People of the Dolmens and Stone Cists
An archaeogenetic investigation of megalithic graves from the Neolithic period on Gotland

Magdalena Fraser
Abstract

The study of ancient genomics of pre-historic human remains has in recent years offered unprecedented knowledge regarding pre-historic migration and population structure on the European continent which has fundamentally altered the current views in the archaeological community. However, the merging of the two fields, archaeology and genetics, is still in its infancy and much work is still needed in order for these fields to integrate. In this thesis I explore how genetic analyses, in combination with contextual radiocarbon dating and isotopic analyses for diet and mobility can be used to investigate demographic events on a local and regional level. This is done through the investigation of people buried in five previously excavated megalithic tombs on the Island of Gotland dated to the Neolithic period. I present the genomic population structure and archaeological background for the pre-historic European reference data and show how this is used to investigate population continuity, demographic shifts, cultural duality, and admixture for local and regional contexts. I present new data and explore the Strontium-baseline for the Gotland biosphere which is used for the mobility analyses. I show that mitochondrial haplogroup data is especially useful in combination with isotopic data, and radiocarbon dating for investigation of demographic shifts on a larger scale. I also show that genomic data gives unique insights into the individuals’ life history which, together with the established demographic background allows for fine scale investigation of population demographic events within and between different archaeological contexts. Finally I show that the different Neolithic contexts on Gotland to a large extent involves immigration of new groups to the island, and that the contextual breaks seen in the archaeological record during the Neolithic period are connected with cultural and population demographic shifts. This dissertation demonstrates that genomic analyses, in combination with archaeology and isotopic analyses, as well as contextual osteological analyses and radiocarbon dating, present unique insights into the life history of the actual people who lived the lives we try to understand.

Keywords: archaeology, aDNA, ancient genomics, archaeogenetics, mtDNA, osteology, radiocarbon dating, Strontium, Carbon, Nitrogen, TRB, PWC, BAC, CWC, dolmen, stone cist, population demography, diet, mobility, cultural duality, admixture, kinship, Neolithic period, Early Bronze Age, Europe, Baltic Sea area, Scandinavia, Gotland

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ISSN 0284-1347
urn:nbn:se:uu:diva-347559 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-347559)
List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.


*These individuals contributed equally to this study

Reprints were made with permission from the publisher
I am also author or co-author of the following articles and book chapters that were published during my graduate studies:


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1 Introduction

The main objective of this thesis is to investigate the demographic developments during the Neolithic period on the island of Gotland. This is done based on investigation of human remains from five megalithic burials using a cross-disciplinary approach that combine archaeology, genetics and stable isotope analysis. The results are used to discuss the population demographic developments from the perspective of these burials.

The Stone Age on Gotland has a complex history and remains from several different archaeological cultures have been identified. These are sometimes overlapping in time, but there are also chronological gaps that complicate interpretations of the demographic development (Fig. 1A). Interestingly, in the sense that Gotland is an island in the center of the southern part of Baltic Sea, the Stone Age material cultures on Gotland exhibit similar developments as seen to the west in southern Scandinavia. However local developments are also seen, and as in other parts of Europe, it has long been debated whether the shifts seen in the archaeological record on Gotland were attributed to migrating people or acculturation by local people adapting new ideas. Do these chronological gaps and changes in material culture also indicate demographic shifts in the local developments seen on the island? Gotland is an ideal area for studying cultural interactions and developments over time due to its relatively small size and natural borders, good preservation of biological remains, as well as long standing archaeological research.

![Fig. 1. A. Gotland cultural timelines (Apel et al., 2018). B: Scandinavian Early Neolithic to Early Bronze Age time divisions.](image)

Gotland has a long history of archaeological exploration, and many of the Stone Age sites were discovered and excavated early (e.g. Hansson, 1897; Hildebrand, 1887; Lithberg, 1914; Nihlén, 1924, 1927; Schnittger, 1913). Hundreds of stray finds of Stone Age axes and other artefacts have also been documented across the island (Andersson, 2016; Bägerfeldt, 1992; Lithberg, 1914; Österholm, 1989). Due to the differences in the excavation methodology however, and also the fact that many of these excavations were done before the invention of radiocarbon dating, there has been some difficulty in trying to reconstruct the chronology of the prehistoric developments on the island.

Much new work regarding the Stone Age on Gotland was initiated in the 1980’s from the “Stone Age Gotland” project led by Inger Österholm and the “Archaeological Exploration Methods” framework led by Göran Burenhult, initially via Stockholm University, and
later via the department of Archeology at Gotland University (e.g. Bartholin and Burenhult, 1997; Burenhult, 2002; Österholm, 2008). Two of the burials included in this thesis (Ansarve and Häffinds) were excavated within the projects in 1984 (Bägerfeldt, 1992; Burenhult, 1986). Additional zooarchaeological and osteological evaluations, as well as new radiocarbon dating were performed in the latter part of the 1990’s by Christian Lindqvist and Göran Possnert which has elucidated and contextualized the chronological occupation on the island, and also the timing of the introduction of new species (Lindqvist, 1997; Lindqvist and Possnert, 1997, 1999).

However, certain Stone Age cultures on Gotland have been more intensely studied than others, e.g. the sub-Neolithic Pitted Ware culture complex (PWC) mainly due to the richness of burials and settlement sites connected with this culture on the island, and also new excavations at the Ajvide site in Eksta Parish (e.g. Andersson, 2016; Bartholin and Burenhult, 1997; Brandt and Burenhult, 2002; Eriksson, 2004; Hansson, 1897; Hildebrand, 1887; Howcroft et al., 2014; Janzon, 1974; Lithberg, 1914; Malmström et al., 2009, 2010, 2015; Martinsson-Wallin, 2008; Molnar, 2008; Nihlén, 1927; Nordéräng, 2007, 2008; Skoglund et al., 2012, 2014a; Storå, 2001; Wallin, 2015, 2016; Wallin and Martinsson-Wallin, 2016; Österholm, 1989, 2008).

Relatively little recent research has been done on the other Neolithic cultures leaving large chronological gaps in our understanding of the demographic developments (Fig. 1A). This is also largely due to the low number of burials from the Late Mesolithic and Early to Middle Neolithic time periods (with the exception of the PWC). The Late Neolithic period is mainly known from the numerous stray finds and also depositions of artefacts within the stone cist burials which, however only have been dated based on artefact typology.

The background of my thesis lies in a research project that was initiated by Paul Wallin (2010) called Neolithic Lifestyles: Dolmens, Earth Burials and Stone Cists. This was part of a larger project called Lifestyles – from Hunter to Urban Mind. The longtime perspective on environmental adaptation and cultural choices in the Baltic Sea Region conducted at the Department of Archaeology and Osteology at Gotland University (now department of archaeology and ancient history, Uppsala University-Campus Gotland), in which old data was compiled and re-analyzed, but also involved specific case studies with new excavations. This has led to much new information, also from new investigations in the Mesolithic period (e.g. Ahlgren et al., 2016; Apel et al., 2015; 2018; Apel & Storå, 2017; Boethius et al., 2017; Günther et al., 2018; Martinsson-Wallin et al., 2015; Martinsson-Wallin and Lidman, 2017; Martinsson-Wallin and Wallin, 2010; Svensson and Fraser, 2017; Wallin, 2015, 2016; Wallin and Martinsson-Wallin, 2016; Wallin and Wehlin, 2010).

The Neolithic Lifestyles project has also evolved into several other large projects and new research on the Stone Age on Gotland have been presented, including case studies of Neolithic pottery, landscape analyses, and also osteological evaluations of which some have been essential for the subsequent analyses in this study (see chapter 6 and Supplement Paper II). As of 2014 my research project is also part of the larger ATLAS of ancient human genomes project led by Mattias Jakobsson, Anders Götherström and Jan Storå (in collaboration with Uppsala and Stockholm Universities) funded by Riksbankens Jubileumsfond and Vetenskapsrådet (VR).
The Scandinavian Neolithic period is divided into three chronological sections Early (EN, c. 4000-3300 cal BCE), Middle (MN, c. 3300-2400 cal BCE), and Late (LN, c. 2400-1800 cal BCE). These archaeological time-periods also have further chronological refinements dependent on the period studied (Fig. 1 B). The temporal focus of this thesis is on the MN period when remains from three different cultural complexes are found; the Neolithic Funnel beaker culture (TRB, from German Trichterbecher), the sub-Neolithic PWC, and the Battle Axe culture (BAC), and also the demographic developments on the island leading into the LN period.

In this thesis I analyze the genetic make-up, diet, and mobility patterns of people in five previously excavated megalithic communal burials:

1. The MN dolmen in the Ansarve meadow associated with the TRB complex (Bägerfeldt, 1992; Hansson, unpublished; Lithberg, 1914) (Paper I and III), and
2. Four stone cist burials (Häffinds, Hägur, Suderkvie, and Utalskog) dated, based on the artefacts found in them, to the Late Neolithic/Early Bronze Age periods (Arne, 1927a; Bergman, 1927; Burenhult, 1986; Hansson, unpublished; Lithberg, 1914; Manneke, 1963a, 1963b; Stenberger, 1944a, 1944b) (paper II). Two of these burials are spatially connected to the chronologically older contexts of either TRB (Suderkvie) or PWC (Hägur).

For information on the research background and the contexts of the burials see chapters 3-6.
2 Research aims and theoretical framework

Some of the methods used here, such as contextual radiocarbon dating and isotopic analyses for diet and mobility, have already become standard approaches in archaeological research (e.g. Bentley, 2006; Katzenberg, 2008; Taylor and Bar-Yosef, 2014). However, the field of ancient DNA (aDNA), and specifically, ancient genomics is a novel and rapidly advancing field in paleoanthropological and archaeological research which allows for new possibilities to study demographic developments in the past (see e.g. Günther and Jakobsson, 2016; Nielsen et al., 2017; Slatkin and Racimo, 2016). This thesis combines the different methods to investigate the demographic changes seen on the island as they provide complementary data regarding the life history of the studied individuals.

2.1 Methodological concepts genetics/genomics

The term Archaeogenetics was coined by Colin Renfrew (Renfrew and Boyle, 2000). Originally it involved using molecular genetics and population genetic methods to the study of present-day populations, in combination with archaeological and paleontological research, to infer prehistoric population events. Today it also includes studies of aDNA which adds another dimension; since direct analyses of archaeological remains reveal information of the people that lived in the past.

The study of aDNA in prehistoric remains is a relatively new research field, as it was just over 30 years ago that the first studies were presented (Higuchi et al., 1984; Pääbo, 1985), for background see (Hagelberg et al., 2015). However, due to technological limitations and methodological challenges the study of aDNA from prehistoric human remains has been problematic. Although, the potential for this type of research in archaeology and evolutionary biology was discovered early, serious problems when working with degraded DNA were soon recognized (Handt et al., 1994; Pääbo, 1989). Especially DNA contamination from external sources was a problem that proved to be difficult to handle (Cooper and Poinar, 2000; Handt et al., 1994; M. Hofreiter et al., 2001; Kolman and Tuross, 2000; Pääbo, 1989; Pääbo et al., 2004). This was particularly problematic in studies of ancient humans (Abbott, 2003; Caramelli et al., 2003; Gilbert et al., 2005; Lindholm et al., 2008; Malmström et al., 2005; Serre et al., 2004). The work was expensive and very time consuming as rigorous controls had to be done to authenticate the data (e.g. Malmström et al., 2007, 2009).

The nature of aDNA being degraded and present in low quantities made it difficult to apply the methodologies used for studying microsatellites and Single Nucleotide Polymorphisms (SNPs) in autosomal and Y chromosomal DNA in present-day DNA and forensics. Thus early work mainly involved analysis of a single genetic loci and also mainly comprised studies of the mitochondrial hypervariable regions (HVR I and HVR II). These uniparental markers contain very limited information on relationships among individuals. In essence they represent one genetic marker, tracing the maternal lineage (mitochondria), or the paternal lineage (Y-chromosome), in contrast to the millions of genetic markers on the autosomes that trace all ancestral lineages (e.g. the maternal grandfather and the paternal grandmother two generations back in time). However, these data can typically help interpretations of strong demographic events (Bramanti et al., 2009; Malmström et al.,
2009, 2015), and distinct differences such as those, for instance, between modern humans and Neanderthals (Krings et al., 1997; see also Nordborg, 1998).

Recent technological developments has allowed for large scale whole genome analyses which has revolutionized the field of aDNA and archaeogenetics (Mardis, 2008; Rizzi et al., 2012). The new technology has allowed for analyses of the whole genome (including DNA in the cell nucleus) which contain information from all of the individuals’ ancestors, as well as specific retrieval of Y chromosomal DNA and high resolution mitochondrial genomes. This has allowed for new ways of analyzing population history and evolutionary processes by using population genetic tools developed for studies of present-day humans. It also has allowed for new ways of verifying authenticity of the data via bioinformatics processing (Sawyer et al., 2012), and estimating external DNA contamination (Fu et al., 2013; e.g. Green et al., 2008; Jun et al., 2012; Korneliussen et al., 2014; Rasmussen et al., 2011; Schiffels et al., 2016; Skoglund et al., 2014b). The laboratory methodology was first optimized for aDNA studies from the research in the ‘Neanderthal genome project’ coordinated by the Max Planck Institute for Evolutionary Anthropology in Germany (http://www.eva.mpg.de/ neandertal/index.html), but new methodologies continues to be presented (e.g. Gamba et al., 2016; Gansauge and Meyer, 2014).

The origin and dispersal of agriculture, and subsequent demographic developments, in Europe has been a major subject of interest not only for archaeologists, anthropologists, and linguists, but also for geneticists (e.g. Ammerman, 1984; Cavalli-Sforza et al., 1996; Childe, 1925; Renfrew and Boyle, 2000; Whittle and Milisauskas, 1997). Specifically the questions of migrating people (demic diffusion) or the spread from ideas (cultural diffusion) has been investigated and studied from genetic analyses of the present-day European population. This work has revealed much information regarding the present-day genetic structure and origins of maternal and paternal lineages, but it could not resolve the question of demic vs cultural diffusion (Günther and Jakobsson, 2016; Novembre et al., 2008).

This is also a topic investigated in studies of aDNA. It had previously been indicated based on analyses of maternally inherited mtDNA in individuals from archaeological contexts in central Europe that there had been discontinuity between Mesolithic hunter-gathers and Early Neolithic farmers (Bramanti et al., 2009), and different maternal haplogroups had been noticed in individuals from TRB and PWC contexts in Sweden (Malmström et al., 2009). Prehistoric key stages that shaped the maternal genetic variation seen in the present-day European population were also identified (Brandt et al., 2013). The new genomic approach however, has provided unprecedented power and resolution to study human prehistory (Günther and Jakobsson, 2016) allowing for the investigation of fine scale genomic structure and admixture, not possible from analyses of uniparental markers alone (Haber et al., 2016). However, mtDNA data is still of interest to archaeological investigations.

An important inspiration for my PhD project was a research paper ‘Origins and Genetic Legacy of Neolithic Farmers and Hunter-Gatherers in Europe’ (Skoglund et al., 2012) which used the new molecular methods to investigate Scandinavian prehistory from genomic analyses of individuals from TRB and PWC contexts. This study presented a new methodology for direct comparisons of individuals from archaeological contexts to address questions directly linked to cultural transformations, migration, and continuity.
Specifically, it showed that the individuals from these contemporaneous but culturally different contexts (involving differences in subsistence strategies and life-style) also had different demographic backgrounds which could be traced in their genomes. This study revealed different biogeographic origins for the two contemporaneous Scandinavian groups showing long distance (over many millennia) migration and mobility in the past. The results together with previous knowledge from ancient mitochondrial DNA (Brmaneti et al., 2009; Malmström et al., 2009) showed that the Neolithization of Scandinavia (seen in the individual from the TRB context) involved migration, and that the individuals from PWC contexts on Gotland had origins in Mesolithic hunter-gatherer (HG) groups.

With my background in osteology and aDNA research on archaeological remains, the new methodology gave me new ways to investigate the demographic processes “behind” cultural transformations seen in the archaeological data on the island. When this project started in 2012 there were only seven individuals presented with genomic data from archaeological contexts in Europe; four individuals from Sweden; from Ajvide and Ire PWC burials on Gotland (ajv52, ajv70 and ire8), and one individual from a passage grave at Frälsegården in Gökhem, Västergötland (gok4) (Skoglund et al., 2012), two 7000 year old hunter-gatherers from Spain (La Braña1 and La Braña2) (Sánchez-Quinto et al., 2012), and also Ötzi, the Iceman from the Alps (Keller et al., 2012). In the years that followed there has been a rapid advancement in archaeogenomics; the laboratory methods have been optimized to retrieve more qualitative data, and hundreds of individuals from different cultural, temporal and geographic contexts have been presented. Sophisticated population genetic tools and methods have now become standard in investigating prehistoric events via ancient genomic data (e.g. Alexander et al., 2009; McQuillan et al., 2008; Patterson et al., 2006; Pritchard et al., 2000; Reich et al., 2009).

The genomic variation of the present-day European population has shown a correlation between genes and geography (Novembre et al., 2008). From the new ancient genomic analyses it has been concluded that the modern-day patterns of genomic variation seen in Europe today were shaped by several major demographic events in the past (see Günther and Jakobsson, 2016). These events include the first peopling of Europe and subsequent migrations to peripheral regions (Fu et al., 2016; Günther et al., 2018; Seguin-Orlando et al., 2014), the Neolithic transition (e.g. Cassidy et al., 2016; Gamba et al., 2014; Hofmanová et al., 2016; Keller et al., 2012; Lazaridis et al., 2014; Martiniano et al., 2017; Mathieson et al., 2015; Olalde et al., 2015; Skoglund et al., 2012, 2014a), and later migrations during the Bronze Age (Allentoft et al., 2015; Haak et al., 2015). The latter event has been related to the large scale migrations associated with the pan-European Corded Ware culture, which has been suggested to originate in the Pontic steppe associated with individuals from Yamnaya culture contexts (ibid). These new findings show that culture and lifestyle were major determinants of genomic differentiation and similarity in prehistoric Europe, rather than geography as is the case today (Günther and Jakobsson, 2016). However, the demographic processes that shaped the genetic variation in the past differ in different regions (e.g. González-Fortes et al., 2017; Jones et al., 2017; Olalde et al., 2018; Valdiosera et al., 2018), and need to be investigated on local and regional levels together with archaeological research.

