


RESEARCH ARTICLE

# The Neolithic Pitted Ware culture foragers were culturally but not genetically influenced by the Battle Axe culture herders

Alexandra Coutinho<sup>1</sup> | Torsten Günther<sup>1</sup> | Arielle R. Munters<sup>1</sup> |  
Emma M. Svensson<sup>1</sup> | Anders Götherström<sup>2</sup> | Jan Storå<sup>3</sup> | Helena Malmström<sup>1,4</sup> |  
Mattias Jakobsson<sup>1,4</sup> 

<sup>1</sup>Human Evolution, Department of Organismal Biology, Uppsala University, Uppsala, Sweden

<sup>2</sup>Archaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, Stockholm, Sweden

<sup>3</sup>Osteoarchaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, Stockholm, Sweden

<sup>4</sup>Centre for Anthropological Research, Department of Anthropology and Development Studies, University of Johannesburg, Auckland Park, South Africa

## Correspondence

Jan Storå, Osteoarchaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, SE-106 91 Stockholm, Sweden.  
Email: jan.stora@ofl.su.se

Helena Malmström and Mattias Jakobsson, Human Evolution, Department of Organismal Biology, Uppsala University, SE-752 36 Uppsala, Sweden.  
Email: helena.malmstrom@ebc.uu.se (H. M.) and mattias.jakobsson@ebc.uu.se (M. J.)

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## Abstract

**Objectives:** In order to understand contacts between cultural spheres in the third millennium BC, we investigated the impact of a new herder culture, the Battle Axe culture, arriving to Scandinavia on the people of the sub-Neolithic hunter-gatherer Pitted Ware culture. By investigating the genetic make-up of Pitted Ware culture people from two types of burials (typical Pitted Ware culture burials and Battle Axe culture-influenced burials), we could determine the impact of migration and the impact of cultural influences.

**Methods:** We sequenced and analyzed the genomes of 25 individuals from typical Pitted Ware culture burials and from Pitted Ware culture burials with Battle Axe culture influences in order to determine if the different burial types were associated with different gene-pools.

**Results:** The genomic data show that all individuals belonged to one genetic population—a population associated with the Pitted Ware culture—irrespective of the burial style.

**Conclusion:** We conclude that the Pitted Ware culture communities were not impacted by gene-flow, that is, via migration or exchange of mates. These different cultural expressions in the Pitted Ware culture burials are instead a consequence of cultural exchange.

## KEYWORDS

admixture, ancient DNA, migration, Stone Age

Helena Malmström and Mattias Jakobsson should be considered joint senior authors.

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## 1 | INTRODUCTION

Archeological interpretations of material culture were for a long time one of the dominant approaches in understanding past human societies and demographic changes. With the recent advancements in

archeogenetic research, we now have the possibility to study both the material culture and the people of past human societies. Based on recent archeogenetic investigations, it has become evident that human mobility, including large-scale migrations has shaped social and cultural development in many areas (Lazaridis et al., 2014; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014). These new results have revitalized the debate on how changes and patterns seen in the archeological material record relate to human populations (Kristiansen et al., 2017). However, there are concerns that interpretations may sometimes be oversimplified, which could lead to narrowing perspectives on both cultural entities and human groups, with potential unwarranted reinforcements of past “explanatory paradigms” (Furholt, 2018; Heyd, 2017; Hofmann, 2015).

The archeological record of northern Europe shows transformations succeeding the Mesolithic, to the appearance of the LBK-complex in the fifth millennia BCE and the Corded Ware complex (CWC) in the third millennium BCE. Both these transformations have been associated with demographic events brought about by migrating human groups (Brandt et al., 2013; Lazaridis et al., 2014; Malmström et al., 2009, 2015; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014). In Scandinavia, the process is similar, although the transition to the Neolithic Stone Age is marked by the appearance of the Funnel Beaker complex (FBC) in the fourth millennium BCE (Malmer, 2002). The introduction of the Battle Axe culture (BAC) in the third millennium BCE marks another important migration and admixture event, which again is related to developments on the continent and the Baltic area (Malmström et al., 2019). In this region, however, hunter-gatherer groups associated with the Pitted Ware culture (PWC), still occur.

The PWC appear in the archeological record between approximately 3400 and 2400 BCE. The emergence and the relation of the PWC people to either Mesolithic hunter-gatherers or to FBC farmers (ca. 4000–2800 BCE), was debated for more than a century (Almgren, 1907; Browall, 1991; Carlsson, 1998; Malmer, 1975, 2002; Stenbäck, 2003). It has now been shown that there is a strong genetic similarity between individuals from PWC contexts and chronologically older Scandinavian Mesolithic hunter-gatherer individuals predating 5000 BCE (Günther et al., 2018; Malmström et al., 2009, 2015; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014), although low levels of admixture between contemporaneous FBC groups and PWC groups have been noted (Günther et al., 2015; Günther et al., 2018; Mitnik et al., 2018; Skoglund, Malmström, et al., 2014). In a later phase, the PWC was also contemporaneous with the BAC (ca. 3000/2800–2300 BCE), which in southern Scandinavia chronologically succeeds the FBC (Brink, 2009; Browall, 1991; Edenmo, 2008; Larsson, 2009; Malmer, 2002). The BAC is considered a Scandinavian variant of the CWC (Wallin & Martinsson-Wallin, 2016; Palmgren & Martinsson-Wallin, 2015; T. D. Price, 2015) and is named after the stone axes associated with the graves of males that mimic metal battle axes. Individuals from BAC contexts from south-central Sweden display a genetic composition similar to individuals of the continental European CWC, demonstrating that the impact of the “Yamnaya” steppe migrations had reached as far north as

mainland Scandinavia by approximately 2800 BCE (Allentoft et al., 2015; Malmström et al., 2019). This massive migration event from the Pontic Steppe had spread to eastern and central Europe around 3,300 BCE and impacted local groups and possibly the emergence of the CWC (Allentoft et al., 2015; Haak et al., 2015), but this process is not fully understood (Furholt, 2018; Heyd, 2017). The demographic, social and cultural interactions between the CWC/BAC and PWC in Scandinavia are not well understood either, even in light of the new genetic data.

