Archaeal community changes in Lateglacial lake sediments: Evidence from ancient DNA

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Abstract

The Lateglacial/early Holocene sediments from the ancient lake at Hässeldala Port, southern Sweden provide an important archive for the environmental and climatic shifts at the end of the last ice age and the transition into the present Interglacial. The existing multi-proxy data set highlights the complex interplay of physical and ecological changes in response to climatic shifts and lake status changes. Yet, it remains unclear how microorganisms, such as Archaea, which do not leave microscopic features in the sedimentary record, were affected by these climatic shifts. Here we present the metagenomic data set of Hässeldala Port with a special focus on the abundance and biodiversity of Archaea. This allows reconstructing for the first time the temporal succession of major Archaea groups between 13.9 and 10.8 ka BP by using ancient environmental DNA metagenomics and fossil archaeal cell membrane lipids. We then evaluate to which extent these findings reflect physical changes of the lake system, due to changes in lake-water summer temperature and seasonal lake-ice cover. We show that variations in archaeal composition and diversity were related to a variety of factors (e.g., changes in lake water temperature, duration of lake ice cover, rapid sediment infilling), which influenced bottom water conditions and the sediment-water interface. Methanogenic Archaea dominated during the Allerød and Younger Dryas pollen zones, when the ancient lake was likely stratified and anoxic for large parts of the year. The increase in archaeal diversity at the Younger Dryas/Holocene transition is explained by sediment infilling and formation of a mire/peatbog.

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1. Introduction

The final stages of the Last Glacial in the Northern Hemisphere, between 19 and 11.7 thousand years before present (ka BP), were punctuated by distinct and alternating warm and cold climatic states before Interglacial temperatures were reached in the early Holocene. These marked climatic shifts influenced past lake ecosystems directly through lake thermal and hydrological budgets, which in turn affected lake biogeochemistry and aquatic organisms, and indirectly through changes in seasonality and catchment processes (e.g., erosion, run-off, vegetation development) (Birks et al., 1990; Leavitt et al., 2009; Fritz and Anderson, 2013).

One of the best studied Lateglacial lake sediment records in Sweden is derived from the ancient lake of Hässeldala Port (Fig. 1A and B) (Muschitiello et al., 2015b; Wohlfarth et al., 2017). Here,
multi-proxy studies combining organic and inorganic geochemistry; pollen, diatom, and chironomid assemblages; biomarkers and hydrogen isotopes; and an excellent chronological framework have allowed reconstruction of local and regional environmental conditions as well as summer temperatures between 14.3 and 9.5 ka BP (WOHLFARTH et al., 2017 and references therein). In particular, the sequence of environmental changes at the transition into and out of the Younger Dryas cold phase (c. 12.7–11.65 ka BP) has been well documented (MUSCHITIELLO et al., 2015b; WOHLFARTH et al., 2017 and references therein) and provides information on how the shallow lake and its catchment responded to abrupt climatic shifts. The available paleoclimatic and paleoenvironmental data sets for Hässeldala Port make the sediments of this site a perfect target for testing the application of ancient DNA (aDNA) analyses. Specifically, aDNA can offer a broader dimension to conventional biological proxies and thus provide the possibility to capture a much larger spectrum of organisms, including non-fossilized microorganisms (e.g. THEROUX et al., 2010).

Ancient DNA from sedimentary records is a new emerging tool used to reconstruct the diversity of past biota (e.g. WILLERSLEV et al., 2003, 2007; 2014; PAWIOWSKA et al., 2014; PARDUCI et al., 2012, 2013; 2015. 2017; GIGUET-COVEX et al., 2014; JØRGENSEN et al., 2012). Mostly, aDNA studies have focused on flora, fauna and phototrophs, while ancient archaeal communities and their response to past climatic and environmental shifts have rarely been investigated (JØRGENSEN et al., 2011; BILLARD et al., 2015; YANG J. et al., 2016; VUILLEMIN et al., 2016). Yet, Archaea are considered as active community members responsible for methanogenesis, methane oxidation and nitrogen transformation in the water column and in the sediment (e.g. LIU et al., 2015; EME and DOOLITTLE, 2015).

Here we explore the metagenomic data set for Hässeldala Port using shotgun sequence analyses of sedimentary aDNA. We specifically focus on the temporal succession of ancient archaeal communities between 13.9 and 10.8 ka BP, a time period characterised by marked shifts between warmer/colder and wetter/drier climates. We compare the composition and diversity of the archaeal communities to sediment organic matter content, to changes in summer water temperatures, to lipid biomarkers (glycerol dialkyl glycerol tetraethers (GDGTs; BROCHEIR-ARMANET et al., 2008; SCHOUTEN et al., 2013)) (KOGA and MORII, 2006) and to lake model simulations. These comparisons allow discussing various factors that might have influenced the archaeal communities in the ancient lake.

2. Site description

Hässeldala Port (56°16′ N; 15°01′ E; 63 m a.s.l.) in Blekinge province, southern Sweden is today a peat bog underlain by a

Fig. 1. (A) Location of the ancient lake of Hässeldala Port in southern Sweden and (B) view on the peat bog, which today exists at Hässeldala Port.
distinct Lateglacial and early Holocene sediment record (Wohlfarth et al., 2017) (Fig. 1A and B). Multiple sediment cores have been obtained from this site and studied using a variety of paleo-environmental and paleo-climatic proxies (Davies et al., 2003, 2004; Andersson, 2004; Wohlfarth et al., 2006; Watson, 2008; Kylander et al., 2013; Steinthorsdottir et al., 2013, 2014; Ampel et al., 2015; Muschitiello et al., 2015a, b; Karlatou-Charalamposopoulou, 2016). Correlations between the various parallel sediment cores and their repetitive lithology were made by statistically aligning their respective loss-on-ignition (LOI) curves (Muschitiello et al., 2015a, b). This made it possible to present the reconstructed environmental and climatic changes on a common time scale (Wohlfarth et al., 2017).

