled plasma-mass spectrometry (LA-MC-ICP-MS). The 87Sr/86Sr values are presented at four decimal places throughout this study.

*II.6.1. Isotope dilution-thermal ionisation mass spectrometry*

ID-TIMS was used for bulk analysis of animal teeth and tree leaves in this study. The tooth samples were washed in an ultrasonic bath; first in ultra-pure water and then in ethanol. A Dremel tool was used for polishing, after which a piece of the polished section was used for strontium extraction, followed by further washing in ultrapure water and ethanol. The extracted samples were treated with 0.1M acetic acid for 4 hours at room temperature (Balasse and Ambrose 2002), followed by an ultra-pure water wash and drying, weighing and dissolution in 8M nitric acid in Savillex beakers on a hot plate (95°C).

The dried and homogenised plant material was weighed and, similar to the teeth, dissolved in Savillex beakers. Nitric acid (8M) and hydrogen peroxide were repeatedly added for oxidation and dissolution. The dried, dissolved samples were converted to chloride form by addition of 6M HCl. After drying, both types of samples were re-dissolved in 6M HCl and purified using a Sr specific ion exchange procedure (Delmonte et al. 2008).

The purified samples were mixed with a silicotungstic ionisation enhancer, loaded on Re single filaments and analysed using a Thermo Scientific Triton thermal ionisation mass spectrometer (TIMS). Two hundred 8 sec. integrations were recorded in multi-collector static mode, applying rotating gain compensation. Measured 87Sr intensities were corrected for Rb interference using 87Rb/85Rb = 0.38600 and ratios were reduced using the exponential fractionation law and 88Sr/86Sr = 8.375209. The isotope data were normalised to the NBS 987 Sr isotope reference, repeated analyses of which during the course of the analytical sessions for animal and plant samples yielded an external reproducibility of 17 ppm (*n* = 12) and 18 ppm (*n* = 20) respectively.

*II.6.2. Laser ablation-multi collector-inductively coupled plasma-mass spectrometry*

LA-MC-ICP-MS was used for the human teeth in this study. *In situ* 87Sr/86Sr analysis was conducted on tooth samples using a NWR193 excimer laser ablation system (Electro Scientific Industries) coupled to a Nu Plasma II multi-collector ICP mass spectrometer (Nu Instruments Ltd.) at the Vegacenter, Swedish Museum of Natural History, Stockholm. The instrument operating conditions are listed in SI1: Table 1 and the isotope data for each ablated tooth are given in SI1: Tables 3-42. The method follows the procedures outlined in Boethius et al. (2021) and Glykou et al. (2018).

Ablations were made on the outer surface of the tooth enamel using line-scans with a 130 μm spot size starting at the tip of the tooth and moving down towards the enamel–dentine junction. The number of ablation lines per tooth ranged from 9 to 20, depending on the size of the tooth. Prior to each ablation, the tooth was pre-ablated using a laser spot size of 150 μm to remove potential surface contamination, which could be caused by its depositional soil environment. The results show no increase in either rare earth elements (REE) or Rb, compared to the reference materials, which indicates pre-ablation was successful. Analyses were also monitored for potential sampling of dentine, which may occur when the enamel layer is thin. Dentine has a lower density and a more porous structure than enamel and can be more easily contaminated. This can lead to anomalous divergence in 87Rb/86Sr, but this was not observed for any analyses.

Possible isobaric interferences were corrected by subtracting a gas blank (84Kr) and by peak stripping (e.g., doubly charged REE, Ca-dimers/argides, 87Rb; cf. Glykou et al. 2018). A polyatomic interference on *m*/*z* 87 has also been reported (Horstwood et al. 2008) and is described as (Ca/Ar)31P16O+. This interference has been reduced by a thorough low oxide tuning of the gases (Willmes et al. 2016). To verify successful removal of all interferences, two reference materials (RM) with known Sr concentrations and ratios were repeatedly analysed throughout analytical sessions (SI1:Table 2). A spine from a velvet belly lantern shark (*Etmopterus spinax*) was used as the primary RM and a tooth from a mountain hare (*Lepus timidus*) was used as the secondary RM. The analyses on the shark spine yielded a 87Sr/86Sr of 0.70919 ± 0.00034 (2SD, *n* = 103), which agrees well with the value of seawater of 0.709179 ± 0.000002 (Mokadem et al. 2015). The hare tooth yielded a 87Sr/86Sr of 0.71002 ± 0.00017 (2SD, *n* = 22). This is in agreement with the value determined by TIMS (0.709988 ± 0.000015; Triton, Thermo Scientific) at the Swedish Museum of Natural History.

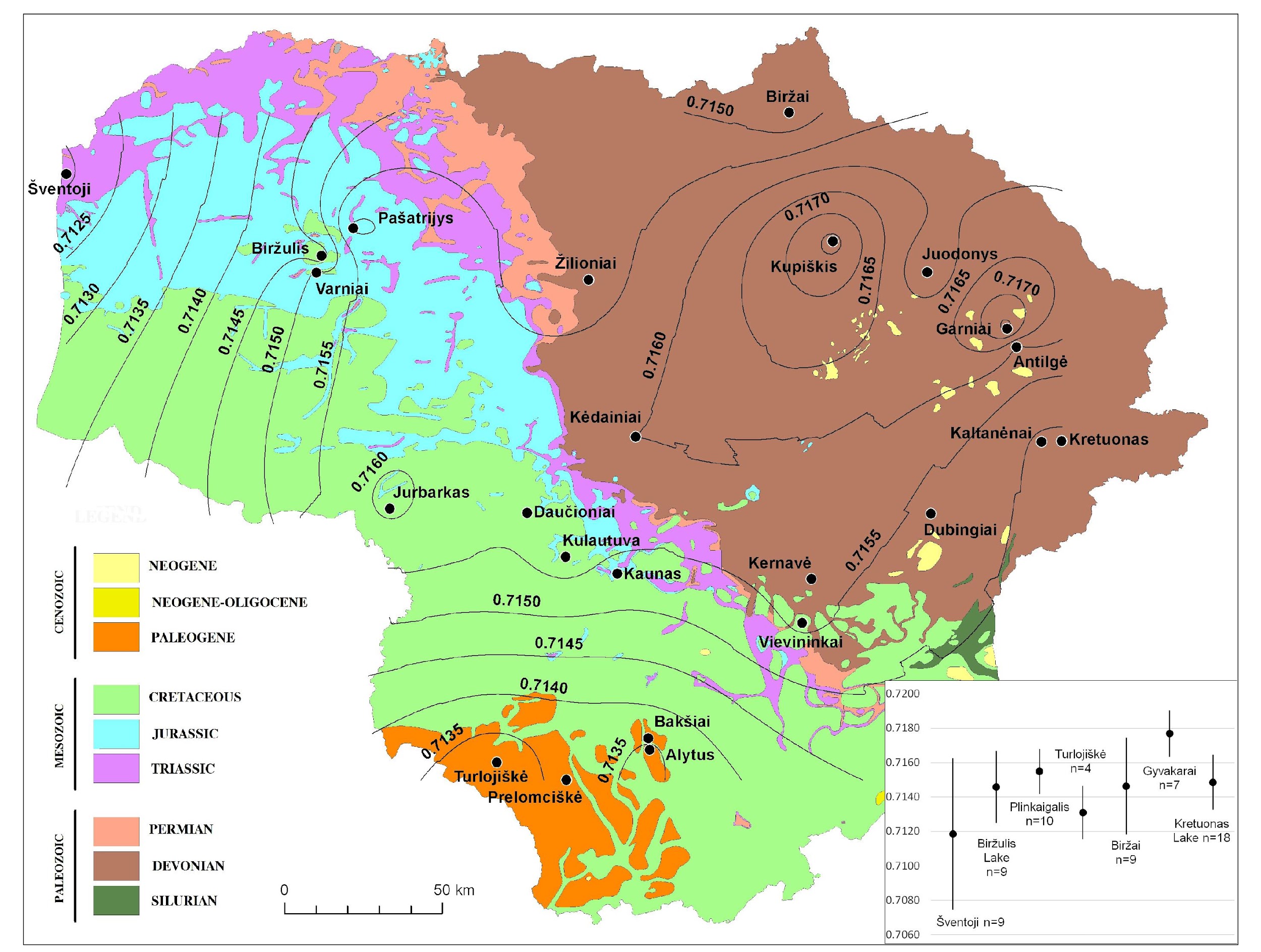
**III. Results**

**III.1.** **87Sr/86Sr measurements and outliers**

LA-ICP-MS measurements on 40 human teeth are presented in Table 1 and Supplementary Information SI1, ID-TIMS measurements on 72 animal teeth enamel samples in Table 2, and ID-TIMS measurements on leaves of 12 modern trees in Table 3. Before reconstruction of local 87Sr/86Sr baselines and a Lithuanian isoscape, two outlier measurements were identified and not used for further interpretations. Among the 72 animal teeth analysed for our project, a pig from Kėdainiai (0.7122) was considered to be an outlier due to an unusually low 87Sr/86Sr ratio for central Lithuania. It could have been transported to the medieval town of Kėdainiai from a distant area, e.g. southwestern or coastal Lithuania. A beaver, from the Kretuonas 1C Neolithic settlement, was considered a second outlier (Piličiauskienė et al. 2022). The notably higher isotopic ratio of the beaver (0.7201) compared to the other animals from the Lake Kretuonas area (0.7136-0.7167) may indicate that either non-local animals had been sampled or it represents a localised anomaly. The analysed beaver tooth was removed from an isolated mandible found in the refuse layer and may have been transported to the site from elsewhere. Animal teeth are commonly used as pendants in this area from this time period (Girininkas and Daugnora 2015).