The archeological material record shows clear differences in cultural expressions between the PWC and CWC/BAC, most obvious in their burial customs, settlement patterns and subsistence economy. The PWC sites are most often found in coastal areas of southern Scandinavia including the Baltic Sea islands of Öland, Gotland and Åland. The BAC finds on the other hand, which largely comprise of battle axes and some 280 graves, are distributed more inland in south and central present-day Sweden. The subsistence economy of the PWC was mainly marine-based, evident from preserved faunal assemblages and stable isotope analyses (Eriksson, 2004; Eriksson et al., 2008; Fornander, Eriksson, & Lidén, 2008; Lindquist & Possnert, 1997; Storå, 2001). The latter studies are, however, still limited to analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in collagen, which reflects protein intake only. The PWC groups probably included a limited amount of “Neolithic” elements in their subsistence as indicated by charred cereal finds and bones from wild boar/domestic pig at some of the sites (Vanhanen et al., 2019). The BAC subsistence economy on the other hand included the utilization of domesticated resources through pastoralism and small-scale horticulture, even though foraging also occurred (Browall, 1991; Eriksson et al., 2008; Fornander, 2013; Hallgren, 2008; Knutsson, 1995; Malmer, 2002). Interpretations are, however, affected by the limited number of excavated settlement remains. The majority of the >220 PWC graves, most of them found on Gotland, are single flat-earth graves where the dead are buried flat on their backs in a supine position (Janzon, 1974; Malmer, 2002; Stenberger, Dahr, & Munthe, 1943; Wallin, 2010). Artifacts accompanying the dead are usually hunting and fishing gear, tooth pendants, pit-decorated pottery and bones and occasionally antlers from wild game (Janzon, 1974; Molnar, 2008). Although BAC burials are also mostly single- or double flat-earth graves, some are cremation burials and secondary burials in association to megalithic monuments (Malmer, 2002; Malmström et al., 2019). The burials have a strictly formalized spatial organization with bodies placed on their side in crouched positions (i.e., hocker position), and including grave gifts such as cord-ornamented pottery, boat shaped battle-axes, grindstones and amber beads (Knutsson, 1995; Malmer, 2002; T. D. Price, 2015).

Interestingly, at the PWC burial sites on the Baltic Sea island of Gotland, there are a number of burials where the dead have either been placed in a hocker position (or in an almost equivalent position), or where BAC associated artifacts have been found, such as battle-axes, grindstones, antler artifacts, and/or amber (Malmer, 1962, 2002). Furthermore, stray-finds of cord-decorated pottery and ~60 battle-axes have been found on Gotland (Palmgren, 2018; Palmgren & Martinsson-Wallin, 2015). These finds show that there were contacts, of some form, across the two

**TABLE 1** Information on the 19 individuals with newly generated genome data included in this study as well as on six additional Pitted Ware culture individuals

Sample ID	Grave No.	Date (cal BCE, 2 sigma)	Haplotype			Contamination estimates				Morphological sex	Burial type <sup>a</sup>		
			mtDNA	Genome coverage	Y-chr	mtDNA	X chr	Autosome	Karyotype				
ajv28	28	2,894–2,670	114.3	1.35	-	U4a2	-	4.1–8.0%	-	0.05%	XX	Female	Hocker, right side?
ajv36	36	3,011–2,873	563.5	0.97	-	U5b2a2	-	2.3–3.6%	-	0.00%	XX	Female	Hocker, left side
ajv59 <sup>b,c</sup>	59	3,011–2,877	50.9	0.16	NA	U5b	NA	0–4.4%	0.73%	-	XY	Male	Supine
ajv58 <sup>b</sup>	58	2,880–2,632 <sup>d</sup>	385.1	2.68	I2a1a1-CTS595	U4d	I2a1a1-CTS595	2.1–3.7%	1.02%	NA	XY	Male	Supine
ajv52 <sup>b</sup>	52	2,914–2,694 <sup>d</sup>	29.2	0.08	NA	V	NA	0–3.7%	0.12%	NA	XY	NA (child)	Supine
ajv54 <sup>b</sup>	54	2,900–2,680 <sup>d</sup>	517.4	0.90	NA	U5b1d	NA	0.7–1.8%	0.64%	NA	XY	Male	Supine
ajv53 <sup>b</sup>	53	2,892–2,491 <sup>d</sup>	1.8	0.02	-	U4d	-	NA	-	NA	XX	Female	Supine
ajv70 <sup>b</sup>	70	2,874–2,621 <sup>d</sup>	105.2	1.29	I2a1a1-CTS595	U4d	I2a1a1-CTS595	0.6–2.6%	0.54%	NA	XY	Male	Supine
ire8 <sup>b</sup>	8	2,909–2,694	24.5	0.04	NA	U4d	NA	1.6–9.6%	0.22%	NA	XY	Male	Possible hocker
vbj001	24	2,862–2,473 <sup>d</sup>	640.9	4.03	-	U4a2	-	2.6–3.9%	-	2.46%	XX	Female	Supine
vbj002	83	2,882–2,632	64.7	0.16	-	U5b2a2	-	0.2–3.4%	-	-	XX	Female	Supine
vbj003	22	2,914–2,698	37.3	0.10	-	K1a3	-	17.8–32.6%	-	-	XX	Female	Supine
vbj004	88	2,875–2,496 <sup>d</sup>	356.1	4.54	-	U5b2a2	-	0.3–0.9%	-	2.56%	XX	Female	Hocker
vbj006	82	2,920–2,705	702.0	3.89	I2a1a3a	I2a-L460	I2a-L460	1.4–2.2%	3.79%	3.19%	XY	Male	Supine
vbj007	84	2,549–2,297	75.5	0.19	-	HV12	-	0–6.4%	0.10%	-	XY	Female	Supine
vbj008	12	2,864–2,468 <sup>d</sup>	276.2	0.90	I2-M438	U5b1d2	I2-M438	0.8–2.8%	1.69%	0.03%	XY	Male	Supine
vbj012	39	3,011–2,878	747.7	1.63	I2a-L460	U5b2a2	I2a-L460	1.0–1.7%	2.01%	0.22%	XY	Male?	Supine, <b>Battle Axe</b>
vbj013	5	2,883–2,631	543.5	3.05	U4a2	I2a1a-CTS595	I2a1a-CTS595	2.0–3.2%	2.67%	1.14%	XY	Male	Supine, <b>amber artifact</b>
vbj014	65	2,899–2,626 <sup>d</sup>	36.9	0.05	NA	U5b1d	NA	0–3.8%	0.73%	-	XY	Male	Supine, <b>antler artifact</b>
vbj015	36	2,908–2,694	72.1	0.02	T2b11	NA	NA	0.5–2.4%	0.01%	-	XY	Male?	<b>Battle Axe, antler artifact</b>
vbj017	76	2,917–2,631 <sup>d</sup>	14.6	0.08	U4a2	U4a2	NA	0–6.1%	0.39%	-	XY	NA	Unknown, from burial near hearth 76, possibly 87, with <b>antler artifact</b>
vbj018	68	2,910–2,694	1,512.4	1.96	U5a2	I2a1b1-L161	I2a1b1-L161	1.4–2.0%	5.47%	2.77%	XY	Male	Hocker
hem001	2	3,011–2,877	997.0	0.29	K1a3a	NA	NA	0.3–0.8%	0.19%	-	XY	NA (child)	Burial 2, <b>hocker</b>
hem004	Ind. 3	3,307–2,912	328.3	0.71	U4a2	I2-M438	I2-M438	0.6–1.5%	1.07%	-	XY	NA	Unknown
hem005	Skel. 2	3,339–3,024	812.2	2.39	U5a1	-	-	0.2–0.7%	-	0.09%	XX	NA	Unknown