Sediment deposition in the ancient lake of Håsseldala Port started around 14.3 ka BP. During this early phase, which is assigned to the regional Older Dryas pollen zone, the catchment vegetation was dominated by herbs, shrubs and dwarf-shrubs (Andersson, 2004). Coleoptera remains suggest that mean summer air temperatures were around 14 °C, while chironomid-based mean July surface water temperatures remained at around 7–8 °C, possibly due to run-off from stagnant ice (Watson, 2008; Wohlfarth et al., 2017). Around 14.1 ka BP, at the start of the regional Allerød pollen zone, lake organic productivity began to increase and the ice-covered season became gradually shorter (Ampel et al., 2015; Wohlfarth et al., 2017). These changes co-occur with a step-wise increase in mean July surface water temperatures to values of 12–13 °C between 13.3 and 13.2 ka BP. Several proxies imply a first climatic shift already around 13.2–13.1 ka BP, when mean July surface water temperatures decline and regionally drier conditions seem to have occurred (Wohlfarth et al., 2017).

A further decline in lake water summer surface temperatures at 12.7 ka BP, i.e. at the start of the regional Younger Dryas pollen zone, coincides with regionally drier conditions and with an expansion of herb and grass vegetation in the catchment (Wohlfarth et al., 2017). Also, the aquatic vegetation in the lake changed as the nutrient level decreased and the ice-covered season became longer (Ampel et al., 2015). Coldest lake water surface summer temperatures were reached at 12.4 ka BP, but started to rise again between 12.4 and 11.9 ka BP from 9 to 12 °C (Wohlfarth et al., 2017). Coincident with the rise in lake surface water summer temperatures, climatic conditions became wetter, the aquatic vegetation changed and the ice-covered season became shorter. The catchment vegetation responded to the change in temperature and precipitation with a delay of a few hundred years as shrubs and trees became only established between 11.8 and 11 ka BP (Wohlfarth et al., 2017). Also at around 11.8–11.7 ka BP, the shallow lake started to fill in and gradually transformed into a mire and later into a peat bog.

3. Materials and methods

3.1. Sediment coring, sampling and sediment description

Sediment core (#5) was obtained in September 2011 and a new sediment core (#7.4) in July 2015 using a Russian corer with a chamber length of 1 m and a diameter of 10 cm. The sediment cores were transported to the Department of Geological Sciences, Stockholm University, where they were stored in a cold room (5 °C) until sub-sampling. Sediment core #5 was sub-sampled in 2012 in contiguous 1-cm increments for lipid biomarker and hydrogen isotope analyses following the procedures described in Muschitiello (2016). Core #5, which has been dated in very high resolution and analysed for various proxies, is the template core for all Håsseldala Port sediment cores (Wohlfarth et al., 2017). The lithology of the new sediment core #7.4 was described in the laboratory prior to sub-sampling in September 2015. After sub-sampling for aDNA (see below), we sub-sampled core #7.4 in contiguous 1-cm increments to analyse the organic matter content of the sediments. Loss-on-ignition (LOI) analyses were performed at 550 °C following the procedures described in Heiri et al. (2001). The LOI % curve for core #7.4 was then statistically correlated to the LOI % curve of core #5 following the core-to-core alignment of Muschitiello et al. (2015a, b). This provided a time scale for core #7.4 and for each of the aDNA samples.

3.2. Precautions during coring, sampling and aDNA analysis

Because aDNA is always degraded, damaged and in low concentration, the potential for contamination of samples and DNA extracts with modern DNA is high. To minimize these risks, we took specific and well established precautions during coring, sampling and DNA analysis of core #7.4. Immediately after collection, the core was wrapped in plastic, placed in PVC liners and quickly transported to the cold room at the Department of Geological Sciences (IGV) at Stockholm University, where it was stored at 5 °C until subsamples were taken for DNA analyses. The cold storage is in a part of the building where no DNA analyses are being performed. Sub-sampling was conducted in September 2015 in a clean laboratory at IGV using gloves and wearing lab coats and masks. The seven DNA samples taken from core #7.4 cover the warm and cold Lateglacial intervals (Allerød, Younger Dryas) and the early Holocene (Wohlfarth et al., 2017) (Supplementary Table S1). For each sample, we removed the top 1.5 cm of the outer sediment with sterilized scalpels, sampled two times circa 5–10 g of uncontaminated material from the innermost part of the core with a new set of sterile scalpels and placed the sample in sterile tubes that were immediately closed. The seven samples were kept cold and frozen within 2 h after sub-sampling and shipped frozen to the Centre for GeoGenetics, University of Copenhagen for molecular analyses.