**III.2. Local 87Sr/86Sr baselines**

In order to identify non-local humans, we reconstructed 87Sr/86Sr baselines, based on the mean value +2 SD of archaeological fauna, for the seven regions where human remains were sampled from (Fig. 2). The robustness of those baselines is, however, greatly variable because of the different number and species of animals analysed, as well as the different distances between the studied sites containing animal and human remains. At Biržai, human remains are located up to 0.5 km from sites from which the animal remains originated, at Turlojiškė up to 1 km, at Šventoji up 4 km, at Kretuonas up to 6.3 km, at Biržulis up to 9 km, at Gyvakarai up to 10 km, and at Plinkaigalis up to 40 km ( SI3).

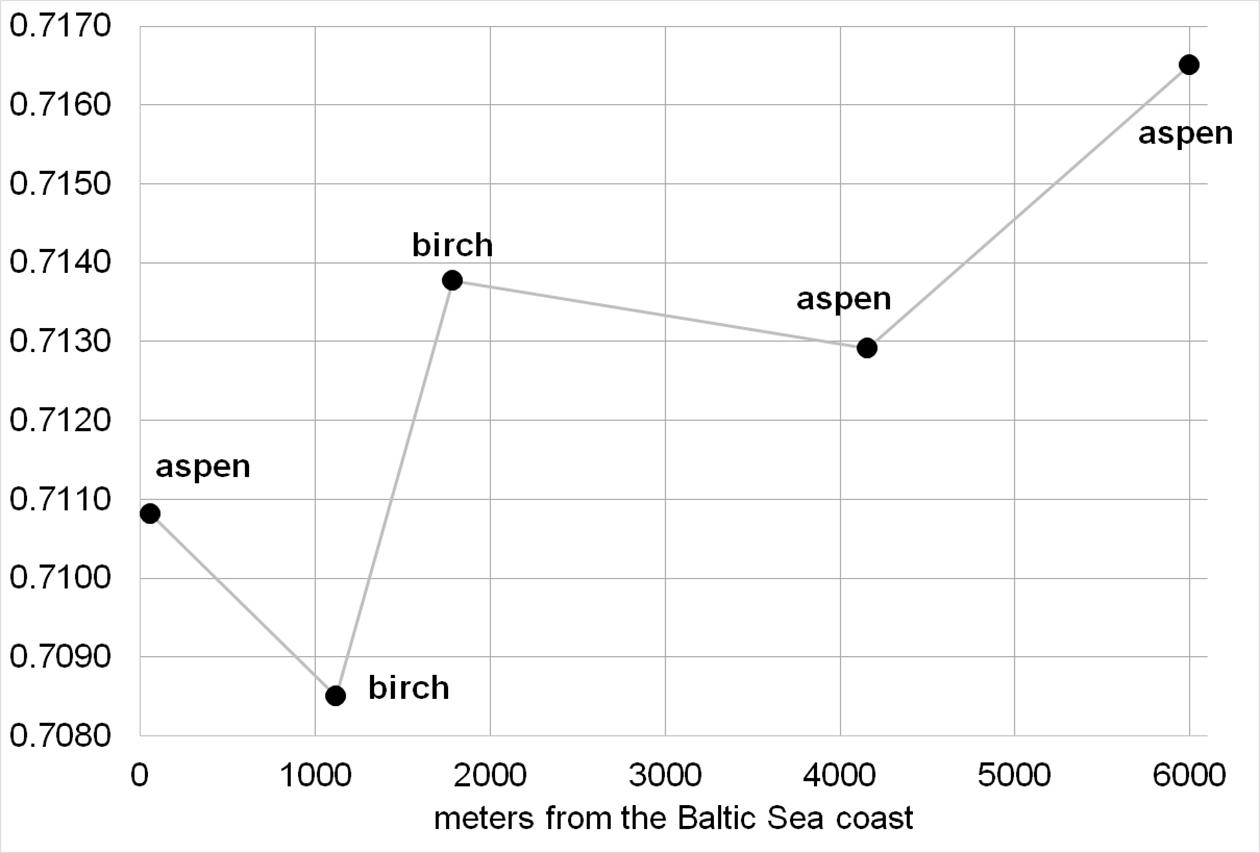


*Fig.*  *2. 87Sr/86Sr isoscape in Lithuania mapped onto a modified Pre-Quaternary geological map 1:200 000 after the Lithuanian Geological Survey (*[*https://www.lgt.lt/epaslaugos/elpaslauga.xhtml*](https://www.lgt.lt/epaslaugos/elpaslauga.xhtml)*) and 87Sr/86Sr baselines based on the mean value + 2 SD of archaeological fauna of the seven regions where human remains were sampled from*

**III.2. 87Sr/86Sr isoscape in Lithuania**

For the reconstruction of the 87Sr/86Sr isoscape in Lithuania, we averaged 87Sr/86Sr ratios of archaeological fauna at each of the 24 localities. In doing so we grouped data from several sites only in cases when they were situated up to 4 km one from another. Then, the obtained means were used for interpolation of the isoscape using the Kriging method (Cressie 1991). The isoscape revealed several geographical trends in the variability of 87Sr/86Sr in the biosphere (Fig. 2). For instance, Garniai and Kupiškis, both situated in northeastern Lithuania, demonstrate the highest faunal averaged 87Sr/86Sr ratios (0.7177) among all of the analysed sites (Fig. 2). It can be assumed that the glacial deposits in this area contain more Precambrian rocks debris with high radiogenic Sr. In the central part of the country, the mean 87Sr/86Sr ratios of archaeological fauna vary between ca. 0.7142-0.7161. Southern Lithuanian appeared to have notably low bioavailable 87Sr/86Sr in the order of ca. 0.7131-0.7137 (Fig. 2). In southwestern Lithuania, calcareous soils are common in which carbonates are found mostly as chalk debris, rather than limestone or dolomite crumbs or boulders. Cretaceous chalk from surface glacial and proglacial deposits may lower the 87Sr/86Sr ratios. However, the impact of *in situ* pre-Quaternary carbonates on the bioavailable Srwas negligible. For instance, at Biržai and Kupiškis, where Devonian dolomite and limestone are covered by only ca. 1-20 m thick glacial deposits, the mean 87Sr/86Sr ratios of archaeological fauna appeared to be higher (0.7146 ± 0.0014 and 0.7177 ± 0.0007 respectively) to that of many other areas in Lithuania with much thicker cover of Quaternary deposits ( SI4).

However, the lowest bioavailable 87Sr/86Sr was recorded at Šventoji on the Baltic coast. The Šventoji animals were sampled at five archaeological sites situated at 800-1100 metres from the modern coastline ( SI:3A) and they have unusually variable 87Sr/86Sr within the range 0.7095-0.7148 and a mean value of 0.7119 (Fig. 2). Some of 87Sr/86Sr values are close to the 87Sr/86Sr ratio of Baltic Sea water (0.7092-0.7093) measured between Gotland and the Latvian coast (Andersson et al. 1992). Therefore, we hypothesised, that bioavailable 87Sr/86Sr at Šventoji was influenced by the sea spray effect (see Alonzi et al. 2020; Snoeck 2014) and that animals with lower 87Sr/86Sr lived closer to the coast than animals with higher 87Sr/86Sr. This has further been confirmed by 87Sr/86Sr in modern tree leaves (Table 3 ). At the Baltic coast, we found a positive correlation between distance from the coast and high radiogenic Sr in the leaves of young modern trees (Fig. 3). It appeared that the sea spray effect is very profound, in a very flat landscape with a similar geology, up to 1.5 km from the coastline, and might still have an impact up to 5 km from the coastline. It has, however, no influence on the biologically available Sr further inland.



