



## The stone cist conundrum: A multidisciplinary approach to investigate Late Neolithic/Early Bronze Age population demography on the island of Gotland

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### ABSTRACT

The Late Neolithic period in Scandinavia [LN, c. 2350–1700 cal BCE] marks a time of considerable changes in settlement patterns, economy, and material culture. This shift also lays the foundation for the demographic developments in the Early Bronze Age [EBA, c. 1700–1100 cal BCE]. However, little is presently known regarding the developments from these time-periods on the island of Gotland in the Baltic Sea. During the Middle Neolithic period [MN, c. 3300–2350 cal BCE], Gotland was inhabited by groups associated with the Funnel Beaker culture [TRB, c. 4000–2700 cal BCE], and the sub-Neolithic Pitted Ware culture [PWC, c. 3300–2300 cal BCE]. Some indications of connections with the Battle Axe/Corded Ware cultures [BAC/CWC, c. 2800–2300 cal BCE] have also been found, but no typical BAC/CWC burials have been located on the island to date.

Here, we investigate the chronological and internal relationship of twenty-three individuals buried in four LN/EBA stone cist burials; Häffinds, Hägur, Suderkvie, and Utalskog on Gotland. We present eleven mitochondrial genomes [from 23 X to 1271 X coverage], and twenty-three new radiocarbon dates, as well as stable isotope data for diet. We examine the local Sr-baseline range for Gotland, and present new Sr-data to discuss mobility patterns of the individuals. The genetic results are compared and discussed in light of earlier cultural periods from Gotland [TRB and PWC], and CWC from the European continent, as well as contemporaneous LN secondary burials in the MN Ansarve dolmen.

We find that all burials were used into the EBA, but only two of the cists showed activity already during the LN. We also see some mobility to Gotland during the LN/EBA period based on Strontium and mitochondrial data. We see a shift in the dietary pattern compared to the preceding period on the island [TRB and PWC], and the two LN individuals from the Ansarve dolmen exhibited different dietary and mobility patterns compared to the individuals from the LN/EBA stone cist burials. We find that most of the cist burials were used by individuals local to the area of the burials, with the exception of the large LN/EBA Häffinds cist burial which showed higher levels of mobility.

Our modeling of ancestral mitochondrial contribution from chronologically older individuals recovered in the cultural contexts of TRB, PWC and CWC show that the best model is a 55/45 mix of CWC and TRB individuals. A 3-way model with a slight influx from PWC [5%] also had a good fit. This is difficult to reconcile with the current archaeological evidence on the island. We suggest that the maternal CWC/TRB contribution we see in the local LN/EBA individuals derives from migrants after the Scandinavian MN period, which possible also admixed with smaller local groups connected with the PWC. Further genomic analyses of these groups on Gotland will help to clarify the demographic history during the MN to EBA time periods.

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### 1. Introduction

The island of Gotland was first populated around c. 7200 cal BCE by Mesolithic hunter-gatherers [HG's] (Fig. 1A) (Apel et al., 2018; Lindqvist and Possnert, 1999, 1997). During the Scandinavian Early- and Middle Neolithic periods [EN-MN] (Fig. 1B) there is evidence from the Funnel Beaker culture [Trichterbecherkultur, TRB], in form of settlement sites, pottery, and domesticated animal remains. As well as, at least one megalithic burial construction; the Ansarve dolmen which is the only confirmed TRB burial on the island to date (Fig. 2B) (e.g. Andersson, 2016; Bägerfeldt, 1992; Lindqvist, 1997; Lithberg, 1914; Österholm, 1989). New radiocarbon analyses of three previously dated (Lindqvist, 1997), plus fourteen additional individuals from the dolmen showed that this burial was used continuously from c. 3300 to 2700 cal BCE (3500–2580 cal BCE, 95% CI) (Fraser et al., 2018). These results make the starting point slightly later than previously estimated (Schulz Paulsson, 2017, 2010), but also extends the main period of usage with > 300 years. Two additional secondary burials during the Late Neolithic period [LN] were also identified (Fig. 1A) (Fraser et al., 2018).

Starting from c. 3200 cal BCE, during the beginning of the MN period, Gotland was also inhabited by sub-Neolithic groups from the Pitted Ware culture [PWC, c. 3300 to 2300 cal BCE] (Fig. 2B) (e.g. Janzon, 1974; Lithberg, 1914; Nihlén, 1927; Wallin, 2016; Wallin and Martinsson-Wallin, 2016; Österholm, 1989). Although, slightly older PWC dates are found in coastal eastern central Sweden (Björck, 2003). Recent genetic analyses of individuals from these contexts [TRB and PWC] from Gotland have shown that the PWC groups show genetic continuity with Mesolithic HG's, but with slight admixture from Neolithic farmers (Günther et al., 2018; Malmström et al., 2015, 2009; Skoglund et al., 2014, 2012). In contrast, the mitochondrial haplogroup composition in the TRB group from the dolmen (Fraser et al., 2018) was most similar to contemporaneous individuals from megalithic burials on the Swedish mainland (Malmström et al., 2015, 2009; Skoglund et al., 2014, 2012), and also showed maternal continuity with EN farmer groups from the continent. Thus, these two contemporaneous but culturally different groups [TRB and PWC] coexisted on the island of Gotland for half a millennium but still maintained their distinct cultural identities and economy (Fraser et al., 2018). The transition following these cultures on the island has remained largely unknown as TRB and PWC disappear from the archaeological record after c. 2700, and c. 2300 cal BCE, respectively.

The second part of the Scandinavian MN period [MNB] (Fig. 1B) marks the introduction and expansion of the Battle Axe culture, a local development of the pan-European Corded Ware culture [BAC/CWC, c. 2800–2300 cal BCE], in Scandinavia and the Baltic Sea area (e.g. Kriiska, 2003; Malmer, 1975). However, the same cultural transformation is not seen on Gotland as the typical hocker style inhumation

burials, and/or cist burials, with BAC artefacts and pottery are absent. A few stray finds of battle axes and some BAC pottery have been found on the island (e.g. Andersson, 2016; Bägerfeldt, 1992; Janzon, 1974; Lithberg, 1914; Malmer, 1975; Rundkvist et al., 2004; Österholm, 1989), suggesting some presence of BAC, or connections with BAC populations on the mainland. Interestingly, the only burials associated with BAC artefacts on Gotland have been found within contemporaneous PWC cemeteries (e.g. Janzon, 1974; Malmer, 1962; Martinsson-Wallin et al., 2015). Moreover, even though secondary BAC reuse of MN megalithic tombs have been noticed in Scandinavia (e.g. Edenmo, 2008; Iversen, 2016; Malmer, 2002, 1975; Sjögren, 2003), no BAC artefacts or pottery has been found in the Ansarve dolmen on Gotland (Bägerfeldt, 1992). Thus, the demographic history and social interactions between the culturally distinct groups [TRB and PWC], as well as to which extent BAC/CWC was present on Gotland, is currently not understood (Fig. 1B). This also has significance for the understanding of the demographic development in the subsequent LN period.

The LN in Scandinavia marks a time with considerable changes in material culture patterns and lifeways. In Jutland, present day Denmark, there is evidence of Bell Beaker Culture [BBC] influence from around c. 2350 to 1950 cal BCE, based on single inhumation burials and settlement sites with BBC pottery and typical BBC stone artefacts (Apel, 2001; Vandkilde, 2005). A similar interpretation has been suggested for southwestern and coastal western Norway (e.g. Prescott and Glørstad, 2015). However, to date, no BBC pottery has been found on Gotland, and single inhumation burials are scarce during this time period. Even though some finds of typical shaft-hole axes and imported flint artefacts such as arrow heads, daggers and scrapers have been located in some LN graves, as well as loose stray finds across the island (e.g. Bägerfeldt, 1992; Wallin, 2010; Österholm, 1989). Their direct or indirect association with the BBC complex remains unknown, indicating the complexity of the LN transformations in different parts of Scandinavia.

A new type of communal megalithic burial is also introduced during this period in Scandinavia, the stone cist burials; a type of gallery grave which also is commonly found on Gotland. More than 1500 cist burials have been found in present day Sweden (Hyenstrand, 1979; Johansson, 1961), and although they are grouped into the same category there are local differences in shape and size (Heimann, 2000). On the Scandinavian mainland they tend to be large, often with several chambers, and sometimes with a gavel stone with a porthole (e.g. Stenberger, 1964; Stensköld, 2004; Vandkilde, 2005). While on Gotland the stone cist burials are smaller and consist mainly of a single rectangular cist [between 0.60 and 3.10 m × 0.35–1.50 m] (Lithberg, 1914; Luthander, 1988; Sjöstrand, 2012; Wallin, 2010). The smaller cist burials across Scandinavia have been suggested to be a continuation of the earlier individual BAC stone cist, or wood coffin burials, whereas the larger cist burials with portholes in western Sweden are similar to those found within the SOM-culture [Seine-Oise-Marne culture, c.

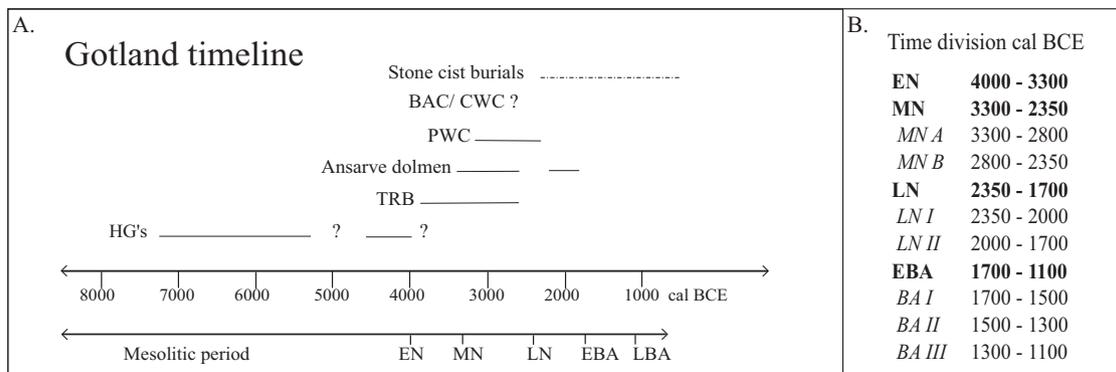
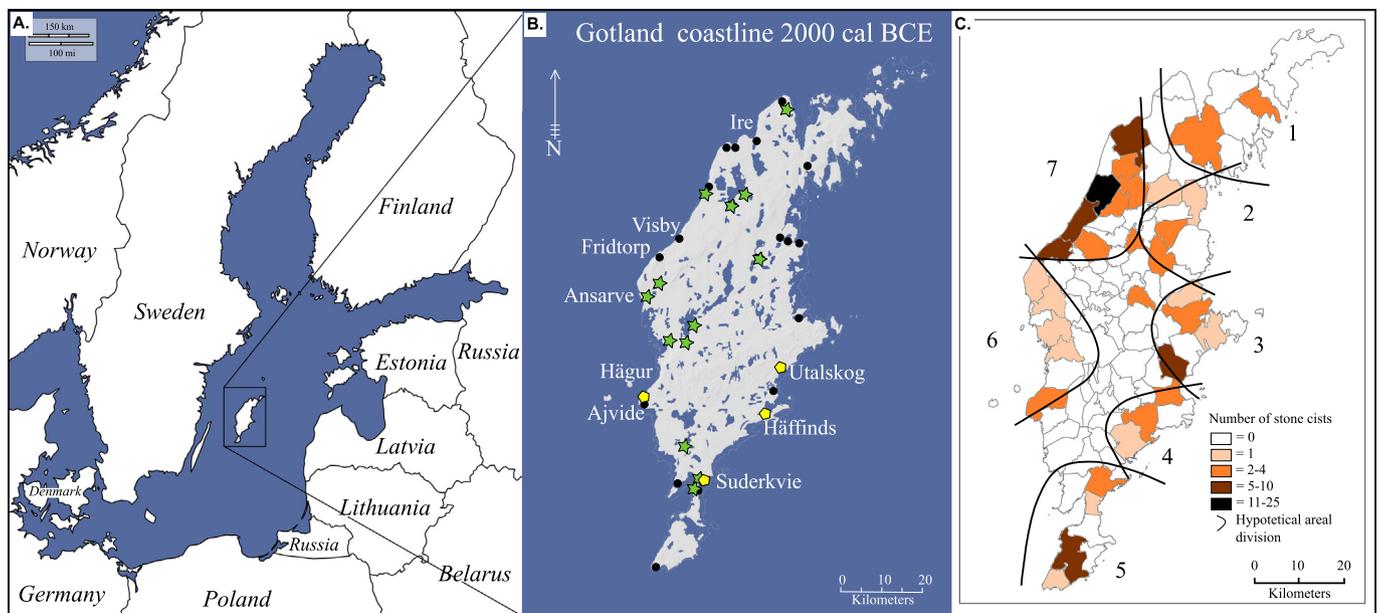


Fig. 1. A. Gotland cultural timelines (Apel et al., 2018; Fraser et al., 2018). B: Approximate dates for the Scandinavian Early Neolithic to Early Bronze Age time divisions; EN: onset of TRB, MN A: onset of PWC, MN B: onset of BAC, LN-EBA time division from Vankilde (1996).