2.2 Methodological concepts diet and mobility
Carbon ($^{13}$C) and Nitrogen ($^{15}$N) stable isotope analyses are used to investigate dietary patterns in prehistoric human remains and have long been used to investigate the dietary
protein in individuals from different contexts in Sweden. Eriksson et al. (2008) investigated diet from the Late Mesolithic to the Viking Age period on the island of Öland, and found a great diversity of food habits which they concluded were more influenced by cultural preferences than natural factors such as climatic changes. This study showed that the people buried in a TRB passage grave during the early phase of usage (MN A) were not full-time farmers. They exhibited a mixed terrestrial diet which previously also has been noticed in some of the coastal megalithic burials in southern Sweden (Eriksson et al., 2008; Lidén et al., 2004). While analyses from inland megalithic TRB mainly have displayed terrestrial dietary signals (Fornander, 2011a; Lidén, 1995a; Linderholm, 2008a; Sjögren, 2004) This is also in contrast to the strict marine diet of the PWC (e.g. Eriksson, 2004; Eriksson et al., 2008; Lidén, 1995b). A marked dietary shift from a mixed marine diet to the use of exclusively terrestrial resources was not noticed until the second half of the third millennium. This showed that the large-scale adoption of a farming to Öland happened almost 2000 years after the onset of the Neolithic expansion in Scandinavia (Eriksson et al., 2008). Similar dietary shifts have been noted from AMS 13C-values from the Mesolithic to the Late Neolithic on Gotland (Apel et al., 2018).

Secondary burials in megalithic tombs are well-known and have also been documented from many MN megalithic burials in Sweden spanning into the LBA and also the Iron Age, seen from ceramics, artefacts, and radiocarbon dating of skeletal remains (Bägerfeldt, 1992; e.g. Eriksson et al., 2008; Fornander, 2011a, 2011b; Persson and Sjögren, 1995; Sjögren, 2003). Individuals from the passage grave burial on Öland connected to the latter part of the Middle Neolithic period (MN B) exhibited the most obvious evidence of dietary variation within the sites studied on Öland. They showed mixed terrestrial/marine diets, and also extreme changes at the individual level, which was suggested reflect intense contacts and interaction between different cultural groups (Eriksson et al., 2008), (i.e. TRB, PWC and BAC). The suggested agro-pastoralist economy of the BAC has further been investigated from stable isotope analyses of individuals found in typical BAC burials in Scania (Fornander, 2013) which revealed a diversity in the dietary pattern showing both marine and terrestrial protein sources, also at inland locations.

Strontium isotope analyses of archaeological remains may aid interpretations and help understand demographic history and mobility patterns by identifying first generation non-local individuals, as well as establishing local and regional groups (Bentley, 2006; Price et al., 2002; Slovak and Paytan, 2012). Sjögren et al. (2009) investigated Sr-isotopes from individuals in MN TRB burials from the Falbygden area in Västergötland, and also the Alvastra dolmen in Östergötland. They found that 23% of the individuals in Falbygden showed non-local childhood Sr-signals, and three of the five individuals studied in Alvastra were also not-local to the area. They also found evidence of both male and female mobility, and also children that were local. However, the individuals studied were not radiocarbon dated and could therefore also show later activity. Some mobility during the MN period at the Alvastra dolmen in Östergötland has later been noted from Sulphur isotope analysis (Fornander, 2011a). Mobility and secondary usage of the megalithic tomb on Öland has also been investigated (Fornander, 2011b; Fornander et al., 2015; Linderholm, 2008b), where Eriksson et al. (2008) previously had identified three phases of usage; a main phase during MN A, and secondary usage during MN B, and also the EBA. Most individuals studied from MN A showed local early childhood signals, whereas increased mobility was noted in MN B, and particularly in the EBA.
2.3 Current debates

The new approaches to investigate prehistoric demographic events have had much momentum in archaeological debate, especially regarding the concept of migration, material culture, science based archaeology, and genetics (e.g. Dommelen, 2014; Furholt, 2017; Härke, 1998; Hofmann, 2015; Kristiansen, 2014; Liden and Eriksson, 2013; Soares et al., 2010; Sørensen, 2017). This is partly because archaeological explanations and theoretical interests have shielded away from migration with the advent of the New, Processual and Post-Processual archaeologies (e.g. Dommelen, 2014). Another reason is because genetic research is frequently interpreted and presented in a manner that recalls aspects of traditional culture-historical archaeology; including the idea that shared material culture indicates shared participation in the same social group, or culture, and that these cultures constitute one-dimensional, homogeneous, and clearly bounded social entities (Furholt, 2017).

Although, there has been some sweeping general statements in the past regarding large-scale migration of people (e.g. Allentoft et al., 2015; Haak et al., 2015), the emergence of new shared genetic signals in individuals spread across vast geographical areas can only be explained by shared ancestry and migration, but it has to be considered that this concerns specifically the demographic process. This process is complicated and unique for each context and needs to be investigated locally together with archaeological research and, actually also with new archaeological perspectives.

Much critique was also made on the earlier studies based on mitochondrial DNA where e.g. Hoffman (2015) pointed out that ‘Geneticists and archaeologists mean quite different things when referring to an individual’s genetic origin. For an archaeologist, the key question is where that individual came from, with a view of finding out about that person’s identity—who were they, or more precisely, who did they think they were? Genetic information acts as a cumulative and long-term archive of population history, but provides no answers’ regarding an individual’s experienced sense of belonging’.

Even if this is true, genetic research is mainly about demography, and not about an individual’s sense of belonging and identity. The aim in this thesis is to investigate demographic change in relation to the archaeological record in Sweden and include both processual and post-processual theoretical archaeological discussions (e.g. Hallgren, 2008; Jennbert, 1984; Malmer, 2002). The lack of well-preserved human remains from different temporal archaeological contexts across Europe leaves large blank areas that unfortunately cannot be investigated through archaeogenetic methods. Thus, the random collection of individuals from different cultural, temporal, and geographic regions, used in genetic research to explain prehistoric cultural events and transitions, is problematic. The early studies of uniparental markers were not sufficient for fine scale analyses but were used to investigate population demographic shifts related to demic and cultural diffusion. The new genomic analyses have provided unprecedented knowledge regarding the pre-history of Europe. However, much work still needs to be done to integrate these different disciplines (archaeology and genetics) for both sides to understand how they complement each other, and also to investigate how genetics can be used for archaeological research to answer questions on a local level.

With this work I hope to bridge the gap between archeological and genetic research and lay the ground for future collaborative research on the prehistory of Scandinavia and the Baltic Sea area.
2.4 Research aims

The aim of this research is to try to find new answers to patterns seen in the material culture record on Gotland from natural science based research of human remains (for research background see chapter 5). Are the periods of transitions seen in the archaeological material record important indicators of demographic change?

Recent genomic analyses have revealed that the ancestral components in Mesolithic foragers across the European continent and Scandinavia differ from that of the individuals associated with the farmer expansion (see chapter 4 for the genetic background in this study). Individuals from EN and MN TRB contexts in Sweden have been found to have ancestry from the Neolithic farmer expansion in continental Europe, but similar to most contemporaneous European farmers, they also show some admixture from hunter-gatherers (Mitnik et al., 2018; Skoglund et al., 2012, 2014a, ). The PWC on Gotland share the majority of their ancestry with Mesolithic foragers, but also show slight admixture with farmers.

Furthermore, individuals from BAC and later contexts in southern Scandinavia have revealed the three main ancestral components derived from the Mesolithic foragers, the European farmer expansion, and the later migration seen in the pan-European Corded Ware culture (Allentoft et al., 2015; Mittnik et al., 2018). The ancestral distinctions in these different groups have also to some extent been identified in uniparental markers (mitochondrial and Y chromosomal DNA) (e.g. Bramanti et al., 2009; Brandt et al., 2013; Haak et al., 2005; Kivisild, 2017; Malmström et al., 2015). As the archeological discussion regarding the demographic developments on Gotland also involve local continuation with adaption of new cultural influences (e.g. Andersson, 2016; Nihlén, 1927; Österholm, 1989), the question here also involves to what extent uniparental markers and genomic analyses can aid in the interpretation of the demographic developments seen on the island.

The specific research aims are to:

I. Investigate the chronology of individuals found in these Middle and Late Neolithic tombs to contextualize burial patterns and determine duration of activity during the different archaeological time-periods.

II. Directly test hypotheses of population structure, admixture, and population continuity/discontinuity on Gotland during the Middle and Late Neolithic periods by analyzing ancient genomes, and uniparental markers from the individuals found in these burials.

III. Establish a Strontium baseline for Gotland, and investigate mobility patterns to infer demographic history by identifying possible first generation non-local individuals, as well as local and regional groups.

IV. Investigate kinship and uniparental inheritance patterns within the burials to identify social structure (matri- and patri-local systems) and marriage exchange.

V. Analyze dietary patterns over time to investigate changes in life-style and dietary culture.
Thus, the main research questions are:

- Were the changes seen in material culture and economy during the MN-LN periods local developments on the island or did it involve migration of new groups of people?
- Who were the people buried in these five megalithic tombs in the sense of genetic affinity to the earlier Mesolithic populations, as well as people from TRB, PWC and BAC contexts?
- Are there detectable dietary shifts that are associated with cultural and/or demographic change?
- What was the duration of usage of the Ansarve dolmen?
- What were the genetic kinship relationships of the individuals in the dolmen?
- What was the internal chronology and activity patterns in these stone cist burials?
- What relationship did the people in the stone cists have with the earlier developments on the island?
- Does genomics allow for fine scale analyses regarding the demographic changes seen in the archaeological record on Gotland?
- To what extent can the combination of the different scientific methods be used to provide new information regarding archaeological research questions concerning population continuity, migration and admixture in different time periods?
- How can this be understood in relation to the current archaeological debates about the way archaeogenetic research is presented and discussed?

2.5 Theoretical framework

The basis for this work lies on a foundation of archaeological research. The Middle Neolithic period in Scandinavia involves cultural remains from three different cultural groups (TRB, PWC, and BAC) and their relationship with each other has thus been one of the larger topics debated in Scandinavian Stone Age research (for background see Andersson, 2016; Edenmo, 2008; Forndamer, 2011b; Hackwitz, 2009; Larsson, 2009; Stensköld, 2004). The purpose of this thesis is to approach this topic in a different way by using novel and proven scientific methods to study the demographic changes seen on the island of Gotland. It is here possible to study people that actually lived the lives we try to understand. These people are found in the contexts of different cultural manifestations that have been linked to similar phenomena in neighboring geographical areas.

Thus, the cultural labels used in this thesis (e.g. TRB, PWC, BAC, CWC) are terms defined by archaeologists to categorize similarities and differences in the material culture such as artefacts, ceramics, economy, and burial customs (Childe, 1925; Clarke, 2014). The archaeological concept of culture is problematic, but here these groupings are used to identify units of analysis provisionally assuming that these categories represent differences in life-style and economy; differences and similarities that are linked with cultural transitions and, possibly, also with demographic changes. Thereby not implying that these groups constitute one-dimensional, homogeneous, and clearly bounded social entities moving across the landscape (Furholt, 2017). The categories are used here as labels to define groups of people with similar way of life to that seen in other locations. For examples of discussions see (e.g. Forndamer, 2011b; Hallgren, 2008). It is important to point out however, that most of the science based approaches (genetics and stable isotope) do
not rely on these categories. Most of these analyses are conducted without categorization information, and it is only after the scientific analyses have been performed that the archaeological categories are added to the interpretation.

Similarly, the archaeological time periods do not correspond to an actual time, but to specific cultural transformations which happen at different time periods in different geographical regions; i.e. the Early Neolithic time period in Scandinavia is contemporaneous with the Chalcolithic time period in southern Europe which has to be taken into consideration when comparing with phenomena in continental Europe.

The term “farmer” in the sense it is used here means that this individual, or group of individuals, belonged to a cultural phenomenon/unit linked with a lifestyle and subsistence economy involving domestication of animals and cultivation of plants (i.e. the Neolithic time period). Similarly, the term hunter-gatherer (HG) is a label for individuals or groups that were hunters and foragers e.g. in the Mesolithic time period. Sub-Neolithic means that these groups had adopted pottery but had a HG life-style at a time when the farming and animal husbandry lifestyle had been introduced and were practiced by other contemporaneous neighboring groups (in the Neolithic time period). Thus, the term TRB, in this sense, equals farming, husbandry, sedentary, communal, and later in time also the construction and use of megalithic burials. The term PWC equals foraging, hunting, fishing, marine, coastal, and flat grave cemeteries. The term BAC/CWC equals the phenomenon seen from these contexts in continental Europe, the Baltic, Finland and Scandinavia, which also to some extent involved nomadism, agro-pastoralism, organized hocker-style burials, and secondary usage of MN megalithic tombs.

2.6 Theoretical methodology

The scientific methods are used to generate many different kinds of data on the studied individuals, (for description of methods see chapter 7). Suitable reference data has been compiled from published research. These datasets are then used to study patterns; i.e. patterns of radiocarbon dates, patterns of skeletal distribution in the graves, patterns of mitochondrial haplogroup frequencies, patterns of genomic structure, dietary patterns, and mobility patterns. The data from each burial is then analyzed as a whole and compared to the archaeological and osteological reports, and further analyzed in the grander scheme of the underlying archaeological research. The method is somewhat comparable to the procedures used in Grounded Theory research in which inductive and deductive methods of analysis are used and the basis lies on ‘the discovery of emerging patterns in the data’ (Glaser and Strauss, 1967). The results are then discussed in a wider archaeological context regarding the prehistory of the island, Scandinavia and continental Europe.

2.7 Limitations

Working with ancient DNA research at a strictly archaeological department has made writing this thesis somewhat difficult as it involves two completely different fields of disciplines (archaeology and genetics). Thus, the structure of this thesis is a compromise for both fields in the conventional way of presenting in Sweden.

The premise for this work has also constantly evolved as new research has continued to be presented that also has affected the underlying research questions. This work progressed into a very large collaborative project that spans over not only over 3000 years in an ever changing time of cultural duality in Scandinavian prehistory, but also entails the
developments in continental Europe from the Mesolithic to the Bronze Age time periods in terms of the reference data collected for the genetic analyses. Thus, time was also a determinate factor of the final outcome of the scope of this thesis, and there had to be some limitations.

The aim of the thesis is to use a combination of several methods to investigate these prehistoric individuals; the choice here therefore, was to present these results together instead of presenting several smaller papers of the different parts. Thus, these papers became quite large and much information had to be presented in the supplementary sections. These sections are included here as they contain important background information in relation to the articles and the manuscript. As this research also investigates how these two fields can be better integrated I have made the choice to combine the current knowledge retrieved from archeogenomics with the archaeological background. Moreover, as the individuals that are genetically investigated in Europe today belong to many different cultural contexts, time periods, as well as being distributed in a few select regions across Europe, only cultures or prehistoric contexts with direct archaeological relevance will be presented in more detail. As the work in genomics is rapidly expanding the main focus in this presentation lies in the work available at the time of the analyses presented here. The only exception is new analyses related to archeological research in the Baltic Sea region.

The LN stone cist analyses presented here is a pilot study on how demographic developments and lifestyle can be investigated from people buried in these communal burials, regardless of cultural definitions to LN and EBA cultures. The choice here is to analyze different types of burials previously attributed to this time period, of which some also have spatial connections with contexts of the chronologically older cultures. The aim is to discuss the demographic changes on Gotland during the LN based on what was known from before during the MN (i.e. TRB, PWC, and BAC). Thus, the LN/EBA stone cist burials will only be discussed in a methodological sense for the developments seen on Gotland.

From the perspective of this thesis, the access to well preserved human skeletal remains is a fundamental prerequisite for the analytical strategy chosen for investigating the population demographic developments on the island. Thus, due to the fragmented and commingled nature of the skeletal remains, poor preservation, and the fact that several of the burials had been disturbed and partially destroyed prior to excavation, only two of the burials were more extensively analyzed (Ansarve and Häffinds). As some of the analyses also are dependent on specific key elements (e.g. specific teeth) all analyses were not possible to do on each of the individual analyzed here.

Moreover, the success of genetic analyses of ancient remains is entirely dependent on the fact that there is endogenous DNA left in the sample, thus the final results at the time of this investigation determined the type of analyses that could be done. As in any comparative research the available reference material also governs the possibilities. Thus, even if hundreds of new samples with genomic data have been presented since this project started; few samples were produced from relevant reference groups and contexts to this study, or with shot-gun data to the level of genomic coverage needed for the population genetic analyses that were done for the analyses in Paper III.
The new genomic research methodology produces massive amounts of data that only can be handled via bioinformatics processing. All genetic data produced here was processed via the bioinformatics support structure at the Jakobsson Lab, Evolutionary Biology center, Uppsala University, developed via the ATLAS of ancient human genomes project. Moreover, as the population genetic analyses on this type of data requires training in computational biology, which is an entirely different field, the genetic research presented here was a collaborative work produced together with professional academic researchers at the Jakobsson’s Lab.
3 Archaeological background

The section below presents a general outline of the underlying archaeology. As Europe is a vast continent to study prehistory, main focus here will be on key events that are relevant to the study area in this thesis.

3.1 The northern European Neolithic expansion

The Neolithic (new Stone Age) is a term used for describing a time in prehistory in which humans went from a hunter-gatherer lifestyle to becoming farmers cultivating land and practicing animal husbandry. This phenomenon has happened independently in different parts of the world at different time periods, forming domestication centers which spread to adjacent regions (e.g. Price, 2000). The Neolithization of Europe started in the Fertile Crescent c. 12,000 years ago and spread into central Europe via Anatolia and the Aegean, and into Southern Europe along the Mediterranean Sea (for a general discussion see: The continuing conversation about the origins of Agriculture. *Current Anthropology*, Volume 50, Number 5, 2009: The Origins of Agriculture: New Data, New Ideas. *Current Anthropology*, Volume 52, Number S4, 2011).

The EN farmer expansion in central Europe is associated with the widespread and culturally homogenous Linearband culture complex (LBK, c. 5500-4500 cal BCE) stretching across Europe from Romania to the Seine Valley (Fig. 2). The LBK are believed to originate from the Starčevo-Cris-Körös culture in the Hungarian Plain dating to c. 5600 cal BCE (Price, 2000). These early farmer settlements were mainly connected with fertile loessic landscapes preferable for cultivation. By c. 5 000 cal BCE peripheral groups had reached as far north as 100 km from the southern Baltic shoreline by the lower Oder region and the Vistula river in present-day Germany and Poland (Hallgren, 2008, pp. 66–67; Midgley, 1992, p. 19; Persson, 1999, pp. 41–43). However, few groups ventured north into the North European Plain which still was inhabited by local Mesolithic foragers for another millennia (Fischer and Kristiansen, 2002; Midgley, 1992; Price, 2015; Sørensen, 2014).