3.3. DNA extraction and metagenome library construction

DNA extractions and pre-PCR preparations of the seven samples were performed in the aDNA laboratory of the Centre for GeoGenetics, University of Copenhagen. Here all facilities are specifically dedicated to aDNA analyses from lake sediments. Total genomic DNA was extracted as described in Pedersen et al. (2016). Each sediment sample was mixed gently before DNA extraction, in order to be representative of the respective sediment layer. For each of the seven samples we used 1 g of material for DNA extraction and replicated the extraction (14 extractions in total). One gram of mixed sediment was added to 3 ml of lysis buffer [68 mM N-laurylsarcosine sodium salt, 50 mM Tris–HCl (pH 8.0)], 150 mM NaCl, and 20 mM EDTA (pH 8.0) with addition of 1.5 ml 2-mercaptoethanol and 1.0 ml 1 M DTT for each 30 ml of lysis buffer, together with 170 μg of proteinase K, and vortexed vigorously for 2 × 20 s using a FastPrep-24 at speed 4.0 ms⁻¹. An additional 170 μg of proteinase K was added to each sample and incubated, then gently rotated overnight at 37 °C. The MOBIOL C2 and C3 buffers (MO BIO Laboratories, Carlsbad, CA) were used for removal of inhibitors, following the manufacturer’s protocol. The extracts were further purified using phenol:chloroform and concentrated using 30 kDa Amicon Ultra-4 centrifugal filters. The phenol:chloroform step was repeated when more purification was needed. All DNA extracts were quantified using the Quant-it dsDNA H5 assay kit (Invitrogen) on a Qubit 2.0 Fluometer according to the manufacturer’s manual. DNA from the 14 sediment samples was extracted in two batches with seven samples each, together with two extraction control blanks per each batch (totally 18 samples).

The 18 samples were then prepared for shotgun metagenome
sequencing using the NEBNext DNA Library Prep Master Mix Set for 454 (New England Biolabs) following the manufacturer’s protocol with the modifications described in Pedersen et al. (2016). Metagenome libraries were amplified in two batches of nine samples each plus one library blank/batch, using AmpliTaq Gold (Applied Biosystems) (14–20 cycles) and quantified using the 2100 Bioanalyzer chip (Agilent). The 20 libraries were purified using the MinElute PCR Purification kit (Qiagen), quantified on the 2100 BioAnalyzer, pooled equimolarily and sequenced using the Illumina HiSeq 2500 platform (100 bp single-end reads). All controls, which included the four extraction blanks plus two library blanks (one from each library batch), were also sequenced as controls for contaminants.

3.4. Bioinformatic analyses

3.4.1. DNA damage analysis

To ensure that our aDNA data was authentic we examined read length and DNA damage patterns due to cytosine deamination, which both are indicators of ancient origin (Ginolhac et al., 2011; Dabney et al., 2013). We also performed k-mer analysis with the k-mer profile analysis library kPAL (Anvar et al., 2014) and performed a principal component analysis (PCA) on the kmer profiles to identify outlier samples. Reads were first trimmed of the Illumina 3’ sequencing adapter with Cutadapt v.1.11 (Martin, 2011). We employed parameter settings -m 30 -trim-n -q 10,10 to discard reads shorter than 30 base pair (bp), trim trailing N’s, and trim low-quality bases (phred score ≤ 10) from both ends of a read. Raw and trimmed reads were quality checked with FASTQC v. 0.11.5 (Andrews, 2010). K-mer analysis indicated that all extraction and library blanks (six in total) were distinctly different from the 14 samples, suggesting that they probably originated from primer-dimers, chimera constructions, contamination from modern human DNA and modern laboratory contaminants (see below). Reads passing quality filters were mapped against a custom database using end-to-end alignment in Bowtie2 v. 2.2.8 (Langmead and Salzberg, 2012). The custom database consisted of all bacterial, fungal, archaeal, protozoan and viral genome sequences, as well as Homo sapiens, available in GenBank (May 2016 version). Bam files were sorted with SAMtools v. 1.3.1 (Li et al., 2009), duplicate reads were removed with Picard v. 2.7.1 (http://broadinstitute.github.io/picard), and mapped reads with mapping quality ≤ 25 were filtered out with BAMTools v. 2.4.0 (Barnett et al., 2011). Filtered bam files were analysed with mapDamage v. 2.0.6 (Jonsson et al., 2013) and the damage pattern analysis showed that all samples consist mainly of trimmed sequences with short read lengths, and C to T and G to A nucleotide substitutions at the end of the reads are drastically elevated (Supplementary Figure S1A, B) compared to the reads from blanks (Supplementary Figure S1C). In order to attest that the archaeal sequences were of ancient origin, we also performed a damage pattern analysis on those mapped sequences that were classified as archaeal based on the taxonomy identifier of the database reference sequence. After removing duplicate sequences as well as filtering on mapping quality, we used in the range 405–1828 for damage pattern modeling. Despite the low number of resulting reads, the ancient signal is present (Supplementary Figure S1D) in contrast to that obtained when running a damage pattern analysis on the blank samples (Supplementary Figure S1C).