**Fig. 2.** A. Map of the Baltic Sea area. B. Map of Gotland with the 2000 cal BCE coastline (modified from Pässe and Andersson, 2006). Archaeological sites mentioned in the text: green stars = EN-MN TRB sites; black dots = MN PWC sites; yellow pentagons = LN/EBA stone cist burials analyzed in this study. C. Map of Gotland with parishes © Lantmäteriet, i2012/921. The numbers of LN/EBA stone cist burials in each parish is highlighted in colors. The core areas are marked with black lines modified from Wallin (2010). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3100–2000 cal BCE] in northern France and Belgium (e.g. Burenhult, 1999; Stenberger, 1964; Vandkilde, 2005).

The LN period has previously not been extensively investigated on Gotland. First, given the difficulty to work with loose stray finds, but also because many of the today excavated stone cists had already been plundered and/or destroyed in the past. LN stone cist burials were also often covered by a large cairn and/or mound during the Early Bronze Age [EBA] (Fig. 1B) (Stenberger, 1964), further complicating its exploration. The exact time of the Scandinavian LN/EBA transition is difficult to pinpoint, and the burials on Gotland have previously been dated mainly by artefact typochronology which often suggest provenance to both time periods. The only directly dated individuals outside PWC context from the LN period on Gotland are the two individuals [ans004 and ans010] from the secondary burials in the MN Ansarve dolmen (Fraser et al., 2018). Secondary Late BA [LBA] and Iron Age [IA] inhumation and cremation burials are also common in all types of megalithic graves on Gotland, including peripheral burials in EBA cairns/mounds.

The LN stone cist burials are located mainly along the former coastline of Gotland (Fig. 2A–C). At least 104 possible stone cist burials distributed at 86 different locations have been suggested to belong to the LN/EBA periods (Luthander, 1988; Sjöstrand, 2012; Wallin, 2010). In contrast to only one confirmed MN dolmen, c. ten TRB sites, and c. eighteen PWC locales (Fig. 2B) (e.g. Österholm, 1989). The geographic distribution of the burials is concentrated in seven spatial clusters, or core regions, where the largest numbers are found along the north-central west coast (Fig. 2C) (Wallin, 2010). Forty-two stone cists have been excavated on Gotland to date showing that they contain both single and multiple burials (e.g. Luthander, 1988; Sjöstrand, 2012; Wallin, 2010). However, most were excavated during the first half of the 20th century and only a few burials have since been osteologically analyzed in detail regarding the human remains. Here we provide new research where we investigate the chronology and individual contexts in four stone cist burials on the island.

## 2. Aims

The focus of this study is to investigate the demographic

development on Gotland during the Scandinavian LN/EBA periods through multidisciplinary analyses of the human remains from four previously excavated stone cist burials. The contexts and chronology of the burials are analyzed together with the archaeological and osteological reports (Sections S1.1–S1.4). We present eleven mitochondrial genomes, twenty-three new radiocarbon dates, as well as isotopic data for investigation of diet and mobility patterns, as well as new environmental Strontium baseline values for the Gotland biosphere. We investigate possible population continuity on the female lineages in regards to the preceding TRB and PWC populations on the island, and also potential population events involving BAC/CWC migration during the latter part of the Scandinavian MN period, through comparative analyses of published mitochondrial data from TRB, PWC and CWC contexts (Brandt et al., 2013; Fraser et al., 2018; Malmström et al., 2015). High resolution mitochondrial genomes can help to decipher the maternal demographic history of the individual burials, as well as demographic developments of the populations. Strontium isotope analyses in combination with radiocarbon dating, dietary analyses, and genetic data aid to interpret and better understand mobility patterns and demography.

## 3. Material

The present study is based on analyses of human remains from four LN/EBA type stone cists burials from four core regions (Wallin, 2010) (Fig. 2B–C and Section S1.1–S1.4). Two sites have a spatial connection with earlier activity; [1] the Suderkvie stone cist to a TRB site (Manneke, 1963a), and [2] the Hägur stone cist to a PWC site (Stenberger, 1944a). The third site “Häffinds” is one of the most elaborate cist burials excavated to date with documentation of several of the individuals positions inside the cist (Burenhult, 1986). The last site “Utalskog” (Arne, 1927) is a burial in a small cave or crevice in a limestone formation in connection to the large LN-IA cemetery of Gålrum. All sites had previously been dated to LN and/or EBA based on artefact typology (Figs. S4A–X, S6B, S7J, and S9). The human remains in all four graves studied were recovered commingled and fragmented, with the exception of some individuals in the Häffinds burial. As some of the burials had been destroyed and plundered prior to excavation,

bone elements from additional individuals outside the cists were also analyzed to better understand the context of those burials. Tooth and/or bone samples were selected from twenty-three individuals for the subsequent analyses: Häffinds [n = 13], Hågur [n = 4], Suderkvie [n = 4], and Utalskog [n = 2] (see Sections S1.1–S1.4 for additional information regarding the burials and sampling).

## 4. Methods

### 4.1. Radiocarbon dating and isotopic analyses

AMS radiocarbon dating was performed at Ångströmlaboratoriet (Uppsala University, Sweden) and BETA analytic Inc. (Miami, Florida) (Section S2.1 and Table S1). The dates were calibrated using Oxcal online software version 4.3 (Bronk Ramsey, 2009), based on the IntCal13 atmospheric curve (Reimer et al., 2013). All dates are presented with the 95% confidence interval [CI] cal BCE, and rounded to nearest tenth value (Table 1). The dating results are discussed based on the Scandinavian Neolithic and EBA time divisions (Fig. 1B).

The IRMS stable isotope analyses were performed at BETA analytic Inc. (Miami, Florida), Ångströmlaboratoriet (Uppsala University, Sweden), and at the Archaeological Research Laboratory (Stockholm University) (Section S2.1 and Table S1). The results were compared to previous stable isotope data from the TRB dolmen (Fraser et al., 2018), as well as, a PWC group and local terrestrial and marine faunal remains from Gotland (Eriksson, 2004; Fraser et al., 2018).

Human and environmental samples were analyzed for strontium isotopes at NERC, Isotope Geosciences Laboratory (Nottingham, UK) (Tables 1, S1 and S2, and Section S2.2). The Sr-isotopic results are discussed in combination with previous Sr data from Gotland (Fraser et al., 2018; Peschel et al., 2017) and further investigated together with geological maps for Gotland from the Geological Survey of Sweden, data © SGU.

**Table 1**

Archaeological site and sample names, biological age, osteological sex, radiocarbon dating, sequencing statistics, mtDNA haplogroup call, contamination estimation, and Strontium results for M1 & M3.

Site	Sample	Biological age	Osteological sex	cal BCE, 95% CI <sup>a</sup>	mtDNA coverage	Read length average	mtDNA haplogroup call	Contamination estimate [%] <sup>b</sup>	Number of sites	Contamination interval [%]	M1: enamel <sup>87</sup> Sr/ <sup>86</sup> Sr	M3: enamel <sup>87</sup> Sr/ <sup>86</sup> Sr
Häffinds	hgb008	> 35 <sup>e,h</sup>	Female? <sup>e,h</sup>	2200–1800	nd	–	–	–	–	–	–	–
	hgb003	20–34 <sup>d,h</sup>	–	2140–1780	nd	–	–	–	–	–	–	–
	hgb011	8 ± 2 <sup>e,h</sup>	–	2140–1770	nd	–	–	–	–	–	0.71205	–
	hgb006	35–45 <sup>d,i</sup>	Male <sup>e,i</sup>	1910–1750	nd	–	–	–	–	–	0.71143 <sup>n</sup>	0.71095
	hgb007	17–25 <sup>d,h</sup>	–	1740–1530	nd	–	–	–	–	–	0.71182	0.71145
	hgb010	> 50 <sup>e,h</sup>	Female? <sup>e,h</sup>	1770–1560	143.08	100	T2b5	4.16	12	2.980–5.331	0.72465	0.72050
	hgb005	17–25 <sup>d,h</sup>	–	1690–1460	179.98	49	HV0a	2.00	4	0.773–3.227	0.71034	0.71056
	hgb012	10–24 <sup>c,h</sup>	–	1630–1500	189.64	75	T1a1	1.68	12	1.041–2.324	–	–
	hgb001	> 45 <sup>d,h</sup>	Male <sup>e,h</sup>	1610–1440	1271.67	64	J1c7a	0.53	14	0.420–0.646	0.71348	0.71467
	hgb002	8 ± 2 <sup>e,h</sup>	–	1500–1320	31.62	54	T2b16	0.89	7	0.000–2.125	0.71350	–
Hågur	hgr001	> 20 <sup>e,j</sup>	–	1750–1570	23.69	85	U5a1c1	2.38	5	0.000–5.043	0.71075	0.71132
	hgr002	10–24 <sup>c,j</sup>	–	1680–1520	27.41	81	H2a5	1.49	5	0.000–3.546	0.71177 <sup>n</sup>	–
	hgr003	> 20 <sup>e,j</sup>	–	1660–1510	56.87	92	H1a	3.27	2	0.451–6.085	0.71107	–
	hgr004	10–24 <sup>c,j</sup>	–	1420–1260	37.19	87	U4a2	4.41	4	0.960–7.863	0.71100	0.71119
Suderkvie	sud003	40–55 <sup>f,k</sup>	Female? <sup>e,k</sup>	2010–1770	nd	–	–	–	–	–	–	–
	sud004	> 20 <sup>c,k</sup>	–	1420–1260	nd	–	–	–	–	–	–	–
	sud002	10–24 <sup>c,k</sup>	–	1400–1130	nd	–	–	–	–	–	–	–
	sud001	~6 <sup>c,k</sup>	–	1380–1120	46.34	67	K1b2a	0.56	4	0.000–1.641	–	–
Utalskog	uta002	> 20 <sup>c,l</sup>	–	1910–1660	nd	–	–	–	–	–	–	0.71218
	uta001	> 20 <sup>c,l</sup>	–	1880–1530	1096.85	57	H1e1a	1.31	6	0.972–1.655	0.71255	–
Ansarve <sup>g</sup>	ans004	> 20 <sup>c,m</sup>	–	2290–2050	nd	–	–	–	–	–	0.71531	–
	ans010	> 20 <sup>c,m</sup>	–	2030–1890	187.75	71	U5b2a1a1	0.89	6	0.234–1.549	0.71760	–

<sup>a</sup>Dates rounded to the nearest tenth value. <sup>b</sup>Green et al. (2008). <sup>c</sup>Sjøvold (1978). <sup>d</sup>Brothwell (1981). <sup>e</sup>Bukistra and Ubelaker (1994). <sup>f</sup>Lovejoy (1985). <sup>g</sup>Fraser et al. (2018). <sup>h</sup>Lindh (1997). <sup>i</sup>Sjöstrand (unpublished). <sup>j</sup>Gytare (2015). <sup>k</sup>Gustavsson (unpublished). <sup>l</sup>Sjöstrand (2012). <sup>m</sup>Wallin and Martinsson (1986). <sup>n</sup>M2.

### 4.2. aDNA analyses: sample preparation, DNA extraction and sequencing, next generation sequence processing, alignment, authentication, and mitochondrial haplogroup assignment

Thirty-six samples from twenty of the individuals were screened for human DNA content (Table S1 and Section S2.3). All samples were prepared in facilities dedicated to analyses of ancient DNA (aDNA) at Campus Gotland according to strict standards for working with degraded samples (Cooper and Poinar, 2000; Gilbert et al., 2005). Blunt-End Illumina libraries (Meyer and Kircher, 2010) were created after DNA extraction, and subsequently sequenced on the Illumina HiSeq 2500 or HiSeqX as described in (Fraser et al., 2018). Sixteen samples stemming from eleven individuals were used for the downstream analyses (Tables 1 and S1). The data showed the characteristic deamination pattern towards the read fragment-ends (Briggs et al., 2007) (Fig. S11), and contamination was estimated based on the Green et al. (2008) approximation (Table 1). Mitochondrial consensus sequences were generated using ANGSD v.0.902 (Korneliusson et al., 2014), and haplogroups were assigned using HaploFind (Vianello et al., 2013), as well as the haplogrep software (<https://haplogrep.uibk.ac.at/>) (Table 1, Table S3 and Section S2.4).

