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Pesonen, Petro Anssi Pellervo; Tallavaara, Miikka

2020-05-30

Elsevier Ltd.

<http://hdl.handle.net/10138/347365>

Pesonen, P A P & Tallavaara, M 2020, 'Human ecodynamics in the north-west coast of Finland 10,000-2000 years ago', *Quaternary International*, vol. 2020, no. 549, pp. 26-35.
<https://doi.org/10.1016/j.quaint.2018.06.032>

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Miikka Tallavaara¹ and Petro Pesonen²

¹Department of Geosciences and Geography, University of Helsinki, Finland

²Archaeological Field Services, National Board of Antiquities, Helsinki, Finland

Human Ecodynamics in the North-West Coast of Finland 10,000–2000 years ago

Abstract

High-quality palaeoenvironmental proxies and well-preserved archaeological record make Fennoscandia as an excellent area for the studies of long-term human-environment interaction in high-latitude settings. Here, we use palaeoenvironmental data and temporal frequency distributions of 754 shoreline dated hunter-gatherer sites to analyse the relationship between environmental changes and hunter-gatherer population dynamics, mobility, social organisation, and conflicts in Baltic sea coast of western Finland. Our results suggest, firstly, that hunter-gatherer population dynamics were strongly influenced by changes in the productivity of terrestrial and marine environments. Secondly, the degree of residential mobility, as indicated by the frequency of house pit sites, was correlated with population size. Thirdly, large villages and large co-residential units were tightly associated with the highest population size and their frequency dropped sharply when population size started to decrease. Fourthly, intensity of conflicts, as indicated by frequency of defensive structures, was the highest slightly after the highest population sizes, when environmental productivity had started to decline. Increased conflicts were probably caused by the imbalance between human population and its resources. Lastly, dramatic population crash (76% within 200 years) occurred just after the intensity peak in conflicts. The crash was partly density dependent (conflicts) and partly density independent phenomenon as it coincided with the onset of the Late Holocene acceleration in the cooling trend in climate. Continuing decline in the environmental productivity during the Late Holocene did not allow hunter-gatherer population to recover from the collapse. All this highlights the importance of environmental forcing on hunter-gatherer populations in northern Europe.

Keywords: Hunter-gatherers, climate change, population dynamics, mobility, conflicts, Finland

1. Introduction

1.1 Background

Questions about human-environment interactions have been highlighted as among the grand challenges in archaeology and palaeocology (Kintigh et al., 2014; Seddon et al., 2014). Drawing valid knowledge about these interactions demands physical proximity of archaeological and environmental records. For example, Greenland ice core data, commonly used as climate proxy by archaeologists, may not adequately reflect environmental variability outside Greenland (Tallavaara and Seppä, 2012). Because Fennoscandian area in northern Europe provides numerous high-quality palaeoenvironmental proxies, well-preserved archaeological record, and detailed historical data, e.g., on demography, it is an excellent region for exploring questions about ecodynamics of pre-industrial human societies. This is reflected by increasing number of studies using data from the area (e.g., Helle and Helama, 2007; Holopainen and Helama, 2009; Rickard et al., 2010; Hayward et al., 2012; Tallavaara and Seppä, 2012; Tallavaara et al., 2014a; Manninen et al., 2018).

Analyses of prehistoric dynamics in Fennoscandia have dealt mainly with dynamics over large areas (e.g., Tallavaara et al., 2010; Tallavaara and Seppä, 2012; Manninen et al., 2018). Here, we

will focus on smaller region on the Baltic Sea coast of Ostrobothnia in western Finland to detect ecodynamics of high latitude coastal hunter-gatherers between 10,000 and 2000 calendar years before present (cal BP). This area (c. 24700 km²) appears to be exceptionally densely populated by hunter-gatherers during certain prehistoric periods (Fig. 1). The wealth of data within relatively compact region gives us an advantage over previous studies, as data gathered from vast areas may average potentially contradicting trends in different subregions yielding a pattern that does not reflect true dynamics in any subregion. Our main data consists of large set of archaeological sites dated using shore displacement chronology. By comparing the temporal distributions of different site types to each other and to palaeoenvironmental proxies, we aim to explore the linkage between environment, hunter-gatherer population size, mobility, and social organisation.

1.2 Regional setting

Currently, our study area in Ostrobothnia western Finland is located in the boreal climate and vegetation zone (Fig. 1), but during the focal period, the region faced several environmental changes. Climate reconstructions from Fennoscandia show rising trend in annual mean temperature 11,000–6000 cal BP with the highest temperatures (c. 2 °C higher than today) between 7000–6000 cal BP (Seppä et al., 2009b). Cooling started c. 6000 cal BP and accelerated after 4000 cal BP (Heikkilä and Seppä, 2003; Seppä et al., 2009b). These long-term trends were punctuated by short-term climate events, most famous of which is the 8200 cal BP cold event (8.2 ka event) that has distinct signal in pollen-based temperature reconstructions (Seppä et al., 2007). Past vegetation tracked climate changes in Fennoscandia and during the Holocene Thermal Maximum (HTM, c. 8000–4000 cal BP) ranges of temperate thermophilous tree taxa were much farther north than today. For example, the distributions of hazel (*Corylus*) and lime (*Tilia*) covered our study area (Huntley and Birks, 1983). The most striking forest ecosystem change in Fennoscandia, however, is partly independent of climate and is associated with the gradual invasion of Norway spruce (*Picea abies*). During this change, the former species-rich mixed forest ecosystem was invaded by spruce and changed to a modern boreal forest, dominated by spruce and pine (*Pinus sylvestris*) (Seppä et al., 2009a). This ecosystem change happened gradually from east to west, so that our study region became part of the typical boreal ecosystem between 5000 and 3000 cal BP (Seppä et al., 2009a). It has been suggested that this ecosystem change had negative impact on hunter-gatherer societies in Fennoscandia (Tallavaara and Seppä, 2012).