Abbreviation: NA, not applicable or not analyzed.

<sup>a</sup>Burial type according to Stenberger et al. (1943)—note also that they state that the bones recovered close to hearth 76 may originate from the burial 87. Text in boldface indicate “BAC influenced” burial style or object.<sup>b</sup>Previously published genome data (Günther et al., 2018; Malmström et al., 2019; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014), see Supporting Table S8.<sup>c</sup>Additional data for ajv59 generated in this study.<sup>d</sup>Previously published radiocarbon dates (Eriksson, 2004; Malmström et al., 2019; Norderäng, 2008; Skoglund, Malmström, et al., 2012; Skoglund, Malmström, et al., 2014; Wallin & Martinsson-Wallin, 2016), see Supporting Table S1.

cultural spheres. The PWC burials on Gotland with cultural influences associated with the BAC (Burenhult, 2002; Janzon, 1974; Malmer, 2002; T. D. Price, 2015; Stenberger et al., 1943) are intriguing cases that can be used to explore the nature of the interaction between the two groups. In this study, we analyze the genomes of 25 individuals from four PWC gravesites on Gotland, and investigate whether these BAC cultural influences were incorporated into PWC contexts through different demographic processes, for example, exogamy and other types of mobility, or through cultural transformation and transmission of ideas.

## 2 | MATERIALS AND METHODS

We investigated 25 individuals from four PWC cemeteries on the Baltic Sea island of Gotland, Sweden (Table 1, Supporting Information 1). Thirteen of these individuals originated from Västertjers (Gothem parish) that comprised at least 50 graves (Janzon, 1974; Stenberger et al., 1943) and 8 individuals originated from Ajvide (Eksta parish) that comprised 85 burials (Burenhult; Wallin & Martinsson-Wallin, 2016; Österholm, 2008). One individual came from Ire (in Hangvar parish) and 3 individuals originated from the three burials excavated at Hemmor (När parish) (Janzon, 1974). Twelve were buried in a supine position typical for PWC and 11 individuals displayed BAC influences by either being buried in a hocker position or having battle axes or other artifacts common to the BAC associated with the grave. When comparing these PWC individuals, we refer to the latter ones as “BAC influenced” individuals. Two of the Hemmor individuals could not, however, be categorized as either type of burial, as not enough skeletal elements were present to determine burial style (supine or hocker) and there were no BAC associated artifacts present in these graves (Table 1). We radiocarbon dated 15 of the individuals and calibrated the dates using OxCal 4.3.2 (Bronk Ramsey, 2009) and IntCal13 (Reimer et al., 2013). These samples were also IRMS analyzed for stable isotope ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Supporting Information 1).

DNA was extracted from bone or tooth elements from 19 individuals (see Supporting Table S1). DNA extraction was carried out using a modified silica-based extraction method (Malmström et al., 2007; Yang, Eng, Waye, Dudar, & Saunders, 1998). Illumina multiplex sequence libraries were constructed for all samples using a blunt-end ligation method to screen for preservation condition of each DNA extract (Günther et al., 2015; Günther et al., 2018; Meyer & Kircher, 2010). Samples were sequenced on the HiSeqXTen platform (Illumina) with 150 bp paired-end v2.5 chemistry. Additional libraries were generated for libraries with a genome coverage of  $>0.1\times$  using Uracil-DNA-glycosylase (UDG) and USER enzyme (Briggs & Heyn, 2012) to remove post mortem de-aminated sites. Libraries with low endogenous human DNA content, low DNA clonality, and less than 20% reads below 35 bp were enriched using Caucasian baits and Mybait Human Whole Genome Capture Kit (MYcroarray, Ann Arbor, MI) under the manufacturer's instructions (Mybaits manual version 2.3.1) to increase genome coverage for these samples for further analysis. The same was applied for damage repair libraries with low

genome coverage. Single stranded libraries were made for particularly degraded samples identified through blunt-end library screening (Gansauge & Meyer, 2013). Further information on the numbers and types of libraries constructed for each sample may be found in Supporting Table S2.

Following (Günther et al., 2018), paired end reads were merged, trimmed (Kircher, 2012) and mapped against the human reference genome (build 36 and 37) using bwa aln (Li & Durbin, 2009). PCR duplicates were collapsed to make consensus sequences (Kircher, 2012). Contamination estimates were calculated based on discordant sites of the mitochondria (Green et al., 2008), the autosomes (Jun et al., 2012) and the X-chromosome in males (Korneliussen, Albrechtsen, & Nielsen, 2014; Rasmussen et al., 2011). Karyotypes of the individuals were assessed using approaches that determine the ratio of sequence fragments that map to the X and Y chromosomes (Skoglund, Storå, Götherström, & Jakobsson, 2013), as well as the ratio of fragments that map to the X chromosome and autosomes (Mittnik, Wang, Svoboda, & Krause, 2016). One sample, vbj003, showed moderate contamination estimates, and we used PMDtools (Skoglund et al., 2014) to remove sequence fragments without post mortem damages potentially originating from the contaminant source.