3.4.2. Taxonomical analysis

For the taxonomical analysis, the data pre-treatment was performed in a similar manner as for DNA damage analysis. Successively, we used the metagenomics pipeline Holi for handling read de-multiplexing, adaptor trimming, quality control, duplicate and low-complexity read removal (Pedersen et al., 2016). Raw reads were de-multiplexed and trimmed using AdapterRemoval v. 1.5 (Lindgreen, 2012) with a minimum base quality of 30 and minimum length of 30 bp. Using Holi, reads with poly-A/T tails >2 bp were removed and low-quality reads and duplicates were removed using String Graph Assembler (SGA) (Simpson and Durbin, 2012) setting the pre-processing tool dust-threshold = 1, the index algorithm = ‘ropewbt’ and using the SGA filter tool to remove exact and contained duplicates. Each quality-controlled (QC) read was thereafter mapped to reference sequences using Bowtie2 v. 2.2.4 (end-to-end alignment and mode – k 50 for example, reads were allowed a total of 500 hits before being parsed). We used the full nucleotide database (nt) from GenBank (downloaded September 2016), which due to size and downstream handling was divided into nine consecutive equal sized databases and indexed using Bowtie2-build (Langmead and Salzberg, 2012). All QC checked fastq files were aligned end-to-end using Bowtie2 default settings. Each alignment was merged using SAMtools (Li et al., 2009), sorted according to read identifier and imported to MEGAN v. 10.5 (Huson et al., 2007). MEGAN allows visual inspection of how sequences are binned along the taxonomy. We used a lowest common ancestor (LCA) algorithm to bin sequences along the NCBI taxonomy (version March 2015) with reads matching 100% in a given database. We estimated the number of sequences with unspecific alignments over multiple taxa (marked as ‘not assigned’), the number of sequences that had no alignments to any comparative sequence in the database (‘no hits’) and the number of sequences assigned to or below taxa from the three domains of cellular life (Bacteria, Archaea and Eukaryotes).

3.4.3. Diversity analysis

For alpha and beta diversity measurements, we used Kraken v. 0.10.5-beta (Wood and Salzberg, 2014) for taxonomic assignments on the same database used for the DNA damage profiling. Low-complexity regions were masked using dustmasker from BLAST + v. 2.6.0 (Camacho et al., 2009). The Kraken filtering parameter was set to 0.2, since it has been suggested to give the best trade-off between sensitivity and specificity on simulated data (Wood and Salzberg, 2014). Duplicate reads were removed before mapping. The diversity calculations were based on binning reads into operational taxonomic units (OTUs) based on their LCA. Only reads mapping to Archaea were taken into account. In order to deal with possible biases in the database due to over- or underrepresentation of certain genera, we performed abundance calculations on genera rather than species level. The Python package scikit-bio v. 0.5.1 was used for calculating alpha and beta diversities based on UniFrac distances. Using the Shannon index as the metric for alpha-diversity, we estimated the biological diversity of a community, taking both genera richness and variance in genera proportion into consideration. The weighted UniFrac metric for beta-diversity was used to compare the composition of archaeal communities with consideration for occurrence and abundance of OTUs. The bioinformatics work was performed using the workflow manager Snakemake v. 3.11.0 (Köster and Rahmann, 2012).

3.5. Lipid biomarkers

Lipid extraction and GDGT analyses were performed on 54 sediment samples (2–8 cm3) from core #5. Samples were freeze-dried and extracted via sonication using the method described in Muschitiello et al. (2015a) and Muschitiello (2016). Three fractions were isolated using a silica gel column and solvent elution and the third, most polar fraction was used for GDGT analysis; it was kept frozen prior to analysis. GDGTs were analysed using a Thermo-Dionex system comprising a Dionex Ultimate 3000RS quaternary pump and an auto-sampler coupled to a Thermo Scientific TSQ
quantum access MAX triple stage quadrupole max mass spectrometer. APCI (Atmospheric Pressure Chemical Ionization) was used as the ionization source in positive mode. Prior to analysis the lipid extract was dissolved in 9:1 methanol: dichloromethane and the injection volume was 10 μL. GDFGs were detected by scanning with selective ion monitoring over m/z 1287.2–1304.8. Chromatographic separation was achieved using a modified method of Zhu et al. (2013).

3.6. Numerical fresh water lake modeling

To simulate the direct climatic impact on a shallow ancient lake like that of Håsseldala Port between the warm state of the late Allerød (~13 ka BP) and the mid-Younger Dryas cold period (~12.17 ka BP), we used the freshwater lake model FLake (Mironov, 2008) to predict key physical lake parameters such as water temperature, lake ice and mixed layer depth. The lake model has undergone thorough testing and is used operationally as part of Numerical Weather Prediction (NWP) models of national weather services, e.g. by Deutscher Wetterdienst (DWD). The source code and an overview of lake studies using FLake can be found online at www.flake.igb-berlin.de. Atmospheric forcing for the lake model was taken from recent high-resolution global climate model simulations of the Allerød and Younger Dryas periods with the Community Earth System Model (CESM1, Schenk, unpublished). The 3 hourly forcing data derived from CESM1 at the closest grid point to Håsseldala Port (56.07° N; 15° E) consisted of down-welling short wave radiation (W/m²), total cloud cover (%), air humidity at 2 m reference height (mbar), air temperature at 2 m reference height (°C) and near-surface wind speeds at 10 m (m/s). Based on today’s topography around the ancient lake, a maximum lake depth of 5 m was chosen. Water transparency was set to transparent water with an extinction coefficient of 0.3 [1/m]. The lake model was initialized on June 1st with an initial temperature of the upper mixed layer of 5 °C, initial bottom temperature of 4 °C and an initial mixed layer thickness of 2 m. The model was insensitive to the initial conditions when started during the warm season. Omitting the first half year used for spin-up, we run 20 years for both time slices, respectively.