For coastal societies, the Baltic Sea has always been an extremely important resource environment. Ringed and grey seals have been hunted throughout the prehistoric and historic times (Ukkonen, 1993; Ukkonen et al., 2014). In addition, the harp seal population of the Baltic Sea was an important source of food during the Mid-Holocene, after which it started to decline and became locally extinct by the Iron Age (Ukkonen, 1993; Storå and Ericson, 2004). The Baltic Sea is also a feeding area for migratory fishes, such as salmon and white fish, whose most important spawning rivers historically flow to the northern half of the Gulf of Bothnia. The prehistoric importance of anadromous fishes in the region is indicated by the archaeological finds of massive stationary fishing structures in the estuary of river Iijoki, some 80 km north of our study region (Koivisto, 2012; Koivisto and Nurminen, 2015). In addition to temperature, the productivity and consequent resource abundance of the Baltic Sea is affected by the inflow of saline North Atlantic waters (Ojaveer et al., 1998; Vuorinen et al., 1998; Westman and Sohlenius, 1999; Möllmann et al., 2000; Sohlenius et al., 2001). During its Holocene history, the Baltic Sea has faced alternating fresh and brackish water stages. The latest brackish water stage, the Litorina Sea, began around 8500 cal BP, when the Danish Straits opened and seawater entered the Baltic basin. The subsequent salinity variation has been controlled by meteorological conditions, freshwater input to the Baltic Sea and

101 the change in the inlet cross-section area at the Danish Straits (Gustafsson and Westman, 2002),
102 which is the most important non-climatic factor. The cross-section area was at its maximum
103 between 6000 and 5000 cal BP (Gustafsson and Westman, 2002).

104

105 The study area became habitable for humans when it emerged gradually from the sea as a result of
106 post-glacial isostatic land uplift. The earliest shoreline dated archaeological sites in the area date to
107 c. 10,000 cal BP, i.e., 1000 years later than the earliest pioneer sites in eastern Finland (Pesonen et
108 al., 2014). The area of Finland was colonised from the east and south-east by human populations
109 related to the so-called Post-Swiderian cultures in north-western Russia (Jussila et al., 2012;
110 Sørensen et al., 2013). Most likely, the earliest inhabitants of our study region were also
111 descendants of these eastern colonisers, but mixing with later immigrant cannot be ruled out. The
112 study area is famous for its rich archaeological material related to the hunter-gatherer populations
113 dating to the Mid-Holocene, especially between 6000 and 4000 cal BP. The material contains
114 numerous and, in some cases, large house pit sites and megastructures (Núñez and Okkonen, 1999;
115 2005; Pesonen, 2002; Mökkönen, 2008; Vaneeckhout, 2010). Hunter-gatherers in Fennoscandia
116 adopted pottery technology c. 7200 cal BP and following eastern European research tradition, these
117 pottery making hunter-gatherer cultures are called Sub-Neolithic and sometimes even Neolithic.
118 Nevertheless, in the study area, hunting and gathering way of life continued well in to the Bronze
119 Age and based on pollen data, agriculture started to gain stronger hold only during the Iron Age
120 (Lahtinen et al., 2017).

121

122

123 1.3 Research questions

124

125 In this study we will explore the dynamics of hunter-gatherer socio-ecological system in the coast
126 of Baltic Sea in Ostrobothnia, western Finland, by analysing temporal distributions of different site
127 types in the region. All the sites have been dated using shoreline dating. Different site types are
128 described in more details in Materials and methods. Our approach is based on the following
129 assumptions: a) The temporal distribution of all sites reflects changes in the population size
130 (population dynamics) in the area, b) temporal distribution of house pit sites reflects changes in the
131 residential mobility as high level of house pit sites correlates with reduced mobility, c) large house
132 pit sites reflect large population concentrations, d) row houses reflect larger co-residential units, and
133 e) megastructures are remains of defensive structures and their distribution reflects intensity of
134 conflicts between groups.

135

136 With these assumptions in mind, we aim to answer, albeit in tentative manner, the following
137 questions:

138

139 1) How the human population size has changed over the study period, and how these population
140 dynamics correspond to the pattern observed in the larger data from the area of modern-day
141 Finland?

142

143 2) Does periods of reduced residential mobility correspond to the periods of high population size in
144 the study region?

145

146 3) How indicators of larger population concentrations and larger co-residential units relate to the
147 overall development in the population size and mobility?

148

149 4) Does the high population size promote tensions and conflicts between groups?

150

5) How the above-mentioned changes in population size, residential mobility, social organisation, and conflict intensity relate to large-scale changes in the climate and the Baltic Sea?