Consensus mitochondrial genomes were constructed using Samtools (v0.1.19, Li et al., 2009) and ANGSD (Korneliussen et al., 2014). The mt haplogroups were determined using Haplofind (Vianello et al., 2013) and PhyloTree mtDNA Build 17 (18 February 2016, van Oven & Kayser, 2009), and are reported against the Reconstructed Sapiens Reference Sequence (RSRS) (Behar et al., 2012). Samtools was used to call Y-chromosome variants (Samtools v 1.3, Li et al., 2009) and PhylotreeY and ISOGG (International Society of Genetic Genealogy, v. 11.224, <http://isogg.org>) enabled Y chromosome haplotyping (van Oven, Van Geystelen, Kayser, Decorte, & Larmuseau, 2014) from bam files generated from UDG treated data. Kinship analysis was performed using the program READ (Monroy Kuhn, Jakobsson, & Günther, 2018) on individuals divided by site location, as well as all together in order to determine first and second degree relatives.

The population genetic data from the 19 individuals sequenced in this study was merged and analyzed together with data from 6 other PWC individuals from Gotland, 3 BAC individuals from Sweden, 17 CWC individuals from Estonia, Latvia, Poland and Germany as well as other relevant comparative groups (Allentoft et al., 2015; Günther et al., 2018; Jones et al., 2017; Malmström et al., 2019; Mathieson et al., 2015; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014) (see Supporting Table S8 for a list of the individuals). All ancient individuals were merged with the Human Origins genotype reference (Patterson et al., 2012), as well as the 1,000 genomes reference dataset (Gibbs et al., 2015) without transitions sites and indels. As some of the individuals had too low coverage to call diploid genotypes, one allele was randomly picked per individual and SNP site. Sequence reads with a base quality and mapping score below 30 were discarded.

Principal components analysis (PCA) was performed on modern western Eurasian populations from the Human Origins dataset.

Ancient individuals were projected on the PCA using the least squares projection (lsq) method and shrinkmode as implemented in the EIGENSOFT package (Patterson, Price, & Reich, 2006; A. L. Price et al., 2006). D-statistics were computed for combinations of ancient individuals merged with the 1,000 genomes reference populations using the package POPSTATS (Skoglund et al., 2015).

We inferred ancestry components using the software ADMIXTURE (Alexander, Novembre, & Lange, 2009) for relevant modern-day populations from the Human Origins reference dataset merged with ancient individuals. Fifty iterations were carried out from  $K = 2$  to  $K = 15$ . The program PONG was used to find common signals between the runs of each  $K$  (Alexander et al., 2009; Behr, Liu, Liu-Fang, Nakka, & Ramachandran, 2016). Results were visualized using R (R Core Team, 2013). A summary admixture graph (Figure 5) was generated using R from the  $Q$ -values of the best iteration run for  $K$ -values which showed the three sources of Eurasian ancestry (hunter-gatherer, farmer and herder ancestry) as described in Haak et al. (2015).

### 3 | RESULTS

#### 3.1 | Genome coverage and contamination estimates

We sequenced DNA from 19 individuals from the three PWC grave sites Ajvide, Västerbjers and Hemmor on Gotland, Sweden, to between 0.02 $\times$  and 4.54 $\times$  genome coverage (Figure 1, Table 1). All individuals were radiocarbon dated, (Supporting Information 1, Supporting Table S1, Supporting Figure S1). Most dates fall within the interval 2900–2500 cal BCE, while two dates from Hemmor appear to be slightly older and one date from Västerbjers slightly younger. Stable carbon and nitrogen isotope analyses show that all individuals had a homogenous diet that was based on marine proteins, (Supporting Table S1, Supporting Figure S2), which replicate results on earlier studies on the PWC diet (Eriksson, 2004). Sequence data was characteristic for ancient DNA in that it showed fragmentation leading to short sequence reads and post mortem nucleotide misincorporations at the ends of DNA fragments (Sawyer, Krause, Guschanski, Savolainen, & Pääbo, 2012) (Supporting Figure S3, Supporting Table S2). Mitochondrial sequence coverage for the 19 samples ranged from 14.6 $\times$  to 1,512.4 $\times$  and produced low contamination estimates <8.0% for all but one individual (vbj003 had a contamination point estimate of 17.8–32.6%, (Table 1, Supporting Table S3). Contamination estimates for the autosomes and for the X chromosome in males were also low (<3.19 and <5.47%, respectively) (Table 1, Supporting Tables S4, S5). Genetic results show that there are 7 females and 12 males in the sample cohort (Table 1).

#### 3.2 | mtDNA and Y chromosome haplogroups

We investigated the mtDNA haplogroup affiliations for the 25 PWC individuals (Table 1, Supporting Table S6). The majority of the