4. Results

4.1. Lithostratigraphy and sediment organic matter content

The basal sediments of core #7.4 are composed of fine sand with low LOI % values (14.1–13.7 ka BP) and clayey algae gyttjas with increasing organic matter content (13.7–12.65 ka BP) (Fig. 2A, B, D). In the silty algae gyttja with fine sand and in the clayey algae gyttja (12.65–11.55 ka BP), the organic matter content is low, but rises again at 11.8 ka BP. The uppermost algae gyttja displays the highest organic matter content of the whole sequence.

4.2. DNA sequencing

We generated 445060968 reads in total for the 14 Håsseldala Port samples, for which the per-sample read count lies in the range of 29–50 million (Supplementary Table S2), except for two failed samples (HÅ3.1.2 and HÅ3.1.2) that were almost devoid of sequence. The sequence data for the 12 Håsseldala Port samples has been submitted to the European Nucleotide Archive (ENA; https://www.ebi.ac.uk/ena/) under study accession number PRJNA378719 (https://www.ebi.ac.uk/ena/data/view/PRJNA378719).

Sequencing of negative controls resulted in 187696052 reads in total for four extraction blanks and two library blanks, despite negligible DNA concentrations as measured by Qubit. Trimming and quality filtering removed 32–71% of the reads for Håsseldala Port’s samples (average 48%), and 80.6% of the reads for blank samples.

A general overview of the data present in Håsseldala Port’s samples is given in Supplementary Figure S2, where we show the number of sequences with unspecified alignments over multiple taxa (not assigned, ~70%) and the number of sequences that had no alignments to any comparative sequence in the database (no hits, ~14%). Eukarya were divided into ten different kingdoms, which also include fungi and animals (Opisthokonta), plants and green algae (Viridiplantae). Whereas most of the reads (~84%) remained unidentified, the majority of the assigned reads (~16%) were assigned to microorganisms with more than 10% assigned to Bacteria, ~5% to Archaea and less than 1% to Eukaryotes. Similar results were recently also obtained by Slon et al. (2017), who analysed seven cave sediment samples using shotgun sequencing; in this study, the percentage of sequences aligned to the database varied from 4.9% to 21%.

Filtered reads were then mapped to a database consisting of 11,635 archaean sequences, 718,548 bacterial sequences, and 298,966 eukaryote sequences. Circa 20% of the blank reads passing QC filters mapped, whereas only 1–3% of Håsseldala Port’s sample reads mapped. Prior to mapdamage analysis, mapping reads were filtered on mapping quality (≈25) and deduplicated, giving in the range 2678–29737 reads for mapdamage analysis (Supplementary Table S2, column “Singleton reads”).

In order to assess potential contamination effects from blank samples, reads were taxonomically assigned, both using Kraken (data not shown) and based on mapping results to superkingdoms Archaea, Bacteria, and Eukarya. Blank samples were almost devoid of archaeal sequence, suggesting that they mostly consist of contaminants. In contrast, the fraction of reads assigned to Archaea is substantially higher for Håsseldala Port’s samples (in the range of 405–1828 reads) (Supplementary Table S2, column “Archaea filtered singletons”). An overview of the Archaea taxa present in Håsseldala Port’s samples is given in Tables 1 and 2 and in Supplementary Table S3, where we show the number of sequences identified at the level of phylum and species, as well as the top 20 most abundant Archaea species.

4.3. Temporal succession of major archaea groups

The aDNA Archaea communities observed in our 12 samples after MEGAN inspection consisted of three phyla, 12 classes, and 54 genera. The archaeal record was mainly affiliated with Eurarchaeota and Crenarchaeota, while only few reads (~1–3%) were affiliated to Thaumarchaeota and Candidatus Batharchaeota (Fig. 2E; Tables 1 and 2 and Supplementary Table S3). The hydrogenotrophic Methanocella (Methanocella paludicola, M. conradii, M. arvoryzae) and Methanoregula (Methanoregula formicica) and the acetoclastic Methanosetae were the most abundant within Eurarchaeota, while uncultured crenarchaeote were most abundant within Crenarchaeota (Table 2 and Supplementary Table S3). In particular, our aDNA data suggest that Håsseldala Port’s ancient lake was mainly dominated by Methanocella paludicola (2593 reads), uncultured archaeon (1645 reads), uncultured crenarchaeote (1385 reads) and Methanocella conradii (611 reads) and by smaller proportions of Methanoregula formicica (240 reads), uncultured euryarchaeote (233 reads), Methanocellii arvoryzae (219 reads), uncultured methanogenic archaeon (191 reads), Methanoregula boonei (154 reads) and Methanoseta concilii (125 reads) (Table 2).

Sediment samples HÅ1.1 (14.0–13.77 ka BP), HÅ3.1 (13.3–13.15 ka BP) and HÅ4.1 (12.94–12.74 ka BP), assigned to the Allerød pollen zone, were dominated by Euryarchaeota (1459, 2130 and 1021 reads, respectively) and to a lesser extent by Crenarchaeota.
(149, 293 and 244, respectively), while Candidatus Bathyarchaeota and Thaumarchaeota were only present in very low numbers (Fig. 2E and Table 1). In samples assigned to the Younger Dryas pollen zone (HÅA5.1, 12.59 ± 12.48 ka BP; HÅA6.1, 12.02 ± 11.94 ka BP), we notice a slight increase of Crenarchaeota (194 and 253 reads, respectively) and a decrease of Euryarchaeota (1110 and 961 reads, respectively), while Candidatus Bathyarchaeota and Thaumarchaeota have similar values as before (Fig. 2E, Table 1). Methanosaeta thermophila was detected only in samples assigned to the Allerød pollen zone (Supplementary Table S3).