3.2 Mesolithic pottery in the Baltic Sea area

The Late Mesolithic foragers of the north European Plain, Scandinavia and the Baltic involve many different groups named from the different lithic assemblages and sites where they have been located. The adoption of pottery can be seen starting around c. 5500 cal BCE on the eastern Baltic coast, in an area stretching from Poland, up to the Fennoscandian arctic coast in Finland and Norway, including the Island of Åland (Hallgren, 2008, p. 57). Pottery is also found along the southern shores of the Baltic Sea from around 5000 cal BCE, and in the southwestern Baltic Sea area in connection with the Ertebølle culture (EBK) from about 4500 cal BCE (Hallgren, 2008, p. 66; Midgley, 1992, p. 11; Persson, 1999, p. 128). These groups expressed differences in pottery style and manufacturing techniques which also were different from the LBK pottery. Although pottery was widespread none of the local forager groups seemed to adopt the new farming economy (Hallgren, 2008; Kriiska, 2003; Midgley, 1992; Nordqvist and Kriiska, 2015).
The EBK was mainly located in southern Scandinavia, Schleswig-Holstein and along the southern shores of the Baltic Sea in East-, and West Pomerania. The EBK pottery was manufactured with similar materials and methods over the whole area, but the design had local variations (Jennbert, 2011, pp. 91–92). Interestingly, EBK pottery did not appear to spread to other Mesolithic forager groups in present-day Sweden, nor did the eastern so-called “Early older Combed Ware” pottery (Sperrings 1) found on Åland from c. 5000 cal BCE (Hallgren, 2008, pp. 57, 69). Neither is there any evidence of Mesolithic pottery on Gotland.

The chronology of archeological time periods differs between the three Baltic countries, as well as Scandinavia, making it difficult to correlate the findings in terms of periods. The Baltic was first populated from the south after the ice retreated by upper Paleolithic foragers. From the Early Mesolithic starting c. 9000 cal BCE there is a succession of cultures starting with the Kunda and Pulli cultures, followed by the introduction of pottery with the Narva culture from c. 5400 cal BCE (somewhat later in Estonia) (Kriiska, 2009, 2003; Mittnik et al., 2018; Törv, 2016). Early pottery in southern Finland (the Sperrings or Early Combed Ware pottery) differs from that of the Narva pottery which points to different directions of origin and reflect different Mesolithic interaction networks (Nordqvist and Kriiska, 2015). Starting from c. 4200 cal BCE there is evidence of the Typical Combed Ware culture (CCC) in the Baltic. The CCC was a wide spread culture with a distribution from Latvia in the south to northern Finland and Karelia, including parts of northern Sweden, and also showed long distance contacts with Russia seen in the distribution of flint, slate and amber (Kriiska, 2003).

3.3 The Neolithization of Scandinavia and TRB

The cultural complexes that chronologically followed the central European LBK were more distinct and more regionally dispersed suggesting local adaption to the social and environmental landscape. These developments are seen in the Rössen culture found in the upper Danube and Rhineland, the Lengyel culture in western Hungary, parts of Austria, Slovakia, the Czech Republic, and Poland, and also the Stroked Pottery culture (Stichbandkeramik, StK) which replaced LBK in the areas of present day southern Poland, the Czech Republic, and also parts of southern and central Germany (Darvill, 2009).

Starting from 4200 cal BCE, the wide-spread TRB culture complex is seen in the archaeological record spanning from the Netherlands to Poland, and from the Czech Republic to southern Scandinavia (Fig. 2) (Bakker, 1979; Fischer and Kristiansen, 2002; Hallgren, 2008; Lithberg, 1914; Malmer, 2002; Midgley, 1992; Müller, 2011; Persson, 1999; Sjögren, 2003; Sørensen, 2014). The TRB cultural complex has been divided into regional groups based on typochronology of pottery (Bakker, 1979; Müller, 2011), and present day Scandinavia and northern Germany belong to the TRB-north group (c. 4000-2800 cal BCE). However, due to the wide distribution of this culture complex there are also local developments which overlap both spatially and temporally, and many different subgroups also belong to this complex (e.g. Midgley, 1992; Müller, 2011). Due to many similarities in material culture and burial customs it has been suggested that TRB derive from the earlier Michelsberg culture (c. 4500-4000 cal BCE) originating from the Rössen culture (for discussions see Sørensen, 2014). The Michelsberg culture had a distribution from Belgium to the Alps, and also show strong affinity with early and middle Neolithic cultures of southern England (Darvill, 2009).
TRB cultural remains have been found across all of Southern Scandinavia up to middle central Sweden and southern Norway, including the islands of Bornholm, Gotland and Öland in the Baltic Sea (e.g. Hallgren, 2008; Malmer, 2002; Sørensen and Karg, 2014) thus the culture dispersed both by land and over water. The northern expansion of the TRB culture into Scandinavia was rapid but regional differences exist in the cultural assemblage indicating different processes for these developments. This has led to much debate regarding internal developments with continuity in Mesolithic networks, or migrating people seeking new land (Fischer and Kristiansen, 2002; Hallgren, 2008; Jennbert, 1984, 2011; Malmer, 2002; Malmström et al., 2009, 2015; Persson, 1999; Rowley-Conwy, 2004, 2011; Skoglund et al., 2012, 2014a; Sørensen, 2014).

The archaeological record supports both theories. Some of the Early TRB sites in southern Sweden and Denmark were placed on top of earlier coastal EBK sites indicating cultural continuity, where also the EBK and TRB artefact assemblages, including pottery, had many similarities (Fischer and Kristiansen, 2002; Jennbert, 2011). Thus some of these sites were defined as transitional. The regional variation seemed to be structured by
previous hunter-gatherer networks indicating some sort of acculturation process (Hallgren, 2008; Knutsson and Knutsson, 2013). Although the southern Scandinavian archaeological record show the presence of cattle, sheep/goat, as well as the introduction to an agricultural subsistence at the onset of the Neolithic period, a marine diet also played a significant role indicated by fossil fauna on the coastal settlement (Apel et al., 1995; Fischer, 2002). The mixed diet also continued in the MN period seen from stable isotope analyses of individuals from coastal megalithic burials (Eriksson et al., 2008; Lidén et al., 2004).

3.4 Middle Neolithic megalithic tombs

The Scandinavian megalithic burial tradition has its roots in the pan-European TRB culture complex starting from c. 3600 cal BCE (Schulz Paulsson, 2017) of which most are found in Denmark and Mecklenburg-Vorpommern in Germany (Midgley, 2008). About 600 megalithic burials have been found in Sweden today mainly in the form of dolmens and passage graves. More than 250 have been found in the large inland complex in the Falbygden area in south-central Sweden. The other megaliths were located mainly along the former coastal areas and islands of southern and western Sweden, three have also been discovered in the northwest by the Oslofjord outlet into Skagerrak in Norway (e.g. Blomqvist, 1989; Sjögren, 2003; Tilley, 1999). Only a few have been found to the east; including the Alvastra dolmen in Östergötland, four on Öland, and one (possibly two) on Gotland (Arne, 1909, 1923; Bägerfeldt, 1992; Janzon, 2009; Lithberg, 1914; Martinsson-Wallin and Wallin, 2010; Papmehl-Dufay, 2015; Tilley, 1999). A grouping of three geographic zones has been suggested based on the typology of the Scandinavian dolmens and passage graves (Kaelas, 1967; Sjögren, 2003):

1. The Southern Baltic Sea area: including Zealand in Denmark, plus Scania and Halland
2. The Kattegat area: including Jutland in Denmark and Bohuslän
3. The Falbygden area, Västergötland

As parallels can be seen on both sides of the sea, social networks communicating by sea transport must have been of great importance (Sjögren, 2003, p. 16). The style of the dolmens on Öland and Gotland are quite unusual compared to the rest of Sweden as they have five or more chamber stones, with the exception of a dolmen in Simrishamn in eastern Scania (Bägerfeldt, 1992). Although they are smaller in size, they have been compared with the “Stordysser” and “Groβdolmens” of Denmark and northern Germany (Bägerfeldt, 1992; Schulz Paulsson, 2017).

The megalithic burial tradition is not found in eastern central Sweden where there instead is evidence of cremation burials in pits on coastal sites (Apel et al., 1995; Hallgren, 2008). During the MN period the inland EN TRB sites in this area were abandoned to favor more permanent usage of earlier coastal sites (Hallgren, 2008; Larsson, 2009). A shift is seen towards a marine economy, also showing transitional pottery connected with PWC (Hallgren, 2008; Larsson, 2009). This shows the complexity in the archaeological record in different areas of Scandinavia, also leading to much debate in the archaeological community regarding the origin and fate of TRB, as well as the origin of PWC.
3.5 Distribution of PWC
The large sub-Neolithic PWC culture complex (c. 3300-2300 cal BCE) found during the Scandinavian MN period were costal and island bound groups with a marine economy. Although pigs were also hunted, they were not a staple food source (Eriksson, 2004; Fornander et al., 2008; Howcroft et al., 2014; Lidén, 1995b) but appears more ritualistic in nature (Wallin, 2015). While regional differences exist, the people of the PWC communities were part of a wide network around the Baltic Sea. PWC sites have been found along the whole former Swedish coastline from Dalarna and Gästrikland in eastern Sweden, to southern parts of Norway, as well as northern Denmark and the Baltic islands of Bornholm, Gotland, Åland, and Öland (Fig. 2) (Larsson, 2009; Malmer, 2002). The communicative value is also confirmed in the archaeological material which contains exotic items that demonstrate long range contacts to the east, and also to the north (Hackwitz, 2009; Larsson, 2009; Malmer, 2002; Wyszomirska, 1984). PWC burials usually contain single individuals buried in supine position in large flat grave cemeteries (Janzon, 1974; Wyszomirska, 1984). However, the rich cosmological and ritualist world of the PWC is not fully understood (Wallin, 2015). Due to the soil conditions on the Swedish mainland the majority of the graves have been found on the islands of Gotland and Öland.

3.6 Surrounded by Battle Axes
Starting from c. 2900-2800 cal BCE new cultural influences from Corded Ware culture (c. 2900-2300 cal BCE) is seen over vast areas in continental Europe, from the Netherlands and Switzerland across central Europe to the Volga River in the East, including Southern Scandinavia, Finland and the Baltic (Fig. 3). These cultural groups are recognized in the archaeological record by similarities in the distinct artefacts, pottery, and strict conventions regarding the burial practice. There are also regional groups i.e. the single grave culture (SGC) in Denmark, Holland and Northern Germany, and the BAC of Sweden, Norway, and also Finland (e.g. Edenmo, 2008; Knutsson, 1988; Kriiska, 2001, 2003; Malmer, 1962, 1975, 2002; Nordqvist, 2016; Sjögren et al., 2016).

The Swedish BAC is also commonly called the Boat Axe culture (e.g. Edenmo, 2008; Hackwitz, 2009). This culture appears in Sweden during MN B, and is mainly known from the distinct inhumation burials of one or two people in a flexed sideways position facing east, also including beakers and axes (Fornander, 2011b; Knutsson, 1995; Larsson, 2009; Malmer, 1962, 1975, 2002). There are c. 250 known BAC graves in Sweden where the majority is found in Scania in southern Sweden (Fornander, 2011b). BAC ceramics is also found in megalithic graves (e.g. Sjögren, 2003), and secondary burials during MN B have been noted in Sweden (e.g. Eriksson et al., 2008). In southern Sweden BAC seem to chronologically follow TRB which has led to discussions of internal developments. BAC settlement sites are usually found inland without connection to water, and also distinct from the costal PWC sites. The fact that BAC also appears alongside PWC in both southern and eastern central Sweden had led to much debate regarding the identity of this culture, and its connection with TRB and PWC.
The Late Neolithic expansion and stone cist burials

The LN (2400-1800 cal BCE) is a time of cultural blending and homogenization in most parts of southern/central Scandinavia. It is the end of the old and at the same time the beginning of what develops later in the EBA. This is also a time of large demographic expansions and cultural transformations in continental Europe, also in connection with the large Bell Beaker complex (BBC) found in Western Europe. The BBC complex is overlapping the earlier SGC/BAC found in northwestern Europe and Scandinavia (e.g. Apel, 2001; Prescott and Glørstad, 2015; Prieto Martínez and Salanova, 2015; Stenberger, 1964; Stensköld, 2004). In central Europe CWC is succeeded by the EBA Únětice culture complex. North Eastern Europe at this time is inhabited by Late CWC groups.

A new type of megalithic grave is also introduced in Scandinavia at this time, the stone cist burials. On the mainland the cist burials tend to be large, often with several chambers, sometimes with a gavel stone with a porthole similar to those found within the SOM-culture (Seine-Oise-Marne culture, c. 3100-2000 cal BCE) in northern France and Belgium (e.g. Burenhult, 1999; Stenberger, 1964; Stensköld, 2004; Vandkilde, 2005). While on Gotland the stone cist burials are smaller and consist mainly of a single rectangular cist (Lithberg, 1914; Luthander, 1988; Sjöstrand, 2012; Wallin, 2010). The smaller cist burials in Scandinavia have been suggested to be a continuation of the earlier individual BAC stone cists (Vandkilde, 2005). 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 also differences in both stone cist shapes and burial customs (e.g. Heimann, 2000; Stensköld, 2004). During the LN the cists were often surrounded by concentric circles and a stone packing. And many were completely covered by a cairn and/or a mound at some point during the subsequent EBA (Stenberger, 1964).

Fig. 3. Map of Europe describing the distribution of the relevant cultures (from Knutsson, 1988; Mallory and Adams, 1997; Nordqvist, 2016), as well as the locations and the radiocarbon dates (cal BCE, 95% CI) for each of the individuals/groups included in the study in paper III (Table S6.1). Distribution and timeline of BAC/CWC (yellow). Symbols correspond to Figure 2.
4 Stone Age Europe seen through ancient genomics

4.1 Mesolithic Hunter-gatherer ancestry

Genomic investigations of Mesolithic foragers stretching across western and central Europe has revealed that, although culturally and geographically distinct, they belong to a relatively homogenous group genetically that has been termed Western Hunter-Gatherers (WHG) (Fu et al., 2016; Gamba et al., 2014; González-Forbes et al., 2017; Jones et al., 2015, 2017; Lazaridis et al., 2014; Mittnik et al., 2018; Olalde et al., 2014; Sánchez-Quinto et al., 2012). Another genetic signal has been identified from eastern Mesolithic foragers first identified in Russia labeled Eastern Hunter-Gatherers (EHG) (Mathieson et al., 2015). Recently a third group with a distinct genetic make-up has been identified in western Georgia which has been isolated from WHG possibly for 45,000 years called Caucasian Hunter-Gatherers (CHG) (Jones et al., 2015).

Early genomic research revealed that Mesolithic foragers from Sweden (Gotland and Motala labeled Scandinavian Hunter-Gatherers (SHG)) showed affinity to both WHG and EHG (Lazaridis et al., 2014; Skoglund et al., 2014a). Recent genomic analyses of additional Mesolithic Scandinavians from Gotland and Norway (Günther et al., 2018) demonstrates that present-day Sweden and Norway was populated via two routes; a southern route involving WHG and a northern route involving EHG, and that Middle Mesolithic SHG shares genetic ancestry with both groups. These two migration patterns coincide with two different distributions of stone tool techniques, which have previously been used to argue for two colonization routes (e.g. Damlien, 2016; Riede and Tallavaara, 2014; Sørensen et al., 2013). The Mesolithic individuals from Gotland (from Stora Bjers and Stora Förvar), together with the individuals from Hummerviksholmen in Norway, are among the earliest human remains in northwestern European analyzed genomically (Fig. 2).

The only Late Mesolithic foragers genetically analyzed in the Baltic Sea area and northern continental Europe to date comes from Estonia and Lithuania. The genomic data was first presented from the large Zvejnieki burial site in Lithuania with affinity to Kunda, Narva, and CCC dated between 6470-3980 cal BCE, 95% CI (Fig. 2) (Jones et al., 2017). Additional individuals from these cultural contexts in Lithuania, and also Estonia, has recently been presented (Mittnik et al., 2018; Saag et al., 2017). These studies have revealed that two individuals (dated between 6440-5740 cal BCE, 95% CI) from the Mesolithic Kunda contexts Spiginas and Donkalnis in Lithuania show close genetic affinity to WHG.

Varying degrees of EHG admixture is noted the later Lithuanian and Estonian Kunda and Narva individuals (Jones et al., 2017; Mittnik et al., 2018), supporting contact networks seen in the Mesolithic pottery and artefacts across the eastern coast of the Baltic Sea (e.g. Nordqvist and Kriiska, 2015). Some of the later individuals from CCC contexts however, also show close genetic affinity to EHG supporting long distance trading contacts to the East seen from imported objects (e.g. Kriiska, 2003; Nordqvist and Kriiska, 2015).
4.2 Neolithization of Europe - genetic evidence

Neolithic individuals from farming contexts showed a distinctly different ancestry (genetic make-up) compared to that of the studied HGs (Skoglund et al., 2012). This was later linked with people associated with EN farming contexts in Anatolia and the Aegean (Hofmanová et al., 2016; Kılıç et al., 2016; Mathieson et al., 2015; Omrak et al., 2016). The two routes for the Neolithic expansion into Europe suggested from archaeological evidence has also been shown from genetics to represent slight differences in the people from central Europe and Iberia (Gamba et al., 2014; Martiniano et al., 2017; Mathieson et al., 2015; Olalde et al., 2015; Valdiosera et al., 2018). However, the complexity behind these migrations needs to be further investigated.

It is also known that the migrating farmers admixed with local populations across Europe. Direct evidence for such an event has been found from a EN Starčevo culture context in Hungary where one individual (KO1, c. 4780-5650 cal BCE, 95% CI) (Fig. 2) show genetic affinity with WHG rather than with the EN farmers (Gamba et al., 2014). At present, our knowledge of the character of the contacts between the HGs and EN farming groups is limited and we need studies investigating more regional patterns. However, the process of admixing continued to some extent across Europe. This is seen from the slight increase of WHG relatedness in individuals so far analyzed from later contexts associated with the Neolithic expansion in Europe (Günther et al., 2015; Günther and Jakobsson, 2016; Haak et al., 2015; Lipson, 2017; Mathieson et al., 2015; Skoglund et al., 2014a). This suggests some levels of continued contact between individuals from both groups as new areas were colonized by immigrating farmers.