2. Materials and methods

2.1 Site data

2.1.1 Site types

The primary data consists of 754 hunter-gatherer settlement sites, of which 256 sites contain house pits or megastructures, rest being settlement sites without visible signs of structures on the ground (Supplementary data 1). Most of the sites are survey finds and only a minor part of them have been excavated. Many of the pit house and megastructure sites in the area have been originally detected in LiDAR images, but all of these have later been confirmed in the field. For this study, we have dated all the sites using their height above the sea level (see below). This holds for excavated sites as well, even if they have yielded radiocarbon dates. Only 12 sites have been radiocarbon dated producing altogether 32 ^{14}C dates ranging between 8000 and 400 cal BP.

We have classified the sites into five categories: 1) sites without house pits, 2) house pit sites, 3) large house pit sites, 4) row house sites, and 5) megastructure sites (Fig. 2). Only categories 1 and 2 are mutually exclusive, while large house pit sites and row-house sites are subcategories of house pit sites and megastructures can, in theory, be present in sites with or without house pits.

A *house pit* is defined usually as larger than 4 meters of diameter depression visible in the ground that, in many cases, has been verified as an archaeological feature with a test pit. House pits are by definition interpreted as remains of pit houses, whose actual design has probably been versatile. Based on excavations, some were rectangular sometimes even log-based structures, while others were lighter round or roundish structures (Katiskoski, 2002; Leskinen, 2002; Pesonen, 2002; Mökkönen, 2011). Construction of pit houses means larger investment in housing than more ephemeral on-ground structures and therefore indicates longer occupation span of the site (Binford, 1990). Thus, the temporal frequency distribution of house pit sites reflects temporal changes in the amount of residential mobility.

We have defined *large house pit site* as a site, where the number of house pits is 20 or more. The three largest site in the area have 130, 115, and 64 house pits, respectively (Kangas in Kaustinen, Miekkakaara in Kokkola, and Hundbacken/Myllykangas in Pedersöre). None of these large house pit sites have been extensively excavated. Therefore, we do not really know how large fraction of the pit houses have been in use simultaneously. Alternatively, it is possible that these sites are formed as a result of repeated visits to favourable location. However, it has been suggested that the arrangement of house pits in large house pit site Rekikylä in Oulu, 55 km north of our study area, indicates that most of the pit houses were in use simultaneously (Pesonen, 1999). The same argument may apply to e.g., Miekkakaara and Hundbacken/Myllykangas sites in our study area. We nevertheless assume that the large house pit sites reflect large, at least seasonal aggregations of residential units.

Row houses are typical to north-western coast of Finland. These are tightly connected house pits usually formed by two or three pits, but some have even five or more pits in a row. Some of these structures have been excavated and it indeed seems that they are multi room house structures (Mökkönen, 2008). Row houses may have had some special function, but we assume that they

reflect different kind of social arrangements than ordinary single room pit houses. These arrangements may relate, e.g., to the problems in cooperation created by scalar stress (Johnson, 1982). Perhaps the most peculiar single site is Kivineva in Kannus, which has at least three row houses and several single house pits in an almost 200 meters long arrangement along the ancient shore of the Baltic Sea. Three of the sites (Kivimaankangas 1 and Turusensaari in Siikajoki and Kurkiniemensaari in Siikalatva feature peculiar “wagon fort” -type formation of house pits where houses have been built on top of the hill or on the promontory with a central empty space between them.

Finally, the area features an enigmatic type of ancient monument which is traditionally called “giant’s church”. These are large rectangular stone embankments, with passages in their walls. Many of such *megastructures* are adjoined by other kind of structures like house pits, burial cairns and heaps of burnt stones (Okkonen, 2003). Size of the megastructures varies between 150 and 3000 m² averaging around 900 m² and the height of the embankments is usually less than 1 m (Okkonen, 2003). Their function is still debated and it has been linked e.g., to hunting or herding activities, food storage, ritual centres, or meeting places (for a review, see Okkonen, 2003; Núñez, 2009; Ridderstad, 2015). All researchers admit that the construction of these megastructures has required unprecedented amount of work, highlighting their importance for the community. We agree with Sipilä and Lahelma (2006), who argue that the most plausible and parsimonious explanation for these sites is that they are remains of defensive structures. In case of hunter-gatherers, it is difficult to imagine any other motivation for such an effort. We assume that the construction of megastructures reflects increased tensions or conflicts between groups.

2.1.2 Shoreline dating

Post glacial shoreline displacement caused by the glacial isostatic adjustment is well-known phenomenon in the Baltic and North Atlantic region making it possible to date archaeological sites located on the ancient sea shores even in the absence of radiometric dates. In this study, all the sites were dated using age-height model, which assigns calendar age to a given height above the current sea level. The model is build using 95 radiocarbon dates that have been associated with heights of ancient shorelines (Supplementary data 2). These ¹⁴C dates include 16 dates from geological contexts, representing dates of isolation of small basins from the Baltic Sea and its predecessors. Majority of the dates are, however, from archaeological sites, where they date the height of the ancient shoreline in front of the site. These data are mainly from north of our study area (Supplementary data 2), but we assume that it reflects shoreline displacement in our area as well.