Table 1
Summarized counts of Archaea reads found in each sample and assigned at the phylum level.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Candidatus Bathyarchaeota</th>
<th>Crenarchaeota</th>
<th>Euryarchaeota</th>
<th>Thaumarchaeota</th>
<th>Sum</th>
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<td>HÅA1.1</td>
<td>6</td>
<td>149</td>
<td>1459</td>
<td>2</td>
<td>1616</td>
</tr>
<tr>
<td>HÅA3.1</td>
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<td>293</td>
<td>2130</td>
<td>5</td>
<td>2448</td>
</tr>
<tr>
<td>HÅA4.1</td>
<td>14</td>
<td>244</td>
<td>1021</td>
<td>5</td>
<td>1284</td>
</tr>
<tr>
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<td>1110</td>
<td>5</td>
<td>1315</td>
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<td>HÅA6.1</td>
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<td>961</td>
<td>8</td>
<td>1235</td>
</tr>
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<td>521</td>
<td>10</td>
<td>951</td>
</tr>
<tr>
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<td>383</td>
<td>293</td>
<td>3</td>
<td>703</td>
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</tbody>
</table>

Table 2
Summarized counts of reads assigned to the top 20 Archaea species found in each sample.

<table>
<thead>
<tr>
<th>Sample ID/species</th>
<th>HA1.1</th>
<th>HA3.1</th>
<th>HA4.1</th>
<th>HA5.1</th>
<th>HA6.1</th>
<th>HA7.1</th>
<th>HA8.1</th>
<th>Sum (counts)</th>
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Sum (counts) | 1137 | 1864 | 1030 | 1054 | 1104 | 1112 | 765 | 8003 |

Fig. 2. Archaeal composition and abundance in Hasseldal Port’s ancient lake sediments compared to other proxies. (A) Simplified lithostratigraphy for core #7.4; (B) loss-on-ignition (LOI) curve for core #7.4; (C) chironomid-derived mean July surface water temperatures established on core #HP4 (Watson, 2008; Wohlfarth et al., 2017); (D) regional pollen zones (Wohlfarth et al., 2017); (E) abundance counts of archaeal phyla and sample ID for core #7.4; (F) Ratio between Euryarchaeota and Crenarchaeota in core #7.4; (H) Relative abundance of GDGT-0 and Crenarchaeol ("Thaumarchaeol") in core #5, both normalized against the sample with highest GDGT-0 concentration.
A distinct change in archaeal composition occurs only in the two youngest samples in our data set assigned to the Holocene (HA7.1, 11.75–11.54 ka BP and HA8.1, 11.10–10.80 ka BP), with Crenarchaeota increasing (377 and 383 reads, respectively) and Euryarchaeota decreasing (521 and 293 reads, respectively), while Candidatus Bathyarchaeota and Thaumarchaeota show a slight increase, but overall remain relatively low in abundance (Fig. 2E, Table 1). This change is also seen in the Euryarchaeota: Crenarchaeota ratio, which displays a gradual increase in Crenarchaeota in the lower five samples and a marked increase in the uppermost two samples (Fig. 2F).

4.4. Diversity changes

In addition to community changes in Archaea composition between 13.9 and 10.8 ka BP, we also detected alpha and beta diversity changes (Fig. 3A). Lowest levels of alpha diversity were found in samples HA1.1 and HA3.1 from the Allerød pollen zone. Archael diversity gradual increased in sample HA4.1 assigned to the later part of the Allerød pollen zone and in Younger Dryas samples (HA5.1, HA6.1) and reached high levels in the two youngest samples (early Holocene, HA7.1 and HA8.1) (Fig. 3A). Dissimilarity values between sample pairs calculated using the weighted UniFrac metric for beta diversity, shows distinct temporal clusters (Fig. 3B). Early Holocene samples (HA7.1 and HA8.1) form one major cluster, while the rest of the samples cluster together and can be subdivided into two main sub-clusters: HA1.1/HA3.1 and HA4.1/HA5.1/HA6.1. Fig. 3B clearly highlights that the two youngest Holocene samples (HA7.1 and HA8.1) are markedly different from all other samples. In order to ascertain that the changes in diversity were not related to differential DNA degradation in the different samples, we compared the level of fragmentation of all our reads and found that there was no substantial change in fragmentation between samples of different ages (Supplementary Figure S3A-D). It should be noted, however that this does not entirely rule out differential fragmentation, nor that there is no effect of differential fragmentation on species composition.

4.5. Lipid biomarkers

The abundance of the generic archaeal membrane lipid GDGT-0 (Schouten et al., 2013) shows an increase during the later part of the Allerød pollen zone, reaches highest concentrations during the Younger Dryas pollen zone (Fig. 2H) and abruptly decreases at the Younger Dryas/Holocene transition around 11.8–11.7 ka BP. Crenarchaeol, which is specific for Thaumarchaeota (formerly group Ia Crenarchaeota) (Schouten et al., 2013), is detected in relatively low concentrations in samples assigned to the Allerød and Younger Dryas pollen zones, but increases in Holocene samples.