*Fig.*  *3. 87Sr/86Sr in modern trees leaves at Šventoji in respect to their distance to the Baltic Sea coast*

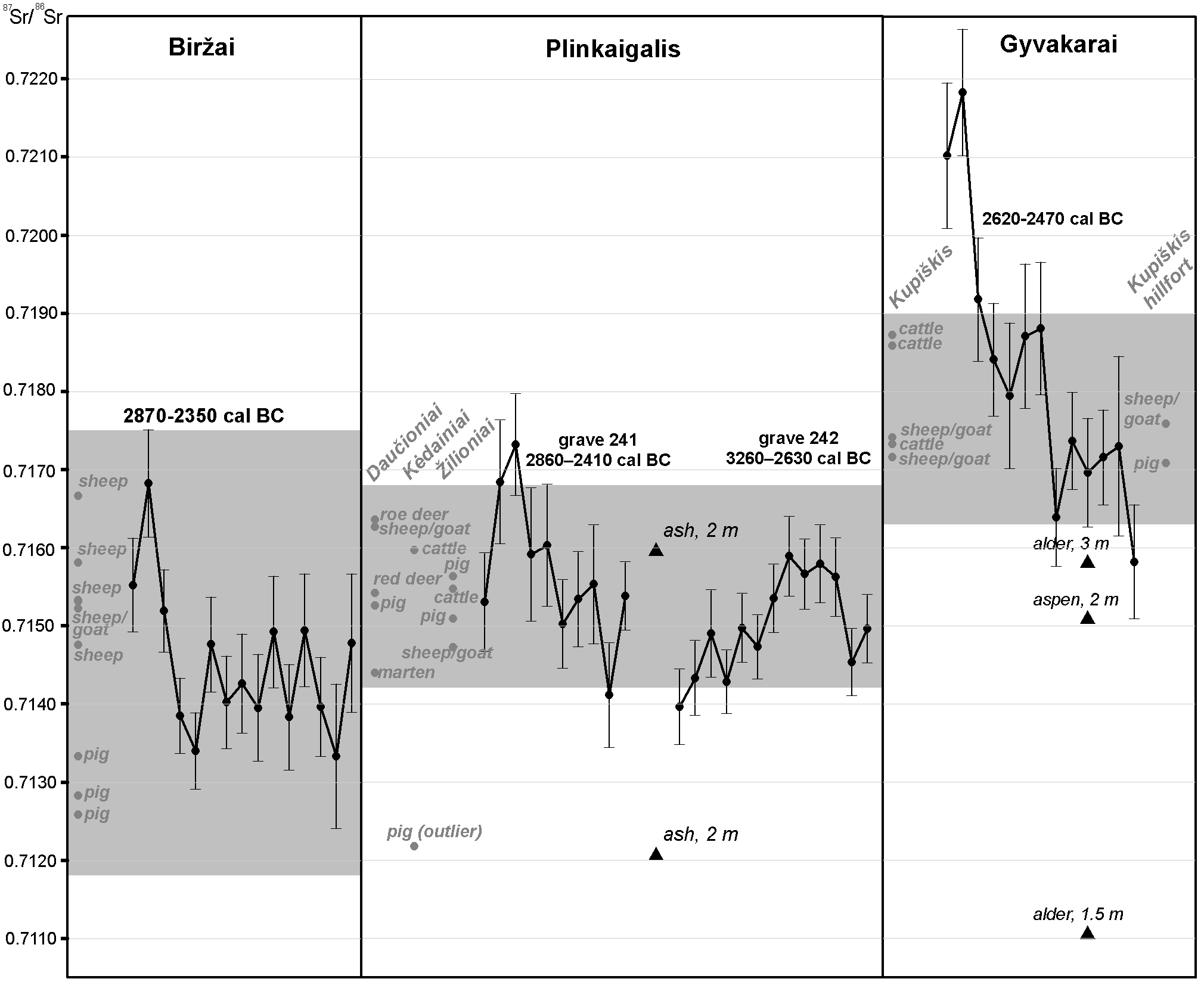
**IV. Discussion**

**IV.1. Modern samples for palaeomobility studies. Are they reliable?**

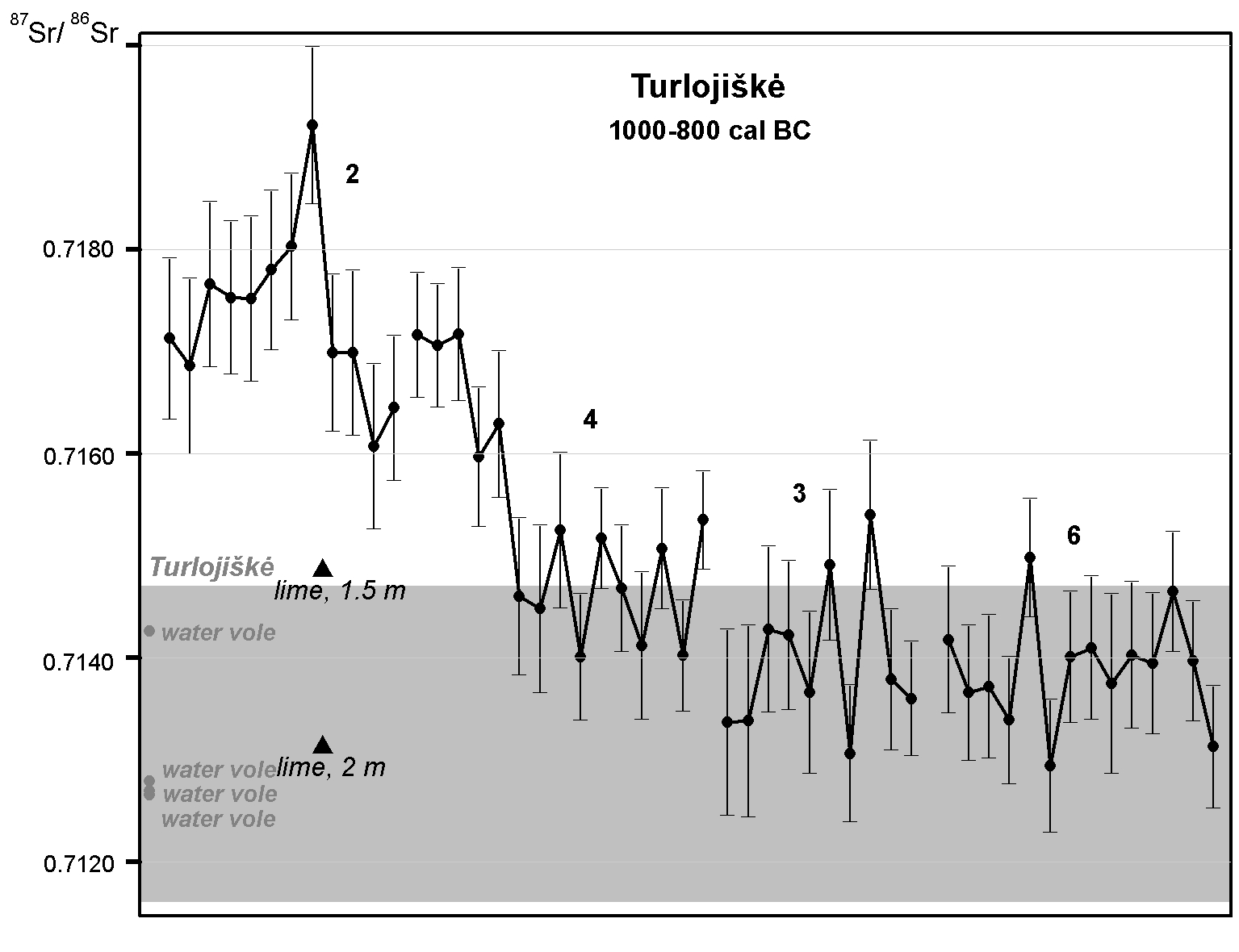
In 2019, Hoogewerff et al. published 87Sr/86Sr ratios obtained from grazing and agricultural soils across a large part of Europe. The study contained measurements from 17 locations in Lithuania, 10 in Latvia, 14 in Estonia, 64 in Poland and 94 in Ukraine. In these countries 87Sr/86Sr values of archaeological fauna were either absent or very few, therefore, Hoogewerff et al.’s data might be useful for reconstructing local baselines in Lithuania. To do this it is essential to know whether 87Sr/86Sr ratios of modern soils are significantly altered by any modern agents. Therefore, we compared 87Sr/86Sr values in modern soils and archaeological animals. Firstly, we interpolated Lithuanian soil data by the Natural Neighbour method (Cressie 1991). Then, we extracted 87Sr/86Sr for each locality from which the animal remains were analysed for our study. Finally we plotted the interpolated soil values against measured faunal values ( SI5). From this plot a statistically significant (a paired-samples t-test, t = 17.71, df = 23, *p* < 0.001) offset between 87Sr/86Sr in modern soils and archaeological fauna is evident, with the former being lower by 0.0081 ± 0.0022. In addition, four small modern rodents from Minaičiai gave a mean 87Sr/86Sr value of 0.7087 which is very close to the soil but inconsistent with the archaeological animals 87Sr/86Sr at any of the closest localities, e.g. Žilioniai (0.7152), Kėdainiai (0.7160) and Pašatrijys (0.7161) (SI5 ). Therefore it seems that 87Sr/86Sr in both soils and modern animals is affected by non-local strontium. Chemical fertilisers may be the reason for this (see Böhlke and Horan 2000). In Lithuania non-natural fertilisers have been extensively used after World War II. In addition, polluted precipitation may also introduce low radiogenic Sr into modern soils and animals. It has been estimated that in some cases precipitation may supply up to 50-75% of the Sr available for plants (Graustein and Armstrong 1983; Sanusi et al. 1995).