The age-height model was built using rbacon package in R, which uses Bayesian statistics to estimate the model (R Core Team, 2017; Blaauw and Christen, 2018). The rbacon algorithm builds the model by dividing the data into many vertical sections, and through millions of Markov Chain Monte Carlo (MCMC) iterations estimates the accumulation rate or, in our case, rate of shore line change (in years/m) for each of these sections. We used prior mean accumulation value of 50 yrs/m. Number of sections affects variability in the model. We used 21 sections (“thickness” of a section being 10m), which gives relatively smooth and robust model (Fig. 3) as compared to the default value (thick=5m). At each run, rbacon algorithm predicts slightly different mean age for each height. To stabilise age estimates, we run the algorithm for 100 times and averaged the mean age over the 100 runs. We had to keep the number of runs low, because rbacon algorithm does not easily lend itself to parallel processing in R. The shore line curve produced by this averaged model is shown in Supplementary figure 1 along with the standard deviation associated with predicted mean

values in the 100 runs. The latter reflects uncertainty associated with age estimates. For example, uncertainty around 8000 cal BP is relatively large (Supplementary figure 1B).

We used the averaged model to assign age estimates to archaeological sites in our data. The height of the shoreline associated with each site was usually visually determined based on the field observations and elevation contours maps and LiDAR data by the National Land Survey. This gives a relatively rough height estimate, accuracy being $\pm 2.5\text{m}$. We emphasize that we measured the height of the ancient shoreline and not the height of the archaeological structures. With megastructure sites, we relied on conventional idea that these structures are not necessarily tightly shore-bound, but are usually located slightly higher than actual dwellings. Had we treated megastructures similarly to other sites and assumed that they are located closer to the ancient shoreline, we would have obtained on average 200 yrs older dates for these structures.

2.2 Radiocarbon date data and reconstruction of the summed probability distribution

We compare temporal distribution of shoreline dated sites from our study region to the summed probability distribution (SPD) of archaeological ^{14}C dates from the total area of Finland (Oinonen et al., 2010; Tallavaara et al., 2010). The ^{14}C dates data contains 1348 individual dates covering the range between 1800 and 10,200 cal BP. The complete dataset is described in more detail in Oinonen et al. (2010) and Tallavaara et al. (2010). The ^{14}C dates were calibrated using IntCal13 calibration curve (Reimer et al., 2013). Calibration, summing of individual probability distributions, and evaluation of the SPD were performed using rcarbon package in R (Bevan and Crema, 2017). To reduce the effect of intensely dated sites with multiple dates per site phases, we followed Tallavaara et al. (2010) and combined dates from the same site falling in 200 ^{14}C -yr intervals. The number of combined ^{14}C dates is 967 and the SPD is based on these combined dates. We evaluated the SPD against random sampling effects and radiocarbon calibration bias using Monte Carlo simulation test with exponential null-model (Shennan et al., 2013; Timpson et al., 2014). The test was based on 1000 simulation rounds.

It is important to note that we used 'normalizing' method when summing ^{14}C dates, although it has been contested whether normalizing the dates in this way after summing is appropriate (Weninger et al., 2015; Bevan et al., 2017). This is because normalizing can make the SPD artificially spiky as a result of non-linearities in calibration curve (Weninger et al., 2015; Bevan et al., 2017). However, the Monte Carlo simulation test is designed to highlight these calibration anomalies (Shennan et al., 2013; Timpson et al., 2014) and test's ability to detect true demographic signals is thoroughly evaluated with known age events and is found to work (Edinborough et al., 2017). Furthermore, using normalized SPDs allows direct comparisons to previous studies (Kuosmanen et al., n.d.; Tallavaara and Seppä, 2012). We could also have used an alternative uniform null-model (Crema et al., 2016; Ritchie et al., 2016) and less conservative 100 year radiocarbon data bins (Ritchie et al., 2016; Edinborough et al., 2017; Shennan et al., 2017), but we relied on longer bins and exponential null-model to ensure more conservative analysis.

2.3 Palaeoenvironmental data

We use palaeoenvironmental data derived from several sedimentary records. The annual mean temperature reconstruction is based on the stacking of four high-resolution pollen records from which the annual mean temperature values ($^{\circ}\text{C}$) are quantitatively derived. The technique is based on using modern pollen–climate calibration sets to create mathematical transfer functions that can

300 be applied to fossil pollen assemblages to obtain quantitative reconstructions of one or two key
301 climate parameters that usually exert the strongest influence on modern and past vegetation patterns
302 and gradients in the study area (Heikkilä and Seppä, 2003; Seppä et al., 2004; Sarmaja-Korjonen
303 and Seppä, 2007; Ojala et al., 2008; Seppä et al., 2009b). Lake Nautajärvi provides also record of
304 the annual accumulation of organic matter, which reflects the autochthonous primary production of
305 the lake (Ojala and Alenius, 2005). This, in turn, is linked to the length and temperature sum of the
306 primary production season (Ojala et al., 2008). Thus, together with temperature reconstruction,
307 Lake Nautajärvi varve record reflects productivity of the terrestrial ecosystem.

308
309 Recently, Warden et al. (2017) published a high-resolution Baltic sea surface temperature (SST)
310 (°C) reconstruction based on the sediment core from the Gotland Basin. They reconstructed SST
311 using TEX₈₆-palaeothermometer, a proxy for reconstructing past sea surface temperature based on
312 the distribution of Thaumarchaeotal membrane lipids. Warden et al. (2017) also published data on
313 the distribution of organic carbon in the core, which reflects primary productivity of the sea. In
314 addition, because the productivity of the Baltic Sea is largely controlled by the temperature and
315 inflow of saline water (Ojaveer et al., 1998; Vuorinen et al., 1998; Westman and Sohlenius, 1999;
316 Möllmann et al., 2000; Sohlenius et al., 2001), we indicate the period of the highest salinity
317 according to proxy data given in Gustafsson and Westman (2002). We assume that the likeliest
318 productivity peak of the sea occurs when the highest temperatures and strongest marine influence
319 coincide.