Several individuals from LBK and Transdanubian LBK contexts from central Germany and Hungary have been genomically analyzed showing close affinity between these groups, and also affinity with the earlier Starčevo culture complex in Hungary, as well as EN contexts in Anatolia (Haak et al., 2015; Lazaridis et al., 2014; Mathieson et al., 2015) (Fig. 2). Additional analyses have been done on mitochondrial data also from Austria supporting these conclusions (Brandt et al., 2013; Haak et al., 2010, 2005; Szécsényi-Nagy et al., 2015) (Supplemental Paper I, Table S4). These individuals are not from the earliest finds of LBK in these areas; however they show low levels of admixing with WHG suggesting that the contacts between these groups at this point had been relatively small.

To date there is only one individual (NE7, 4490-4360 cal BCE, 95% CI) associated with the Lengyel culture from Hungary that has been genomically analyzed showing affinity with the earlier Neolithic groups in the area (Gamba et al., 2014), and also the central European LBK (Fig. 2). The rest of northwestern continental Europe is blank at this stage in terms of genomic analyses from these archaeological groups. However, there has been some work on mitochondrial data confirming the Neolithic maternal affinity in individuals associated with a Lengyel group in Poland (Lorkiewicz et al., 2015), as well as Rössen and Schöningen contexts in central Germany (Brandt et al., 2013), and also from the contemporaneous Neolithic Gurgy necropolis in the Paris basin (Rivollat et al., 2015) (Supplement Paper I, Table S4).

Apart from the individuals analyzed from the MN passage grave in Gökhem in present-day Sweden (Skoglund et al., 2012, 2014a) there are only three individuals genomically analyzed connected with TRB south of the Baltic Sea. They derive from different con-
texts from the successive Baalberge, Salzmünde, and Bernburg cultures in Saxony-Anhalt in central Germany (Mathieson et al., 2015) (Fig. 2). The only other individuals with genomic data from this time period in western and central Europe derive from Otzi, and two individuals from the Chalcolithic Remedello di Sotto cemetery in northern Italy, a female from the MN passage grave Ballynahatty in Ireland, several Iberian MN-Chalcolithic groups, and an individual from the Late Copper Age Baden culture in Hungary (Fig. 2) (Allentoft et al., 2015; Cassidy et al., 2016; Günther et al., 2015; Keller et al., 2012; Martiniano et al., 2017; Mathieson et al., 2015).

They all show affinity to the EN farmer groups and slightly elevated WHG admixture compared to the EN farmers. They also show some stratification which seem to correlate with geography, where all the western European MN-Chalcolithic groups including the Scandinavian MN TRB show close affinity to each other. Recently, the genetic farmer affinity was also confirmed in an individual from the EN TRB context Saxtorp in Scania (Mittnik et al., 2018) showing close affinity to the MN TRB from Gökhem. Unfortunately, this individual was not published at the time of this investigation and is thus not included in the analyses for paper III.

Additional mitochondrial data has been presented from several additional groups connected with TRB from MN megalithic burials in mainland Sweden and Öland (Malmström et al., 2015), the Ostorf burial site in Northern Germany (Bramanti et al., 2009), collective burials in Odagsen, Panker, and Calden (Lee et al., 2014), as well as from the Baalberge, Salzmünde, and Bernburg cultures in Saxony-Anhalt (Brandt et al., 2013) which are used my analyses in paper I (Supplement Paper I, Table S4).

4.3 Pitted Ware Culture

The sub-Neolithic PWC on Gotland has been investigated through six individuals from the Ajvide and Ire burials sites showing affinity to WHG and SHG (Skoglund et al., 2014a, 2012), but they also show slight admixture from the component found in farmers (Skoglund et al., 2014a). The proportion of farmer admixture has recently been estimated to c. 10%, and, although the origin of PWC on Gotland has not been determined, a model of largely an SHG continuity and a small contribution of Scandinavian TRB could not be rejected (Mittnik et al., 2018). There is also mitochondrial data from 28 individuals from Ajvide, Ire, Fridtorg, and Visby on Gotland and four individuals from Köpingsvik on Öland (Malmström et al., 2015), which I include in my investigation in Paper I and II (see Supplement Paper I, table S4 and Supplement Paper II, Table S4).

4.4 Battle Axe Culture

Recent genomic analyses of individuals buried in the typical CWC burials in continental Europe has showed ancestry from an additional ancestral component not previously found in the farmer and forager populations in Europe (Fig. 3) (Allentoft et al., 2015; Haak et al., 2015). Thus, they show ancestry from three different ancestral groups. This ancestry component is maximized in the CHG foragers from Caucasus (Jones et al., 2015), and is also found in individuals from the Yamnaya complex in the Pontic steppe which have shown to share ancestry with CHG and EHG (Allentoft et al., 2015; Haak et al., 2015).

The new ancestral component is spread across Europe in association with the CWC, and has also been identified in an individual from the Viby BAC burial in Scania (2620-2470 cal BCE, 95% CI), and from a secondary burial in the Kyndelose megalithic tomb in
Denmark (2850-2490 cal BCE, 95% CI) (Fig. 3) (Allentoft et al., 2015). These individuals show a combination of the three major admixture components in the present-day European population derived from the Mesolithic foragers, the Neolithic expansion, and the large expansion associated with CWC (Günther and Jakobsson, 2016). This combination become common in Scandinavia already in the subsequent LN period, and has today been found in twelve later individuals from different Scandinavian LN-BA contexts (Allentoft et al., 2015; Mittnik et al., 2018), showing that the BAC in Scandinavia to some extent also involved migration of new groups. This ancestral combination has also been found in individuals from Early CWC burials in central Germany and Poland (Fig. 3) as well as in later contexts across Europe (Allentoft et al., 2015; Haak et al., 2015).

Today, very little genetic research has been done on mitochondrial DNA from BAC contexts in Scandinavia. In addition to the above mentioned individuals there is one individual analyzed from Bergsgraven in Östergötland showing a unique lineage compared to what has been found earlier in Scandinavia (Malmström et al., 2015). There is however, a large dataset available from several CWC groups in Saxony-Anhalt (Brandt et al., 2013) which show a blending of Mesolithic, Neolithic and additional maternal lineages introduced from the CWC expansion which is used in my analyses in Paper II (see Supplement Paper II, Table S4).
5 Research background

5.1 The Late Mesolithic/Early Neolithic transition

The initial human settlement on Gotland started over 9 000 years ago. However there seems to have been a population decline on Gotland between c. 5600 and 4500 cal BCE as little activity has been recorded from this time (e.g. Apel et al., 2018; Lindqvist and Possnert, 1999). From around 4500 cal BCE there is evidence of the so called axe-sites; e.g. Nasume, Krooks, Kroksstäd in Tofta Parish and Norrbys in Hall Parish (Andersson, 2016; e.g. Isendal, 1985; Lithberg, 1914; Nihlén, 1924, 1927; Österholm, 1989), but no confirmed Ertebølle pottery has been found on the island to date. Most of the LM dates come from seal bones, also from the Stora Förvar cave on Stora Karlsö Island on the west coast of Gotland (Apel and Storå, 2017; Lindqvist, 1997; Lindqvist and Possnert, 1999; Rundkvist et al., 2004). As there are no graves from the LM/EN transition on the island little is known about the demography of these people.

From the beginning of the Scandinavian EN there is evidence from the TRB culture in form of axes, stone tools, ceramics, and domesticated animal remains. Investigation of flint has shown both local origin and imports from Southern Scandinavia implying exchange networks with the mainland (Norderäng, 1997). Zooarchaeological investigations from the Mesolithic to the MN Neolithic, and radiocarbon dating of domesticated animal bones show that they were introduced in the EN time period (Lindqvist, 1997; Lindqvist and Possnert, 1999; Rundkvist et al., 2004). Several sites with TRB pottery have been found, as in other parts of Scandinavia they are all situated in connection with sandy soils preferable for cultivation. However, few of these have radiocarbon dated finds.

They are mainly distributed in three spatial clusters on Gotland (from Bágerfeldt, 1992; Stenberger, 1964; Österholm, 1989):

- A northwestern cluster in the Lummelunda, Lokrumme, Martebo area where also wet-land depositions of TRB pottery has been located.
- A large western central cluster between the area of Visby, Ekeby, Väte, Roma, and Västergarn where depositions of large collections of oversized thin-butted flint axes also have been found in Kopparsvik (11), Hogrân (15) and Vall (7).
- A southern cluster in the Hablingbo-Grötlingbo area.

These areas also correspond to the main distribution of the different types of axes connected with TRB, but single stray finds have been located across the whole island (Andersson, 2016; Bágerfeldt, 1992; Lithberg, 1914; Österholm, 1989). Only a few settlement sites have so far been assigned to the EN period based on analyses of pottery; Ardags, Ekeby Parish, Mõlner & Grâne, Väte Parish and Suderkvie in Grötlingbo Parish (Apel and Storå 2017; Lidman, 2014; Martinsson-Wallin and Lidman, 2017; Österholm, 1989).

The Suderkvie site was discovered in connection with the 1959 excavation of a destroyed stone cist burial (Manneke, 1963a, 1963b). The cist was found to have been placed on top of an earlier TRB site located on top of beach sand. A skeleton from a female was also located adjacent to the cist, and scattered burnt and unburnt human remains and TRB
pottery were located across the whole site. The TRB ceramics from Suderkvie has shown
different characteristics than that found at other sites and has been suggested to have been
imported from areas south of the Baltic Sea (Althin, 1967; Österholm, 1989). Erika Lid-
man (2014) investigated the ceramics at Suderkvie where she also found similarities with
TRB ceramics on Öland, she also concluded that there probably also were ceramics from
other time-periods in this material. New radiocarbon dating of hazelnut shells located in
pits at the Suderkvie TRB site were dated to 3520-3350 cal BCE, 95% CI (Lidman, 2015;
Martinsson-Wallin and Lidman, 2017). Thus, the question if this site also being a de-
stroyed megalithic burial needed further investigation.

Lidman (2015) conducted a detailed study of the site in her master’s thesis in archaeology
at Campus Gotland where she modelled the surrounding landscape in different time peri-
ods. She found that the site was located on a small peninsula 190 - 350 m from the shore
during the EN TRB phase, which is in line with other coastal TRB megalithic burials.
Based on the advanced ceramics she also concluded that it could have been so called
“megalithic ceramics” connected with TRB megalithic burials. However, the location of
such a burial monument at this site has not been identified, and new radiocarbon dating of
the skeletal remains in connection with this thesis showed LN-EBA dates. Thus, the site
had evidence of long usage which also is seen from the artefacts found spanning from the
EN to historical times (Gräslund, 1964; Lidman, 2015; Manneke, 1963a). The osteologi-
cal evaluation of the bones found in the pits connected with the EN TRB phase showed
mainly burnt and unburnt faunal remains, but two small unburnt human hand bones were
also located (Gustavsson, unpublished; Lidman, 2015). Unfortunately, they were poorly
preserved and were not included in the genetic analyses. This stone cist burial is further
presented in the analysis in (Supplement Paper II).

5.2 The Early/Middle Neolithic transition and the Ansarve dolmen
There are at least one, possibly two, partly destroyed megalithic tombs located in Ansarve
and Lixarve in Tofta Parish (e.g. Lithberg, 1914; Martinsson-Wallin and Wallin, 2010;
Nihlén, 1924; Wallin, 2010; Wallin and Wehlin, 2010). The Lixarve dolmen remains to
be excavated to confirm the affinity to TRB. However, the Ansarve dolmen has been
evacuated twice (1912 and 1984), and in the latter excavation it was established that is
was a so called rectangular dolmen (Fig. 4) (Bägerfeldt, 1992; Fraser, 2017; Hansson,
unpublished; Lithberg, 1914; Nihlén, 1924). Thus the form and the dating of the dolmen
on Gotland is in line with the developments seen at this time period within the TRB cul-
ture in continental Europe and Scandinavia (e.g. Blomqvist, 1989; Midgley, 1992, 2008,;
Müller, 2011; Sjögren, 2003; Tilley, 1999).

The artefacts included flint (local and Scandinavian), amber, round butted pecked axes,
and a carved sandstone, but no ceramics were found (Bägerfeldt, 1992). It has previously
been noted on Öland and the Swedish mainland that TRB-pottery deposits are common
both inside the chamber, outside the entrance, and along the surrounding curb, but the
distribution of pottery varies in different locations (Janzon, 2009). Pottery from secondary
BAC and later usage also occur in megalithic burials (e.g. Sjögren, 2003).

Human remains were located at both excavations and at least 31 individuals were buried
in the tomb, but since the skeletal remains from both excavation has not been evaluated
together there were probably more (Lindqvist, 1997; Wallin and Martinsson, 1986).
Three individuals from this burial were dated to the beginning of the MN period (3630-
3030 cal BCE, 95% CI) (Lindqvist, 1997), which showed some of the earliest dates for this type of burial in Scandinavia (Persson and Sjögren, 1995; Schulz Paulsson, 2010, 2017). Other radiocarbon dates from this burial revealed later usage from the Bronze Age to the Migration period (Bägerfeldt, 1992; Wehlin, 2011). The $^{13}$C-values from the AMS radiocarbon dating suggested a terrestrial diet with some marine protein input (Lindqvist, 1997).

Recent summed probability distribution modeling suggests a population increase at the beginning of the EN in connection with the appearance of TRB (Apel et al., 2018). The limited number of radiocarbon dated TRB contexts on the island is problematic and the chronology and duration of the length of usage of the dolmen has not been determined. The TRB phase on Gotland seems to end around c. 3000 cal BCE (Apel et al., 2018; Lindqvist, 1997; Rundkvist et al., 2004; Österholm, 1989).

5.3 Middle Neolithic A (MN A, c. 3300-2800 cal BCE)
Starting from c. 3200 cal BCE there is evidence of the sub-Neolithic PWC complex (e.g. Apel et al., 2018; Norderäng, 2008; Wallin and Martinsson-Wallin, 2016). Radiocarbon dating from eastern central Sweden (Björck, 2003) are slightly earlier than the developments seen on Gotland. There are at least eighteen known PWC localities on the island all situated along the former coast line, including several large burial sites (e.g. Janzon, 1974; Österholm, 1989). Thus, the TRB complex appears to be contemporaneous for at least 200 years with the PWC on Gotland. In line with the discussions in Scandinavia much debate has focused on the TRB and PWC cultural manifestations and their relationship; did they represent distinct groups, or where they rather the result of successive developments (e.g. Browall, 1991; Carlsson, 1987; Malmer, 2002). Previous studies of aDNA and stable isotopes suggest distinction between these two groups in Scandinavia (Eriksson, 2004; Eriksson et al., 2008; Lidén et al., 2004; Malmström et al., 2009, 2015; Skoglund et al., 2012, 2014a).
5.4 Middle Neolithic B (MN B, c. 2800-2400 cal BCE)
Starting from c. 2800 cal BCE cultural remains from the Battle Axe culture (BAC) are found in Scandinavia. However, the classic archaeological debate regarding the contemporaneity and succession of the three different cultural groups (TRB, PWC, and BAC) and their relationship to each other as seen in the archaeological record on the Scandinavian mainland (e.g. Hackwitz, 2009; Larsson, 2009; Malmer, 2002) has not had the same momentum on Gotland. Only a few stray finds of battle axes have been found distributed mainly on the upper mid-western part of the island (Bägerfeldt, 1992). As no BAC settlement sites have been located it has been suggested that these finds reflect contacts with this culture on the mainland (Bägerfeldt, 1992; Lindkvist, 1993; Malmer, 1975; Martinsson-Wallin et al., 2015). BAC pottery is uncommon on Gotland but a few cases have been noted at the cave Stora Förvar on Stora Karlsö, Ardags in Ekeby, at the coastal site Rojrhage (Barshardershed) in Grötlingbo, and in two graves (no 3 and 10) at the Ire PWC site (Palmgren, 2014; Rundkvist et al., 2004; Schnittger and Rydh, 1940).

The Rojrhage site is located very close to the Suderkvie TRB pottery site and has evidence of pottery from TRB, PWC, and BAC; however there appears to have been three consecutive phases. The first phase show dates somewhat earlier than those found at the Suderkvie site and includes only a small amount of TRB pottery, the main phase (MN A) is associated with the PWC and an abundant amount of PWC pottery, flint, a bone harpoon point, and also bones of pig, cattle, and seal is connected to this phase. The third phase dates to the beginning of the LN period and includes a small amount of BAC pottery and some bones of grey seal (Rundkvist et al., 2004).

The only BAC influenced burials on Gotland to date have been found within the MN PWC contexts, and BAC associated artefacts have been located at Ajvide, Västerbjer, Ire, Visby, and Fridtorp (Janzon, 1974; Lindkvist, 1993; Malmer, 1962; Palmgren, 2014). A Battle Axe and a dagger made from dear antler has also been located at the Mölner TRB site in Väte Parish (for a summary see Palmgren, 2014, pp. 61–62). Thus, even if our knowledge is restricted, the extent of the BAC cultural influences during the latter part of the MN period on Gotland appears to have been limited. Individuals in PWC burials with possible BAC influence are currently the focus of archaeogenetic analyses conducted by Alexandra Coutinho, PhD student at the Evolutionary biology center, Uppsala University. However, secondary BAC burials in MN megalithic tombs are common in Scandinavia (e.g. Kaelas, 1967; Sjögren, 2003), thus there is also a possibility that the Ansarve dolmen was used for this purpose.

5.5 The Late Neolithic Stone cist burials
The Late Neolithic period (c. 2400-1800 cal BCE) on the island shows the introduction of new cultural influences seen in the burial traditions, material culture, as well as a possible demographic expansion shown by an abundance of megalithic graves (stone cist burials). This is also a time of large demographic expansions and cultural transformations in continental Europe, in connection with the appearance of the large Bell Beaker complex (BBC) which also can be seen in mainland Scandinavia (e.g. Apel, 2001; Prescott and Glørstad, 2015; Prieto Martinez and Salanova, 2015; Stenberger, 1964; Stensköld, 2004). Some typical shaft-hole axes and imported flint arrow heads, daggers and scrapers have been located in some LN graves, as well as some loose stray finds (Bägerfeldt, 1992; e.g. Österholm, 1989; Wallin, 2010). However, their association with BBC has not been es-
established, and no typical BBC pottery has been found. The artefacts show similarities with the developments seen in Scandinavia, but also with continental Europe (e.g. Apel, 2001; Bägerfeldt, 1992; Edenmo, 2008; Heimann, 2000; Lithberg, 1914; Stenberger, 1964; Stensköld, 2004)

At present little is known of the LN developments on Gotland represented by a 600 year timespan. Many cists were excavated during the first half of the 20th century (e.g. Hansson, 1927; Lithberg, 1914), and many had already been plundered and/or destroyed prior to excavation (e.g. Manneke, 1963a; Stenberger, 1944a), and their relationship to the earlier developments on the island is not known. No settlement sites have been located, and the chronology of the burials needs to be established as stone cists were also used into the Early Bronze Age (EBA). Stone cist continues to be built also in the Iron Age.