Furthermore, we also found that the 87Sr/86Sr ratios of modern plants (5/12) were incompatible with those of archaeological animals. The uptake of strontium by vegetation is dependent on many factors including fungi, root-depth and taxon (Dijkstra et al. 2003; Isermann 1981). Local anomalies in the geological background may also greatly influence the 87Sr/86Sr in plants, for instance these may be caused by clastic carbonate components within glacial deposits. For example, at Gyvakarai, 2.0-3.0 m high alder and aspen trees, have only slightly lower ratios (0.7158 and 0.7151 respectively) compared to the local baseline based on archaeological fauna (0.7163-0.7190), while another 1.5 m high aspen had a much lower 87Sr/86Sr value of 0.7111 (Fig. 4). This aspen with the lowest 87Sr/86Sr value was growing on calcareous subsoil, whilst the remaining two were growing on non-calcareous subsoil (Table 3). At Turlojiškė, from two young 1.5-2.0 m high lime trees that were growing 2.2 km apart, one had a 87Sr/86Sr value of 0.7131, which is within the local baseline (0.7116-7147), whilst the other had a higher 87Sr/86Sr value of 0.7149 (Fig. 5). Once again, the tree growing on calcareous clay had a lower 87Sr/86Sr value than the one growing on non-calcareous clay loam (Table 3). At Plinkaigalis, two ash trees that were both 2.0 m high and growing on calcareous subsoil showed very distant 87Sr/86Sr values of 0.7160 and 0.7121. While the higher value is within the local baseline based on archaeological fauna (0.7142-0.7168), the other is much lower (Fig. 4). In this case, a more thorough analysis of the carbonate content in surface deposits is required in order to explain the anomalously low radiogenic value. Finally, the best fit between modern plant and archaeological animal ratios was found in the coastal area at Šventoji (Fig. 6). However, this could be due to the sea spray effect, which is affecting the area today as well as in prehistory.

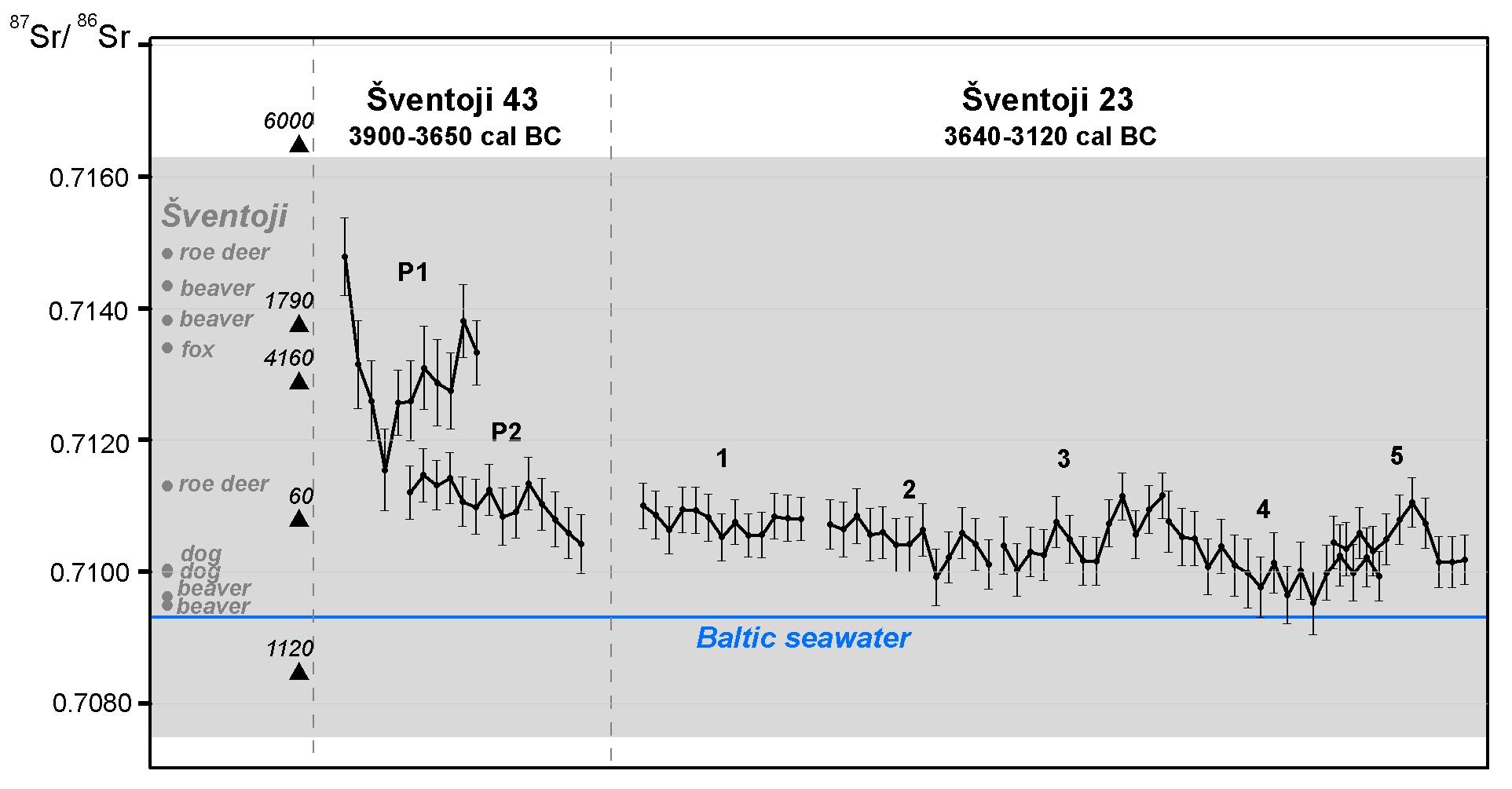
To summarise, we identified lower 87Sr/86Sr in modern soils and animals and in some cases also modern plant samples compared to the archaeological fauna throughout Lithuania, however, the reasons for this are far from clear. Based on these offsets we advise caution when using modern samples for the reconstruction of local baselines and isoscapes in Lithuania.