320
321 To track the changes in the importance of marine resources in hunter-gatherer subsistence, we used
322 mean percentage of seal bones per period in coastal archaeological bone assemblages in Finland (N
323 of assemblages = 72, total N of identified fragments = 37810). These data (seal bone NISP per
324 assemblage) were extracted from the archives of osteological reports compiled by PhD Pirkko
325 Ukkonen and PhD Kristiina Mannermaa at the Finnish Museum of Natural History, and from
326 osteological reports at the National Board of Antiquities. For the osteological data, we used relative
327 simple periodisation: Early Mesolithic (11,000–8500 cal BP), Late Mesolithic (8500–7200 cal BP),
328 Early Sub-Neolithic (7200–6000 cal BP), Middle Sub-Neolithic (6000–5400 cal BP), and Late Sub-
329 Neolithic (5400–3500 cal BP). Assemblages were assigned to these broad periods based on artefact
330 typological information or ¹⁴C dates.

333 3. Results

334
335 Figure 4A shows the temporal distribution of all shore-bound sites (TDS) in the study region.
336 Assuming that this distribution reflects changes in the size of the coastal human population, it
337 reveals an interesting pattern of three population boom-and-bust cycles that culminate at c. 9500,
338 7700, and 5500 cal BP. The first two of the population booms are rather modest, whereas the
339 magnitude of the last boom is over twice as large as the magnitudes of the earlier booms. The TDS
340 suggests that after this last population boom-and-bust cycle, human population in the study region
341 didn't recover and basically disappeared by 3500 cal BP. The strongest decrease in population size
342 occurs from 4800 to 4600 cal BP when the number of sites drops from 55 to 13. The lowest site
343 frequency between 10 000 and 4000 cal BP occurs around 8300 cal BP, which coincides with the
344 8.2 ka cold event. However, one has to keep in mind the large uncertainty related to shoreline dating
345 around 8000 cal BP (Supplementary figure 1B).

346
347 Comparison of the TDS to the summed probability distribution (SPD) of ¹⁴C dates from the total
348 area of Finland (Fig 4B) shows striking similarities between the two proxies until 3500 cal BP. The
349 SPD shows the identical pattern of three population boom-and-bust cycles, with the last one of the

cycles being the most profound. However, the peaks of the last two cycles date some 200 yr earlier in the SPD of Finnish ^{14}C dates than in the TDS from the study region. Although it is possible that this reflects true differences in the population dynamics between small sub-region and the total area of Finland, we consider it much more likely that the difference in the timings of the peaks reflects differences in the accuracy of radiocarbon and shore line dating. It is, however, difficult to determine which one of the methods is giving more reliable results. Because most of the ^{14}C dates in the dataset are charcoal dates (Oinonen et al., 2010; Tallavaara et al., 2010), own age of the ^{14}C samples may contribute to the difference making SPD to show slightly older peaks. Another difference between the two distributions is that the SPD does not show any response to 8.2 ka cold event. Interestingly, the Monte Carlo simulation test of the SPD suggests that the earliest boom-and-bust cycles around 9500 and 7700 cal BP are not statistically significant deviations from the exponential null model (Supplementary figure 2). This indicates that the test might be too conservative. Because of the correspondence between TDS and SPD and because TDS is not affected by radiocarbon calibration, it is reasonable to assume that also these earlier boom-and-bust cycles in SPD are not calibration or sampling anomalies.

The biggest difference between the TDS in the study region and the SPD of ^{14}C dates from the total area of Finland occurs after 3500 cal BP. While the population in the study region appears to vanish, the SPD indicates a new growth starting from 3500 cal BP. Again, this may reflect true differences, where the coastal hunter-gatherer population in smaller sub-region dies out or remains extremely small and archaeologically almost invisible. However, it may also reflect changes in the settlement pattern. Increasing influence of agriculture may have led to the new preferences in the choice of the settlement sites and diminishing importance of the shore. This is known to have happened in southern Finland. At least in the southern parts of Ostrobothnia, intensification of land use began during the Bronze Age (Holmblad, 2010). In the radiocarbon dates from our study area, there are weak indications that some sites continue to be in use even after 3000 cal BP, but as the data is very small (see above) these cannot be used as a reliable evidence. In our study area, Bronze Age does not feature prominently, but those few sites that are known still appear to be shore-bound (e.g., Ikäheimo, 2005; Pesonen, 2016). This suggests that profound decrease in the population size visible in the TDS may be real phenomenon.

Figure 5 compares temporal distributions of different site types (Fig. 5B—F) to the distribution of all sites (Fig. 5A). The distribution of sites without house pits (Fig. 5B) shows the same pattern of three boom-and-bust cycles as the distribution of all sites (Fig. 5A). However, the last and the most prominent of the booms in the TDS of all sites is mainly composed of house pit sites (Fig. 5C). Two subcategories of house pit sites, large house pit sites (Fig. 5D) and row house sites (Fig. 5E), show roughly the same distribution as house pit sites in general, although frequencies in these subcategories fall much earlier and sharper than the frequency of house pit sites. Actually, all the above-mentioned distributions have mode at around 5500 cal BP. The distribution of megastructures, however, is different as the highest frequency occurs 600 years later around 4900–4700 cal BP (Fig. 5F). This means that, while house pit sites peak at the time of the highest inferred population levels, the height of the megastructure building occurs when population had already started to decline.