### 4.3. Mitochondrial demographic modeling

We incorporated the LN individual [ans010] from the Ansarve dolmen (Fraser et al., 2018) within the LN/EBA dataset reported here [n = 12] (see Section 5.3.1 below and Table 1). We merged our LN/EBA data with previously reported mitochondrial haplotypes from TRB and PWC contexts from Gotland (Fraser et al., 2018; Malmström et al., 2015, 2009; Skoglund et al., 2014, 2012). To get a wide range of the mtDNA haplogroup composition within CWC groups from similar contexts, we chose the larger mitochondrial dataset [n = 50] from the Saxony-Anhalt region in Germany, as reported in Brandt et al. (2013), as a proxy for BAC/CWC influences on Gotland (Section S5.2).

To investigate the origin of the maternal lineages in the LN/EBA individuals we modeled LN/EBA as a mixture from the PWC, CWC and/or TRB data and tested for goodness of fit for each of the models (see

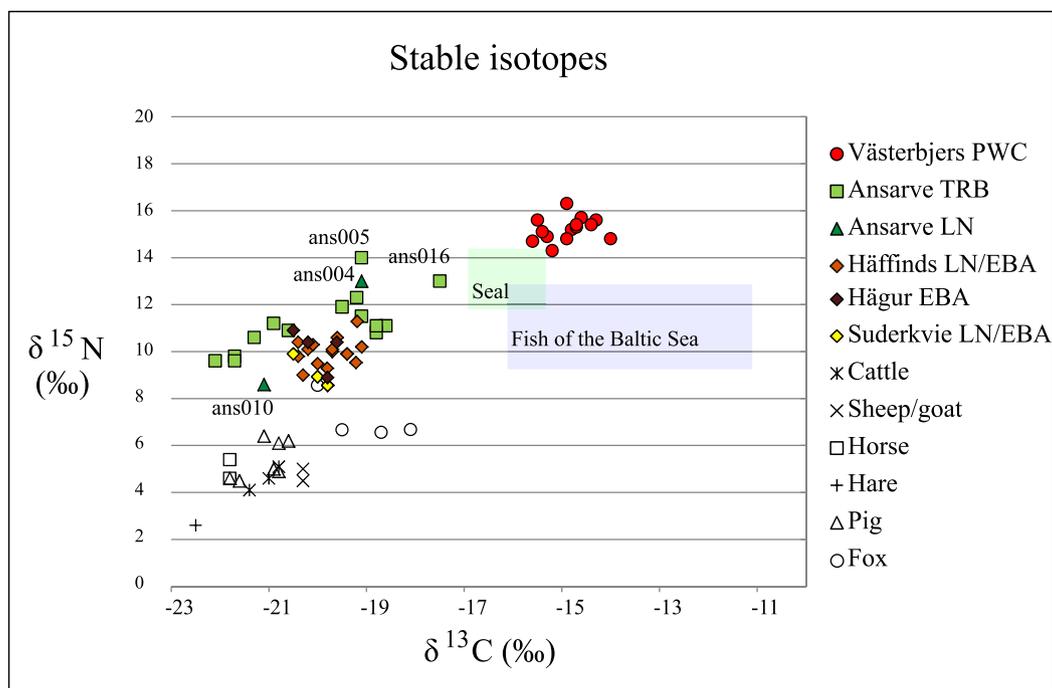


Fig. 3. Plot of stable isotope values for the LN/EBA individuals in this study [teeth and/or bone], compared with the Ansarve dolmen [M1] (Fraser et al., 2018), and PWC from Västerbjers [M1], plus local terrestrial and marine fauna (Eriksson, 2004).

Section 4.3.1 below). We used the published mitochondrial data for TRB [ $n = 9$ ] and PWC from Gotland [ $n = 26$ ], as well as the CWC dataset from Saxony-Anhalt, Germany. Unfortunately, not all of the individuals' mtDNA haplotypes from these different datasets have been reported to the same phylogenetic resolution level (Table S4), i.e. some calls were based on HVS I data (Malmström et al., 2015), and in some cases also HVS II, or diagnostic control region SNPs (Brandt et al., 2013). Thus, the analyses below required some initial data filtering. In order to get the most information out of the different datasets, we manually attempted to strike a good balance between haplotype resolution and sample size for each of the four groups (see Section S2.5). This filtering kept the most information, but lowered the number of individuals in the PWC and CWC groups [ $n = 21$  and  $n = 30$ , respectively] (Fig. S12 and Table S4).

#### 4.3.1. Modeling LN/EBA as a mixture from PWC, CWC and TRB

Neglecting effects of genetic drift, it is possible to model the sample from LN/EBA as a draw from an admixed source where the different non-admixed parts of the source are represented by the samples from CWC, PWC and TRB. We tried two approaches, one where we only used two (non-admixed) parts, and one where we set up a 3-way model including all three groups (Section S2.5).

We first modeled a hypothetical LN/EBA population as a pair-wise mixture of populations A and B using all combinations of TRB, PWC and/or CWC. We model a sample from population LN/EBA as a draw from the mixed distribution  $c f_A + (1-c) f_B$  where: 1)  $c$  is the admixture proportion of population A, and  $1-c$  is the admixture proportion of population B. 2)  $f_A$  is the multi-allelic distribution (a Dirichlet-multinomial distribution) in population A based on the observed allelic counts in the sample from population A. 3)  $f_B$  is the multi-allelic distribution in population B based on the observed allelic counts in the sample from population B. Here, "multi-allelic" refers to the different haplotypes defined in Table S4. Using this formula, we calculate the likelihood of the observed sample from population LN/EBA given  $c$ , and the observed samples from population A and B, and find the maximum likelihood estimate for  $c$  by trying out values of  $c$  in the range from 0 to 1 with 0.05 steps. The likelihood as a function of  $c$  was plotted using R

(Section S2.5).

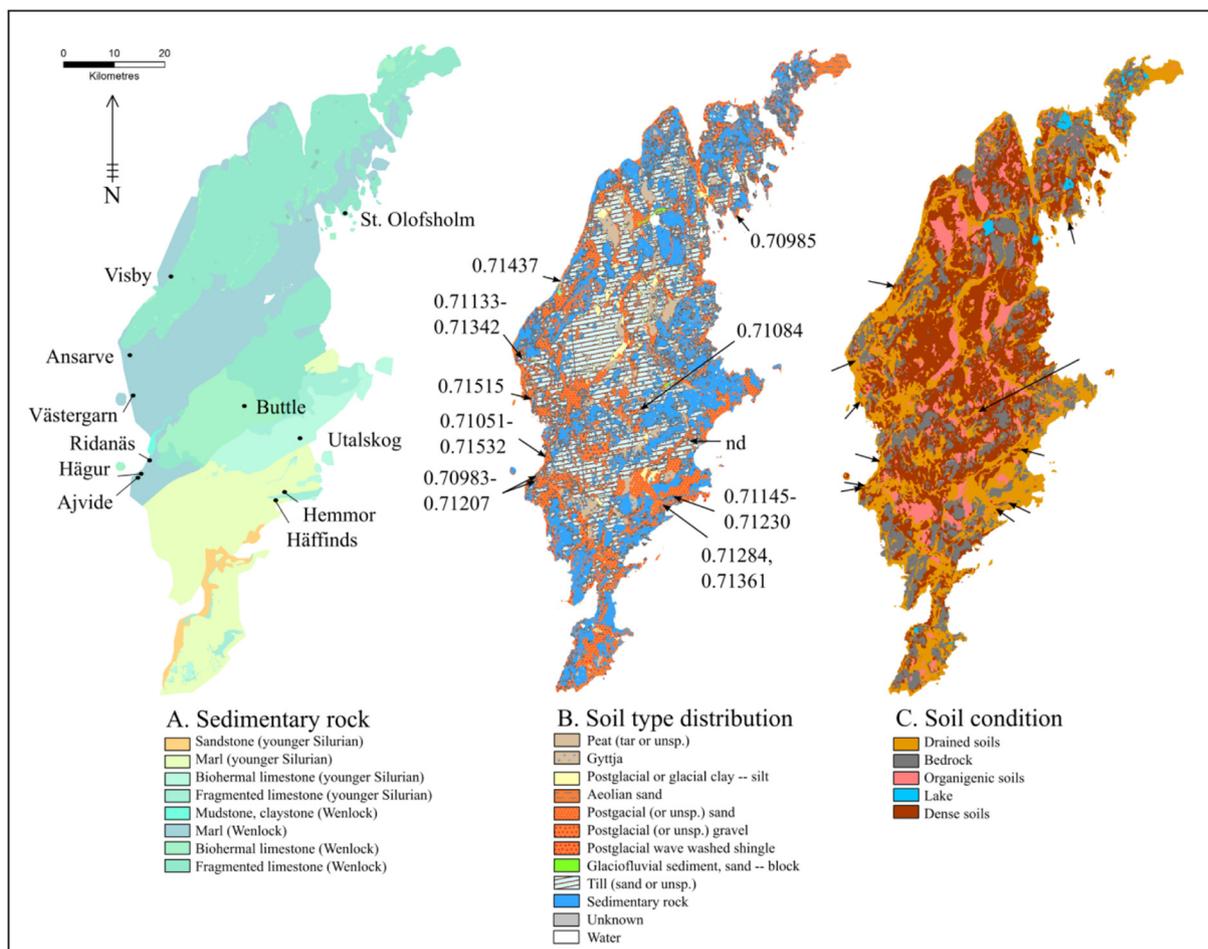
We then set up a 3-way model where we model a sample from population LN/EBA from the mixed distribution  $c_1 f_{PWC} + c_2 f_{CWC} + (1-c_1-c_2) f_{TRB}$  (where  $f_X$  is the Dirichlet-multinomial distribution of the haplotype frequencies in population X based on the observed sample from population X). Using this formula, we calculate the likelihood of the observed sample from population LN/EBA given  $c_1$  and  $c_2$ , and the observed samples from population A, B and C, and find the maximum likelihood estimate for  $c_1$  and  $c_2$  by trying out values of  $c_1$  and  $c_2$  in the range from 0 to 1 with 0.05 steps. The likelihood as a function of  $c_1$  and  $c_2$  was plotted using R (Section S2.5).

To assess the goodness of fit of a pair-wise model with a fixed  $c$ , a sample from population A and a sample from population B, we simply draw a sample of the same size as the sample from LN/EBA from the distribution  $c f_A + (1-c) f_B$  and count how often the likelihood of this random sample is lower than the likelihood of the observed sample from LN/EBA. The same process was done for the 3-way model using the distribution  $c_1 f_{PWC} + c_2 f_{CWC} + (1-c_1-c_2) f_{TRB}$ . If a random sample often has a higher likelihood than the likelihood of the observed sample, this is an indication that the model fits poorly (Section S2.5).

## 5. Results

### 5.1. Radiocarbon dating and diet

The radiocarbon results show that the burial activities at these four sites span from the LN into the EBA [c. 2200–1100 cal BCE, 95% CI] (Fig. S9 and Table S1). However, each site is unique, see Section 5.4 below for detailed analyses of the burials. Interestingly, the stable isotope results show that the individuals in the cist burials displayed a homogeneous terrestrial diet (Fig. 3). This is in contrast to the strict marine diet of the PWC individuals (Eriksson, 2004), as well as the more varied terrestrial diet of the individuals from the Ansarve dolmen (Fraser et al., 2018). The dietary pattern of the two LN individuals from the dolmen also deviates from each other, as well as the cist burials (Fig. 3). As the LN/EBA individuals showed a terrestrial diet these dating results did not need to be corrected for reservoir age. The slightly



**Fig. 4.** Base maps: Geological maps of Gotland from the Geological Survey of Sweden, data © SGU (Section S2.2). A. Sedimentary carbonate platforms with Strontium sample locations this study and (Fraser et al., 2018), and Ridanäs Viking Age trading port (Peschel et al., 2017). B. Soil type distribution with current environmental Sr-values. C. Soil condition on Gotland showing sampled locations.

elevated Nitrogen value for the LN individual [ans004] could be an indication of some freshwater fish in the diet, however a freshwater carbon offset has yet to be established for Gotland. For a discussion regarding the radiocarbon calibrations for the Ansarve dolmen see Fraser et al. (2018).