A first attempt to chronologically categorize these burials on Gotland was done by Ann Luthander (1988). At least 42 stone cists have been excavated on the island which she categorized into different time periods based on the artefacts found in the cists. These cists contained both single and multiple burials but only a few have been osteologically analyzed in detail. Thus the number of individuals estimated in many of the burials is only approximations. The stone cists were further discussed by Bägerfelt (1992) who also compared them to LN stray finds on the island.

New research initiated in the Neolithic Lifestyles project by Wallin (2010) concluded that at least 104 possible stone cist burials, distributed at 86 different locations belong to the LN/EBA periods. These were identified based on cists with LN artefacts or connections with later Bronze Age cairns. Seven different core areas were identified across the island: 1) Bunge/Lärbro, 2) Boge/Vallstena/Hörsne, 3) Kraklingbo/Gammelgarn/Alskog, 4) Lau/Burs/Rone, 5) Vamlingbo/Sundre/Grötlingbo/Fide, 6) Klinte/Eskelhem/Tofta, 7) Visby/Väskinde/Martebo. The highest number of burials was found in the upper mid-western part in #7 in Västerhejde, Visby, Väskinde, and Stenkyrka. Larger groupings were also found in #3 Alskog (on the central east-coast of the island), and in the south #5 in Vamlingbo.

Alexander Sjöstrand further analyzed LN/EBA cists in more detail, and plotted the spatial distribution of these burials according to size, and also position of the cist, in his masters-thesis in archaeology at Campus Gotland (Sjöstrand, 2012). He also osteologically analyzed the natural stone cist burial “Utalskog” in Alskog which is further analyzed in this thesis. Two additional stone cist burials from Häffinds in Burs Parish, and Hägur, Eksta parish are included in the study for Paper II (see below).
6 Material

6.1 The Ansarve dolmen (RAÄ Tofta 14:3)
This megalithic burial in Ansarve meadow in Tofta parish on the central west coast of Gotland, was first excavated in 1912 (Hansson, unpublished), and again in 1984 (Bägerfeldt, 1992) (Fig. 4). Human remains were located from both excavations. At least eight individuals were determined from the 1912 excavation (SHM 31173); five adults men and women, and three children, and three mandibles have been dated which revealed some of the earliest dates for this type of burial in present-day Scandinavia 3630-3030 cal BCE, 95% CI (Ua-3783: 4595 ± 65 BP, δ13C -19.3; Ua-3784: 4555 ± 60 BP, δ13C -19.3; Ua-3785: 4640 ± 70 BP, δ13C -18.6) (Lindqvist, 1997; Schulz Paulsson, 2017, 2010). The δ13C-values suggested a terrestrial diet with some marine protein input (Lindqvist, 1997). A minimum of 31 individuals were identified from the 1984 excavation; 16 adults (males and females), and 15 children from infants to juveniles (Wallin and Martinsson, 1986), an additional burial was located in the stone packing (Bägerfeldt, 1992).

Conventional radiocarbon dating (preAMS) was performed on a human bone from inside the chamber (St-10960: 3379 ± 130 BP, δ13C -19.7), charcoal underneath one of the stones in the south eastern part (St-9597: 1515 ± 75 BP, δ13C -23.6), and the female skeleton located outside the chamber (St-10961: 2530 ± 275 BP, δ13C -21.6) (Table S1) only revealed later usage from the Bronze Age to the Migration period (Bägerfeldt, 1992). These datings, however, has to be considered unreliable. The female skeleton has since been re-dated with AMS (Ua-39877: 1965 ± 30 BP, δ13C -22.3) to the Roman Iron Age (Wallin, 2010; Wehlin, 2011) (See Supplement Paper I, Table S1). The second excavation revealed that the burial was a partly destroyed rectangular dolmen (Fig. 4) (Bägerfeldt, 1992). This fact, together with the results of the 14C dated mandibles, showed that the people buried within the dolmen had connections with the megalithic burial tradition found in the much larger TRB culture complex (e.g. Blomqvist, 1989; Midgley, 2008; Müller, 2011; Schulz Paulsson, 2017; Sjögren, 2003; Tilley, 1999). For more information see Supplement Paper I.

6.2 The Häffinds stone cist (RAÄ Burs 9:1)
A stone cist burial with a large central cairn and earthen mound located on a field in Burs parish on the south-central east coast of Gotland, excavated and removed in 1984 (Burenhult, 1986). The cist has been dated to Late Neolithic to Early Bronze Age based on the bone and bronze artefacts which were found both inside and surrounding the cist. Artefacts inside the cairn were dated to the Late Bronze Age (BA IV to BA V). The cairn also included a secondary cremated urn burial dated to BA V (feature 2). A BA V bronze shaving knife was found when sifting the soil (Burenhult, 1986).
The individuals in the cist were buried tightly together in a supine position with their heads to the east, except one female (No.10) who was placed in the opposite direction (Fig. 5). An osteological analysis of the individuals inside the cist was conducted by Barbro Lind in connection with her undergraduate thesis in osteoarchaeology at the osteological research laboratory, SU (Lindh, 1997). At least 20 individuals were identified from the analyses; ten children including two infants, two sub-adults and eight adult male and female individuals between 20 to >50 years of age. One adult male was missing in the assemblage in Lind’s analysis, this individual was located during this research and has now been osteologically analyzed by Alexander Sjöstrand at the osteological laboratory Campus Gotland in 2014 (Sjöstrand, unpublished). For more information see Supplement Paper II.
6.3 The Hägur stone cist (RAÄ: Eksta 72:1)

A partially destroyed and plundered stone cist burial with overlying cairn located in Hägur, Eksta Parish on the south-west coast of Gotland excavated in 1944 (Stenberger, 1944a, 1944b). This burial is just 1 km northwest of the MN PWC burial site of Ajvide. The cist has been dated to the EBA based on a tooth pearl and bronze ring found inside.
and next to the cist, a stone disc was found in the upper western part of the cairn (Fig. 6). A partial Iron Age sword sheath fitting was found close to the human remains in feature 4 (Stenberger, 1944a).

The human remains were retrieved from five spatially separated concentrations within the cist and cairn (#1-5) (Fig. 6). The osteological evaluation was conducted by Sandra Gytare in connection with her undergraduate thesis in archaeoosteology at Campus Gotland (Gytare, 2015). All five concentrations contained very fragmented remains of several individuals; the minimum number of individuals (MNI) was estimated for the assemblage as a whole. At least thirteen individuals were present (adult and juveniles, males and females, and small children). For more information see Supplement Paper II.

6.4 The Suderkvie stone cist (RAÄ: Grötlingbo 13:1)

A damaged and partly destroyed stone cist burial located in Suderkvie, Grötlingbo Parish on the southeast coast of Gotland excavated and removed in 1959 (Manneke, 1963a, 1963b). During the excavation it became evident that the cist had been placed on top of an EN settlement site. TRB pottery was found scattered across the whole site, and also in some of the pits (Features IV-VII (Fig. 7) (Manneke, 1963a). Burnt and unburnt pieces of human and animal bones were also located across the whole site. Two hazelnut shells in Features IV (R13) and V (R5) were dated to 3520-3350 cal BCE, 95% CI) (Lidman, 2015; Martinsson-Wallin and Lidman, 2017). Ceramics, flint flakes, animal bones and charcoal were also located within the cist, as well as a tooth pearl and two bronze items (Manneke, 1963a).

The Suderkvie stone cist (RAÄ: Grötlingbo 13:1) is a damaged and partly destroyed stone cist burial located in Suderkvie, Grötlingbo Parish. It was excavated and removed in 1959. During the excavation, it became evident that the cist had been placed on top of an EN settlement site. TRB pottery was found scattered across the whole site, and also in some of the pits (Features IV-VII (Fig. 7) (Manneke, 1963a). Burnt and unburnt pieces of human and animal bones were also located across the whole site. Two hazelnut shells in Features IV (R13) and V (R5) were dated to 3520-3350 cal BCE, 95% CI) (Lidman, 2015; Martinsson-Wallin and Lidman, 2017). Ceramics, flint flakes, animal bones and charcoal were also located within the cist, as well as a tooth pearl and two bronze items (Manneke, 1963a).

The osteological evaluation was conducted by Anders Gustavsson at the osteological laboratory Campus Gotland in 2015 (Gustavsson, unpublished). A number of long bones...
and other skeletal elements from at least thirteen individuals; four adults, and eight children (three infants, one c. 2-4 years, three c. 6 years, and one c. 8-10 years of age) were recovered. The bones were comingled in piles inside the cist, mainly in the central part and the southeast corner (Fig. 7). The remains of a female skeleton (Skeleton A, SKA) was located two meters west of the cist in Square R.5, and skeletal remains from at least one additional adult was located in Square R.7 to the east of the cist (Fig.7) (Gustavsson, unpublished; Manneke, 1963a, 1963b). For more information see Supplement Paper II.

6.5 The Utalskog stone cist (RAÄ: Alskog 48:1)
A natural limestone cave burial located at Utalskog, Alskog parish on the east coast of Gotland excavated in 1926 (Fig. 8) (Arne, 1927a, 1927b; Bergman, 1927). The cist is part of the large Late Neolithic–Iron Age burial site of Gålrum just 14.0 km northeast of the Häffinds stone cist burial. Part of the formation had been removed by dynamite by the landowner before the grave was discovered (Fig.8). The burial was dated to the LN period based on the bone and amber artefacts.

Fig. 8. Top: The limestone formation in 1929 (Photo Nihlén, ATA 4412/1929). Bottom left: The limestone formation today, the burial is to the right in the photograph in front of the tree (Photo Fraser). Bottom right: Close up of the burial (photo Fraser).
The individuals had been packed tightly together with their heads to the north inside the crevice, and some individuals had been moved to the sides to make room for the last individuals buried (Bergman, 1927). An osteological evaluation was conducted by Alexander Sjöstrand in connection with his MA thesis in archaeoosteology at Campus Gotland (Sjöstrand, 2012). At least 26 individuals were present based on the left petrous bone. Due to the fragmented state age estimation could only be determined on a few bone elements; which showed eight adult males and females, as well as two children and one juvenile. For more information see Supplement Paper II.
7 Methods

This chapter describes the ideas of and purposes behind the different methodologies used in my thesis. Technical details of how this was done are described in the supplements.

7.1 Sampling

The human remains studied in this thesis were stored at the Swedish History Museum in Stockholm: Ansarve 1912 excavation (SHM 31173), Suderkvie (SHM 27151), Hägur (SHM 23293), and Utalskog (SHM 18589), as well as at the Osteoarchaeological Research Laboratory at Stockholm University (Häffinds), and at Uppsala University-Campus Gotland (formerly Gotland University) (Ansarve 1984 excavation). The assessments and collection of the materials were based on published and unpublished osteological reports, archaeoosteological BA and Masters Student thesis, discussions during the student evaluations, plus evaluation of excavation documentation, photographs and plan drawings.

Sampling and documentation was conducted at the osteological laboratory and/or the DNA laboratory at Campus Gotland. As most of the analyses conducted are dependent on the permanent molars (M1-M3) sampling was mainly done on teeth (loose and in situ). The Häffinds burial was the only burial with documentation on several individuals’ position within the grave. For the other burials sampling was dependent of the fragmentation grade and preservation of the materials, as well as available molar tooth elements. In some burials only key individuals from selected locations were included in the analyses due to poor preservation. Additional cranial bone elements were also sampled for the DNA analyses (See Supplement Paper I, Table S2 and Supplement Paper II, Table S1 for information on the collected samples). Permission for sampling for radiocarbon, isotope and DNA analyses was given by the Swedish Historical Museum (SHM31173, SHM27151, SHM23293, and SHM18589; Dr nr: 610-613-2011, Dr nr: 610-732-2011, Dr nr: 3.3.323.2013, Dr nr: 331-493-2015, and the archaeologists in charge of the materials (Göran Burenhult; Häffinds, and Paul Wallin; Ansarve 1984).

7.2 The time aspect

One purpose of this investigation was to establish the chronology of usage for these different burials by radiocarbon dating. As these were mass burials with fragmented commingled remains, used and re-used over extended time-periods, the radiocarbon dating was also paramount for the sample provenance, and also for understanding the context and chronology of the LN burials. Two of the previously dated mandibles from the Ansarve dolmen also showed older radiocarbon dates compared to similar contexts in Scandinavia, thus they were re-dated, combined and recalibrated.

The reservoir effect from marine and freshwater fish food consumption affects radiocarbon dating results. This is caused by an apparent age of the source reservoir that differs from the contemporary atmospheric surface $^{14}$C value, resulting in anomalously old radiocarbon ages of samples from different bodies of water (Jull et al., 2013; Philippsen, 2013). The Baltic Sea has a complex natural history (Andrén et al., 2011) and the marine reservoir effect has fluctuated over time and thus varies temporally. This value also fluctuates spatially due to the topography of the sea floor affecting the circulation, the saline
inflow, and freshwater runoff from different river systems (Lougheed et al., 2013). Similarly, the freshwater reservoir effect in inland lakes and rivers can be problematic to evaluate as it fluctuates heavily, even within the same body of water, and time is also a factor (Philippsen, 2013). The Marine reservoir offset of 70 ± 4 for the strict marine diet of the PWC on Gotland (Eriksson, 2004) (mean δ13C-value -15.4 ± 1.2‰), was used to calibrate for reservoir age during the MN period in this study using an isotopic cut-off point at Carbon values higher than −18.0‰ (Eriksson et al., 2008). Different offsets have been suggested for other areas in the Baltic (e.g. Piličiauskas and Heron, 2015), as well as from other time periods on Gotland when the salinity was different (Boethius et al., 2017). To date there is no offset value for freshwater fish consumption on Gotland; however establishing this goes beyond the scope of this thesis. Thirty-nine radiocarbon dates are presented in Supplement Paper I, Table S2 and Supplement Paper II, Table S1. Additionally, all the radiocarbon dates for the genetic reference groups needed to be investigated and recalibrated as they were collected from different publications which used different ways to present this data, or the radiocarbon dating for some individuals were presented in later publications from the same research group. This was then used to create new temporal groups for the comparisons. Calibration and plots were done using Oxcal online software version 4.3 (Bronk Ramsey, 2009), based on the IntCal13 atmospheric curve (Reimer et al., 2013) (See Supplements paper I and III for details).

7.3 Diet as a cultural definer
The stable isotope analysis was used to examine dietary patterns and general differences in subsistence economy from investigation of the main source of protein intake in the diet. Carbon and Nitrogen stable isotope analyses (13C/ 15N) have shown to be a valuable tool in archaeological research for investigating diet in prehistoric populations (e.g. Katzenberg, 2008). The Carbon isotopes reflect the level of marine and terrestrial protein intake in the diet, and Nitrogen isotopes reflect trophic level in the food chain, plotted together the results will indicate the individuals’ dietary habits. Carbon and Nitrogen isotopic signatures enter the body through the diet. Isotopic ratios in teeth are fixed during the formation of the tooth as dentine does not show extensive remodeling. This is contrary to bone which is continuously remodeled (for a comparison of different bone elements see Reitsema, 2013). For first molars (M1) the root is finalized at around 9-10 years of age (Hillson, 1996), thus stable isotope analyses of collagen from dentine of M1 will show the dietary pattern during childhood, whereas collagen in bone will show the last c. 10-15 years of the person’s life time and thus reflect different ages dependent on the persons age at death. Due to the fragmented nature of the material in these burials the sampling did not allow for the same bone element in all the individuals studied, thus the results reflects different time-periods in some of the individuals and is mainly used here as an indicator of an individual’s diet (see Supplement Paper I, Table S2 and Supplement Paper II, Table S1 for details). Dietary analyses are also important for establishing main source of protein for the calibration reservoir age in radiocarbon dates (see above), and also to evaluate Strontium isotopic values (see below).

7.4 Mobility patterns
The aim here was to address questions concerning human mobility patterns and to identify individuals with a local and non-local geographic origin by analysis of strontium isotope ratios (87Sr/86Sr) in human tooth enamel (Bentley, 2006). Strontium analyses in combination with osteology and genetic data has also shown to be very useful in archaeological research (e.g. Alt et al., 2016; Haak et al., 2008; Knipper et al., 2017). Mobility anal-
yses are used to investigate ongoing migration, social structure, and marriage patterns among individuals, which can be used to make hypotheses about demographic changes within groups. Uniparental markers such as mitochondrial DNA (mtDNA) and non-recombining Y chromosomal DNA can be used to investigate maternal and paternal inheritance patterns, and population continuity. Thus aid in investigation of migration and also identify social structure (matri- and patri-local systems), and marriage exchange (e.g. Bentley et al., 2002; Knipper et al., 2017; Sjögren et al., 2016).

Strontium from the local geology incorporates into skeletal tissue through the food chain, where Strontium replaces calcium in the bone or tooth enamel matrix (Bentley, 2006). As tooth enamel is not remodeled the $^{87}$Sr/$^{86}$Sr ratio remains unchanged through life and is commonly not affected by diagenetic alteration. This is in contrast to skeletal bone remains which instead can be analyzed for the local Sr-signals from the geological background, together with local fauna, and soil samples (Slovak and Paytan, 2012). A consideration of diet is relevant for mobility studies as high levels of marine protein in the diet can change the Sr-isotopic signal towards the seawater ratio (Bentley, 2006). The Baltic Sea is brackish and the Sr-isotope values differ from that of oceanic water and range between 0.7092-0.7097 (Andersson et al., 1992). Strontium enters tooth enamel during its formation, as the teeth develop during different stages in life, different teeth will show different time-periods in an individuals’ life time (Bentley, 2006). The permanent first molars are mineralized broadly from c. 0.5 months in utero to c. 3 years of age (Hillson, 2005, 1996), thus, analyses of the first molar (M1) will show the first years in a person’s lifetime, and analysis of the additional molars (M2 and M3) will show if there has been mobility and residential change during different stages of childhood to adulthood. The Strontium ratios are compared to the local geological Sr-baseline, and outliers indicate non-locality (Price et al., 2002; Slovak and Paytan, 2012) (see Supplement Paper I, Table S2 and Supplement Paper II, Table S1 for details).