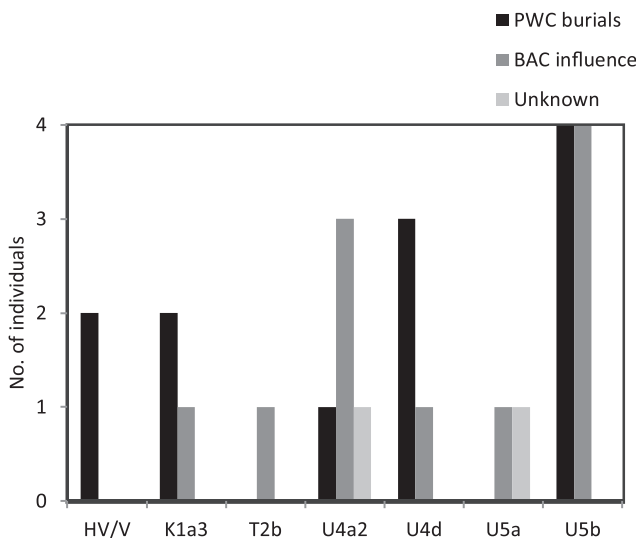
11 “BAC influenced” PWC individuals belonged to haplogroup U lineages, where U5b was most prevalent (36.4%) followed by U4a2 (27.3%), U4d (9.0%), and U5a (9.0%) (Figure 2, Supporting Table S6). Other haplogroups seen among the individuals of the “BAC influenced” burials were K1a3 (9.0%) and T2b (9.0%). All lineages found among these individuals, except for T2b, were shared with the other PWC individuals, who displayed some additional haplogroups (HV and V, Table 1). Overall, the haplogroup distribution is similar to that previously found among PWC individuals using Hypervariable Region 1 (HVR1) data (Malmström et al., 2009, 2015), where T2b was also found in two PWC individuals from Ire on Gotland and Köpingsvik on Öland. The high prevalence of U-lineages is something PWC shares with Scandinavian Mesolithic hunter-gatherers (Günther et al., 2018; Haak et al., 2015; Lazaridis et al., 2014; Mathieson et al., 2015). The three Swedish BAC individuals from present-day Sweden studied this far belonged to other sublineages than the individuals in the “BAC influenced” PWC burials in this study, namely K1a2a, U4c1a, and N1a1a1a1 (Allentoft et al., 2015; Malmström et al., 2015, 2019). CWC individuals south and east of the Baltic Sea generally displayed both typical Neolithic farmer haplogroups such as H, J, K, T and X, and haplogroups associated with hunter-gatherers, such as U4 and U5 (Allentoft et al., 2015; Brandt et al., 2013; Fernandes et al., 2018; Jones et al., 2017; Mathieson et al., 2015; Mathieson et al., 2018; Saag et al., 2017), and some of these lineages overlapped with the lineages found among the PWC individuals, including those individuals buried in “BAC influenced” burials.

We successfully retrieved Y-chromosomal haplotypes from six of the PWC males, while two additional males were typed previously (Table 1, Supporting Table S7) (Günther et al., 2018; Skoglund, Malmström, et al., 2014). All males, both from typical PWC burials ( $n = 4$ ) and from “BAC influenced” burials ( $n = 3$ ), belonged to haplogroup I, and individuals with greater genome coverage displayed haplogroups I2a1a and I2a1b lineages. I2-lineages have previously been found in Mesolithic Scandinavian hunter-gatherers (Günther et al., 2018; Haak et al., 2015; Lazaridis et al., 2014; Mathieson et al., 2015). Although I2a-lineages have been found in three CWC males (from Pikutkowo in Poland, Fernandes et al., 2018, and Brandýsek in the Czech Republic, Olalde et al., 2018), the vast majority of both BAC and CWC males, including the BAC males from Bergsgraven and Viby in present-day Sweden, belonged to R1a (Allentoft et al., 2015; Haak et al., 2015; Malmström et al., 2019; Mathieson et al., 2015, 2018; Saag et al., 2017). The distribution of uniparental variants suggest that the individuals in the “BAC influenced” burials in this study are genetically analogous to the distribution among other individuals associated with the PWC.

#### 3.3 | Kinship analysis

We investigated possible kinship to determine whether the “BAC influenced” individuals were closely related to each other. Three sets of kin relations were found among all 25 individuals; two second-

**FIGURE 1** Map of Scandinavia (modified from Fraser, 2018 and Vanhanen et al., 2019) with sample location for the 25 individuals from PWC burials on Gotland (Ajvide, Ire, Västerbjers and Hemmor), as well as sample location for comparative BAC individuals (Bergsgraven and Viby) and the approximate cultural range of PWC and BAC/CWC. BAC, Battle Axe culture; CWC, Corded Ware complex; PWC, Pitted Ware culture



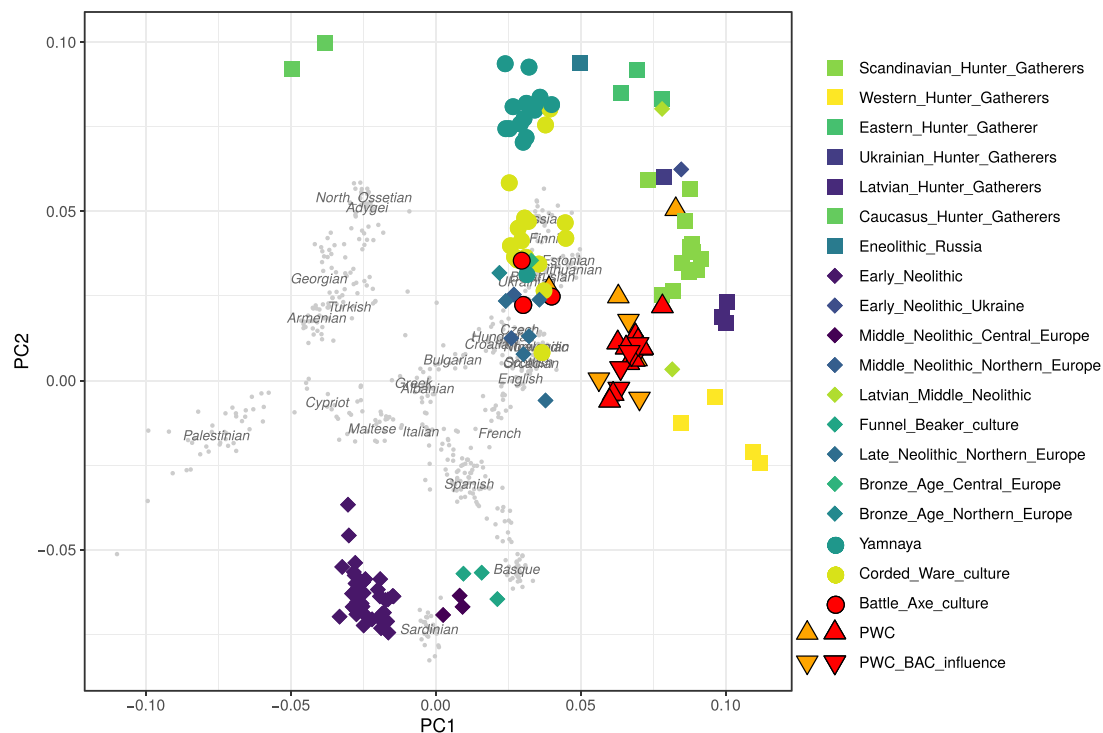
**FIGURE 2** Mitochondrial haplogroup frequencies for the 25 individuals from PWC burials. PWC, Pitted Ware culture