5.2. Strontium isotopes [<sup>87</sup>Sr/<sup>86</sup>Sr] and mobility patterns

The exposed sedimentary bedrock of Gotland reflects a series of stacked carbonate platform generations, as well as a thin streak of sandstone in the southern part of the island, that formed during the Silurian time period (Fig. 4A) (Calner, 2005; Jeppsson et al., 2006). This should provide a relatively homogenous Sr-isotopic background value for the Gotland biosphere. However, the soil type distribution on the island, especially inland, show large areas of till [moraine] consisting of heterogeneous sediments from older formations brought by glacial ice (Fig. 4B–C). Other areas consist of exposed carbonate bedrock with postglacial deposits of sand, wave washed gravel and shingle. As Gotland is an island the effect of sea spray and precipitation also has to be taken into consideration. This creates a broad range of Sr-values making it difficult to evaluate the baseline for the Gotland biosphere (Fraser et al., 2018; Peschel et al., 2017). Here we present ten new environmental Sr-ratios from Häffinds, Hemmor, Högur, St. Olofsholm, and Buttle (Table S2). All sampled sites (Fig. 4A–C) consist mainly of bedrock and postglacial layers; however some areas also comprise partial distributions of till which could affect soil sample results (Section S2.2). When combining the environmental Sr-isotope ratios for the

different locales from this study and earlier published data (Fraser et al., 2018), extreme outliers within sites were identified and removed from the analyses (Fig. S10A). These results are also affected by the sample location distribution which mainly comprises locations along the former coastline, with the exception of the Buttle site (Fig. 4A). The low sample numbers for some of these sites, the higher single values at Visby and Västergarn (Fraser et al., 2018), and in the case for Ridanäs (Peschel et al., 2017) the uncertainty of the faunal remains actually being local, also have to be considered (Fig. 4A–B and Table S2).

Previous attempts for determining the local Sr-baseline for Gotland showed a broad range (Fraser et al., 2018; Peschel et al., 2017), the additional environmental samples from this study [n = 10] reduces this range slightly (Table 2). Although, more environmental sampling is needed in order to further establish this range for Gotland, as well as to confirm the higher values from Visby, Västergarn, and Ridanäs. However, we find some regional Sr-isotopic variation which fall within

**Table 2**  
Table listing details of the Strontium baseline calculations.

Sample	N	No of sampled sites	Mean	1SD
Ridanäs faunal <sup>a</sup>	11	1	0.71242	0.0016
Faunal and soil <sup>b</sup>	15	6	0.71183	0.0017
Combined results <sup>a,b</sup>	26	7	0.71208	0.0016
Combined results with this study	36	10	0.71195	0.0015

<sup>a</sup> Peschel et al. (2017).

<sup>b</sup> Fraser et al. (2018).

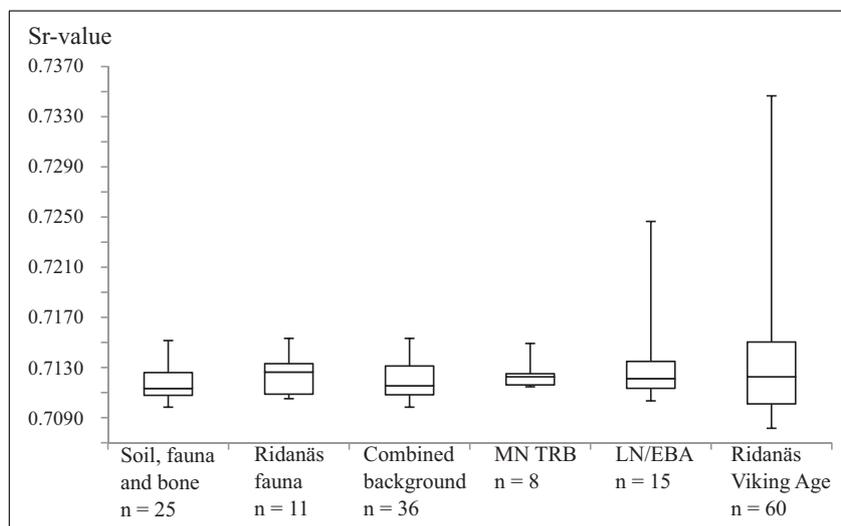


Fig. 5. Strontium values for the environmental sampling and early childhood Sr-values for the human groups from different time periods on Gotland this study and (Fraser et al., 2018; Peschel et al., 2017). The box represents the median and the 2nd and 3rd quartile, and the whiskers the 1st and 4th quartiles.

0.70980–0.71361 [n = 23, 7 sites], thus this range could be more realistic for the limestone environment of the Gotland biosphere (Fig. S10A). The combined mean for all environmental Sr-data available from Gotland to date, including the higher values from the three sites, gives a more conservative measure of 0.70890–0.71500, 2 SD (Fig. S10C and Table 2) which we use as Sr-baseline for Gotland in this study. Local Sr-ranges for the sites were also detected and used for the analyses of the burials (Fig. 4A–B).

As the baseline presented here still has uncertainties, it is possible that this range will change when more Sr-data is available in the future. Thus, individuals with Sr-values close to the upper and lower boundaries, may in fact be non-locals (Fig. S10C). Most of the individuals in this study exhibit Sr-isotopic ratios expected of local individuals. Apart from the two nonlocal LN individuals in the dolmen (Fig. S10C) we also find one obvious nonlocal individual in the Häffinds burial dated to BA I. Based on the median and quartile values for each of the groups (Fig. 5), we can also detect an increase of migration to Gotland during the LN and EBA compared to the MN period, which becomes even more evident during the Viking Age. For details on the Strontium analyses for the individual sites see Section 5.4 below.

### 5.3. Mitochondrial haplogroups

We generated eleven mitochondrial genomes ranging between 23 X and 1271 X coverage (Table 1). While we were able to retrieve enough genetic data from several of the EBA individuals to make haplotype call, unfortunately none of the LN individuals in this study harbored sufficient data. All samples presented a typical for ancient DNA average read length, and mtDNA contamination estimates for all samples were predicted to be low (Table 1). All individuals were classified into unique mitochondrial haplotypes [HV0a, H1a, H1e1a, H2a5, J1c7a, T1a1, T2b5, T2b16, U4a2, U5a1c, K1b2a] (Table S3 and Section S2.4).

#### 5.3.1. Modeling LN/EBA as a mixture of the ancient MN groups

Although our dataset mainly comprise EBA individuals, we incorporated the mitochondrial haplogroup for the single LN individual [ans010, U5b2a1a1] (Fraser et al., 2018) with the EBA dataset [n = 12] (Table 1), as it was later in time than the TRB cultural phase on the Island, and also later in time than the other individuals included in the comparative data; the PWC and the CWC datasets which were used in this study (Brandt et al., 2013; Malmström et al., 2015) (Table S4 and Fig. S12). To assess the maternal ancestral contribution to the LN and EBA individuals we modeled the haplotype distribution of the LN/EBA

group as a mixture between population A and B using all pair-wise combinations of the PWC, CWC and TRB data as a source, but neglecting for effects of genetic drift (see Section 4.3.1 and Section S2.5). We find that the best pair-wise combinations consisted of 60/40 TRB/PWC, 75/25 CWC/PWC, and 55/45 CWC/TRB (Fig. S13). We then assessed goodness of fit for these different models, as well as a 100% contribution from either of the groups, and found that the only model that showed a good fit was the CWC/TRB combination (Fig. 6 and Table S5). Interestingly, the TRB/PWC and CWC/PWC models did not show a good fit, and 100% PWC had the worst fit of all models.

Additionally, we modeled a 3-way combination including all groups and found that the best 3-way combination was 55% CWC, 40% TRB, and 5% PWC (Fig. S14A–B). This combination also showed a good fit and a small contribution from PWC could thus not be excluded (Fig. S15 and Section S2.5). Even though the goodness of fit of this 3-way configuration is basically identical to a model without any PWC contribution (Fig. S15), and the model with 45% TRB and 55% CWC (the best model among the pair-wise combinations above), a partial, albeit small maternal PWC contribution should probably not be ruled out. Additionally, due to the lower resolution of the PWC dataset, we filtered out unspecific haplogroups [U and U4, n = 5] (Section S2.5), thus further genetic analyses will help to clarify the mitochondrial gene pool of the PWC on the island. Furthermore, here we are analyzing the female lineages, hence analyses of nuclear DNA is needed to fully investigate the ancestral contribution and demographic development on Gotland.

### 5.4. The case studies of the four LN/EBA cist burials

#### 5.4.1. Häffinds

Ten of the individuals from the cist burial were analyzed, plus three individuals in additional features within the burial structure were dated (Table S1 Section S1.1 and Fig. S2). Four dated to the LN phase; two mature adults and a child [hgb003, hgb008, and hgb011, respectively] dated to LN I, and another mature adult [hgb006] dated to LN II (Fig. 7A–B). The majority of the other individuals dated to BA I; three young adults [hgb005, hgb007, hgb012], an older female [hgb010], and an older male [hgb001]. As well as, the individuals from the contexts outside the cist; an adult and a small child [hgb013 and hgb015] located north of the cist, and a juvenile [hgb014] from feature 3 (Fig. S2). Another child [hgb002] from inside the cist dated to BA II (Fig. 7A–B). Seven individuals were Sr-analyzed; four adults and two 10–12 year old children revealed local early childhood Sr-signals

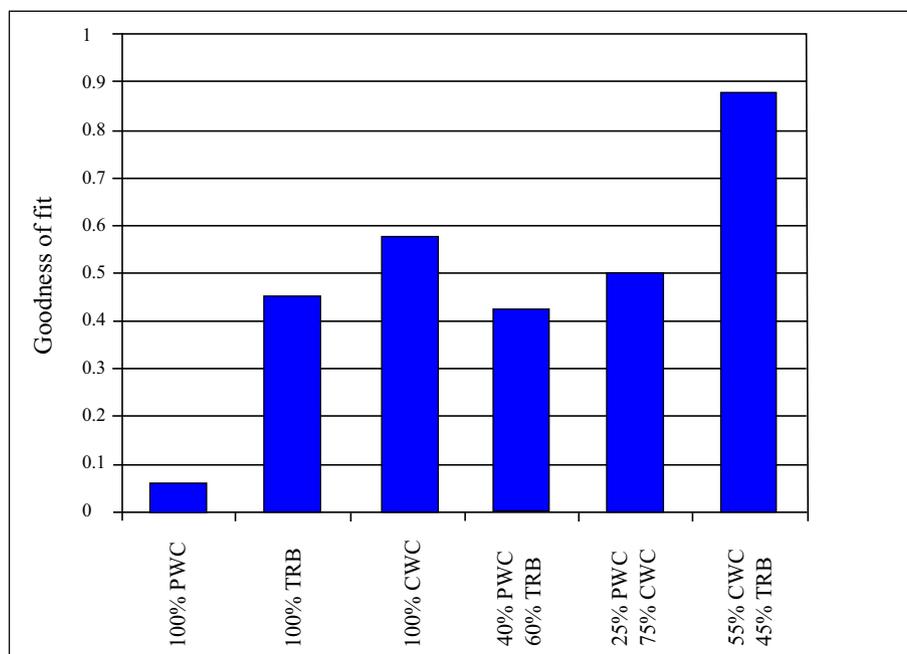


Fig. 6. Goodness of fit for the different pair-wise models of the maternal ancestral contribution to LN/EBA group displayed as proportion of simulated draws from the tested model that has a lower log likelihood than the observed sample (Table S5).

(Fig. 7C and Table 1), and although divided into two clusters, five of them also showed local Sr-values for the region. However, they seem to have changed residence during their life-time before returning to the Burs area. The older female [hgb010] (Fig. 7A) showed obvious non-local signals, and she had also moved between early childhood and early adolescence before she came to the island. Mitochondrial lineage calls were produced for five of the EBA individuals [hgb001, hgb002, hgb005, hgb010, hgb012], which all belonged to different haplotypes [J1c7a, T2b16, HV0a, T2b5, and T1a1, respectively] (Table 1).

#### 5.4.2. Hägur

Four individuals from this disturbed burial were analyzed (Table S1 and Section S1.2). All individuals were dated to EBA; an adult and a juvenile [hgr001 and hgr002] from location #2 were contemporaneous with the adult [hgr003] from location #3 and dated to BA I, the other juvenile [hgr004, also from #3] dated to BA II (Fig. 8A–B). All four individuals show local childhood Sr-values for the Eksta region where this burial is situated and they do not seem to have changed residence during their lifetime (Fig. 8C). Mitochondrial lineage calls were obtained for all four individuals, which belonged to different haplotypes [U5a1c1, H2a5, H1a, and U4a2, respectively] (Table 1).