When population trajectory is compared to environmental proxies (Fig. 6), it becomes clear that the last boom-and-bust cycle between 6000 and 5000 cal BP coincides with high temperature and intensity of the primary production season (Fig. 6B—E), as well as with the salinity of the Baltic Sea (Fig. 6F). The link between environmental changes and the earlier boom-and-bust cycles is not that clear, although the second cycle (8000–6800 cal BP) coincides with the post 8.2 ka event warming and a cooler dip at around 6900 cal BP. The first cycle, in turn, coincides with warm and

400 cold spikes at 9500 and 9400 cal BP, respectively. However, these climate fluctuations are visible
401 only in the pollen-based annual mean temperature reconstruction (Fig. 6B) and their robustness is
402 therefore not clear.

403
404 The fact that high temperatures coincide with high salinity (Fig. 6F) in the Baltic Sea suggests that
405 both, terrestrial and marine productivity were high between 6000 and 5000 cal BP. Also, the organic
406 carbon data from the Baltic Sea sediments suggest high primary productivity of the sea between
407 6000 and 4500 cal BP (Fig. 6E). The importance of the Baltic Sea during this period is highlighted
408 by the intensive use of marine resources by coastal populations: The average percentage of seal
409 bone fragments is over 70 in bone assemblages of the Finnish coastal sites dated to the Middle Sub-
410 Neolithic between 6000 and 5400 cal BP (Fig. 6G). As argued previously for the larger area in
411 eastern Fennoscandia (Tallavaara and Seppä, 2012), the population boom-and-bust between 6000
412 and 5000 cal BP appears to coincide with a period of distinctively high terrestrial and aquatic
413 resource abundance. This holds well for our smaller study region as well.

414

415

416 4. Discussion

417

418 This study adds to a growing number of population proxy comparisons that show how different
419 types of regional and even continental population proxy records yield consistent patterns
420 (Tallavaara et al., 2010; Williams, 2012; Downey et al., 2014; Tallavaara et al., 2014b; French,
421 2015; French and Collins, 2015; Tallavaara et al., 2015; Palmisano et al., 2017). Here, we were able
422 to reproduce the pattern in the SPD of ^{14}C dates covering the whole Finland using independent data
423 from small subregion not well-represented in the ^{14}C data. This lends support to the idea that the
424 SPD of ^{14}C dates reflects the general demographic trend over large area, although the northernmost
425 part of Finland may deviate from this general pattern (Tallavaara et al., 2010). Previous proxy
426 comparisons have already corroborated the general trend and especially the presence of the
427 prominent boom-and-bust between 6000 and 5000 cal BP (Tallavaara et al., 2014b). Here, we
428 showed that also smaller scale features – earlier boom-and-bust cycles – occur consistently in the
429 two independent proxy data. Despite small and more or less systematic difference in the dating of
430 the cycles between the two proxy data, the overall similarity in the patterns strongly suggests that
431 the both proxies are reflecting true prehistoric human population dynamics.

432

433 Distributions of different types of sites suggest interesting patterns. First, the period of the highest
434 hunter-gatherer population levels was also the period of reduced residential mobility. Most of the
435 sites between 5800 and 5000 cal BP had pit houses, which indicates larger investment in housing
436 and longer occupation spans of sites and, consequently, less mobile way of life (Binford, 1990). The
437 return to more mobile way of life occurred around 5000 cal BP when most of the dwelling sites
438 didn't have pit houses. The link between mobility and population size or density is not unexpected,
439 as ethnographic data shows that hunter-gatherer populations living under high densities were also
440 residentially less mobile and sometimes even sedentary (Binford, 2001; Kelly, 2013). However, our
441 data do not permit us to make inferences about the causes of reduced mobility. For now, we cannot
442 say if it was the high population size and consequent population packing that forced hunter-
443 gatherers to reduce their mobility, or the favourable environmental conditions allowed both reduced
444 mobility and high population levels.

445

446 Secondly, the formation of larger co-residential units indicated by row houses and large population
447 concentrations indicated by large villages were probably driven by partly different factors than the
448 construction of pit houses in general. The number of large pit house villages and sites with row-
449 houses both peak around 5500 cal BP, like the distribution of all sites, but then decline sharply and

level off until falling to zero by 4500 cal BP. Thus, the distributions of the two subcategories of pit house sites do not follow the overall distribution of pit house sites that show smoother decline after the peak. Short-lived florescence of large villages and co-residential units may imply a threshold in population size that triggered and dampened the formation of these new social organisations.

Finally, intensity of conflicts, reflected in the building activity of megastructures, was the highest after the population peak when population size was still large, but had started to decrease along with declining environmental productivity. At the outset, this pattern does not seem to fit in the idea that high population size and density promotes conflicts among hunter-gatherers – only few megastructures were built during the population peak. However, the interplay of still-large population size and deteriorating resource availability may have created imbalance between hunter-gatherer population and its resources, which facilitated intensification of conflicts that culminated 4900–4700 cal BP. Furthermore, it is tempting to speculate that the tensions within and between communities were reflected already in the dissolution of large villages and co-residential units c. 5400 cal BP, a process that accelerated as environmental suitability started to decline and, within five hundred years, lead to intensive building of defensive structures.