degree relations at Västerbjers (vbj002-vbj007 and vbj001-vbj008) and one first degree relation at Ajvide (ajv59-ajv70) (Supporting Information 3, Supporting Figures S5.1 and S5.2). All of these were, however, between individuals from typical PWC burials. Further, many of the pairwise estimates for individuals across the four sites fell toward

the lower end of the graph curve, indicating genetic similarity between populations that are higher than expected (see Supporting Figures S5.4 and S6).

### 3.4 | Genomic analysis

Similar to previous studies (Allentoft et al., 2015; Günther et al., 2018; Haak et al., 2015; Mathieson et al., 2015; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014), a principal component analysis (PCA) separated Neolithic farmers (purple and turquoise diamonds), hunter-gatherers (HG) (e.g., Eastern HGs in green squares, Scandinavian HGs in light-green squares and Western HGs in yellow squares), and Yamnaya steppe herders (green-blue circles) (Figure 3). The individuals from typical PWC burials (red upward-pointing triangles), as well as the “BAC influenced” PWC burials (red downward-pointing triangles), with genome coverage corresponding to >10,000 overlapping SNPs cluster with previously analyzed individuals from PWC contexts (Figure 3) (Günther et al., 2018; Malmström et al., 2019; Skoglund, Malmström, et al., 2014). The Scandinavian BAC and continental CWC individuals, on the other hand, clustered between the Yamnaya group and modern northern Europeans (Figure 3), similar to what has been observed previously (Allentoft et al., 2015; Haak et al., 2015; Malmström et al., 2019). There was, however, one exception among



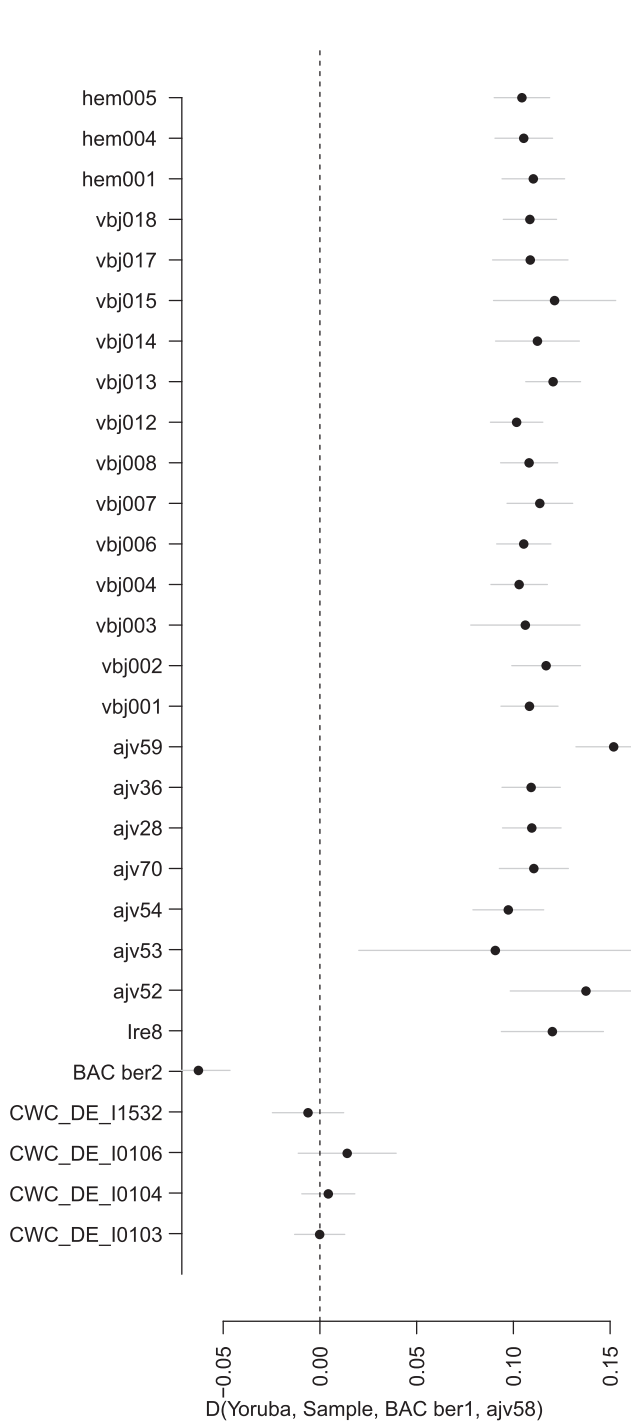
**FIGURE 3** Principle components analysis for the 25 individuals from PWC contexts and other relevant prehistoric individuals from different cultures and time-periods (see Supporting Table S8). Modern-day individuals from the Human Origins Dataset (Patterson et al., 2012) are used as background variation. The individuals from PWC contexts found in graves with BAC influences are shown as downward-pointing triangles. Individuals from PWC contexts with less than 10,000 SNPs are shown as orange triangles, the individuals with >10,000 SNPs are shown as red triangles. BAC, Battle Axe culture; PWC, Pitted Ware culture

the PWC individuals, as vbj003 cluster outside of the PWC group and closer to the BAC/CWC individuals (Figure 3). This is a spurious result caused by the low coverage of this sample ( $\times 0.03$ ) and low number of overlapping SNPs (4879) after contamination removal using PMDtools (Skoglund, Northoff, et al., 2014). vbj003 affiliation with the other individuals from PWC contexts was verified by a *D*-test (Figure 4).