**

*Fig.*  *4. 87Sr/86Sr intra-tooth variation of the human individuals from the Biržai, Plinkaigalis and Gyvakarai CWC graves plotted onto a local baselines, which were constructed from data obtained from archaeological animals (shaded in grey; at 2 SD). ID-TIMS measurements of modern tree leaves are denoted by black triangles*

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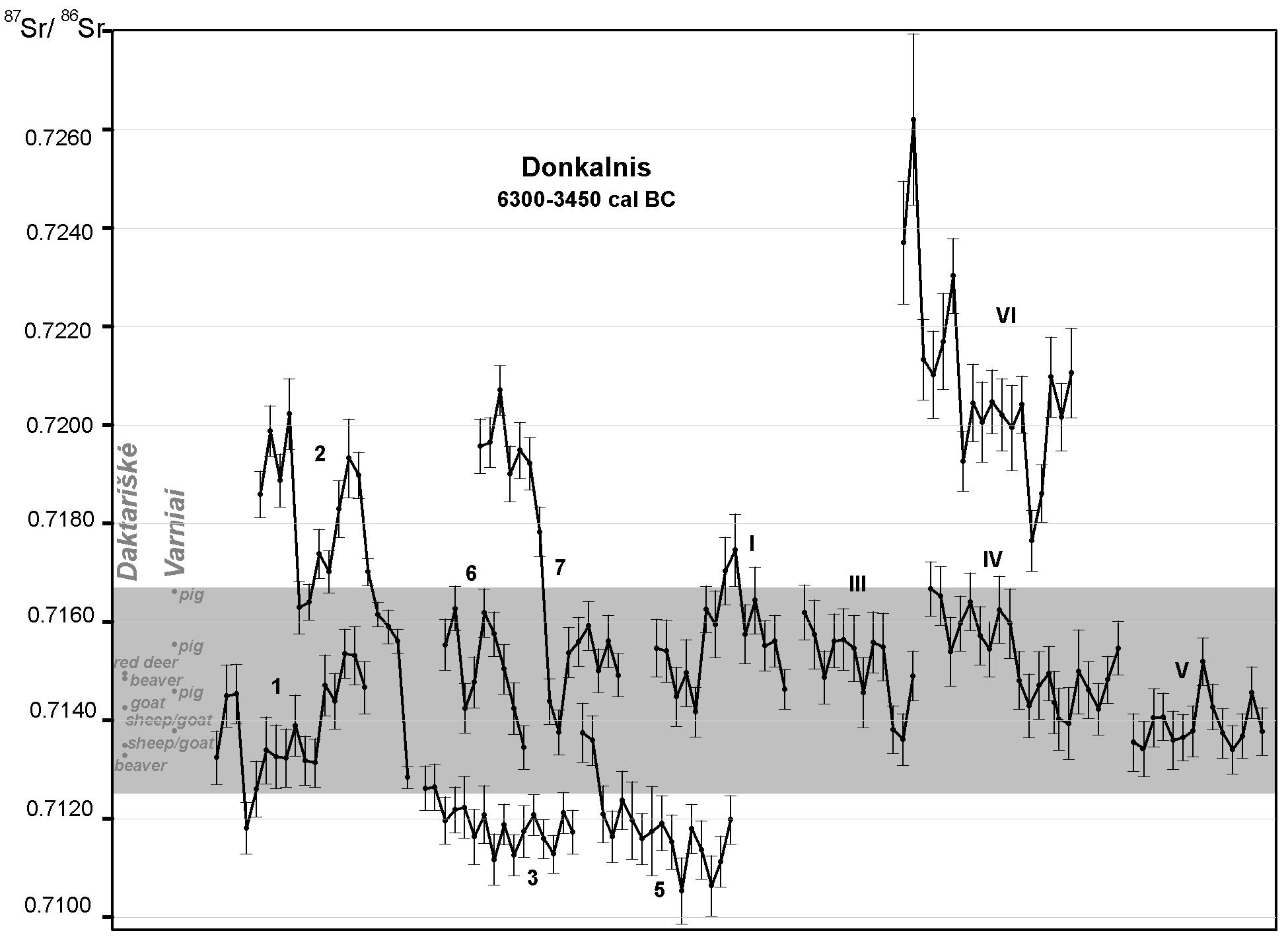
*Fig.*  *5. 87Sr/86Sr intra-tooth variation of the four human individuals from the Turlojiškė Late Bronze wetland deposition plotted onto a local baseline, which was constructed from data obtained from archaeological animals (shaded in grey; at 2 SD). ID-TIMS measurements of modern tree leaves are denoted by black triangles*

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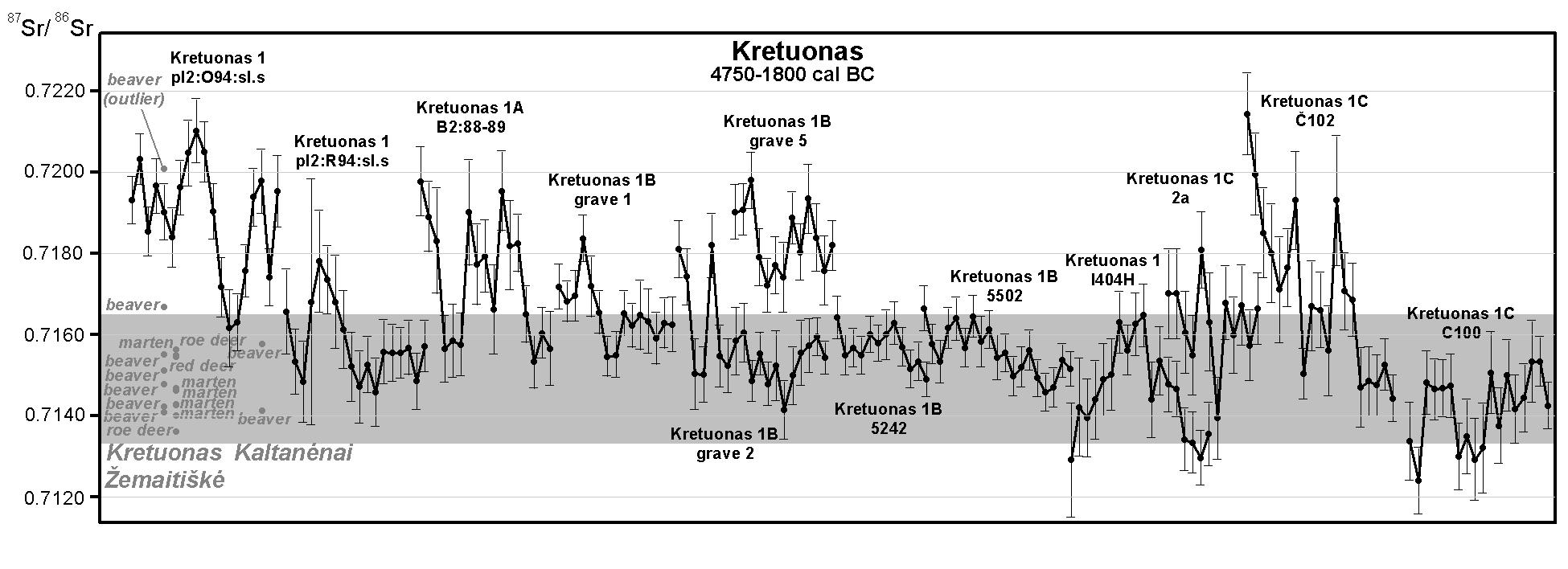
*Fig.*  *6. 87Sr/86Sr intra-tooth variation of seven human individuals from the Šventoji Subneolithic dwelling sites plotted onto a local baseline, which was constructed from data obtained from archaeological animals (shaded in grey; at 2 SD). ID-TIMS measurements of modern tree leaves are denoted by black triangles while accompanying numbers show their distance to the Baltic coastline*