#### 5.4.3. Suderkvie

Four individuals from this destroyed site were analyzed (Table S1 and Section S1.3). An older female located 2 m west of the cist in square R5 [Skeleton A; sud003] was dated to LN II (Fig. 9A–B). An adult individual [sud004] in square R7 just outside the eastern side of the cist was contemporaneous with a juvenile inside the cist [sud002] and dated to BA II, and a small child [sud001] inside the cist was dated to BA III. Mitochondrial DNA was only retrieved from the child that showed a unique haplotype [K1b2a] (Table 1).

#### 5.4.4. Utalskog

Two adult individuals were analyzed (Table S1 and Section S1.4). One of the individuals [uta002] dated to LN II, and the other [uta001]

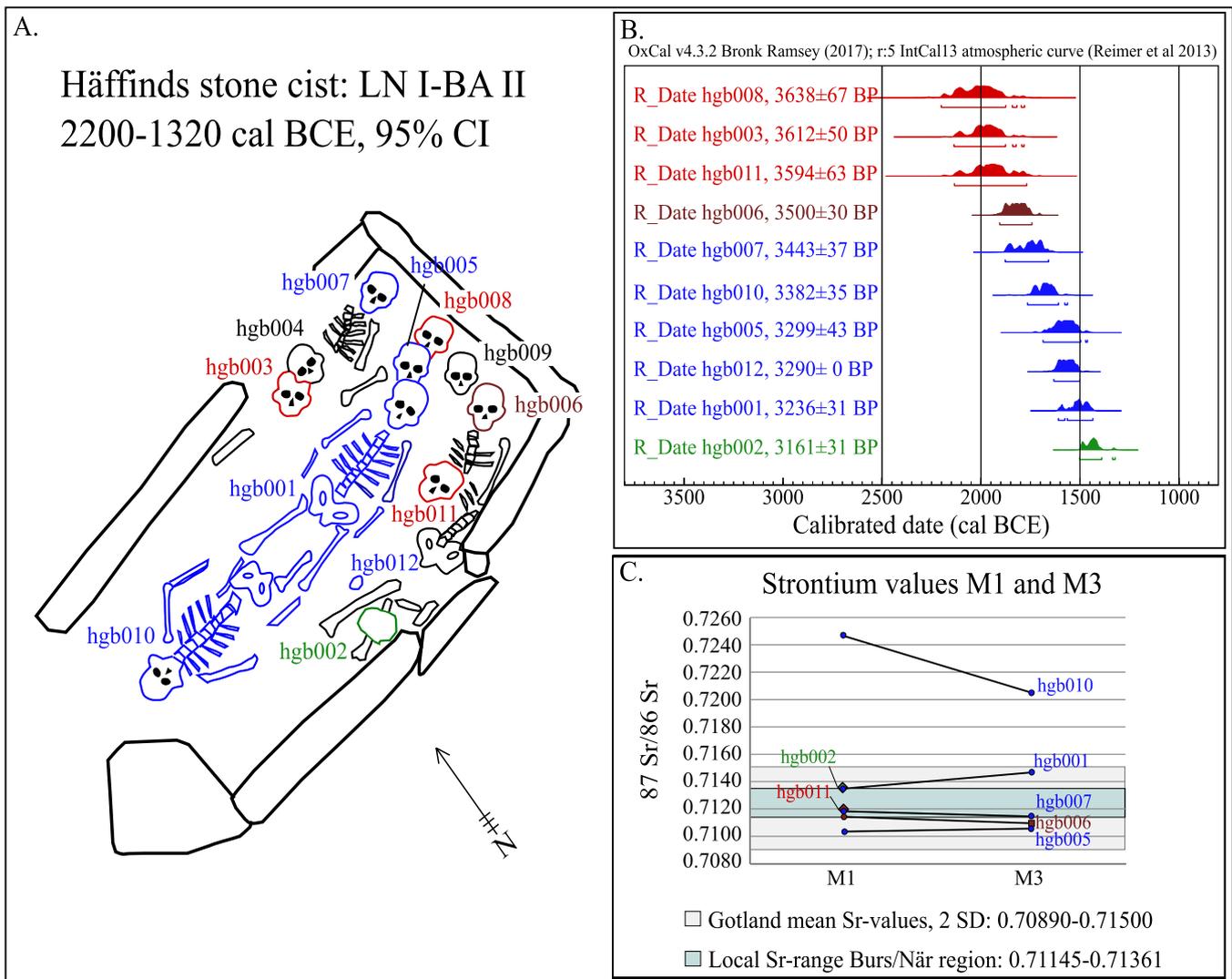
to BA I (Fig. 10A). Both individuals showed local Sr-signals equivalent to that of the Burs/När area (Fig. 10B), which is within c. 10 km from this burial. This local Sr-range is used as a proxy for the Alskog area where this burial is located as we currently do not have environmental Sr-data from this site (Fig. 4B). Only one of the individuals gave results for mitochondrial DNA which showed a unique haplotype [uta001; H1e1a] (Table 1).

## 6. Discussion

Several of the graves analyzed here have been plundered and destroyed and the excavations were carried out long ago and were not recorded in sufficient detail. Therefore, the interpretations presented have to be understood in this context and there can be unknown biases of the data. We find that only one of the burials dated to LN I [Häffinds], this stone cist grave was also in use continuously into BA II. Two additional burials showed results from LN II [Utalskog and the SKA female at Suderkvie]. The other two stone cists [Hägur and Suderkvie] only showed EBA usage, however more individuals need to be dated in order to fully understand the chronology of these burials. We also found extensive usage during BA I, and the individuals dated outside the cist context at Hägur, Häffinds and Suderkvie also revealed BA I to BA II dates, thus they were contemporaneous with individuals in the cists. Only the Suderkvie cist burial showed usage in BA III (for further discussions see below). These results indicate that all four cist burials ended in the EBA. New types of burial traditions entered the island in the LBA [c. 1100–500 cal BCE] mainly in form of cremation urn burials. Either as secondary burials inside EBA cairns/mounds, inside small LBA stone cists, and/or within ship settings or other types of LBA stone settings and cairns (e.g. Stenberger, 1964; Wehlin, 2013). A secondary LBA cremation urn burial was also located in the cairn of the Häffinds burial analyzed in this study (Fig. S2 and Section S1.1) (Burenhult, 1986).

### 6.1. The Late Neolithic burials

The Häffinds stone cist [n = 20], the largest and most elaborate burial in terms of size, had also been used for the longest time-period, as



**Fig. 7.** A. The Häffinds stone cist burial (modified from Burenhult, 1986) (Section S1.1). Colors indicate time periods: red = LN I; brown = LN II; blue = BA I; green = BA II; black = not included in the analyses. B. Radiocarbon dating series for ten individuals from inside the cist, 95% CI. C. Strontium values for seven individuals inside the cist: Circles depict M1 and M3; Diamonds depict individuals with only M1 values; Square depict only M2. Gray area depicts current mean Sr-values, 2 SD for Gotland, and light green area depicts local Sr-range for the Burs/När region presented in the text. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

it had been used continuously from LN I to BA II (Fig. 7). At least four individuals were buried within the cist during the LN period [three adults and a child]. One adult and the child was also analyzed for childhood mobility and showed local Sr-signals. It seems as the remains of their bodies had been moved to the sides when additional individuals were added to this burial. This is also consistent with the ritual burial activities documented for these types of graves in Sweden (e.g. Stensköld, 2004). As there were at least twenty individuals buried inside the cist at Häffinds we have probably not identified all individuals from the LN period.

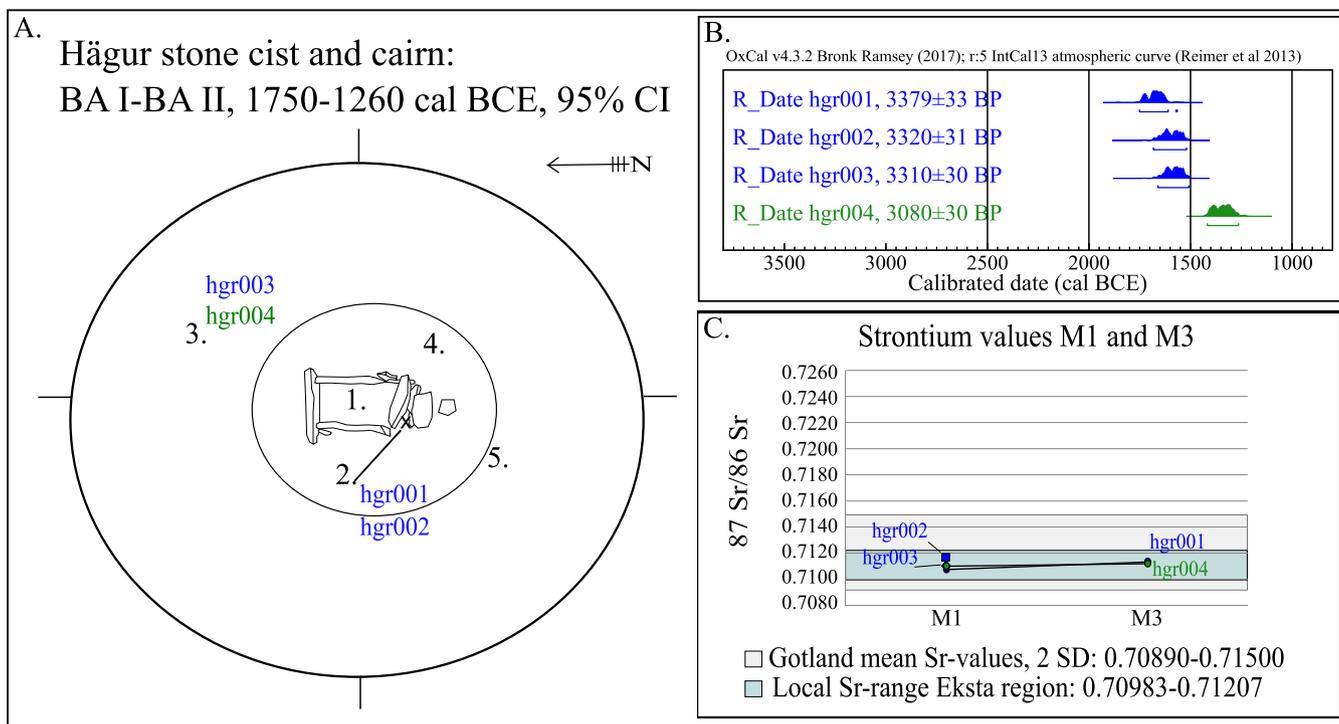
The natural limestone burial in Utalskog [n = 26] was the largest of the four in terms of number of individuals. Although very fragmented, both males and females of all age groups, including several children were noticed (Sjöstrand, 2012). The individuals had been packed tightly together, and it appeared as if some had been moved to make room for others (Bergman, 1927) (Section S1.4). The dating showed that it had been in use for at least 200–400 years [1910–1530 cal BCE, 95% CI] bordering the LN/EBA transition and continuing into BA I. However, it could have been in use longer as, due to the fragmented state of the material, we only analyzed two individuals from this burial. Both individuals analyzed presented similar local Sr-signals indicating

that they came from the same area (Fig. 10B). The BA I individual belonged to a unique haplotype [H1e] (Tables 1 and S4).

The find circumstances for the partial skeleton [SKA] outside the cist at Suderkvie is more difficult to evaluate (Fig. 9 and Section S1.2) (Gustavsson, unpublished; Manneke, 1963b, 1963a). Her LN II dating is several hundred years older than the other individuals at this burial site. Some of her skeletal elements were found in correct anatomical position whereas all the other individuals inside the cist were completely disarticulated and commingled (Fig. S7E–G). She could have belonged to another burial which since has been destroyed (Section S1.2). Further dating of the other human remains found scattered across this site, will help to clarify the context of this burial.