To test the specific ancestry of all sequenced PWC individuals relative to published individuals, we calculated *D* statistics to measure the allele sharing of the PWC individuals with the highest coverage BAC individual, ber1 (Malmström et al., 2019), and the highest coverage PWC individual, ajv58 (Günther et al., 2018; Skoglund, Malmström, et al., 2014). All investigated individuals from the four PWC sites (Ajvide, Ire, Västerbjers and Hemmor) showed genetic similarity to the reference PWC individual in comparison to the reference BAC individual as shown by the positive *D*-values (Figure 4). Note that vbj003 showed an unexpected clustering on the PCA, likely due to modest contamination and low coverage, but the individual is clearly genetically similar to other PWC individuals (Figure 4). In contrast, the individual ber2, also from a mainland Scandinavian BAC context, presented a negative *D*-value and a closer relation to the ber1 individual. Furthermore, four CWC individuals from modern-day Germany displayed genetic affinities closer to ber1 compared to the other PWC individuals that all displayed strong affinities to ajv58.

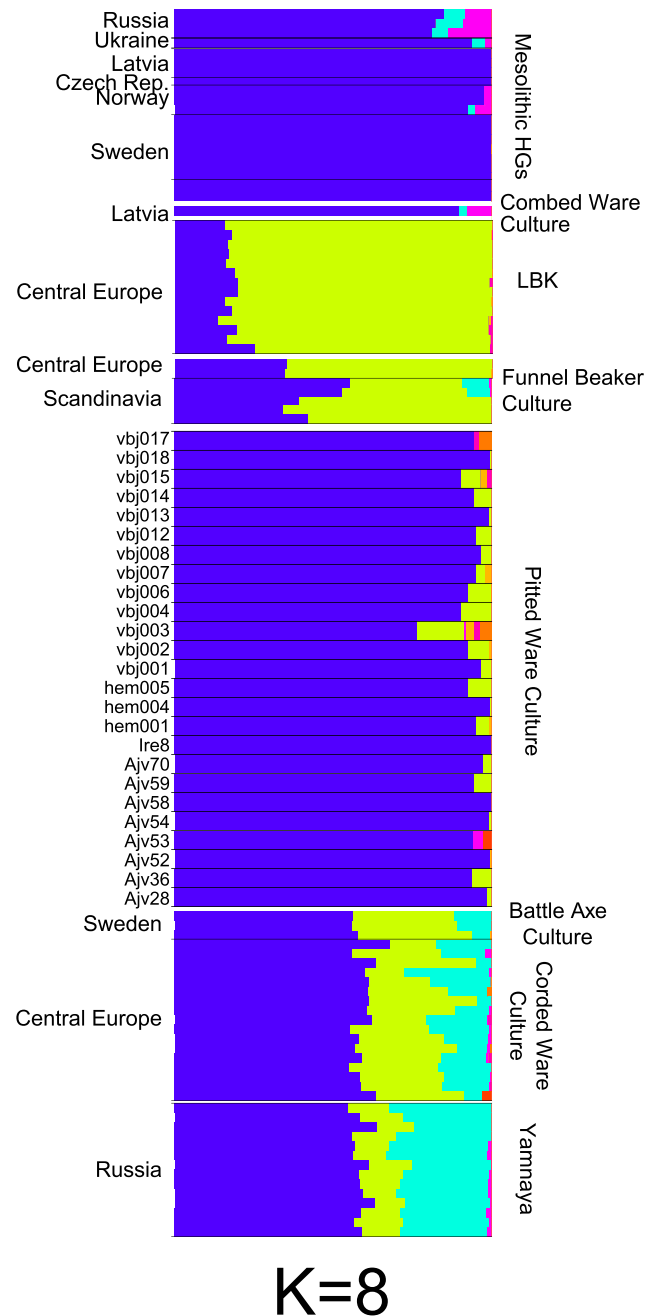
In an unsupervised clustering analysis with ADMIXTURE (Alexander et al., 2009), prehistoric individuals from farmer, herder and hunter-gatherer context have been found to harbor different genetic ancestry components reflecting their distinct histories (Allentoft et al., 2015; Günther et al., 2018; Günther et al., 2015; Haak et al., 2015; Lazaridis et al., 2014; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014). In this case, the component representing "hunter-gatherer" ancestry is shown in blue, the component representing "farmer" ancestry is shown in yellow-green, and "herder"-related ancestry component is shown in turquoise (Figure 5). Regardless of burial position, type of grave goods or burial site, the 19 PWC individuals from this study, as well as for the six PWC individuals from Skoglund et al. (Skoglund et al., 2012; Skoglund, Malmström, et al., 2014) and Günther et al. (Günther et al., 2018), displayed a large fraction of the blue hunter-gatherer ancestry component (Figure 5, Supporting Figure S4). The BAC individuals from (modern-day) Sweden also shared approximately 50% of this (blue) component, but a large fraction of their ancestry was also made up of the yellow component (which is common in Neolithic farmers) and the light blue component (common in the Yamnaya steppe herders and in CWC) (Figure 5).

Most PWC individuals, regardless of burial position, also exhibited a small fraction of farmer ancestry (Figure 5). This indicates a low level of gene-flow between the FBC and PWC populations and suggests



**FIGURE 4** D-statistics values for 24 individuals from PWC burials, one individual from a BAC context and four CWC individuals from Germany. Individuals with a positive D-value are more related to the PWC group (here represented by ajv58), and individuals with a negative D-value are more related to the BAC group (here represented by ber1). Error bars indicate  $\pm 2$  SEs. BAC, Battle Axe culture; CWC, Corded Ware complex; PWC, Pitted Ware culture

that the groups were not completely isolated from one another (Günther et al., 2015; Mittnik et al., 2018; Skoglund, Malmström, et al., 2014). None of the 25 PWC individuals however, presented herder-related ancestry.



**FIGURE 5** Ancestry fractions for individuals from PWC burials, analyzed together with a large set of comparative individuals (see Supporting Table S8). The ancestry fractions were estimated using the Admixture software (Alexander et al., 2009), and the figure displays the result of assuming eight distinct ancestries ( $K = 8$ ). PWC, Pitted Ware culture

In summary, the 25 PWC individuals are genetically similar but not identical to Mesolithic Scandinavian hunter-gatherers (Günther et al., 2018; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014) and different from the individuals from the preceding FBC contexts on Gotland (dated ca. 3300–2700 BCE) (Fraser et al., 2018; Sánchez-Quinto et al., 2019). As seen before, low levels of admixture with farmer-related individuals can be found in PWC individuals (Mittnik et al., 2018; Skoglund, Malmström, et al., 2014).