**IV. 1. Mobility patterns**

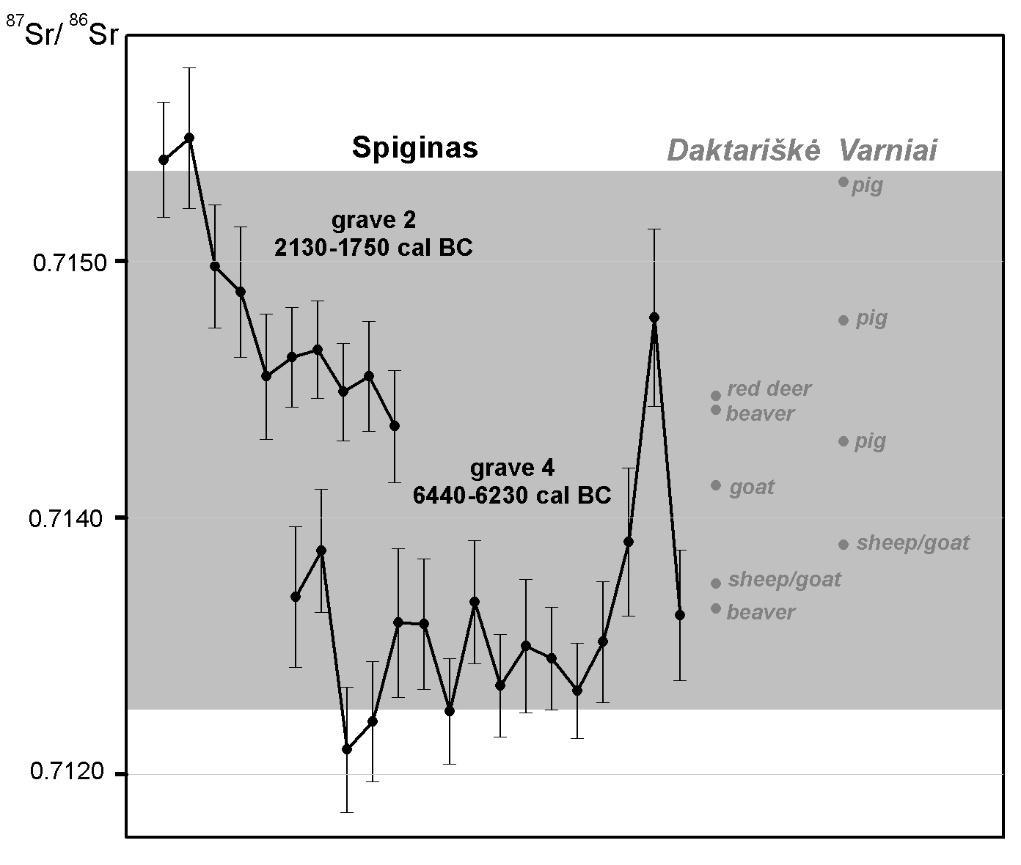
We compiled 87Sr/86Sr intra-tooth variation curves from multiple 87Sr/86Sr measurements for each human tooth and plotted them onto local baselines reconstructed from 87Sr/86Sr ratios (2 SD) of archaeological fauna (Fig. 4-9). According to radiographic and histological studies, enamel of the permanent M1 tooth forms at the age of 0-3 years, 3-6 years for M2, 8-11 years for M3, 2-6 years for premolars, and prior to birth and up to 0.5 years for dM1 (Massler et al. 1941; Reid and Dean 2006). Since we preferentially sampled permanent M1 and M2 teeth from humans, the majority of the intra-tooth variation curves reflect the chronological sequence during early childhood (0-6 years). Despite this, there were several exceptions, the permanent M3 teeth from Šventoji 23 ‘grave’ 1 and Donkalnis grave 3, both of which mineralised during late childhood (8-11 years), and the deciduous dM1 from Šventoji 43, which mineralised prior to birth and during early infancy.

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*Fig.*  *7. 87Sr/86Sr intra-tooth variation for 11 human individuals from the Donkalnis Mesolithic-Subneolithic cemetery plotted onto a local baseline, which was constructed from data obtained from archaeological animals (shaded in grey; at 2 SD)*

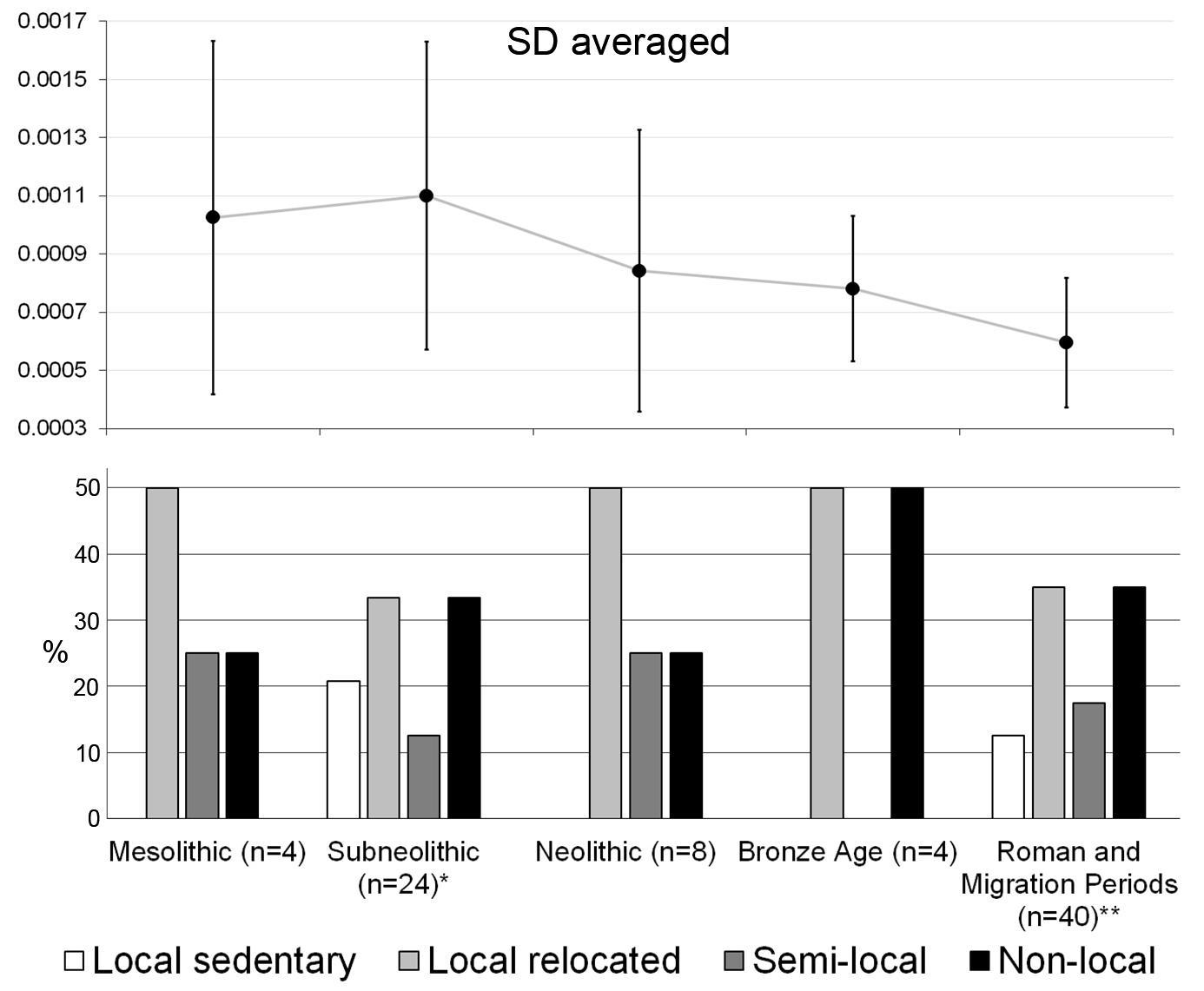
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*Fig.*  *8. 87Sr/86Sr intra-tooth variation for 12 human individuals from the Kretuonas Subneolithic-Neolithic site plotted onto a local baseline, which was constructed from data obtained from archaeological animals (shaded in grey; at 2 SD)*

**

*Fig.*  *9. 87Sr/86Sr intra-tooth variation for two individuals from the Spiginas Mesolithic-Neolithic cemetery plotted onto a local baseline, which was constructed from data obtained from archaeological animals (shaded in grey; 2 SD)*

On the basis of 87Sr/86Sr intra-tooth variation curves and SD values, which were calculated for each individual from multiple 87Sr/86Sr measurements on the same tooth, we grouped human teeth measurements into four clusters termed here as local sedentary, local relocated, semi-local and non-local. Under local sedentary, we assume individuals whose 87Sr/86Sr intra-tooth variation range does not exceed the local baseline and demonstrates low SD up to ±0.00035, i.e. individuals that are likely to have been born locally and did not leave the region during mineralisation of the tooth enamel. Individuals bearing local 87Sr/86Sr but exhibiting significant 87Sr/86Sr intra-tooth variation (SD > ±0.00035) were grouped together as local relocated. They were most likely locally born but changed their place of residence within an analysed region or moved between several areas with overlapping bioavailable 87Sr/86Sr. Alternatively, high intra-tooth variation inside of the local baseline range may indicate dietary shifts to seasonally available resources (e.g. migratory fish or waterfowl) or changes in the place of foraging, fishing or hunting without relocation of a whole group. Under the non-local category, we placed individuals whose all or at least two first measurements are outside of the local baseline. They had to be born outside the region of death. Some of these people had already moved into the local region during mineralisation of the analysed tooth throughout their childhood (e.g. Kretuonas 1B grave 2) but some did so later as is shown by their 87Sr/86Sr intra-tooth variation curves. The final group is semi-locals. In this case 87Sr/86Sr in the oldest part of the enamel (tooth crown) is within the local baseline. However, subsequent measurements exceed the local 87Sr/86Sr range. This implies that these individuals were most likely born locally but during childhood they changed their place of residence, entering an area with different bioavailable 87Sr/86Sr values.