5. Temporal changes in archaeal community abundance and diversity

Earlier analysed proxies in Hasseldala Port’s sediment cores show that the lake basin registered the marked climatic shifts that characterised the last glacial/interglacial transition, both in terms of summer temperatures and evaporation (Watson, 2008; Muschitiello et al., 2015b), and that it started to fill in around 11.8–11.7 ka BP and gradually transformed into a mire and later
into a peat bog (Wohlfarth et al., 2017). The sediment composition of core #7.4 mirrors these changes with rising organic matter content during the (warmer) Allerød pollen zone, lower organic matter content during the (cold and dry) Younger Dryas pollen zone and high organic matter content during the (warm and wetter) early Holocene. As shown by several studies (e.g., Björck and Møller, 1987; Wohlfarth et al., 2017), changes in organic matter content in late-glacial lake sediments in southern Sweden can be used as an indirect proxy of climatic conditions as lake aquatic productivity increased and detrital input into a lake decreased during warmer climate states and vice versa. However, sediment organic matter content is not only coupled to climatic conditions, but also to lake status changes and to natural sediment infilling.

Our aDNA analyses show that archaeal community composition and diversity changed through time in Hässeldala Port’s sediments and that the most distinct shift occurred at the Younger Dryas/Holocene transition, i.e. when air and lake water surface summer temperatures rose distinctly (Wohlfarth et al., 2017) and sediment organic matter content started to increase markedly. Beta diversity and BI values rose distinctly (Wohlfarth et al., 2017) and sediment organic matter content is not only coupled to climatic conditions, but also to lake status changes and to natural sediment infilling. Archaeal abundance is highest in Allerød and Younger Dryas samples and decreases in early Holocene samples (Fig. 2E). Lipid biomarker analysis supports this and shows high relative abundances of GDGT-0 (Schouten et al., 2013) during the later part of the Allerød pollen zone and during the Younger Dryas pollen zone and an abrupt decrease at the Younger Dryas/Holocene transition (Fig. 2H). Euryarchaeota, which dominate in Allerød and Younger Dryas samples, decrease in abundance in early Holocene samples where Crenarchaeota and partly also Candidatus Batharchaeota increase (Fig. 2E and F and Table 1). Thaumarchaeota, on the other hand, have slightly higher abundances in samples HA6.1 and HA7.1 only (Table 1), i.e. below and above the Younger Dryas/Holocene transition. These observations generally agree with the lipid biomarker analyses, which detect an increase in Crenarchaeol (‘Thaumarchaeota’; formerly group Ia Crenarchaeota; Schouten et al., 2013) concentrations around 11.8 ka BP (Fig. 2H). This increase suggests that nitrogen-based redox processes, including

<table>
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<th>Depth (cm)</th>
<th>LOI (%) averaged</th>
<th>Candidatus Batharchaeota</th>
<th>Crenarchaeota</th>
<th>Euryarchaeota</th>
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Table 3

Comparison between inferred lake water July surface water temperatures (Fig. 2C) and the most abundant Euryarchaeota in Hässeldala Port’s sediments.

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<th>Age interval (ka BP)</th>
<th>HA1.1</th>
<th>HA3.1</th>
<th>HA4.1</th>
<th>HA5.1</th>
<th>HA6.1</th>
<th>HA7.1</th>
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<tr>
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<td>13.3–13.1</td>
<td>12.9–12.7</td>
<td>12.6–12.5</td>
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</table>

| Methanocella paludicola | 415 | 858 | 391 | 374 | 294 | 187 | 187 |
| Methanococcus conradii | 97  | 198 | 102 | 85  | 61  | 55  | 13  |
| Methanoregula formica | 48  | 63  | 14  | 42  | 19  | 15  | 9   |
| uncultured euryarchaeote | 51  | 52  | 23  | 34  | 32  | 11  | 30  |
| Methanocella arvoryzae | 56  | 71  | 31  | 18  | 17  | 19  | 7   |
| uncultured methanogenic archaean | 43  | 49  | 24  | 29  | 28  | 9   | 9   |
| Methanoregula boonei | 26  | 35  | 13  | 35  | 23  | 13  | 9   |
| Methanosaeta concilii | 9   | 16  | 14  | 31  | 43  | 10  | 2   |
| Methanospirillum palustre | 15  | 22  | 7   | 17  | 16  | 4   | 3   |
| Candidatus Methanomassiliicoccus intestinalis | 26  | 8   | 0   | 12  | 5   | 5   | 3   |
| uncultured soil archaean | 1   | 2   | 8   | 13  | 14  | 14  | 4   |
| Methanosaeta harundinacea | 6   | 14  | 10  | 3   | 4   | 5   | 2   |
| uncultured Desulfurococcales archaean | 1   | 12  | 3   | 0   | 2   | 0   | 0   |
Correlations between the sediment organic matter content (LOI %) and the four archaeal groups show that Crenarchaeota correlate positively with LOI% ($r^2 = 0.597$; $P$-value 0.041), while Candidatus Bathyarchaeota, Euryarchaeota and Thaumarchaeota display no significant correlations (Table 3). Higher organic matter content in the uppermost analysed samples (H7.1, H8.1) can therefore explain the increase in abundance of Crenarchaeota. The increase in organic matter content in Hässeldala Port occurs around 11.8–11.7 ka BP and coincides with infilling of the ancient lake and the transition into a lake and later into a peat bog (Wohlfarth et al., 2017). This transition also concurs with an important climatic transition, which led to a rapid rise in summer water temperatures (Fig. 2C) and ambient air temperatures and to marked changes in catchment vegetation (Wohlfarth et al., 2017). Although the coincidence of a climatic shift and natural lake infilling make it difficult to disentangle the importance of these factors on past archaeal abundances, we hypothesize that lake infilling and the accompanying changes in sediment organic matter content were the underlying causes for the observed increase in Crenarchaeota.