## 4 | DISCUSSION

There are certain limitations to the study of archeological material record alone. For instance, it cannot inform about relationships among groups of people or groups of individuals. Archeogenetic investigations have that specific utility; in that genetic data is particularly useful for deciphering kin relations as well as larger-scale population relations (Günther & Jakobsson, 2019). Archeogenetic research has recently revealed some large-scale population genetic patterns among prehistoric people associated with certain archeological contexts. For instance, distinct ancestry components associated with Mesolithic hunter-gatherers, with Early Neolithic farmers and with steppe herders (Allentoft et al., 2015; Haak et al., 2015; Lazaridis et al., 2014; Skoglund et al., 2012; Skoglund, Malmström, et al., 2014). In Scandinavia during the third millennium, three genetically distinct groups exist; FBC with mostly farmer ancestry, PWC with mostly hunter-gatherer ancestry and BAC with a steppe component in their ancestry.

These broad scale studies laid the foundation for other, more detailed questions about social processes and links to variability in the material culture record (this study and Mittnik et al., 2019). We can now investigate more fine-scale patterns of interactions that utilize information on specific material culture expressions and burial patterns to help our understanding of transmission of knowledge, beliefs and objects among cultural spheres.

Given the distinct ancestries of BAC and PWC (Malmström et al., 2019), it would be straightforward to detect recent migrants from the BAC into the PWC community. However, all the 25 sequenced individuals from four PWC burial grounds on Gotland, Sweden, appear to have been a part of a genetically homogeneous population associated with the PWC. None of these individuals, including the 11 individuals in burials displaying cultural characteristics of the BAC, share a close genetic affinity to individuals from BAC or CWC contexts. Nor do we find any evidence for the 11 individuals buried with BAC-influences to share kinship. Hence, the "BAC influenced" graves were likely the consequence of trade and cultural contacts (Malmer, 1962, 2002; Palmgren & Martinsson-Wallin, 2015; Wallin & Martinsson-Wallin, 2016), but without any signs of migration or admixture between the two groups.

The lack of admixture between the BAC and the PWC indicates that PWC communities interacted with BAC communities, but without genetically mixing with them to any notable degree. Therefore, the appearance of specific BAC elements and practices and perhaps ritual elements among PWC burials on Gotland was likely the result of exchange of ideas, artifacts, and cultural influences. The PWC group show additional signs of occasionally adopting practices from other groups including sparse utilization of cereals, possibly through contacts with local FBC groups (Vanhanen et al., 2019), and, based on analysis of stable isotopes, there are indications of some level of differentiation in the dietary pattern at the Ajvide site (Howcroft, Eriksson, & Lidén, 2014). Further, the PWC pottery in its earliest phases include some FBC-style like

elements (Vanhanen et al., 2019). There is also evidence of low levels of admixture from FBC groups into PWC groups (Günther et al., 2015).

Due to contrasts in material culture expressions (variations in the making of pottery, the designs on vessels, and the raw material of axes and grinding stones), Palmgren and Martinsson-Wallin (Palmgren & Martinsson-Wallin, 2015) speculated that the PWC community on the island utilized characteristics from the BAC culture to distinguish themselves from other groups within the larger PWC community. It has further been suggested that the two groups—the BAC and the PWC—were not separate at all, and that they only utilized the landscape in different ways (Hallgren, 2008; Malmer, 2002). However, this latter idea can now be rejected as (a) individuals from BAC contexts on the Scandinavian mainland are clearly part of a greater CWC group that encompasses individuals from continental Europe (Malmström et al., 2019), (b) the steppe-related ancestry that is characteristic for BAC/CWC associated individuals is not present in individuals from PWC contexts, and (c) as all individuals from PWC burial sites, including individuals in "BAC influenced" burials, had a heavily marine-based diet, which differs from the terrestrial diet seen in BAC (Fornander, 2013).

The last decade has reinstated migration as a driver of cultural change, but we need to continue to examine the interactions among individuals from different (and similar) cultural groups based on genetic and isotope information to decipher both the characteristics of the studied case, and general patterns across many cases. The cultural spheres were often not isolated entities as the archeological records show, also for the PWC, and the cultural contacts were likely different in different geographic regions and time-periods. This is also true for demographic developments. The PWC complex and the people associated with it is in many aspects intriguing. This case study shows that genetic data and the archeological record provide complementary information on the complexity and variability of the social dynamics and practices of the people associated with the PWC.

We conclude that all individuals buried in the PWC gravesites on Gotland were from the same population, irrespective of whether the burials demonstrated cultural influences from the BAC. This implies that the expression of BAC characteristics at these gravesites, such as being buried in the hocker position and/or having battle-axes, antler artifacts or amber associated with the grave, likely reflects cultural exchange between the coexisting PWC and BAC groups. The two groups remained genetically distinct for several centuries demonstrating low or no admixture between the groups despite obvious evidence of cultural contact.

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## CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

## DATA AVAILABILITY STATEMENT

The genome data generated for this study can be accessed through the European Nucleotide Archive under accession number PRJEB33128.

## AUTHOR CONTRIBUTIONS

Anders Götherström, Jan Storå, Helena Malmström, and Mattias Jakobsson designed research; Alexandra Coutinho, Helena Malmström, Torsten Günther, Emma M. Svensson, Arielle R. Munters, Anders Götherström, Jan Storå, and Mattias Jakobsson performed research; Alexandra Coutinho, Helena Malmström, Anders Götherström, and Jan Storå contributed samples and conducted archeological analyses; Alexandra Coutinho, Helena Malmström, and Torsten Günther analyzed data; and Alexandra Coutinho, Helena Malmström, Torsten Günther, Anders Götherström, Jan Storå, and Mattias Jakobsson wrote the article with input from all authors.

## ORCID

Mattias Jakobsson  <https://orcid.org/0000-0001-7840-7853>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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