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*Fig.*  *10. 87Sr/86Sr intra-tooth variation SDs estimated for different prehistoric periods and*  *mobility patterns revealed by strontium isotope ratios*  *in Lithuania.*

*\* Four individuals supposedly dating to the Subneolithic-Neolithic were attributed to the Subneolithic here.*

*\*\* Data for the Roman and Migration periods (ca. 1-600 cal AD)* *of the Iron Age are from Kurila et al. (in prep)*

In order to reveal trends in mobility patterns during the Stone and Bronze Ages, we estimated the percentages of local sedentary, local relocated, semi-local and non-local 87Sr/86Sr intra-tooth values for the Late Mesolithic (ca. 7000-5000 cal BC), the Subneolithic (ca. 5000-2900 cal BC), the Neolithic (ca. 2900-1800 cal BC), and the Bronze Age (ca. 1800-500 cal BC) periods (Fig. 10 ). Not surprisingly, likely locally born individuals, classified as local relocated, local sedentary or semi-local, made the core of the population (50-75%) during all periods. Non-locals made up a substantial part (25-50%) of the Stone and Bronze Age individuals. An increase of non-locals during the Subneolithic (33%) and the Bronze Age (50%) periods compared to the Mesolithic (25%) and the Neolithic (25%) periods was present. However, this overrepresentation may be due to the very low number of sampled individuals from the Mesolithic, Neolithic and Bronze Age periods and also due to the very likely sacrificial nature of the Turlojiškė Late Bronze Age site. We should also wish to point out that in many areas of Lithuania the bioavailable 87Sr/86Sr values overlap at 0.7140-0.7160 (Fig. 2). This range could also be expected for neighbouring countries with similar geology. Furthermore, it has been estimated that more than 90% of the terrestrial samples throughout the world have 87Sr/86Sr that fall within the range of 0.7060 and 0.7200 (Bataille et al. 2020). Overlapping baselines across large areas reduce the possibility of identifying non-locals via 87Sr/86Sr analysis. Therefore, we should consider 25-50% non-locals as a minimum value.

Profound, and in many cases cyclic, variation in 87Sr/86Sr intra-tooth values in an individual is classified by us as a local relocated or semi-local individual, suggesting seasonal mobility to be a common phenomenon. This was identified in the Mesolithic, Subneolithic and Neolithic individuals, and perhaps some of the Bronze Age individuals. This finding fits well with the mixed-type economy recently proposed for the southeastern Baltic population during the Neolithic and the Early Bronze periods, based on carbon and nitrogen stable isotope data, organic residue analysis of ceramic vessels, and recent macrobotanical analyses (Piličiauskas et al. 2017a, 2020, 2021; Robson et al. 2019). It seems that mobile stockbreeding and extensive barley farming was supplemented by the continued exploitation of wild resources for some time. Strontium isotopic data from Turlojiškė argues for the continuation of a mobile way of life and perhaps also extensive farming into the Late Bronze Age, despite evidence for intensive farming around fortified settlements (Minkevičius et al. 2020). Our interpretation of the 87Sr/86Sr values of the Turlojiškė humans may, however, be incorrect (i.e. evidence for increasing mobility) due to the sacrificial nature of the site. Nevertheless, it seems that several types of economies involving different degrees of sedentism are likely to have coexisted in the southeastern Baltic during the Bronze Age. Sedentary populations may have ploughed permanent fields and practised manuring in the vicinity of the fortified settlements. However, further away from the local centres, in forested areas, semi-nomadic communities may have practised slash-and-burn agriculture.

We demonstrate that under conditions of similar geology, in this case glacial and proglacial surface deposits, intra-tooth 87Sr/86Sr standard deviations may be used as proxy data for ascertaining the degree of mobility among prehistoric communities. We averaged intra-tooth 87Sr/86Sr standard deviations for five prehistoric periods, Mesolithic, Subneolithic, Neolithic, Bronze Age, and Iron Age (Fig. 10) and found that the beginning of pottery technology at ca. 5000 cal BC did not reduce the mobility of hunter-gatherers in Lithuania. Furthermore, decreasing intra-tooth 87Sr/86Sr variation from the Neolithic to the Iron Age is in agreement with the introduction and subsequent slow and long-lasting intensification of farming and transition to a more sedentary way of life.

Based on 87Sr/86Sr analysis, Stone Age year-round settlements may only have existed on the Baltic coast in Lithuania. At the coastal Šventoji sites, five of the seven Subneolithic individuals had a very low 87Sr/86Sr intra-tooth variation with standard deviations between 0.0002 and 0.0003. Here, very rich marine and lagoonal food resources were available (Piličiauskas et al. 2017b). However, neither the 87Sr/86Sr ratios within the local baseline nor the very low intra-tooth variation curves contradict the hypothesis that coastal fishers moved up and down the Baltic coast. Further, it is interesting to note that none of the inland Stone or Bronze Age individuals showed intra-tooth 87Sr/86Sr standard deviations below 0.0004. Such low variation only reappears during the Iron Age (Fig. 10), which may be connected with the intensification of agriculture, in connection to the introduction of iron tools, at the beginning of the Roman Period (Michelbertas 1986).

Sex-biased mobility patterns were not possible to examine for the Neolithic and the Bronze Age due to the relatively low number of individuals (*n* = 8 and 4 respectively), and the few secure sex determinations among them. However, if we combine all of the analysed Mesolithic and Subneolithic hunter-gatherers into a single group, 13 individuals have been sexed. According to the 87Sr/86Sr data, two out of five females and four out of eight males were non-local. Thus, there is no significant difference in mobility patterns between males and females in the southeastern Baltic hunters-gatherer communities.

Comparing the degree of mobility of the inhabitants of the southeastern Baltic during the Stone and Bronze Ages to that of other European regions is challenging, not least due to the different geologies but also the different methods applied. In previous mobility studies, TIMS was mostly used, which measures the 87Sr/86Sr ratio of bulk enamel samples and does not provide any data on intra-tooth variation. In our study LA-ICP-MS was employed which records intra-tooth variation that can further be used as proxy data to infer mobility patterns. Unfortunately, there are too few studies from Estonia and Finland (Oras et al. 2016) and they also derive from different periods (Lahtinen et al. 2021) to compare with our data from Lithuania. More extensive studies have been undertaken on Swedish and Danish individuals. Intriguingly, the number of non-locals dating to the Neolithic in Lithuania compared to those from the Early-Middle Neolithic in southwestern Sweden appear to be somewhat comparable (25 and 18% respectively); whilst the number of non-locals dating to the Bronze Age in Lithuania was similar to those from the Neolithic to Early Bronze Age of southwestern Sweden (50 and 47% respectively) (Blank et al. 2021). Furthermore, the mobility patterns of coastal Subneolithic fishers at Šventoji, show no or only a single non-local (14%) which is similar to the Neolithic Pitted Ware culture people on Gotland (9% of non-locals) (Ahlström and Price 2021). However, in both regions the low number of non-local 87Sr/86Sr ratios in humans is most likely the effect of the significant consumption of marine-derived protein or at Šventoji by the sea spray effect rather than reduced mobility. On the same island of Gotland, 23 individuals dated to the Middle Neolithic (ca. 3300-2350 cal BC) and Late Neolithic-Early Bronze Age showed increased migration to Gotland during the latter period based on 87Sr/86Sr data (Fraser at al. 2018). On the island of Öland, 87Sr/86Sr ratios from nine individuals from the passage grave at Resmo, dating to the Neolithic and the Bronze Age (ca. 3500-1000 cal BC), have been analysed and at least five non-local individuals representing at least two different geographical regions of origin were identified. It was also noted that non-local individuals were more frequent during the Bronze Age than during previous periods (Fornander et al. 2015). In Denmark, also based on 87Sr/86Sr data, mobility increased as well as the variation in the geographical origin of the migrants during the Early Bronze Age (ca. 1700-1100 cal BC) in parallel to the emergence of long-distance metal trade (Frei et al. 2019). However, Lithuania in contrast to southwestern Sweden, Gotland, Öland, and Denmark, did not demonstrate a significant increase in mobility during the Neolithic or Bronze Age (Fig. 10). Perhaps this may partly be explained by the delayed adoption of agriculture in the southeastern Baltic, which occurred ca. 1500 years later than the spread of stockbreeding (Piličiauskas et al. 2021). In addition, inland Lithuania was a periphery of the metal trade network during the Bronze Age (Luchtanas and Sidrys 1999).