## 6.2. The Early Bronze Age burials

The EBA usage in Häffinds shows a different burial pattern than that of the LN. Most individuals were dated to BA I; the mature male and female, and three young adults inside the cist. An additional small child and a juvenile located in feature #3, as well as one adult located just outside the cist also dated to BA I (Figs. S2 and S9), indicating some type of burial activity involving disarticulated human remains. Partial

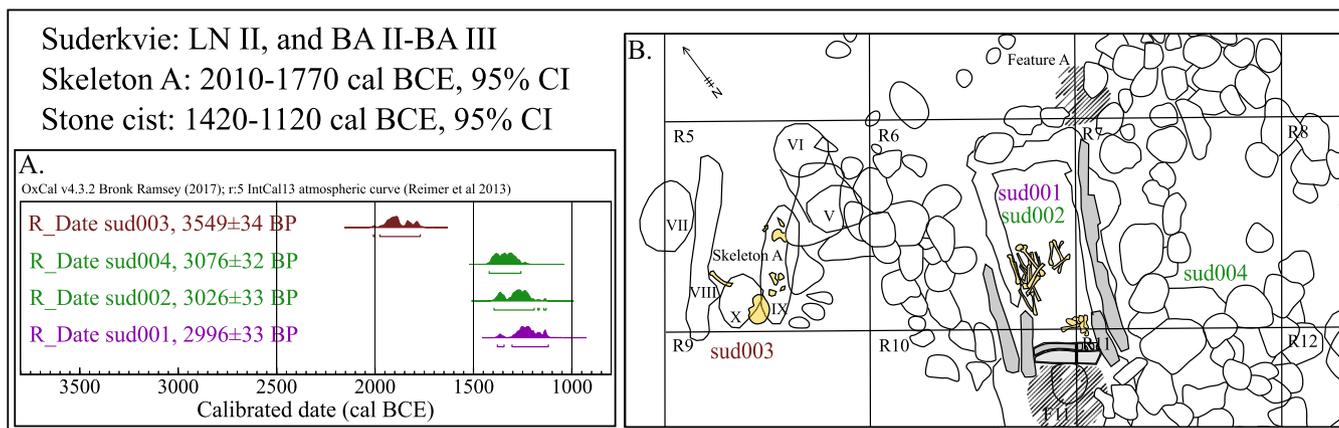


**Fig. 8.** A. The Hägur stone cist burial and cairn [outer oval] (modified from Stenberger, 1944b) (Section S1.2). Locations of human remains are depicted by numbers: 1. inside the cist; 2. inside the south part of the cist; 3. North-northeast part of the cairn; 4. findings place C; 5. inner circle depicts the area around the cist on a high level. B. Radiocarbon dating series, 95% CI. C. Strontium values. Symbols, colors and Sr-baseline values are displayed as in (Fig. 7A–C).

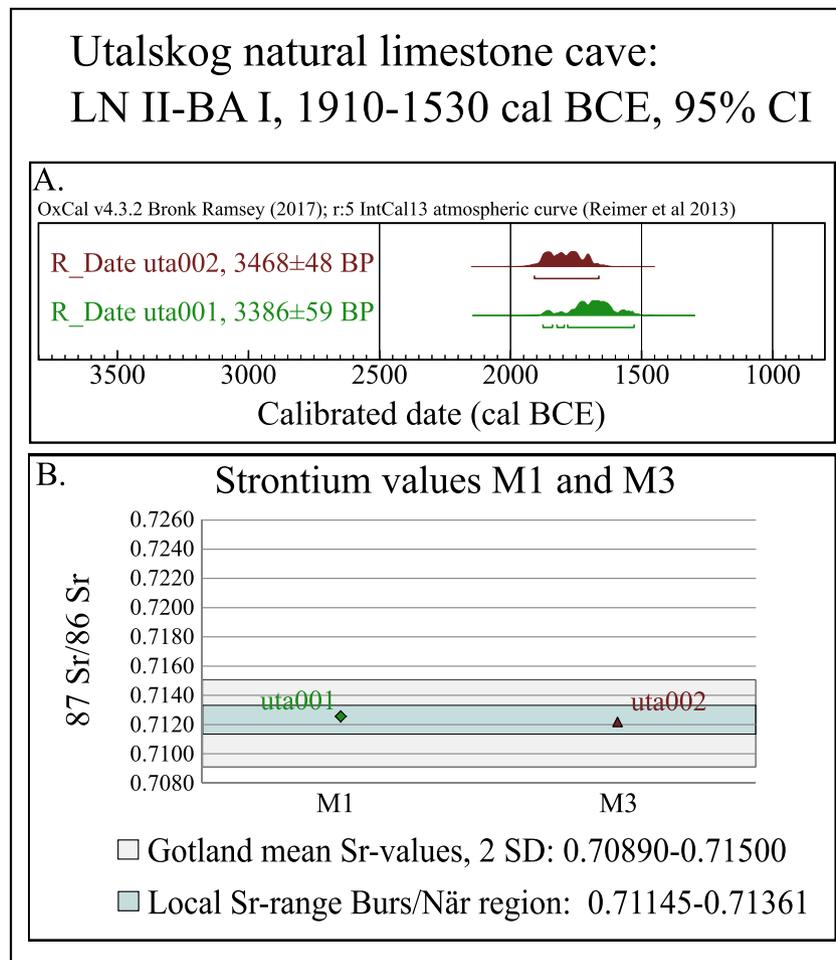
remains from several individuals were found in each of the three features outside the cist (Persson, unpublished) (Fig. S2 and Section S1.1). An additional child from the cist was dated to BA II (Fig. 7). The two older male and female individuals were placed in anatomical position in the center of the grave but were separated temporally by c. 100 years (Fig. 7A). The mature female did not grow up on Gotland, and she was also placed in the opposite direction to that of the other individuals buried in the cist. The older male and two of the young adults from BA I, plus the young child dated to BA II, all showed local early childhood Sr-signals. The mature male and the young child were among the last to be buried in the cist. The male was represented by an almost complete skeleton, whereas the child was completely disarticulated and commingled. The top cover of the cist was missing, and the top layer in the cist was also reported to have been disturbed (Lindh, 1997) (Section

S1.1). The burial was later completely covered by a cairn and a large earthen mound (Burenhult, 1986). The different haplotypes in the five individuals reported indicated that they were not related maternally. However, the nonlocal female [hgb010] and the child [hgb002] both belonged to the haplogroup lineage T2b which has been found in TRB, PWC and CWC individuals in the datasets analyzed here (Fig. S12 and Table S4). The haplogroup lineage J1c has been found in both TRB and CWC individuals, and lineages HV0a and T1a has been found exclusively in TRB and CWC individuals, respectively.

The Suderkvie cist burial [n = 12] had been destroyed and plundered and skeletal remains were found scattered across the whole site (Gustavsson, unpublished; Manneke, 1963a, 1963b). Although, this stone cist burial must have been destroyed a very long time ago as the whole site was covered by a thick humic layer and not visible above



**Fig. 9.** A. Partial plan of the Suderkvie stone cist and Skeleton A (modified from Lidman, 2015; and Manneke, 1963b) (Section S1.3). The squares are 2 m<sup>2</sup>. Skeletal remains from inside the cist and Skeleton A have been colored in yellow. B. Radiocarbon dating series, 95% CI. Colors indicate same time periods as in (Fig. 7A–C) with the addition of the color purple which indicate BA III. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 10.** A. Radiocarbon dating series for the two individuals, 95% CI. B. Strontium values for the individuals. Symbols, colors and Sr-baseline values are displayed as in (Fig. 7A–C), pyramid depicts only M3.

ground (Fig. S6A, B and H). This is in contrast to many of the other destroyed burials on Gotland that were plundered and damaged in the near past during historical times (Lindquist, 2007). The long bones of several individuals had been piled up in the center of the cist, and partial skeletal remains of at least four adults, and eight smaller children and infants were present (Gustavsson, unpublished) (Fig. S6E–F and Section S1.3). However, these assemblages do not necessarily indicate a primary prehistoric ritual burial activity as the different bone concentrations may have been associated with the destruction of the cist. A juvenile from the cist and the adult in square R7 were contemporaneous and dated to BA II. A small child in the cist dated to BA III, this is the only individual from this study that belong to this time-period.

If the LN [SKA] female belonged to another cist burial the stone packing surrounding the EBA stone cist connected these two burials spatially (Fig. S6B, C and G). Interestingly, both graves were situated on top of a MN TRB-pottery site, and TRB pottery was scattered across the whole site and was also found in pits located below the stone packing (Section S1.3) (Lidman, 2014; Manneke, 1963a, 1963b). However, these features might not have been visible above ground at the time when the cist burial was constructed over 2000 years later. The burials were constructed on top of beach sand which at the time of the MN TRB site was c. 190 to 350 m from the shore (Lidman, 2015). However, due to the isostatic uplift, the distance to the shoreline was c. 700 m at the end of the LN period, and c. 1400 m at the end of the EBA, presenting different landscapes for the activities at this site during the different time periods. The preservation of DNA for these individuals was also

poor. We only retrieved mtDNA from the young child which showed a unique haplogroup lineage [K1b] (Table S4).

The final burial at Hägur [n = 16] consisted of a cist with a cairn. This burial had also been plundered and partially destroyed prior to excavation. The cist cover had been pushed to the side, and the cist was filled with large cobblestones. Human remains were found commingled in five locations within the cist, and in the cairn surrounding the cist (Fig. 8A–C and Section S1.2) (Stenberger, 1944b, 1944a). Four juvenile and adult individuals from two locations were analyzed which showed that at least three were contemporaneous and dated to BA I, and the fourth dated to BA II. Although separated in time by at least 500 years, this burial site is located only 1 km north of the large MN PWC burial site of Ajvide. The four individuals showed local Sr-values for the area and they seem to have resided in the same location for their lifetime (Fig. 8C). All four individuals displayed different haplotypes, thus they were not related maternally (Table 1). One unique haplogroup lineage [H1a] was found (Table S4). The U5a lineage has been found in both PWC and CWC datasets, and the H2a and U4a lineages have been found exclusively in CWC (Table S4). Although, the U4-lineages in some of the PWC individuals on Gotland has not been fully resolved (Table S4).

### 6.3. Demography

Interestingly, we find that most individuals studied showed local Sr-signals. However, we detected an increase of migration to Gotland compared to the MN period but mainly in the individuals buried in the Ansarve Dolmen (Fig. 5). Only one individual [hgb010, BA I] from the

Häffinds burial showed an obvious nonlocal Sr-signal. Although still within the local baseline range for Gotland, the Häffinds individuals [ $n = 8$ ] seem to have been quite mobile during their lifetime, and also appeared to have originated from different locations (Fig. 7C). In contrast, the individuals from the EBA Högur stone cist [ $n = 4$ ] seem to have resided in the same location during their lifetime (Fig. 8C). Although, the local Sr-range for the Alskog area has not been determined both individuals showed similar Sr-values which fall within the local Sr-range found for the Burs/När area in close vicinity (Fig. 10B).

The individual [ans016] from the end of the MN phase with the deviating Sr-value (Fraser et al., 2018) is close to the upper Sr-baseline boundary and could thus be of nonlocal origin (Fig. S10C). The two LN individuals [ans004 and ans010] from the dolmen also display nonlocal early childhood Sr-signals (Fig. S10C). While the sample size for the MN usage of the Ansarve dolmen is small [ $n = 8$ ], these individuals are evenly distributed over the whole period of usage showing that there were local groups on the island throughout this time period (Fraser et al., 2018). Interestingly, the LN Ansarve individuals, buried in what may be considered a deviating burial context, also exhibited different diet and life history patterns than those of the individuals buried in the cists (Fig. 3 and Fig. S10C). The stable isotope analyses revealed a strict terrestrial diet in the LN/EBA individuals in this study [ $n = 21$ ], also in contrast to the earlier TRB and PWC groups (Fig. 3). Only two of the seventeen dated individuals from the dolmen [ $n = 31$ ] were from the LN period (Fraser et al., 2018; Lindqvist, 1997), indicating an infrequent, but still recurrent, use of the dolmen in the LN period by people not local to the island (Table 1).

Unfortunately, due to poor preservation, mitochondrial haplotype calls were only obtained from the EBA individuals in this study. However, some interesting findings were observed. We find two adult local individuals with unique haplogroup lineages [H1a, H1e], and two juvenile individuals with haplogroup lineages [H2a and T1a] previously found exclusively in the CWC individuals analyzed here, all four dated to BA I showing that new lineages had already been established on Gotland at this time period. Another unique haplogroup lineage [K1b] is found in the child dated to BA III at Suderkvie, indicating continued migration to the island. Additionally, the two nonlocal individuals [LN II; ans010 and BA I; hgb010], were adding to the already existing haplogroup lineages [U5b and T2b, respectively] previously found in the PWC individuals analyzed here. The T2b lineage has also been found in the TRB individuals from the dolmen (Table S4).