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). However, the soil type distribution on the island, especially inland, contain layers of till (moraine) consisting of heterogeneous sediments from older formations brought by glacial ice which could show deviating signals to that of the local bedrock. 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 (Bentley, 2006; Slovak and Paytan, 2012). Previously, little research had been done to establish the Sr-baseline for the Gotland biosphere. A mean Sr-value of $0.7106 \pm 0.0003 (0.71000-0.71200, 2 SD)$ had been suggested based on human and faunal remains from seven individuals from three sites on the island (Price et al., 2014; Wilhelmson and Ahlström, 2015).

Thus, an important objective for this thesis was to establish the Sr-baseline for the geological background on Gotland by sampling and analyzing local animals and soil samples from different archaeological sites, also in connection with the burials analyzed here (Paper I and II). A new Sr-range was also published recently based on eleven teeth from domestic fauna (cattle, goat, and pig) from the Viking Age trading port in Fröjel (Peschel et al., 2017), which is included in this study. The results from Fröjel however, showed a much broader span from a single location (mean value $0.71242 \pm 0.0016$, Sr-range
0.70921–0.715629, 2 SD). As this was a trading port it is possible that some of these animals were non-local, there is also the possibility that they came from different regions on the island thus representing Sr-signals from several areas which is further explored here (see Supplement Paper I, Table S2 and Supplement Paper II, Table S2 for details).

7.5 Genetic markers, inheritance patterns and variation
The prehistoric individuals’ ancestral inheritance patterns are investigated in order to identify relationships between individuals and groups, and also to identify demographic shifts. This is done from analysis of the maternally inherited mitochondrial DNA, the paternally inherited Y chromosomal DNA (YDNA), and autosomal DNA, which is inherited from both parents and contains genetic information of all ancestors of an individual (Fig. 9).

A living organism contains all the genetic material needed for the functioning of the organism. The genetic information is stored in DNA (Deoxyribonucleic acid). DNA can be described as a chain constructed of four building blocks, so called nucleotides (A, T, G, and C). Together, in different combinations, they build up an individual's entire genome (all the genetic information in a cell). The human genome consists of two separate parts; nuclear DNA contained in the cell nucleus, and mitochondrial DNA in the mitochondrial organelles in the cytoplasm. Nuclear DNA consists of 22 homologues autosomal chromosome-pairs and two sex chromosomes (XX in females and XY in males) (n = 46).

During the process of meiosis (when sex cells are created) the homologous chromosome-pairs recombine (exchange genetic material with each other, also called crossover), and the number of chromosomes in each cell are reduced to only contain one copy of each chromosome (n = 23). The homologues autosomal chromosome-pairs (and the XX karyotype in females) contain identical genes from each parent, and recombine. Most of genes on the Y chromosome and the X chromosome differ from each other and they only recombine in the outer ends, in the so called pseudo-autosomal regions. Thus, the majority of the Y chromosome is inherited as is from father to son with the exception of possible mutations. As the 22 autosomes always are present in both males and females, they are inherited in equal proportions from all ancestors; thus one individual has inherited 1/2
from its parents, 1/4 from all grandparents, 1/8th from all great-grandparents, and so on (Fig. 9). Mitochondrial DNA is inherited separate from the DNA in the cell nucleus. Everybody has mitochondria but in humans it is inherited from the mother only. Mitochondrial DNA does not recombine and is thus also inherited as is with the exception of possible mutations.

Genetic variation arises from the process of mutation; this can be anything from one base change to large structural changes in the genome. A polymorphic locus that is used for genetic analysis is often referred to as a genetic marker. Uniparental markers (mtDNA and non-recombinant YDNA) are inherited from one parent only. MtDNA allows for tracing lineages back in time for an individual’s mother, back to the maternal grandmother, continuing back in time over the generations (Fig. 9). Similarly, YDNA follow the male lineage, from son to father, and back in time. Many present-day individuals have been studied for mtDNA and YDNA and the different variants that individuals carry are defined as haplogroups. These haplogroups lineages form the evolutionary history of the mitochondrial genome and the Y chromosome, which in turn are correlated, and can be informative about, the evolutionary history of carriers of the particular haplogroups. The mtDNA and YDNA haplogroups are described by letters and numbers and the worldwide human variation is constantly updated as new haplotypes (variant within a group) are identified (see http://www.phylotree.org/ (mtDNA), and https://isogg.org/tree/ (Y DNA)).

The other genetic markers used here are Single Nucleotide Polymorphisms (SNPs). A SNP describes a single base difference between two DNA sequences (i.e. between the nucleotide bases A, T, C, or G). SNP exist on both uniparental markers and on autosomes. As uniparental markers are haploid there is only one version within an individual. The autosomes have homologues pairs which can have alternate variants within the same gene on each gene copy. Alternative genetic variants in the same position in the genome are called alleles. If the individual has inherited the same allele from each parent it is homozygote on this position, if the alleles are different the individual is heterozygote on the position. Heterozygosity can be used to measure diversity in populations (see 7.8 below).

Different frequencies of alleles at polymorphic loci provide information about population relationships, diversity, and history. SNPs are a valuable genetic marker in population genetic studies because of their low mutation rate, which means that a common variant is likely to be identical by descent. SNPs are also abundant in the genome. In population genetic studies, the process of recombination (during meiosis) is also beneficial as this creates statistical independence between markers. If two loci are statistically independent, they can be seen as independent stochastic outcomes of the same ancestral process, thus the resolution of population genetic structure and evolutionary history tends to be greater the more genetic markers that are analyzed (see e.g. Hollfelder, 2018; Skoglund, 2013).

The majority of the human genome is identical, 99.9% when comparing two individuals. The human genome contains 3 billion base-pairs, thus there are c. 3 million variable sites between a pair of individuals. Most of these sites are mapped and are thus very informative for studying variation within and between individuals and populations. Since the nucleotides in each position represent a specific part of an individual’s genetic history, we see the complex combined story when analyzing the whole, or large parts, of an individu-
als’ genome. The centuries of geographical separation have made it possible to genetically separate individuals from different areas due to variation in frequency in large numbers of genetic variants (Novembre et al., 2008). Although these random changes in the genome can, eventually, become either fixed or completely disappear due to finite population sizes, a process called genetic drift. In humans, and in many other species, these variants vary in frequency across geographic space due to hindrances in gene-flow (e.g. geography), a process often referred to as population structure or genetic stratification. In theory, it means that an allele will eventually be fixed or disappear from a population the fewer individuals there are in a population, the stronger the effect of genetic drift, but genetic exchange (gene flow) with other populations typically counteracts this process.

7.6 Ancient genomes from ancient people

The methods used here are based on shot-gun sequencing DNA libraries (See supplements Paper I-III for details). The initial work is done in a DNA laboratory specifically set up for aDNA work where first the materials (bone and teeth) are decontaminated, and DNA is extracted and purified. The following process involves converting all DNA sequences in a sample extract to a uniquely indexed sequencing library, which then is pooled together with other libraries for massive parallel sequencing with Next Generation Sequencing technology (NGS). Once generated and processed, the sequence data is sorted by index. The data is then bioinformatically processed using a pipeline for aDNA analysis, which in this case has been performed by the bioinformaticians at the Jakobsson Lab. This pipeline uses a combination of programs and scripts especially suited to handle large aDNA data sets generated with NGS methods, where the data is processed and mapped to the human reference genome (Günther et al., 2018).

The shot-gun sequencing approach of DNA libraries does not target specific genetic data in a sample, thus exogenous sequences are also generated (e.g. environmental, bacterial, and contaminant DNA). Although it varies for each library dependent on the quality of the sample, usually only a few percent of the DNA recovered is endogenous DNA from the individual studied and every library therefore need to be investigated prior further sequencing.

The sequencing result from each sample library is presented in form of statistics providing information on the proportion human DNA, average read length of the sequences, the percentage of duplicate sequences, percentage of sequences that were too short to map, amount of nuclear and mitochondrial DNA coverage, and estimation of biological sex (Günther et al., 2018). The screening statistics information is used to determine if additional libraries can be built from the same extracts to retrieve more data, and also if new extractions need to be made and tested for endogenous DNA content. As the libraries are screened in batches (of ~ 20), the full potential of each library is not seen in the screening, but has to be estimated based on the different parameters shown in the sequencing statistics. The screened libraries that have been determined to be potentially sufficient for DNA retrieval need to be repooled in smaller batches and sequenced again until they are depleted (which means that every DNA fragment has been sequenced) based on the ‘clonality’ estimate of each sequence run.

The sequence data need to be quality checked and authenticated. This is first done by analyzing natural properties found in aDNA (Fig. 10). Ancient DNA molecules are broken down into short sequences due to chemical damage in the DNA backbone, sugar
molecules, and nitrogenous bases (Pääbo et al., 2004), thus an average short sequence length is an indicator for aDNA data (Fig. 10A). Another property that is used for authentication is the chemical damage pattern induced from cytosine deamination accumulating in the DNA sequences (Briggs et al., 2007; Sawyer et al., 2012). This pattern is especially noted in the 5’ and 3’ overhangs which can be calculated and plotted to visually inspect the data (Fig. 10B) (See Supplements Papers I-III).

Contamination is estimated to determine if there is DNA from more than one individual present in the sample; this is done from direct analyses of known positions in the mitochondrial genomes (Fu et al., 2013; Green et al., 2008), also in the X chromosome in the case of males (Korneliussen et al., 2014; Rasmussen et al., 2011), and can also be estimated in autosomal DNA (Jun et al., 2012) See Supplements Papers I-III). Libraries with indications of >4% human DNA contamination often are discarded from further investigation. However there are also ways of filtering for postmortem damage (PMD) bioinformatically which reduces present-day DNA contamination (Skoglund et al., 2014b).

Libraries with <2% human DNA content are costly to work with as they produce very little endogenous DNA in each sequencing run. However, there are other methods that can be used to retrieve more data from important samples. Libraries with low human DNA content can be enriched for human DNA using capture methodology. There are several different ways to “fish out” DNA by using probes, e.g. biotinylated baits specifically targeting only human DNA based on the nuclear or mitochondrial genomes (Briggs et al., 2009; Carpenter et al., 2013). In this way all the noise that comes with direct sequencing of shot-gun data is eliminated and more data is retrieved during sequencing.

DNA libraries can also be damage repaired by adding an initial DNA repair step in the library building process by using UDG and endonuclease VIII, or USER enzyme (NEB) treatment to remove deaminated cytosines (Briggs and Heyn, 2012). This is especially good for high coverage genomes (>20x average coverage per base position in the genome) which subsequently allows for fine scale analyses of the whole genome. Damage repaired high coverage genomes can be used for advanced population genetic analyses.
e.g. to estimate genetic variation within an individual, infer the so-called effective population size, or to call novel genetic variants (e.g. Günther et al., 2018).

When all the sequence data from one individual has been obtained, it is then merged into a single data file and remapped, filtered, and rechecked for DNA contamination (for details see Supplements Papers I-III). New sequencing stats are produced for the total coverages for each individual and the quantity of nuclear and mitochondrial coverage determines what type of population genetic analysis that can be done. At least 10x coverage of the mitochondrial genome is recommended to estimate modern DNA contamination, thus samples with low coverage genomic data and insufficient amounts of mtDNA cannot be used for the downstream analyses.

The shot-gun approach is completely random and a 1x coverage genome is an average measure and does not mean that every position in the genome is covered; some stretches in the genome can have higher coverage, whereas others areas are completely lacking. This means that direct comparisons of many low coverage individuals involves different overlapping parts in each of the individuals, which affects the power in the analyses, and also limits what can be achieved.

There are two types of nucleotide substitutions; Transitions (C/T or G/A) and Transversions (C/G, A/T, C/A, T/G). The most common type of DNA damage in ancient DNA involves transition substitutions from deamination of cytosines (Michael Hofreiter et al., 2001; Lindahl, 1996), thus ancient DNA analyses sometimes (e.g. for low coverage sequence data and SNP data) only involves transversion SNPs in order to avoid errors induced from DNA damage.

Genomic coverage of a few percent (>2%) allows for estimation of biological sex (Skoglund et al., 2013), estimation of 1st and 2nd degree kinship relationships (Kuhn et al., 2017), and estimating genetic affinity to present-day and ancient populations from principal component analysis (PCA) (Skoglund et al., 2012). Genomic coverage of >10% (0.1x coverage) allows for more specific hypothesis tests regarding the relationship between individuals (Patterson et al., 2012). Genomic coverage >1x allows for more fine scale analyses of genetic diversity, definition of Y chromosome haplogroup, and direct comparisons of ancient individuals. If the entire genome has good coverage (>10x - 20x) fine scale analyses across the whole genome can be implemented and detailed investigation of the individual’s evolutionary history can be obtained. As an individual has two parents, four grandparents, eight great-grandparents, and so forth, and this individual’s genome is made up of the ancestors’ genetic material, the individual’s genome is then informative also about the individual’s ancestor’s evolutionary history.

7.7 Frequency patterns of mitochondrial haplogroups

The mitochondrial data is used here to assess ancestral maternal inheritance by direct comparisons to archaeological groups, and also to identify maternal relationship within the burials. Mitochondrial haplogroup frequency analyses have been used for a long time to investigate population genetic affinities between prehistoric groups and much reference data (both aDNA and from the present-day European population) is available for this type of investigation. Here two different approaches are used:
The maternal ancestral affinity in the Ansarve group is investigated from principal component analysis (PCA) of mitochondrial haplogroup frequencies. PCA is a statistical method used to investigate large datasets with many different variables. It is used in genetics to visualize genetic distance and relatedness between and among populations. The haplogroups from 25 different archaeological groups were condensed into 21 haplogroups: K, I, J, U5b, U5a, U4, U3, U2, U, T2, T1, J, V, H, HV, X, W, I, N1a, N*, C and compared to the Ansarve group (see Supplement Paper I, Table S4). The frequency pattern was also visualized in histograms (see Supplement Paper I for details).

The origin of the maternal lineages in the Late Neolithic/Bronze Age individuals is investigated for ancestral contribution from three different archaeological groups; TRB (Ansarve), and PWC from Gotland, and a CWC group based on the large dataset from Saxony-Anhalt (see Supplement Paper II, Table S4 for details). The haplogroup resolution was also extended to get more power in the analyses. The haplogroup frequencies are visualized in pie charts. 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. Two approaches are used here, one using two (non-admixed) parts, and one using a 3-way model including all three groups, the models were then tested for goodness of fit (see Paper II for details).

### 7.8 Kinship analysis

Mitochondrial and Y-chromosome haplogroups are commonly used to infer family relationships; however, they are mainly used to exclude certain direct relationships as most mtDNA and YDNA haplogroups are common in unrelated individuals. Thus, they cannot be used to infer the actual degree of relationship between individuals. Paper III utilizes a method that investigates 1st to 3rd degree relationship in individuals based on autosomal DNA (Kuhn et al., 2017) (see Supplement Paper III).

### 7.9 Investigating population structure

It has been shown from PCA analysis of a large number of SNPs from present-day Europeans across the continent that, despite low average levels of genetic differentiation, there is a close correspondence between genetic and geographic distance (Novembre et al., 2008). The results showed that an efficient geographical map of Europe can be visualized from the two dimensional summary of genetic variation in Europeans. This is used as a backdrop to investigate genetic affinity of prehistoric individuals. PCA analyzes can be done completely without pre-defining the individual's group affiliation. Individuals based on low coverage data are analyzed separately together with the present-day data and then each individual is projected on top of the PCA space (see e.g. Skoglund et al., 2012). In this way as little as 2% genomic coverage is sufficient to compare individuals to each other. This allows for a first inspection on the genomic relationship between the individuals studied, and also to compare with other ancient individuals from various archaeological contexts and to present-day European groups (see Supplement Paper III).

Another estimation of ancestry in unrelated individuals which is used for admixture and population structure inferences utilize model-based clustering approaches (Alexander et al., 2009; Pritchard et al., 2000). Clustering methods can infer ancestry components in individuals based on the genetic variation found in them. This can be done both unsupervised (without predefinition) and supervised in which some populations are pre-defined.
Unsupervised admixture will estimate the different ancestry components for each individual. The results are presented in clusters (defined as K) where the different ancestral components are often visualized using different colors corresponding to the size of the ancestry component (see Paper III and Supplement). The unsupervised admixture proportions gives an indication of the ancestral admixture components in each individual.

Both these methods are often used as a first choice of approach to get an overview of the pattern of ancestral components in each individual. This initial exploration of the genetic data can be further analyzed through more specific model-based tests.

### 7.10 Three-population and four-population tests

The methods; 3-population tests ($f_3$-statistics) and 4-population tests ($f_4$-statistics) are formal model-based tests for investigating admixture and shared drift. These tests are commonly used to measure the shared genetic drift between populations and individuals, which is interpreted as shared ancestry.

The $f_3$ statistic is designed to test whether a population 'C' descends from the admixture of two populations, referred as 'A' and 'B'. The $f_3$-statistic is generally set up as $f_3(C: A, B)$ where C is the target population that is tested for being an admixed group of populations A and B.

**Outgroup $f_3$ statistic** is a special case of the $f_3$ statistics which provides a direct estimate for the shared genetic drift between the reference populations A and B, thus reflecting their genetic proximity (Leonardi et al., 2017; Patterson et al., 2012). Making C a true outgroup (a population that has not shared any gene flow with populations A and B since they diverged) results in a positive value for the $f_3$-statistics proportional to the length of the shared drift between populations A and B. By using a fixed population (e.g. A), and only population B is exchanged, a relative measure of genetic similarity for all populations B to A can be inferred based on the value of the $f_3$ statistic (Sell, 2017). The outgroup $f_3$ statistics is set up as e.g. $f_3$(outgroup: population A, test). Population A is either an individual or a group, and the test will be substituted for all groups/individuals for which the similarity of the sample is of interest (see Supplement Paper III). The $f_3$ outgroup statistics is used here to find trends of shared ancestry in the different populations which then can be further tested.