Tallavaara and Seppä (2012) have previously highlighted the important role of climate and climate-independent environmental changes in shaping hunter-gatherer population dynamics in eastern Fennoscandia and especially the boom-and-bust between 6000 and 5000 cal BP. Our study, which is focused on small subregion, supports this role. In addition to driving the most prominent boom-and-bust cycle in the region, our study shows evidence, albeit weaker, that climate may have had links to earlier and smaller boom-and-bust cycles. It has been suggested that the influence of climate is mainly indirect filtered through its effect on ecosystem productivity and consequent resource abundance (Tallavaara and Seppä, 2012). This effect was exemplified by changes in forest composition that were partly independent from climate changes (Seppä et al., 2009a; Tallavaara and Seppä, 2012). During 8.2 ka cold event, climate may have had more direct effects as well. The cooling took place most likely in winter (Seppä et al., 2007), which may have created harsh wintering conditions and increased winter mortality among hunter-gatherers as reflected by the drop in site frequency.

It is natural to assume that changes in marine productivity have played important role driving coastal hunter-gatherer population dynamics in our study region. Corresponding peaks of temperature and salinity between 6000 and 5000 cal BP likely created high-productivity conditions in the Baltic Sea, which would have significantly contributed to the coinciding peak of human population. However, Warden et al. (2017) have recently shown that while increased temperature increased primary productivity of the Baltic sea, it also resulted in hypoxic conditions across the entire sea. Based on modern analogue, Warden et al. (2017) argue that hypoxia would have had negative effect on the availability of many important marine resources such as cod, herring, and harp seal between 6000 and 4000 cal BP. If the availability of marine resources was decreased during the HTM, marine resources would not have played important role in the Mid-Holocene population boom-and-bust cycle. Decreased availability of marine resources would imply that the importance of these resources would have decreased in the diet of hunter-gatherers.

However, as the archaeological bone assemblages from coastal sites in Finland show, the use of marine resources, mainly ringed seal (*Phoca hispida*) (Ukkonen, 1993; Ukkonen et al., 2014), was the most intensive at the time of the population peak. It is possible that in the northern Baltic sea, seals and their main food source herring were not negatively affected by hypoxia. On the other hand, as Warden et al. (2017) themselves show, the overall proportion of marine resources in the diet did not decline as a result of hypoxia in the southern Baltic sea either. Maybe the stronger

inflow of saline oceanic waters during the Mid-Holocene created conditions that were not analogous to modern hypoxic conditions. Whatever the reason for marine resource availability not declining despite hypoxia, it is evident that, at least in the northern Baltic sea, the importance of marine resources increased during the Mid-Holocene and peaked simultaneously with human population size.

An intriguing feature of the population history in the region is that the coastal population didn't recover from its last and the most prominent bust. Prior to 6000/5500 cal BP the long-term trend in population growth was positive despite some temporary inversions. The main difference in the drivers of population dynamics between periods prior and after 6000/5500 cal BP is that before this point, long-term trend in the productivity was also positive, whereas after the point, it was negative. Although resource availability was the main driver of long-term population dynamics, intensified conflicts may have amplified the negative effect of decreasing environmental productivity at the early stages of the last population bust. The main collapse of almost 80% drop in the population size occurred only 100 years after the most intense period of conflicts at around 4700 cal BP. At this time, cooling and decline in marine productivity really kicked in as well. The continuing decline in the carrying capacity ensured that human population didn't recover until much later as a result of the beginning of farming economy.

Here, we have analysed the data from the perspective of internal development of the regional population within environmental context. We have not taken into account the possible role of outside influence in the observed changes. Immigration is commonly evoked as an explanation for the changes in the material culture and organizational structure of prehistoric societies in eastern Fennoscandia. One of the most prominent and archaeologically visible periods in the prehistory of Finland took place between 5900-5500 cal BP, coinciding with the population peak. This so-called Typical Comb Ware culture has sometimes been seen as a result of immigration that brought in wide contact network, hierarchical social organization, and new type of housing (pit houses) (Meinander, 1984; Carpelan, 1994; Edgren, 1999). Thus, immigration can be taken as a complement to our purely demographic-environmental explanation of the changes in the settlement pattern.

5. Conclusion

In this paper, we have been able to demonstrate links between broad-scale environmental changes, hunter-gatherer population dynamics, mobility, social organisation and conflicts. However, some dimensions of the observed pattern and especially causal explanations remain speculative due to many unknowns. For example, the function of megastructures is debated and we have leaned on one, albeit plausible, suggested function of megastructures as being remains of defensive structures. Also, the exact dating of the megastructures remains ambiguous and depends on strong assumptions. In addition, besides few small scale excavations, large house pit village sites have not been properly studied. This means that our knowledge on the internal chronology of these sites is limited and we cannot conclude whether village sites represent large aggregations of more or less contemporaneous houses, or an accumulated result of repeated visits to topographically suitable place over few centuries. Future research on the supposed village sites will hopefully shed light also on whether the last use phases of these sites show evidence of increased tensions within communities. Despite these uncertainties, we would like to summarise our results with the following tentative story of human ecodynamics in the region.