Our ancestral contribution modeling for the maternal lineages showed that, among the models tested, the only models with a good fit were 55/45 CWC/TRB contribution (Fig. 6), or a 3-way mixture of 55% CWC, 40% TRB, and 5% PWC (Fig. S15). All other models had poor support, including the models with 100% contribution from either group present on Gotland in the preceding period. The PWC group had the weakest fit of all models which is quite surprising as the PWC was the only preceding group that was established on the island in the beginning of the LN period. Although separated temporally by more than 500 years, the individuals from the Högur burial seems to have been well established in the Eksta area which previously was inhabited by PWC groups. However, the new haplogroup lineages [H1a and H2a] in the Högur burial suggest some migration to Gotland in a period succeeding the PWC. Archaeologically, it is difficult to reconcile a 55/45 CWC/TRB contribution on Gotland as the temporal range of the TRB culture ends around c. 2700 cal BCE, and presently there is little archaeological evidence of assimilation of TRB and BAC/CWC on Gotland during the latter part of the MN period (e.g. Andersson, 2016).

The apparent decline of human activity on the island post TRB, and also later postPWC is intriguing. As we do not see cultural assimilation of TRB and PWC on Gotland one can only speculate as to why TRB disappears from the archaeological record. We know that there was TRB connected activity at several sites spanning between c. 4000 to 3000 cal BCE. However, only one burial has been confirmed to date, also showing later activity up to c. 2700 cal BCE. The fluctuations in

settlement intensity on Gotland have recently been identified through modeling of summed probability distributions of radiocarbon dates from the Mesolithic to the LN, which indicated multiple population events (Apel et al., 2018). Gotland was settled for different reasons during the different time-periods, which are seen in the differences in subsistence patterns, reflected by stable isotopes and material culture.

The LN period is a paradox as the apparent lack of settlement sites, and directly dated finds, is in contrast to the high number of stray finds and burial monuments. This is, however due the fact that settlement sites are difficult to find in the landscape without the large scale exploitation-excavations performed in connection with new infrastructure, as has been done on the Swedish mainland. The same problem has been noted for the apparent lack of BA settlement sites on the island (Runesson, 2014).

The introduction of new female lineages and the mtDNA haplogroup variation within these stone cist burials, together with an increase of nonlocal individuals, and a dietary shift, indicates that a demographic event has happened. The LN period shows traces of activity all over the island compared to the MN period with ten TRB, and eighteen PWC sites (e.g. Bäckerfeldt, 1992; Luthander, 1988; Wallin, 2010; Österholm, 1989). This pattern seems to continue into the EBA as seen by the well-established local groups identified by their Sr-signals, as well as the monumental burials.

It has been shown that the CWC migration across central Europe was based predominantly on migrating males (Goldberg et al., 2017). Our genetic results show that there also were incoming females to Gotland as new maternal lineages were introduced and established in local populations. This has recently also been shown in mtDNA analyses of LN/EBA populations in southern Germany (Knipper et al., 2017). As we had very limited genetic data from the LN period in this study, we can only base our interpretation on what we found in the local EBA individuals. Moreover, as we are analyzing mtDNA we only see the female lineages and a very small fraction of the human genome. Thus, the full extent of population continuity from the local PWC groups is not known. However, we can show that there has been a clear shift in the population demography from that of the MN period on Gotland. Further genomic analyses of these groups on Gotland [TRB, PWC, and the LN/EBA cist burials] will help to clarify the demographic history of the Gotlandic island inhabitants during the Stone Age and Early Bronze Age.

## 7. Conclusion

We use a multidisciplinary approach to investigate the LN to EBA population demographic developments on the island of Gotland via analyses of individuals buried in four previously excavated stone cist burials. LN activity is recorded at three of the sites, and the stone cist most extensively dated showed continuous burial activity from LN I to BA II. We find an increased intensity in burial activity during BA I, where there also appear to be some activities outside the cists involving human remains. Only one burial revealed usage in BA III.

We find a shift in population demography compared to the preceding cultural developments on the island recorded from the Neolithic TRB, and sub-Neolithic PWC groups. We find that these burials were used by local groups that were well established in the regions where the burials were situated. These individuals also displayed a different dietary pattern than that noted for the preceding TRB and PWC groups on the island. We also detect sporadic reuse of the MN TRB dolmen in the LN period by nonlocal individuals, who also shows deviating dietary patterns to the LN/EBA individuals in the stone cist burials.

We see an increase of new mitochondrial lineages in the EBA individuals, of which some also were noted in the CWC reference dataset used in this study. Our modeling for maternal ancestry suggests a 3-way model of 55% CWC, 40% TRB, and 5% PWC. Given the broad absence of archaeological evidence for the typical BAC/CWC burials, as well as no archaeological evidence of assimilation of TRB and PWC during the

latter part of the MN period on Gotland, it seems probable that the major process of admixture did not occur on the island. Instead, the data indicates an admixture process that occurred elsewhere and prior to migrating to Gotland. Thus, our results suggest later migration to the island during the LN period by people with a new economy, as well as new burial customs. A likely scenario, taking all these factors into account, is a sizable migration of people, with a ~50/50 (maternal) ancestry in TRB and CWC associated groups, possibly admixing with much smaller local groups of PWC associated individuals on the island.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2018.02.045>.

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## References

Andersson, H., 2016. Gotländska stenåldersstudier Människor och djur, platser och landskap. Stockholm Studies in Archaeology 68.

Apel, J., 2001. Daggers, Knowledge & Power: The Social Aspects of Flint-dagger Technology in Scandinavia 2350–1500 cal BC, Kust till kust-böcker. Dept. of Archaeology and Ancient History, Univ. of Uppsala, Uppsala.

Apel, J., Wallin, P., Storå, J., Possnert, G., 2018. Early Holocene human population events on the island of Gotland in the Baltic Sea (9200–3800 cal. BP). *Quat. Int.* 465 (Part B), 276–286.

Arne, T.J., 1927. Rapport rörande undersökning av en-mansgrav, sannolikt från stenåldern, belägen på gården till Utalskog i Alskogs socken, Gotland. Brev till Riksantikvarien. Stockholm den 2 September 1927. Rapport Utalskog, Dickarbacke. (ATA - rapport. No. Dnr: 3530/27). Riksantikvarieämbetet, Stockholm.

Bägerfeldt, L., 1992. Neolitikum på Gotland. Problem och konsekvenser. ARKEO-Förlaget, Gamleby.

Bergman, B., 1927. Brev till Riksantikvarien. Ekse, Ardre, Ljugarn den 8 september 1927. Slutrapport. Utalskog, Dickarbacke.

Björck, N., 2003. In: Samuelsson, C., Ytterberg, N. (Eds.), *The Neolithic Coastal Settlements – Cosmology and Ideology in a Baltic Sea Perspective*. I: C. Samuelsson & N. Ytterberg (red) *Uniting Sea. Stone Age societies in the Baltic Sea region*. Proceedings from the first Uniting Sea Workshop at Uppsala University, Sweden, January 26–27, 2002. Presented at the Uniting Sea Workshop 1pp. 20–42 (Sweden).

Brandt, G., Haak, W., Adler, C.J., Roth, C., Szécsényi-Nagy, A., Karimnia, S., Möller-Rieker, S., Meller, H., Ganslmeier, R., Friederich, S., Dresely, V., Nicklisch, N., Pickrell, J.K., Sirocko, F., Reich, D., Cooper, A., Alt, K.W., 2013. Ancient DNA reveals key stages in the formation of central European mitochondrial genetic diversity. *Science* 342, 257. <http://dx.doi.org/10.1126/science.1241844>.

Briggs, A.W., Stenzel, U., Johnson, P.L., Green, R.E., Kelso, J., Prüfer, K., Meyer, M., Krause, J., Ronan, M.T., Lachmann, M., et al., 2007. Patterns of damage in genomic DNA sequences from a Neandertal. *Proc. Natl. Acad. Sci.* 104, 14616–14621. <http://dx.doi.org/10.1073/pnas.0704665104>.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337–360.

Brothwell, D.R., 1981. *Digging up Bones: The Excavation, Treatment and Study of Human Skeletal Remains*, 3. ed. Cornell Univ. Press, Ithaca, N.Y. [rev. and updated].

Bukstina, J.E., Ubelaker, D., 1994. Standards for data collection from human skeletal remains. In: *Arkansas Archeological Survey Research Series no 44*, Fayetteville, Arkansas.

Burenhult, G., 1986. *Speglingar av det förflutna*. Wiken, Höganäs.

Burenhult, G. (Ed.), 1999. *Arkeologi i Norden*. Natur och Kultur, Stockholm.

Calner, M., 2005. Silurian carbonate platforms and extinction events—ecosystem changes exemplified from Gotland, Sweden. *Facies* 51, 584–591. <http://dx.doi.org/10.1007/s10347-005-0050-0>.

Cooper, A., Poinar, H.N., 2000. Ancient DNA: do it right or not at all. *Science* 289, 1139. <http://dx.doi.org/10.1126/science.289.5482.1139b>.

Edenro, R., 2008. Prestigeekonomi under yngre stenåldern: gåvoutbyten och regionala identiteter i den svenska båtbyxekulturen, *Occasional papers in archaeology*. Inst. för Arkeologi och Antik Historia, Univ. Uppsala.

Eriksson, G., 2004. Part-time farmers or hard-core sealers? Västerbjers studied by means of stable isotope analysis. *J. Anthropol. Archaeol.* 23, 135–162.

Fraser, M., Sanchez-Quinto, F., Evans, J., Storå, J., Götherström, A., Wallin, P., Knutsson, K., Jakobsson, M., 2018. New insights on cultural dualism and population structure in the Middle Neolithic Funnel Beaker culture on the island of Gotland. *J. Archaeol. Sci. Rep.* 17, 325–334. Available online. <https://doi.org/10.1016/j.jasrep.2017.09.002>.

Gilbert, M.T.P., Bandelt, H.-J., Hofreiter, M., Barnes, I., 2005. Assessing ancient DNA studies. *Trends Ecol. Evol.* 20, 541–544. <http://dx.doi.org/10.1016/j.tree.2005.07.005>.

Goldberg, A., Günther, T., Rosenberg, N.A., Jakobsson, M., 2017. Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc. Natl. Acad. Sci.* 114, 2657–2662.

Green, R.E., Malaspina, A.-S., Krause, J., Briggs, A.W., Johnson, P.L.F., Uhler, C., Meyer, M., Good, J.M., Maricic, T., Stenzel, U., Prüfer, K., Siebauer, M., Burbano, H.A., Ronan, M., Rothberg, J.M., Egholm, M., Rudan, P., Brajković, D., Kučan, Ž., Gušić, I., Wikström, M., Laakkonen, L., Kelso, J., Slatkin, M., Pääbo, S., 2008. A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. *Cell* 134, 416–426. <http://dx.doi.org/10.1016/j.cell.2008.06.021>.

Günther, T., Malmström, H., Svensson, E.M., Omrak, A., Sánchez-Quinto, F., Kilinc, G.M., Krzewińska, M., Eriksson, G., Fraser, M., Edlund, H., Munters, A.R., Coutinho, A., Simões, L.G., Vicente, M., Sjölander, A., Sellevold, B.J., Jørgensen, R., Claes, P., Shriver, M.D., Valdiosera, C., Netea, M.G., Apel, J., Lidén, K., Skar, B., Storå, J., Götherström, A., Jakobsson, M., 2018. Population genomics of Mesolithic Scandinavia: investigating early postglacial migration routes and high-latitude adaptation. *PLoS Biol.* 16, e2003703. <http://dx.doi.org/10.1371/journal.pbio.2003703>.

Gustavsson A., Osteologisk analys av skelettmaterialet från en hällkista i Suderkvie 1:14, Grötlingbo 13:1, Grötlingbo socken, Gotland, (Osteologisk rapport), *Osteologisk Rapportserie Uppsala universitet Campus Gotland*, Uppsala University, (unpublished).

Gytare, S., 2015. *Who were Buried in the Gallery Grave in Hägur? : A Case Study of a Possible Late Neolithic Gallery Grave on the Island of Gotland*. Independent thesis Basic level (Bachelor Student thesis). Uppsala University, Department of Archaeology and Ancient History.

Heimann, C., 2000. The landscapes of gallery graves in Sweden. The use of gallery graves in the transformation of Neolithic landscapes. In: Darvill, Red T., Gajda, M. (Eds.), *One Land: Many Landscapes*. BAR.

Hyenstrand, Å., 1979. Arkeologisk regionindelning av Sverige. Riksantikvarieämbetet.

Iversen, R., 2016. Was there ever a single grave culture in East Denmark? Traditions and transformations in the 3rd millennium BC. In: Furrholt, Martin, Großmann, Ralph, Szmyt, Marzena (Eds.), *Proceedings of the International Workshop "Socio-Environmental Dynamics Over the Last 12,000 Years: The Creation of Landscapes III (15th–18th April 2013)"* in Kiel. In Kommission bei Verlag Dr. Rudolf Habelt GmbH, Bonn, pp. 159–170.