The $f_4$-statistics is used to estimate the relationship between four populations e.g. $f_4(A,B;C,D)$, where, a *priori*, A and B are assumed to be closely related, and C and D are assumed to be more closely related. Exchanging A for a true outgroup to all populations e.g. $f_4$(O, test; C,D) limits the test results to show (relatively) recent admixture between the test and C (if positive), or the test and D (if negative). Standard errors (SE) and Z scores for $f_4$ statistics are estimated using a weighted block jackknife strategy incorporated into the ADMIXTOOLS suit (Patterson et al., 2012). The Z score show significance of the test, and $|Z| \leq 3$ (for negative values), and $|Z| > 3$ (for positive values) shows a significant result. The SE can be displayed as error bars in the plots. The more data available for each sample in the comparisons the smaller the SE, and as many of the samples included in paper III comprise low coverage data, using 2 SE in some analyses show large error bars. Thus, displaying 1 SE error bars in some of the analyses here indicates trends and not significant results.
7.11 Population diversity
Genetic diversity, e.g. individual or population heterozygosity, can be estimated from sequence data and is informative about effective population size in the prehistoric groups. Effective population size, which is a measure of genetic drift in a population, is not the same as the census size, but these two parameters can be correlated. A large effective population size typically indicates a large population size over the relatively recent past of the population. Comparative genetic diversity estimation can identify signs of isolation, or bottleneck events in the population’s history, such as serial founder effect.
8 Synopses of the papers

There are three papers making up this PhD thesis each of them exploring different aspects of the population demography during the Neolithic period on Gotland through multidisciplinary analyses of human remains from the megalithic burials.

**Paper I. New insights on cultural dualism and population structure in the Middle Neolithic Funnel Beaker culture on the island of Gotland.**

This paper presents the internal chronology, maternal inheritance, mobility, and dietary patterns of individuals buried in the Ansarve dolmen on Gotland. Additionally, sixteen new environmental Sr-values from six locales are presented for the Gotland Strontium biosphere and discussed in relation to newly presented Sr-data from the Viking Age harbor in Fröjel. These results are used as a background for the mobility analysis in this study. This paper gives the empirical background and grounding for this thesis in regards to the population demographic development on the island during MN A, and investigates the maternal relationship of this group to Neolithic farmer and HG groups in Europe. Specifically, the maternal relationships to TRB groups in Sweden and continental Europe, and the sub-Neolithic PWC related groups on the island are investigated. The dietary pattern from these individuals is compared to that seen from investigation of contemporaneous TRB megalithic burials in Sweden, as well as a local PWC group from Västerbjer. This paper also lays the foundation for the analyses performed in Paper II and Paper III.

The results show that the dolmen was used continuously over a 600 year period (from c. 3300-2700 cal BCE) which extends the TRB phase on Gotland 300 years forward. Thus, this burial was contemporaneous with PWC on Gotland for at least 500 years. Two secondary burials in the LN period were also noticed. Nine of the individuals from the MN phase gave results for mtDNA which showed maternal continuity with central European farming populations. The high haplogroup variation within the group indicated that the burial site was not dominated (maternally) by one closely related group. The mtDNA haplogroup composition closely resembled individuals buried in MN passage graves in Sweden, but differed from the PWC groups on Gotland. This was further supported by the dietary patterns which resembled a slightly mixed terrestrial diet similar to other TRB groups in Sweden, distinct from the strict marine diet of the PWC.

Eleven individuals evenly distributed across the whole phase of usage (including the two LN individuals) were analyzed for childhood mobility. A conservative Sr-baseline value was calculated based on the combination of the local Sr-data in this study and the Fröjel data which gave a broad range 0.70981–0.71534, 2 SD (n = 26, 7 locales) and needs to be further refined with more data from additional locations. Regional Sr-ranges were also detected at some locales. One individual from the end of the phase of usage showed a deviating Sr-value to that of the others which, although divided in two clusters, showed Sr-values within the range found for the Ansarve dolmen. At least one of the LN individuals was of non-local origin, but possibly both, as well as the other individual with a deviating signal from the end of the MN phase. These results indicated that individuals from two different cultural complexes, TRB and PWC, coexisted on the island of Gotland for half a millennium with different cultural affiliations and subsistence strategies.
Paper II. The Stone Cist Conundrum. A multidisciplinary approach to investigate Late Neolithic/Early Bronze Age population demography on the Island of Gotland

This paper presents the internal chronology of four LN/EBA stone cist burials on Gotland, as well as maternal inheritance, mobility, and dietary patterns of individuals buried in these graves. Additional environmental Sr-data is also presented and the Strontium biosphere for Gotland is further refined and discussed in regards to the geological background of the island, and used for the mobility analyses. In this study, individuals are analyzed for mobility during different periods of their life-time, and are also, when possibly, compared to the regional Sr-values from the location of the particular burials. This paper gives the empirical background, and grounding for this thesis in regards to the population demographic development on Gotland during the LN period, after the TRB, PWC and, possible, BAC phases on the island. Specifically, the maternal ancestral contributions from TRB, PWC and BAC to the LN people are investigated. The mtDNA haplogroup variation within the burials is compared to the haplogroup frequencies seen from the local TRB (Ansarve dolmen) and PWC groups on the island. The ancestral contribution from BAC was examined on the basis of individuals from CWC contexts in Saxony-Anhalt in central Germany as a proxy for BAC groups in Scandinavia.

The results show that the stone cist burials were used by local groups that were well established in the areas of the burials, and the one burial (Häffinds) that was most extensively dated was used continuously from LN I to BA II (see Fig. 1B for LN-EBA timeline divisions). Two other sites revealed activity starting from LN II (Utalskog and Suderkvie). However, most burial activity was noted in the BA I period at which time some activity involving the manipulation of human remains outside the cists also was conducted. Only one burial gave result for BA III. The individuals displayed a strict terrestrial diet in contrast to the preceding archaeological groups on the island. Secondary LN reuse of the Ansarve dolmen was noted by nonlocal individuals with displayed deviating dietary patterns from that of the individuals in the cist burials. Additionally, a nonlocal female at the Häffinds burial was buried in the opposite direction to that of the others in one of the burials during BA I.

Due to poor preservation, only individuals dated from EBA gave results for mtDNA and all individuals (n = 11) showed unique haplotypes. Thus, none of these individuals belonged to the same maternal lineage. Some of the haplogroups had previously been noted in individuals from local TRB and/or PWC contexts, as well as, in the CWC group from Saxony-Anhalt, but some were also unique to the EBA cists. The modeling for ancestral contribution favored a model with 55% CWC and 45% TRB, but a model with 50% CWC, 45% TRB and 5% PWC also showed a good fit. These results are difficult to reconcile with the archaeological record on Gotland. Thus, the maternal inheritance patterns, together with the Sr-results and the archaeological record, suggest sizable migration to the island during the LN period by people with a new economy, as well as new burial customs. However, some levels of admixture with smaller local groups of PWC-related individuals could also have occurred on the island.

Paper III. The genetic history of the people buried in the Ansarve Dolmen on Gotland and the northeastern most expansion of the Funnel Beaker Culture

This paper presents genomic data from six individuals buried in the Ansarve dolmen on Gotland from three different time-periods during the main phase of usage. This paper investigates the genomic affinity and admixture components of these individual in rela-
tion to the three main ancestral admixture components linked with Mesolithic HGs, and the Neolithic and Bronze Age expansions in continental Europe. This paper adds to the empirical background and grounding for this thesis in regards to the internal relationship in this burial as well as population demographic development on the island during MN A. Specifically, it investigates kinship within the burial, and ancestry in the Ansarve individuals in relation to different Mesolithic groups, Neolithic farmers and individuals from contemporaneous Scandinavian contexts such as TRB (Gökhem), and sub-Neolithic PWC, but also contexts with potential ancestral links to individuals from BAC/CWC contexts on the mainland. It also investigates HG admixture over time, specifically in relation to the contemporaneous PWC on the island.

The results give direct evidence that the six individuals from the dolmen show ancestral affinity with the Neolithic farmer expansion driven by migrating groups with distinct genetic make-up, and show close affinity with the contemporaneous TRB on the Swedish mainland. We find that the Ansarve individuals show slightly elevated HG admixture to that of other contemporaneous individuals from farming contexts, but it does not increase over time. The HG admixture source in the Ansarve group does not seem to derive from the contemporaneous local PWC on the island, or Scandinavian SHG. Instead, we suggest that the HG admixture happened in the ancestors of the Ansarve individuals, prior to arriving on Gotland. This is, however, in contrast to the individual from TRB context on the Swedish mainland which showed strong affinity to a PWC related source. There also seem to be differences in the farmer demographic origins in the Ansarve and Gökhem groups. Both Scandinavian groups show low diversity to that of other EN-MN farming groups in continental Europe. We also find a 2nd degree relation between two contemporaneous males, and all four males analyzed from this burial shared the same Y haplogroup. We did not see evidence of extensive admixture in the chronologically later Ansarve individuals in relation to the admixture component found in contemporaneous individuals from BAC/CWC contexts.
9 Discussion

9.1 Chronology and population demographic developments seen through genetics

A new Stone Age on Gotland is starting to emerge from the results from this thesis, as the demographic developments during the Neolithic period are becoming clearer. Previous summed probability distribution modeling of radiocarbon dates (SPDRD:s) (Apel et al., 2018) has identified several different population booms and declines during the Stone Age on Gotland. The first boom is associated with the Middle Mesolithic pioneer settlement, starting around 7200 BCE. Four individuals from Stora Bjers and the Stora Förvar cave from the pioneer phase on the island have recently been genetically analyzed and they show shared ancestry with other European Mesolithic hunter-gatherers, both from the west and from the east, which makes the genetic ancestry of these SHG individuals distinct (Skoglund et al. 2014a, Günther et al., 2018). They also display similar genetic affinities with the later SHG from Motala (Lazaridis et al 2014). There is a marked population decline on the island around c. 5600 cal BCE. This is followed by a hiatus period up to c. 4500 cal BCE when a second boom is noticed in the SPDRD model associated with Late Mesolithic activity, and another population boom is noted just after 4000 cal BCE associated with EN TRB activity (Apel et al., 2018).

The archaeogenetic analyses in this thesis show direct evidence that people buried in the Ansarve dolmen had origins in the Neolithic farmer expansion on the European mainland (Paper III). They show close genetic affinity to individuals from MN TRB context on the Swedish mainland which, together with the archaeological record on Gotland, shows that these individuals were part of the large TRB complex that is also associated with the Neolithicization of Scandinavia. Individuals associated with an EN TRB context in Sweden (Mittnik et al., 2018) show the same genetic make-up as the MN TRB groups connected with the Neolithic expansion (Skoglund et al., 2012, 2014a), thus the EN introduction of TRB on Gotland most likely also involved migration of new groups of people.

The fact that these people also built a megalithic tomb several hundred years after the introduction of the TRB culture to the island shows that the people connected with TRB contexts on Gotland stayed in contact with other TRB groups on the mainland. The exact genetic origin of the Ansarve individuals can unfortunately not be established until more reference data is available from relevant archaeological groups, however they appear to show a different genetic ancestry compared to that of the contemporaneous individual from Gökhem (Paper III). The new radiocarbon datings from the dolmen (Fig. 11) show that it was used continuously for at least 600 years and thus extends the TRB phase on Gotland with at least 300 years up to c. 2700 cal BCE (Paper I).
The next population boom on the island seen in the SPDRD model is associated with the large PWC complex with a peak around c. 3000 cal BCE followed by a decline towards the end of the MN period (Apel et al., 2018). The new dating of the dolmen shows that the TRB and PWC cultural complexes on Gotland overlap for at least 500 years. The Ansarve individuals’ show some limited HG admixture, but this admixture does not seem to derive from Mesolithic SHG, or the local PWC on the island, but rather a WHG source from continental Europe (Paper III). Thus, it appears that most of the HG admixture already had happened in the ancestors of these individuals prior to arriving to Gotland. Some increased levels of HG admixture has also been noted in other MN farmer groups compared to the EN farmers in continental Europe (e.g. Günther et al., 2015; Mathieson et al., 2015). However, the HG ancestry does not seem to increase over time in the Ansarve group suggesting that there was little contact between these individuals and the local PWC groups.

As there is some archaeological evidence of LM activity on the island prior to the arrival of EN TRB, there is also a possibility that the EN TRB admixed to some extent with local Late Mesolithic HG groups on the island. This would, however mean that the LM population boom on Gotland seen from the SPDRD model also involved migration of new groups with WHG ancestry, and does not reflect population continuity from the Middle Mesolithic SHG on the island, or the Scandinavian mainland. Future analyses of LM individuals from the southern and southwestern Baltic Sea area, and also from Gotland, are needed to further investigate this topic.

The fate of the TRB on Gotland is not known, but from the archaeological record, and also the genetic studies in this thesis, they do not seem to be absorbed into the PWC complexes on the island. The Ansarve group shows low diversity compared to continental farmer groups from the EN to the Chalcolithic (Paper III). However, the diversity of the Ansarve group is in line with what is seen from the MN TRB group on the Swedish mainland, and may be a general pattern of Neolithic populations at the fringes of their geographical distribution. Further investigation is needed in order to identify if the Ansarve group were isolated on the island.
Previous research has shown that the PWC individuals have ancestral origin in Mesolithic SHGs, but also show slight admixture with farmers (Mittnik et al., 2018; Skoglund et al., 2012, 2014a). Interestingly, in contrast to the Ansarve group, the individual from Gökhem showed significant results for admixture with a PWC related HG source (Paper III), which also has been noted previously (Günther et al., 2015; Skoglund et al., 2014a). Future analyses will reveal if the PWC admixture component in the Gökhem individual is a result from admixture with local PWC groups on the mainland, meaning that there was gene flow from a PWC related source.

The arrival of PWC on Gotland is also somewhat later in time than what is seen in eastern central Sweden (Björck, 2003) which could mean that PWC and TRB populations already were admixed on the Swedish mainland, prior to the PWC groups arriving on the island. The mitochondrial haplogroup composition in individuals from the Swedish mainland TRB and PWC contexts from Öland and Gotland, although mainly distinct, also shows a slight overlap (Malmström et al., 2015). This was also noted in the Gotland TRB group from the Ansarve dolmen showing some levels of shared maternal ancestry with PWC individuals (Paper I). Future genomic analyses of additional individuals from PWC and TRB contexts will reveal to which extent these different groups interacted in Scandinavia.

The third genetic admixture component most evident in individuals associated with the continental CWC and Yamnaya complexes during Scandinavian MN B has not been identified in any of the Gotland PWC individuals included in this thesis (Skoglund et al., 2012, 2014a), neither was it detected in any of the Ansarve individuals from the later part of the MN phase of usage (Paper III). The radiocarbon dating from the dolmen also revealed secondary usage during LN I and LN II (Fig. 11) which is at least 400 years after the TRB, and also just after the PWC, phases on the island. Only one of these individuals (from LN II) yielded enough genetic data to confirm mitochondrial haplogroup showing mtDNA haplogroup U5b (Paper I). This haplogroup has previously been found in individuals from both PWC and CWC contexts (Brandt et al., 2013; Malmström et al., 2009, 2015).

Only one of the stone cists, Häffinds, which was more extensively dated, revealed LN I dates and also showed continuous usage into BA II (Paper II) (Fig. 11). Thus, the initial phase was overlapping with the secondary usage in the dolmen. Two additional burials were also dated to LN II; the natural stone cist at Utalskog, and the female skeleton next to the stone cist burial at Suderkvie. However, the Suderkvie stone cists only revealed EBA dates indicating that this burial and the female skeleton derived from two separate burials. Interestingly, BAC pottery has been found in connection with the Early LN period at the Rojhage site (Rundkvist et al., 2004) in close vicinity to Suderkvie, thus there is a possibility that the female burial at Suderkvie is connected with this archaeological cultural phase. The stone cist at Hägur also only showed EBA dates. However, all the cist burials included many individuals, and thus it is possible that they also were used for longer time-periods.

Unfortunately, due to poor preservation only individuals from the EBA periods in the stone cists yielded sufficient mitochondrial data. They all revealed unique haplotypes, but some of these haplogroups have previously also been found in individuals from TRB, PWC and/or CWC contexts (Paper II). No specific correlation could be found in the maternal lineages of these individuals with spatial connection to the earlier manifestations.
such as TRB at the Suderkvie site, and at the Hägur burial in close vicinity to the Ajvide PWC site on the Eksta coast. The modeling for maternal ancestral contribution based on the haplogroups in individuals from the Ansarve dolmen (Paper I), and from PWC contexts on Gotland (Malmström et al., 2015), as well as the CWC group from Saxony-Anhalt (Brandt et al., 2013) showed that the PWC group, which is the only archaeological group that had persisted on Gotland up until the LN period, contributed little to the mitochondrial genepool found in these burials during the EBA period (Paper II). Instead the main maternal ancestral contribution seems to derive from haplogroups associated with the Neolithic expansion and the combination of haplogroups found within the CWC in continental Europe (Paper II). This result is difficult to reconcile with the archaeological evidence found on Gotland during the MN/LN transition and is best explained if the admixture seen in these individuals had happened prior to arrival to Gotland. Thus, these results suggest migration of new groups to the island, which is also supported by the unique haplogroups found in some of these EBA individuals.

9.2 Dietary patterns over time

The stable isotope analyses have given important insights into the life history of the studied individuals, and the results also complement the archaeogenetic data. The dietary analyses revealed that the people in the Ansarve dolmen mainly had a terrestrial diet distinct from that of the local PWC individuals, but some individuals also displayed a mixed diet including some input of freshwater fish or marine protein dividing these individuals into two clusters (Paper I). However, there was no obvious change in diet over time, but it appears as the people buried around c. 3000-2800 cal BCE displayed a more strict terrestrial diet in comparison to the individuals in the beginning, and also to some extent in the end, of the MN phase of usage. The individuals analyzed from the MN period in the Alvastra dolmen in Östergötland (Fornander, 2011a), close to the large inland Lake Vättern, were intermediate to the clusters found within the Ansarve group. However, there had also been some mobility within this burial as people not local to the area was revealed (Fornander, 2011b). Some of the individuals from the contemporaneous passage grave on Öland, used by mainly local individuals (Fornander et al., 2015), displayed a more marine diet (Eriksson et al., 2008) in comparison to the Ansarve group (Paper I). The LN/EBA individuals revealed a dietary shift from that of the individuals in the preceding archaeological groups and displayed a uniform terrestrial diet across all burials (Paper II). Interestingly, the individuals from contemporaneous secondary LN burials in the dolmen showed a deviating dietary pattern, both from each other, as well as from that of the individuals in the stone cist burials.

Thus, contrary to what was noted on Öland, it appears as farming and/or animal husbandry played a more significant role in the TRB populations on Gotland, (seen through the individuals buried in the dolmen), starting around the beginning of the third millennium BCE. This also coincides with the population peak of the sub-Neolithic PWC complexes on the island that had a strict marine economy based on sea mammals and fish. The final shift to the use of exclusively terrestrial resources happened in the second half of the third millennium BCE in connection with the people buried in the stone cists (Paper II), similar to the developments seen on Öland (Eriksson et al., 2008). This development happens after the final phase of the PWC complexes on the island, which suggests that new groups started to arrive to Gotland in the LN period with a new economy, as well as new burial customs, supporting the conclusions made from mitochondrial DNA, and also indicating
the timing of these events. Thus, dietary culture seems to be an important indicator of demographic change also in these different Neolithic groups on Gotland.