Alpha diversity generally increases from the oldest to the youngest samples and displays highest diversity in the two Holocene samples H7.1 and H8.1 (Fig. 3A). The increase in archaeal diversity during the early Holocene was accompanied by a decrease in archaeal abundance, except for Candidatus Bathyarchaeota and partly also Thaumarchaeota (Table 1). The two Holocene samples also stand out in the similarity/dissimilarity analysis as clearly different from all other samples (Fig. 3B) and imply a distinct change in ecosystem functioning and restructuring of the archaeal communities. Higher diversity is readily explained by the formation of many micro-environments within a lake or a peat bog and the much larger temporal and spatial physicochemical gradients and variations compared to a relatively simple lake environment.

Beta diversity analysis moreover suggests two sub-clusters within the Allerød-Younger Dryas pollen zones, comprising samples H1.1/H3.1 (Allerød) and H4.1/H5.1/H6.1 (late Allerød and Younger Dryas) (Fig. 3B). These two sub-clusters correlate to some extent with reconstructed July lake surface water temperatures derived from chironomids (Fig. 2C), which could indicate that summer lake water temperatures might have been important for archaeal communities during Hässeldala Port’s lake phase. Specifically, samples H1.1 and H6.1 compare in time to low lake water July surface temperatures, while sample H3.1 temporally corresponds to higher lake water temperatures and samples H4.1 and H5.1 concur with a decrease in temperatures. To test this further we compare the most abundant Euryarchaeota genera with Allerød and Younger Dryas summer lake surface water temperatures inferred from chironomid assemblages (Fig. 2C; Table 4). We observe that Methanocella paludicola, Methanocella conradii, Methanoregula formica and Methanocella arvoryzae have highest abundances in sample H3.1 (highest summer lake surface water temperatures), while Methanoseta concilii increases in abundance in samples H5.1 and H6.1 (lower summer lake surface water temperatures) (Table 4).

To test if lake physical properties had an influence on the diversity of methanogenic Archaea we use a lake model simulation and focus on a specific warmer and colder time interval (13 ka BP– AL and 12.17 ka BP – YD, respectively). Compared to AL, simulated lake water temperatures for YD are dominated by severe winter cooling and cold spring temperatures lasting throughout May (Fig. 4A). Consequently, the lake model simulates thicker lake ice cover (Fig. 4B) and a significantly longer ice-covered season for YD as compared to AL (Fig. 4C). On average, the ice-free season of ~18 weeks (126.1 ± 1.75 days) is significantly reduced by around two weeks (~14.7 ± 2.24 days, $p = 2 \cdot 10^{-7}$) in YD. As a result, the lake starts to warm up later leading to a significantly shorter growing season length (N days > 5.5 °C per year) of around one week (~7.25 ± 2.91 days, $p = 0.0211$). The onset of the growing season does not occur before mid (~16th of June, AL) to late (~23th of June, YD) June and ends in late September (~24th of September). The simulated lower YD mean summer (June, July and August) temperatures of ~12.75 °C can mainly be attributed to a roughly 3 K colder June, while July temperatures remain on average warm with 17.56 °C (17.46 °C in AL) (Fig. 4A). These very warm conditions last however for a very short period only during YD.

Extrapolating these results to the diversity differences observed among the late-glacial archaeal assemblages (Fig. 3B), we suggest that the length of the growing season and of the lake-ice season were more important factors than warm peak July temperatures only. Higher abundances of certain methanogenic Euryarchaeota in sample H3.1 on the other hand, may be related to a combination of
a longer growing season, a shorter lake ice cover season and higher July lake water temperatures. Taken all proxies together, it appears that the conditions in Håsseldala Port’s ancient lake were most favourable for methanogenic Archaea during the Allerød and Younger Dryas pollen zones, when the lake might have been stratified and anoxic for a large part of the year. In contrast, the increase in archael diversity towards the end of the Younger Dryas pollen zone and during the early Holocene is related to the formation of a mire/peat bog with larger temporal and spatial physicochemical gradients and where nitrogen-based redox processes, including archael ammonium oxidation, became more important.

6. Conclusion

This study of Lateglacial/early Holocene lake sediments in southern Sweden demonstrates that Archaela communities formed an important part of past ecosystems and that such ecosystems can only be studied using environmental aDNA. By combining shotgun sequencing aDNA data, lipid biomarkers and lake model simulations with earlier observations, we show that minor shifts in archael composition were linked to climatic changes, but that the most distinct shifts were associated with the transformation of the lake into a mire and peat bog. We therefore hypothesize that archael community changes (diversity and total abundance) are driven by a variety of factors (e.g., changes in lake water temperature, duration of lake ice cover, rapid sediment inflilling), which influence bottom water conditions and the sediment-water interface. Conditions in Håsseldala Port’s ancient lake were most favourable for methanogenic Archaela during the Allerød and Younger Dryas pollen zones, when the lake was likely stratified and anoxic for a large part of the year. The increase in archael diversity towards the end of the Younger Dryas pollen zone and during the early Holocene is linked to sediment inflilling and formation of a mire/peat bog with larger temporal and spatial physicochemical gradients and variations compared to a relatively simple lake environment. Archaela community changes only detectable by aDNA, can thus be an indirect proxy for changes in lake status. Their paleoecological importance however needs to be further studied in concert with other paleoenvironmental indicators.

Acknowledgement

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2017.11.037.

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