**IV.2. The origins of non-locals**

Another very important question arises after identifying non-locally born individuals –– where did they come from? It is, however, rather hard to suggest potential areas of origin for the identified migrants due to the very few 87Sr/86Sr measurements available from Eastern Europe as well as the overlapping local baselines inside Lithuania and adjoining countries and territories. For instance, two Late Bronze Age non-locals at Turlojiškė (2 and 4) (Fig. 5) and four Subneolithic-Neolithic non-locals at Kretuonas (Kretuonas 1A B2, Kretuonas 1B graves 1, 2 and 5) (Fig. 8) may have come from multiple areas in Lithuania having bioavailable 87Sr/86Sr ranges ofca. 0.7160-0.7190 (Fig. 2). Only in extreme cases with higher and lower 87Sr/86Sr, more specific places of origin may be suggested for several individuals. For instance, 6/13 Mesolithic-Neolithic non-locals show 87Sr/86Sr intra-tooth values which begin from above 0.7200. Such high ratios are not known in Lithuania with the exception of a single beaver from Kretuonas 1C (0.7201). Therefore, these people most likely arrived from outside of modern day Lithuania. Such high 87Sr/86Sr values are known from Fennoscandia where Precambrian rocks with high radiogenic Sr are exposed (Fig. 1; Åberg and Wickman 1987; Voerkelius et al. 2010; Lahtinen et al. 2021). However, there is currently no evidence that Stone Age peoples were able to cross the Baltic Sea in other places than through Denmark or the Åland Islands. The shortest way to the Baltic Shield from the southeastern Baltic was through Karelia or southern Finland. Therefore, it may be speculated that the Mesolithic individual at Donkalnis 2, the Subneolithic individuals Donkalnis 7 and VI (Fig. 7 ), the Subneolithic-Neolithic individuals Kretuonas 1 (pl2:O94) and Kretuonas 1C (Č102) (Fig. 8), as well as the Neolithic individual from the Gyvakarai CWC grave (Fig. 4) were born in the northeastern Baltic region rather than the southeastern. Such a distant origin (ca. 500-700 km) for a relatively high number of analysed Lithuanian Stone Age people (6/36) is not unexpected in light of aDNA and archaeological data. The individual from Donkalnis 7, dated to 3521-3371 cal BC, has previously been reported as having a substantial part of its ancestry from Eastern Hunter-Gatherers (30%) compared to other people from Donkalnis and Spiginas that have a Western Hunter-Gatherer ancestry, without or with a very small Eastern Hunter-Gatherer genetic component (0-10%) (Mittnik et al. 2018). Archaeologically, the Eastern Hunter-Gatherer ancestry in the eastern Baltic, including Lithuania, is the Comb Ware culture. Its pottery spread widely throughout the region from ca. 3900-3500 cal BC (Nordqvist 2018; Piličiauskas et al. 2019). Furthermore, at the same time amber, Carboniferous flint and slate tools started to be transported routinely in large quantities between southeastern Baltic, northwestern Russia and southern Finland (Núñez and Franzén 2011; Piličiauskas et al. 2019; Tarasov and Nordqvist 2021; Zhulnikov 2008). Based on the aDNA and 87Sr/86Sr data, these contacts involved long-distance migration of individuals or perhaps even groups of hunter-gatherers. Furthermore, it seems that these routes were already active during the Late Mesolithic as demonstrated by the non-local (according to the Sr data) individual from Donkalnis 2 that dates from ca. 6400-6110 cal BC (Antanaitis-Jacobs et al. 2009).

A different picture concerns the male in the CWC grave at Gyvakarai, dated to ca. 2620-2470 cal BC (Piličiauskas et al. 2017a), which according to aDNA data, lacks the minor Anatolian component which is very common for other CWC people (Mittnik et al. 2018). Genetically, he stands very close to the nomadic Yamnaya culture people. However, bioavailable 87Sr/86Sr above 0.7200 is so far unknown from the southeastern European steppe while in central Europe, high radiogenic Sr is found in isolated patches in the Carpathian Mountains (Gerling 2015). Therefore, southern Finland and Karelia appear to be the most plausible candidates of origin for the Mesolithic and Subneolithic people as well as the Gyvakarai individual. Thus, Gyvakarai may represent a case of long-distance trade or a return migration by CWC individual(s) who entered southern Finland at ca. 2800 cal BC (Nordqvist 2018).

Finally, it might be possible to suggest the origin of humans with 87Sr/86Sr lower than the local baselines. At the Donkalnis cemetery –– Mesolithic grave 5 and Subneolithic grave 3 (Fig. 7) represent two such cases. Animals with 87Sr/86Sr ratios in-between 0.7100-0.7120 are only known from a single place in Lithuania, which is Šventoji on the Baltic coast (Fig. 2). Such low bioavailable 87Sr/86Sr ratios are determined by the seawater Sr transported onto the coast via sea spray. Human mobility between Lake Biržulis and the Baltic Sea, a distance of 85 km, may have been a common practice during the Subneolithic. Numerous amber finds at the Daktariškė 5 dwelling site situated at a distance of 2.6 km from the Donkalnis cemetery on the same Biržulis Lake supports this (Piličiauskas 2018).

**V. Conclusions**

* Even in areas entirely covered by glacial deposits, it is possible to identify patterns of migration due to significant variation of bioavailable 87Sr/86Sr.
* We documented significant and systematic 87Sr/86Sr offsets between modern soils, animals and in some cases plants and archaeological animal samples. Thus, this finding cautions against the use of modern samples for palaeomobility studies at least in the southeastern Baltic region.
* Strontium isotope analysis via LA-MC-ICP-MS not only allowed us to identify migration but also enabled us to evaluate the degree of mobility through recorded 87Sr/86Sr intra-tooth variation. Furthermore, using LA-MC-ICP-MS it is possible to trace immigrants who moved to their places of death/burial even before final mineralisation of tooth enamel.
* According to 87Sr/86Sr ratios, non-locally born individuals made up at least 25-50% of the population during the Stone and Bronze Ages. Their numbers may have been higher due to the overlapping 87Sr/86Sr baselines.
* Six of the 11 Mesolithic and Subneolithic non-locals had higher 87Sr/86Sr ratios than 0.7200, indicating that they might have come from southern Finland and/or Karelia. Two Mesolithic and Subneolithic individuals from the Donkalnis cemetery with 87Sr/86Sr lower than 0.7120 are suggested to have come from the Lithuanian coast of the Baltic sea indicating a mobility between the coast and the inland up to 85 km. Overlapping 87Sr/86Sr baselines as well as an absence or scarcity of bioavailable 87Sr/86Sr data from the neighbouring countries complicates the interpretation of places of origin for other non-locals.
* Medium/high 87Sr/86Sr intra-tooth variation (SD range 0.0004-0.0023) appeared to be a characteristic of inland people from the Mesolithic, Subneolithic, Neolithic, and the Bronze Age periods while the lowest (SD range 0.0002-0.0003) were only found among the coastal Subneolithic fishers and seal hunters. This suggests that seasonal mobility has been practised widely not only by inland Mesolithic-Subneolithic hunter-gatherers but also by the first animal herders and farmers. 87Sr/86Sr data suggests that the most sedentary way of life was among Subneolithic coastal people during the 4th millennium cal BC for whom numerous marine and lagoonal food resources were available. Alternatively, the lowest intra-tooth variation at the coastal zone may be caused by the sea spray effect which, according to 87Sr/86Sr ratios of modern tree leaves, is significant up to 5 km from the Baltic coast.

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**Supplementary information**

*SI1. 87Sr/86Sr measurements (LA-MC-ICP-MS) on human teeth enamel*

*SI2. Pre-Quaternary geological map of Eastern and Northern Europe (based on IGME5000, 2005) and the maximum extent of the last glaciation ice sheet with trajectories of the major ice streams which existed during the decay of the ice sheet according to Boulton et al. (2001)*

*SI3. Fig. 3. Archaeological sites with human, animal and plant samples analysed mapped onto a Quaternary geological map 1:200 000 after Lithuanian Geological Survey (*[*https://www.lgt.lt/epaslaugos/elpaslauga.xhtml*](https://www.lgt.lt/epaslaugos/elpaslauga.xhtml)*). H – Holocene, LP – Late Pleistocene, MP – Middle Pleistocene*

*SI4. Mean 87Sr/86Sr ratios of archaeological fauna from this study and from Piličiauskienė et al. (in prep) plotted on the interpolation of thickness of Quaternary deposits (from Aleksa 2007 with permission)*

*SI5. Measured 87Sr/86Sr ratios of fauna and interpolated 87Sr/86Sr ratios of modern grazing and agricultural soil (from data published by Hoogewerff et al. 2019). Note that all animals are from archaeological sites with a single exception of Minaičiai (marked with \*) in which four modern small rodents were analysed*