9.3 Strontium baseline
The Sr-baseline for Gotland has been further established based on the analyses in Papers I and II, and also together with the faunal data from the Ridanäs Viking Age harbor in Fröjel (Peschel et al., 2017). The earlier Sr-baseline (0.71000-0.71200, 2 SD) reported from Price et al. (2014) and Wilhelmson and Ahlström (2015) was not included as the individual results had not been published. The combination of results from the different locales retrieved in this thesis allowed for exclusion of outlier results based on soil samples (Supplement Paper II). However, some single Sr-values, that are high in comparison, still need to be confirmed from (i.e. Visby, Västergarn, and also Ridanäs, see Fig. 12). The other locales showed some regional Sr-isotopic variation which fall within 0.70980-0.71361 (n = 23, 7 sites), thus this range could be more realistic for the limestone environment of the Gotland biosphere. The Sr-baseline used in this thesis includes the higher Sr-values mentioned above and gives a more conservative measure of 0.70890-0.71500, 2SD (n = 36, 10 sites) (Paper II), thus individual results close to the upper and lower baseline boundaries may in fact show nonlocal results. All sampled sites consisted mainly of bedrock and postglacial layers; however some areas also comprise partial distributions of till (moraine) which could affect soil sample results with signals from nonlocal older geological formations (Fig. 12). As most of these locales are based on sites along the former coastline (with the exception of Buttle), additional sampling at these and other locales will help to fine tune the Sr-baseline for the Gotland biosphere.
Fig. 12. Base maps: Geological maps of Gotland from the Geological Survey of Sweden, data © SGU (modified from Paper II). Left. Sedimentary carbonate platforms with Strontium sample locations (Paper I and Paper II), and Ridanäs Viking Age trading port (Peschel et al. 2017). Right. Soil type distribution with current environmental Sr-values.

### 9.4 Mobility patterns

The Sr-isotope analyses have given important insights into the demographic developments in the different time periods, as well as within the burials, and the results also further complement the archaeogenetic data. Interestingly, most of the individuals Sr-analyzed from these burials showed local early childhood Sr-signals indicating well-established groups on the island (Papers I and II).

The Ansarve analysis showed local individuals from the whole main phase of usage and, although distributed in two groups, the Sr-values fell within the local range found in the area showing that there were local TRB groups present on Gotland at least up to c. 2700 cal BCE. Only one individual from the end of the main phase of usage (2810-2580 cal BCE, 95% CI) showed a deviating Sr-value close to the upper 2SD boundary and could thus be of nonlocal origin. This individual also displayed a different dietary pattern with higher levels of marine protein, which could have some effect also on the Sr-value. Although, living at the time of the BAC/CWC expansion, this individual showed genetic
affinity to the Ansarve and Göhem individuals, as well as other contemporaneous farmers from continental Europe, rather than individuals from BAC/CWC contexts on the mainland (Paper III). Interestingly, both LN individuals displayed nonlocal early childhood Sr-signals showing mobility to the island. Unfortunately, only one yielded genetic results and it was not possible to retrieve nuclear data. However, this result shows that incoming people were adding to the already existing mitochondrial gene pool previously found in PWC individuals on the island (Paper II).

The analyses from the stone cist burials (Häffinds, Hägur, and Utalskog) revealed that most of individuals analyzed were local to the area where the burials were situated (Paper II). The Häffinds burial showed some mobility in the individuals across time, but most individuals still showed local Sr-values. Several of these individuals showed that they had moved numerous times during their life-time, in contrast to what was noted from the other burials. Only one nonlocal individual was identified; one female buried in the Häffinds burial during BA I. She had also moved several times before arriving on Gotland. Interestingly, she was buried in the opposite direction to that of the others in this cist burial (Paper II).

These results show that the megalithic burials originally were mainly used by local groups, whereas the secondary usage of the dolmen was made by nonlocal people at the same time as stone cists were started to be built on the island. Thus, it is plausible that secondary usage of megalithic burials from non-local individuals could be an indication of demographic changes that happen before new groups had become established in the area and had the possibility to claim their own land, and/or lacked the resources to build a burial monument of their own.

9.5 Kinship and internal relationships within the burials

As most of the genetic data retrieved at the time of these analyses were based on mitochondrial DNA it was only possible to investigate kinship in the Ansarve burial (Papers I and III). The skeletal remains in the burial were fragmented and commingled, thus the internal relationship within the burial could not be determined. Nine individuals gave results for mtDNA and showed seven unique haplotypes. The nuclear analyses revealed two females from the early phase of burial that shared much drift but they were not close kin related; they also displayed different maternal lineages. The other four individuals were all males; three were contemporaneous and shared the Y haplogroup I2a1b1a1a, the other individual was the nonlocal individual from the end of the usage phase. Due to some missing data his YDNA haplogroup could only be resolved to the level of I2a1b. Two of the contemporaneous males were related to 2nd degree and could be half-brothers, uncle-nephew, grandfather-grandson, or double cousins. Thus, it appears from these results that there were more male than female kin relations in this burial, suggestive of a patrilocal society.

The Häffinds cist is the only burial that contained information on individuals’ positions inside this cist and also showed continued usage over a long period (LN I-BA II) (Paper II). The radiocarbon dating showed that the skeletal remains were moved to the sides to make room for new individuals buried during BA I. The BA I period was the most active phase in the burial where there also seemed to be additional manipulation of skeletal remains outside the cist. There were also differences in the treatment of the buried, where some were placed in anatomical position in the center of the cist cist and in many cases
the skeletons/bodies were kept intact even if new burials occurred. Other individuals, even if they were chronologically younger, were sometimes completely disarticulated and commingled. Additionally, the nonlocal older female at Häffinds was buried in the opposite direction which shows interesting behavior in terms of the burial practice (see Paper II for details).

9.6 Does genomics allow for fine scale analyses regarding the demographic changes seen in the archaeological record on Gotland?

The work of my thesis have provided new insights into the demographic developments on Gotland, results that were previously not possible to infer. From analyses of the genomes of human remains we can trace the population history in individuals from different contexts and, even if the archaeological record is lacking burials for certain time-periods and cultural contexts, the genetic distinction found between the individuals show direct evidence of specific population events. These studies are specifically well suited in analysis of distinct groups. It is more difficult to analyze affinity to different groups with similar ancestry (e.g. affinity to different WHG groups across Europe, or different farmer groups) as the differences are so subtle that they can rarely be supported by significance, it also varies on individual levels. The differences of admixture levels within the different groups; e.g. the different HG admixture levels among farmer groups also pose a challenge for fine-scale investigations of the relations among the different farmer groups. However, it is possible to detect trends, and as more individuals are analyzed in the future, we might also find evidence of direct association between similar groups from different geographic regions.

The depth of the analyses however is governed by the genomic coverage retrieved from the studied individuals, levels of contamination, and also the available reference material (both in terms of genomic coverage and archaeological relevance to the group studied). Individuals exhibiting genome coverage of <1x has few overlapping SNPs with each other, and cannot always be directly compared on a significant level. Some of the interpretations can thus only be derived from what we do not observe, instead of what we do see which leaves some questions unanswered. The methodology used in this study was designed based on the data available at the time; however, there are also many other types of analyses that can be implemented to answer research questions, especially on higher coverage samples.

Again, it needs to be emphasized that the conclusions drawn here are based on the life-history of single individuals, or groups of individuals from specific contexts. Thus, they should only be interpreted as such; the genomic analyses show snapshots of time in specific individuals’ ancestry that should not be extrapolated as absolute facts for the total developments for an entire archaeological cultural context. For instance, the Ansarve burial is unique in terms of the TRB manifestation on Gotland. We do not know where the individuals associated with the EN TRB were buried; neither do we know what happened to the other people that were contemporaneous with the individuals within this burial. Thus, the conclusions drawn here regarding the interaction between individuals from the different cultural contexts only refers to these specific individuals analyzed here. We do not know the genetic ancestry of the other people buried in the dolmen. But, we can see that these particular individuals show similar ancestry and life-history to each other, even across time, which allows for certain conclusions regarding this particular
group of individuals. They were the decedents of the local TRB groups that did not seem to interact much with other local distinct groups on the island.

9.7 To what extent can the combination of the different scientific methods be used to provide new information regarding archaeological research questions concerning population continuity, migration and admixture in different time periods?

Mitochondrial DNA is very useful for detecting strong demographic shifts and population continuity during these time periods, and is especially informative when contextualized from the results generated from the other methods. As seen in the stone cist analyses, even though mitochondrial data only was retrieved from some of the EBA individuals studied in the graves, the combination of the results generated from the dating, dietary and mobility analyses, together with the archeological background allowed for inferences even in the Late Neolithic period.

However, the fact that most individuals studied showed local Sr-signals made the questions regarding endogamy and exogamy in these particular burials not applicable. For these types of questions the sex of the individuals also has to be known. Most of these samples in these studies were small skeletal parts, loose teeth, or juvenile individuals that could not be assesses for sex. Thus the possibility to include biological sex determination based on low coverage nuclear data in these types of studies is very valuable from an archaeological stand point. Additionally, low coverage nuclear data of >2% can be used for close kinship analyses, and also to estimate genetic affinity via PCA analysis which would be a very valuable and informative asset for the contextual interpretation of the burials.

The possibility to combine the above mentioned data on many individuals from the same context together with finer scale analyses of genomic structure, admixture, and ancestral contribution on a subset of individuals provides enormous insights into these people lives. The analyses used in this thesis provided information on the ancestors of these individuals showing their origins and demographic history, as well as interactions with other groups on the island. Further, analyses on admixture proportions and diversity will reveal more in-depth insights on the history of these individuals.

9.8 Reflections

The field of archaeogenomics has evolved around me as my thesis project progressed. New methodology and new insights were constantly presented which transformed the field. I have had the privilege to work in close collaboration with professional computational biologists in my project which has allowed me to address some of the specific research questions I have set up for my materials. In this PhD project I have designed the research questions, collected and contextualized my own research materials, and generated my own genetic data. The Atlas project allowed me to expand my research and work freely; it also allowed me to include the additional Strontium analyses, and more radiocarbon dating in this project which brought the analyses to a different level.

The data has become “easy” to retrieve in the lab, but requires many different steps and analyses for the sequencing process to be able to generate enough data for the analyses. The bioinformatics support structure developed simultaneously with my laboratory work,
and the sequencing center (SciLifeLab), as well as the computational environment in Uppmax had to expand to keep up with the massive amount of data that have been generated within the Atlas project. This also created long queues and even pauses, and sometimes it took as long as six months to get results from one screening of samples. However, the infrastructure and workflow has evolved and become much more streamlined over the years which have improved the speed of the data retrieval process.

The genomic data analyses, however, demand several years of specialist training to master. From a PhD students’ perspective then the main focus needs to be on laboratory methodology, bioinformatics, and computational biology, and little time is left for in-depth research in the other fields. However, one need to know the archeology to be able to set up the questions, one also need to know European pre-history and archaeology in order to work with the genomic reference materials available today, and to be able to design the different analyses accordingly. Thus, a large part of my work involved researching, interpreting, and explaining the archaeology behind my project and reference datasets to my collaborators, and learning how the different computational tests can be used, in order to set up the proper analyses that were used to interpret the data.

9.9 Future prospects

I can only see that these new methods are here to stay as they are extremely valuable for archaeological research, but there needs to be more developments towards integration between the different disciplines in order to use the full potential of genomics in archaeology. The emergence of new data in the future from more relevant reference groups will also provide additional fine-scale information of the population structure and demographies during these time periods in Scandinavia and the Baltic Sea area. This will further the possibilities to study demographic and social processes on regional levels and with a higher resolution.

For these fields to truly integrate in the future, however, there needs to be more collaborative projects where the individual researchers do different parts in larger collaborative archaeological research projects. More money also needs to be invested in archaeological research projects in general to be able to implement radiocarbon dating and isotopic analyses as standard tools for contextualizing the materials. As is seen in the work from this thesis; in here lays the fundamental background for the interpretation of the in-depth genetic analyses.
10 Acknowledgements

There are so many people that I would like to thank for helping me finishing this work, and I sincerely hope that I am not forgetting someone.

First I want to thank my husband Simon Höjeberg and our boys Tore and Knut for your enormous patience and support!

I would like to thank my supervisor Kjel Knutsson for taking on this project, and for all the support and guidance. And my co-supervisors; Paul Wallin at Campus at Gotland for your positive attitude and feedback and interesting research projects, Mattias Jakobsson at EBC, UU for your generosity and support which allowed me to perform the genetic analyses on Gotland, and also for inviting me into your incredibly inspiring research group, and Anders Götherström at AFL, SU for all the years and interesting conversations. I also want to give a special thanks to Jan Storå at OFL, SU for your enormous generosity with your time, support with the dating and isotope analyses, and also feedback in manuscript writing.

I want to thank my collaborators; Federico Sanchéz-Quinto at EBC for great discussions, your time and patience, and for processing the genetic data and computing the analyses in Paper I and III. Per Sjödin at EBC for all the interesting discussions and for designing and computing the mitochondrial analyses for Paper II. Jane Evans at NERC, Isotope Geosciences Laboratory, UK for producing the Strontium data and discussions regarding the analyses in paper I and II. Gustaf Svedjemo at Campus Gotland for providing the geological maps in Paper II. Emma Svensson at EBC for producing the Kolin data for Paper III. Radka Šumberová and Hana Brzobohatá for providing the Kolin samples and the archaeological background for this site in Paper III. And Helena Malmström for assigning the YDNA haplogroups in Paper III. I also want to thank Jan, Mattias, Kjel, Paul, Emma, Federico, Per, and Torsten Günther for valuable discussions and proof reading manuscripts. And also Kjel, Jan, and Mattias for the race in getting this thesis finalized in time.

I would also like to thank several people that have helped me over the years in the Jakobsson lab, EBC; Helena, Emma, and Irene Ureña for getting me started with the library building, and also Pontus Skoglund and Torsten Günther for processing the early sequence data. Emma and Hanna Edlund for all the post-PCR and sequencing organizational support. Hanna, Irene, Ricardo Rodríguez Varela, Luciana Simões, Mario Vicente, Alexandra Coutinho, Ayca Wärja, Berenice Villegas, and Lena Granhäll for helping me with the bioanalyzing or other lab support when I couldn’t make it to Uppsala. And a special thank you to Arielle Reivant Munters for all the bioinformatics support, organization, and contamination checks, and also Robin Ohlsson for processing sequence stats.

I would also like to thank Alexander Sjöstrand, Anders Gustavsson and Sandra Gytare at Campus Gotland for interesting discussions regarding the osteological evaluations, and Alexander for the osteological analysis of the missing individual. Markus Fjellström at AFL for producing stable isotope data. Thank you Leena Drenzell at SHM and Lena Ideström at Gotlands Museum for providing samples. And Göran Burenhult for discussions and photographs regarding the Häffinds burial context.

Thank you Anders Eriksson, Thomas Holmgren and Camilla Widegren at Campus Gotland for putting up with all my deliveries. A special thank you to Anders for all the help with installing things and handy work in the lab. And also P.O. and Ola from Region Gotland for maintenance. I also want to thank Björn Broman, Kristian Söderholm, Svante
Agnestig, Pierre Westergren at Campus Gotland for all the IT technical support in the lab. A special thank you to Kristian for fixing the burned out connection in the clean bench after the power out. I also want to thank Barbro Thiele, Arne Häglund, Jane Klasson at Campus Gotland, Carina Ehn at Engelska parken, and Frida Svedbergh and Hanna Edlund at EBC for support in financial matters and for handling all the bills. And thank you to Olle Jansson, Bengt Jönsson, and Petra Eriksson at Campus Gotland, and also Kirs Höglund for helping me when I needed it. Thank you Margareta and Tommy Berglund for permission to photograph the Utalskog natural cist burial.

I also like to thank Mattias, Anders, and Jan for inviting me to be a part of the ATLAS research group, and for the financial support for laboratory costs, radiocarbon dating and isotopic analyses. And thank you for all the inspiring ATLAS meetings, excursions, and workshops over the years. And a special thank you to all the team members in the ATLAS project Torsten, Emma, Helena, Federico, Ricardo, Arielle, Ayca, Hanna, Luciana, Alexandra, Anna Kjellström, Torun Zachrisson, Maja Krzewsinska, Jonatan Lindström, Gulsah Merve Dal Klinic, Jan Apel, Olaf Thalman, Rita Peyroteo Stjerna, Natalja Kashuba, and Linus Flink for all the great discussions and support!

I also want to thank all the current and former Jakobsson lab members and associates who are not part of the ATLAS for always making me feel welcome and for all great discussions Pontus, Per, Mário, Lena, Robin, Berenice, Carina Schlebusch, Agnes Sjöstrand, Lucie Gatепaille, Gwenna Breton, Nina Hollfelder, Thijessen Naidoo, Tatiana Ruiz, Maximilian Larena, Amy Goldberg, and Cristina Valdiosera.

I would like to thank all the people at the department, and Campus on Gotland who have supported me over all these years. I want to make a special dedication to the late Inger Österholm, and also late Lars Beckman whose work on setting up the course in archaeogenetics on Campus (already in 2001), and also setting up the original aDNA lab (in 2003) has made my work here on Gotland possible. I thank Gustav Malmborg for letting over the gauntlet to me in 2007. And a special thank you to Sabine Sten for all the support over all the years, and also Helene Martins-son-Wallin, Gunilla Runesson and Karin Bengtsson, and De Badande Wännernas stiftelse. A special thank you to Mikael Eklund who helped me build the new aDNA lab on Campus in 2009. And to Anders Götherström for all the support over the 12 years that had lead up to this point; it has been a long and windy road since the hedgehogs... I want to thank my office roommates Alexander Andreeff and Alexander Sjöstrand, and also Gustaf Svedjemo, Jan Apel and Paul for all the great conversations and pep. I would like to thank Gullög Nordqvist, Lars Karlsson, Susanne Carlsson, and Neil Price at Engelska parken for all the support, and also all the people, especially all my fellow doctorands, at the department for always making me feel welcome and for all the good conversations. Finally a special thank you to all my former and present students for all the great conversations and for keeping me on my toes.

Thank you to Berit Wallenbergs stiftelse for my PhD funding, and also Gunvor och Josef Arnér stiftelse, and Helge Ax:son Johnssons stiftelse for grants.

Last but not least I would like to thank my family and friends for all your patience and encouragement over the years. This work is especially dedicated to my mother and my father whom unfortunately no longer are with us.
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