Janzon, G.O., 1974. Gotlands mellanneolitiska gravar, *Acta Universitatis Stockholmiensis*. In: *Studies in North-European Archaeology*, 6. Almqvist & Wiksell, Stockh.

Jeppsson, L., Eriksson, M.E., Calner, M., 2006. A latest Llandovery to latest Ludlow high-resolution biostratigraphy based on the Silurian of Gotland—a summary. *GFF* 128, 109–114.

Johansson, B.O.H., 1961. Stenåldershällkistor från svensk-norska gränslandskap. TOR XII.

Knipper, C., Mittnik, A., Massy, K., Kocumaka, C., Kucukkalipci, I., Maus, M., Wittenborn, F., Metz, S.E., Staskiewicz, A., Krause, J., 2017. Female exogamy and gene pool diversification at the transition from the final Neolithic to the Early Bronze Age in central Europe. *Proc. Natl. Acad. Sci.* 114 (38), 10083–10088. [10083–10088](https://doi.org/10.1073/pnas.1706355114).

Korneliusson, T.S., Albrechtsen, A., Nielsen, R., 2014. ANGSD: analysis of next generation sequencing data. *BMC Bioinf.* 15 (1).

Kriiska, A., 2003. From Hunter-fisher-gatherer to Farmer - Changes in the Neolithic Economy and Settlement on Estonian Territory.

Lidman, E., 2014. *Kulturen med en twist: En studie av fyra lokaler från trattbågarkulturen på Gotland*. (BA-thesis in archaeology). Uppsala University, Department of Archaeology and Ancient History.

Lidman, E., 2015. *Suderkvie—en plats med ett glömt minne?: En mikrostudie av lokalen Suderkvie på Gotland*. (Masterlevel thesis in archaeology). Uppsala University, Department of Archaeology and Ancient History.

Lindh, B., 1997. *Monument i förändringens tid. En arkeoosteologisk studie av en senneolitisk hällkista i Häffinds, Burs socken på Gotland*. (Bachelor thesis in archaeoosteology). University of Stockholm, Archaeoosteological Research Laboratory.

Lindqvist, M., 2007. *Gotländsk arkeologi under 150 år*. In: Pettersson, Ann-Marie (Ed.), *Arkeologi, Gotländskt Arkiv. Läsnmuseet på Gotland, Visby*, pp. 5–14.

Lindqvist, C., 1997. *Ansarve hage-dösen. Tvärvetenskapliga aspekter på kontext och den neolitiska förändringen på Gotland*. In: Åkerlund, A., Bergh, S., Nordblad, J., Taffinder, J. (Eds.), *Till Gunborg. Arkeologiska samtal*. Stockholm Archaeological Reports. 33. pp. 361–378.

Lindqvist, C., Possnert, G., 1997. The subsistence economy and diet at Jakobs/Ajvide and Stora Förvar, Eksta parish and other prehistoric dwelling and burial sites on Gotland in long-term perspective. In: Burenhult, G. (Ed.), *Remote Sensing*. vol. I. Department of Archaeology, Stockholm Universit, Stockholm, pp. 29–90.

Lindqvist, C., Possnert, G., 1999. The first seal hunter families on Gotland. On the Mesolithic occupation of the Stora Förvar Cave. *Curr. Swed. Archaeol.* 65–88.

Lithberg, N., 1914. *Gotlands stenålder*. Bagge, Stockholm.

Lovejoy, C., 1985. Dental wear in the Libben populations: its functional patterns and role in determination of adult skeletal age at death. *Am. J. Phys. Anthropol.* 47–56.

Luthander, A., 1988. *Senneolitiska gravar på Gotland* (BA-thesis). (Stockholm).

- Malmer, M.P., 1962. Junge Neolithischen Studien, Acta archaeologica Lundensia in 8°, 2. (Lund).
- Malmer, M.P., 1975. Stridsyxekulturen i Sverige och Norge. LiberLäromedel, Lund.
- Malmer, M.P., 2002. The Neolithic of South Sweden: TRB, GRK, and STR. Royal Swedish Academy of Letters, History, and Antiquities: Distributed by Almqvist & Wiksell International, Stockholm.
- Malmström, H., Gilbert, M.T.P., Thomas, M.G., Brandström, M., Storå, J., Molnar, P., Andersen, P.K., Bendixen, C., Holmlund, G., Götherström, A., Willerslev, E., 2009. Ancient DNA reveals lack of continuity between Neolithic hunter-gatherers and contemporary Scandinavians. *Curr. Biol.* 19, 1758–1762. <http://dx.doi.org/10.1016/j.cub.2009.09.017>.
- Malmström, H., Linderholm, A., Skoglund, P., Stora, J., Sjödin, P., Gilbert, M.T.P., Holmlund, G., Willerslev, E., Jakobsson, M., Liden, K., Götherström, A., 2015. Ancient mitochondrial DNA from the northern fringe of the Neolithic farming expansion in Europe sheds light on the dispersion process. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 370, 20130373. <http://dx.doi.org/10.1098/rstb.2013.0373>.
- Manneke, P., 1963a. Rapport över arkeologisk utgrävning år 1959 vid Sudervkie, i Grötlingbo Socken. (ATA - rapport. No. Inv. nr: 27151. Dnr: 1669/63). Riksantikvarieämbetet, Stockholm.
- Manneke, P., 1963b. Bilder och planer från den arkeologiska utgrävningen år 1959 vid Sudervkie, i Grötlingbo Socken (ATA-document No. Inv. nr: 27151. Dnr: 1669/63). Riksantikvarieämbetet, Stockholm.
- Martinsson-Wallin, H., Wallin, P., Apel, J., 2015. Prehistoric lifestyles on Gotland—diachronic and synchronic perspectives. *Archaeol. Liturg.* 142–153.
- Meyer, M., Kircher, M., 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb Protoc* 2010(<http://dx.doi.org/10.1101/pdb.prot5448>). (pdb.prot5448-pdb.prot5448).
- Nihlén, J., 1927. Gotlands stenåldersboplatser, Kungliga Vitterhets historie och antikvitets akademiens handlingar. Viktor Petterssons bokindustriaktiebolag, Stockholm.
- Påsse, T., Andersson, L., 2006. Paleogeografiska kartor, SGU information januari 2006. SGU Uppsala.
- Persson, O., 2018. Häffinds Godsbacken. Anteckningar från den preliminära osteologiska undersökningen (Osteological report, 1984). Stockholm University (unpublished).
- Peschel, E.M., Carlsson, D., Bethard, J., Beaudry, M.C., 2017. Who resided in Ridånäs: A study of mobility on a Viking Age trading port in Gotland, Sweden. *J. Archaeol. Sci. Rep.* 13, 175–184. <http://dx.doi.org/10.1016/j.jasrep.2017.03.049>.
- Prescott, C., Gløstad, H., 2015. Expanding 3rd millennium transformations: Norway. In: Martinez, M.P.P., Salanova, L. (Eds.), *The Bell Beaker Transition in Europe. Mobility and Local Evolution during the 3rd Millennium BC*. Oxbow Books, Oxford and Philadelphia, pp. 77–87.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., et al., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 years cal BP.
- Rundkvist, M., Lindqvist, C., Thorsberg, K., 2004. Barshalder. 3: Rojrhage in Grötlingbo: a multi-component Neolithic shore site on Gotland, Stockholm archaeological reports. Dep. of Archaeology, Univ. of Stockholm, Stockholm.
- Ruñsson, G., 2014. Bronsålderns bosättningsområden och boplatser på Gotland: många syns inte men finns ändå (Doctoral thesis). Stockholms universitet, Stockholm.
- Schulz Paulsson, B., 2010. Scandinavian models: radiocarbon dates and the origin and spreading of passage graves in Sweden and Denmark. In: Jull, A.J.T. (Ed.), *Radiocarbon, Proceedings of the 20th International Radiocarbon Conference*. 52. pp. 1002–1017.
- Schulz Paulsson, B., 2017. Time and Stone: The Emergence and Development of Megaliths and Megalithic Societies in Europe. Archaeopress Archaeology, Oxford.
- Sjögren, K.-G., 2003. Mångfaldige uhrminnes grafar: Megalitgravar och samhälle i Västsverige. GOTARC. Series B, Gothenburg archaeological theses 27 (Göteborg 2003).
- Sjöstrand, A. Den bortglömda individen Osteologisk analys av individ 6 från hällkistan i Häffinds, Burs 9:1, Gotland, unpublished (Osteological report). Uppsala University Campus Gotland.
- Sjöstrand, A., 2012. The Stone Cist Phenomenon: A Study of Stone Cists on the Island of Gotland and Their Role in the late Neolithic - early Bronze Age society (MA-thesis). Gotland University, Department of Osteology.
- Sjøvold, T., 1978. Inference concerning the Age Distribution of Skeletal Populations and some Consequences for Palaeodemography. *Anthropologie Kozlemenenyek* 22, 99–114.
- Skoglund, P., Malmström, H., Raghavan, M., Stora, J., Hall, P., Willerslev, E., Gilbert, M.T.P., Götherström, A., Jakobsson, M., 2012. Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. *Science* 336, 466–469. <http://dx.doi.org/10.1126/science.1216304>.
- Skoglund, P., Malmström, H., Omrak, A., Raghavan, M., Valdiosera, C., Günther, T., Hall, P., Tambets, K., Parik, J., Sjögren, K.-G., et al., 2014. Genomic diversity and admixture differs for Stone-Age Scandinavian foragers and farmers. *Science* 344, 747–750.
- Stenberger, M., 1944a. Slutrapport Hägur 1:15 B.
- Stenberger, M., 1944b. Plan av och sektioner genom gravröse, Hägur 1:15 B. Eksta sn, Gotland.
- Stenberger, M., 1964. Det forntida Sverige. Almqvist & Wiksell, Stockholm.
- Stensköld, E., 2004. Att berätta en senneolithisk historia: sten och metall i södra Sverige 2350 - 1700 f. Kr. Stockholm Studies in Archaeology. Univ, Stockholm.
- Vandkilde, H., 1996. From Stone to Bronze. The Metalwork of the Late Neolithic and Earliest Bronze Age in Denmark. Jutland Archaeological Society Publications XXXII. Aarhus, Jutland Archaeological Society, Moesgård.
- Vandkilde, H., 2005. A review of the early Late Neolithic period in Denmark: practice, identity and connectivity. *J. Neolit. Archaeol.* 1–51 (December 15th).
- Vianello, D., Sevini, F., Castellani, G., Lomartie, L., Carpi, M., Francheschi, C., 2013. HAPLOFIND: a new method for high-throughput mtDNA Haplogroup assignment. *Hum. Mutat.* 34, 1189–1194. <http://dx.doi.org/10.1002/humu.22356>.
- Wallin, P., 2010. Neolithic monuments on Gotland: Material expressions of the domestication process. In: Martinsson-Wallin, H. (Ed.), *Baltic Prehistoric Interactions and Transformations: The Neolithic to the Bronze Age*. Gotland University Press, Visby, pp. 39–61 (No. 5).
- Wallin, P., 2016. The use and organisation of a Middle-Neolithic pitted ware coastal site on the island of Gotland in the Baltic Sea. In: Dupont, Catherine, Marchand, Gregor (Eds.), *Archaeology of maritime hunter-gatherers. From settlement function to the organization of the coastal zone Actes de la séance de la Société préhistorique française de Rennes, 10–11 avril 2014*. Société préhistorique française, Paris.
- Wallin, P., Martinsson, H., 1986. Osteologisk analys av skelettmaterialet från megalitgraven i Ansarve, Tofta Socken, Gotland. Osteologisk rapport.
- Wallin, P., Martinsson-Wallin, H., 2016. Collective spaces and material expressions: ritual practice and island identities in Neolithic Gotland. In: Nash, George, Townsend, Andrew (Eds.), *Decoding the Neolithic and Mediterranean Island Ritual*. Oxford Books, Philadelphia, pp. 1–15.
- Wehlin, J., 2013. Östersjöns skeppssättningar. Monument och mötesplatser under yngre bronsålder (GOTARC series B. Gothenburg Archaeological Theses 59). Gothenburg University, Gothenburg.
- Österholm, I., 1989. Bosättningsmönstret på Gotland under stenåldern. En analys av fysisk miljö, ekonomi och social miljö. Theses and papers in Archaeology 3. Stockholms universitet.