The main driver of hunter-gatherer ecodynamics was resource availability controlled by the productivity of terrestrial and marine environments. Long-term trend in the productivity was

550 positive until 6000/5500 cal BP. This positive trend was punctuated by cooler anomalies that
551 temporarily hampered population growth of the coastal hunter-gatherers in the region. Due to the
552 increasing trend in productivity, the regional population was nevertheless able to recover and
553 sustain its long-term growth despite these interruptions. Changes in climate and in the Baltic sea
554 around 6000 cal BP created unprecedentedly favourable conditions for hunter-gatherers, which lead
555 to prominent population boom. Interplay of environment and population size reduced residential
556 mobility and induced the formation of large villages and co-residential units.

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558 As a result of population packing, conflicts within and between communities started to emerge.
559 These conflicts increased with the start of the climatic cooling and culminated 4900–4700 cal BP as
560 manifested by intense building of defensive structures. Although climate was the main driver in the
561 population bust, conflicts may have amplified still rather weak effect of climate at the beginning of
562 the population bust. The population decline started slowly, but the crash was about to come.
563 Between 4800 and 4600 cal BP hunter-gatherer population size crashed and never truly recovered.
564 This coincided with the end of the HTM when the cooling trend steepened and marine productivity
565 decreased. Contrary to Early and Mid Holocene, Late Holocene trend in environmental productivity
566 and resource availability was negative and, consequently, the recovery of hunter-gatherer population
567 was not possible. The region was not completely deserted, but human population remained
568 diminutive and archaeologically hardly visible as compared to the heydays of the HTM.

570 571 **Acknowledgements**

572 MT acknowledge financial support from the Kone Foundation.

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600 **References**

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602 **Figure captions**

603

604 Figure 1. Study area and the distribution of the archaeological data. A: Map showing the location of
605 the study area in Finland between modern towns of Oulu and Vaasa and in wider European
606 context. The map also shows the distribution of radiocarbon dates that are used for population proxy
607 covering the area of Finland. The study area is not very well represented in the radiocarbon dates
608 data. B: Detailed map of the study area and the distribution of different site types.

609

610 Figure 2. LiDAR images of different house pit and megastructure sites. A: House pit site with
611 number of individual house pits (Haukkanevan Palokangas 1 in Siikalatva). B: Large house pit site
612 (Miekkakaara in Kokkola). C: Row house site (Vanhakorsu 2 in Siikajoki). D: Megastructure site
613 (Kastelli Linnakangas in Raahe). The megastructure is also shown in the inset photograph. Photo by
614 Timo Pärssinen, National Board of Antiquities.

615

616 Figure 3. Age-height model produced by rbacon algorithm. The figure shows the result of one run.
617 Red curve represents the weighted average of different MCMC iterations and can be taken as a
618 shore displacement curve for the area. Grey curves delineate the 95% confidence interval.
619 Calibrated distributions of individual radiocarbon dates are shown in blue. The model averaged over
620 100 runs is shown in Supplementary figure 1A.

621

622 Figure 4. Comparison between temporal frequency distribution of shoreline dated sites in the study
623 area (A) and summed probability distribution of archaeological radiocarbon dates from the area of
624 Finland (B). The figure also shows grey bands that indicate corresponding boom-and-bust cycles in
625 both population proxies. In addition to histogram, A shows a kernel density curve with bandwidth of
626 80 yrs.

627

628 Figure 5. Temporal frequency distributions of all sites (A) and different site types (B—G). In
629 addition to histograms, the figure shows kernel density curves with a bandwidth of 80 yrs.

630

631 Figure 6. Relationship between human population dynamics and environmental changes. A: Human
632 population size dynamics based on the temporal frequency distribution of sites. B: Annual mean
633 temperature based on four pollen based reconstructions. C: Growing season intensity based on the
634 annual accumulation of organic matter in annually laminated lake. D: Summer sea surface
635 temperature derived from a sediment core from Gotland Basin in the Baltic Sea using TEX86-
636 palaeothermometer. E: Marine net primary productivity based on total organic carbon content of the
637 same core as in D. F: Model-based salinity of the Baltic Sea. G: Mean percentage of seal bones per
638 archaeological period in archaeological bone assemblages from coastal sites in Finland. The figure
639 also shows grey and blue bands indicating features in the population proxy that are associated with
640 environmental changes. 1: The earliest boom-and-bust cycle coincides with warm and subsequent
641 cold spike in pollen-based temperature reconstruction. 2: Low population size around 8300 cal BP
642 coincides with 8.2 ka cold event. 3: The second boom-and-bust cycle coincides with post 8.2. ka
643 event warming. 4: Low population size 6900 cal BP coincide with cold event in pollen-based
644 temperature reconstruction. 5: The most prominent boom-and-bust cycle coincides with the highest
645 temperature and ecosystems productivity. 6: Population crash coincides with the onset of the Late
646 Holocene cooling. The red band indicates the most intense occurrence of conflicts based on the
647 peak period of megastructure construction.

648

649 Supplementary figure 1. The age-height model that is used to date archaeological sites in the study
650 area. A: The final model that is average of weighted mean age values over 100 runs of rbacon
651 algorithm. B: The standard deviation associated with predicted weighted mean values in the 100

652 rbacon runs. High standard deviation indicates that between-run difference in mean age values is
653 large and, consequently, that age estimate assigned to certain sites is more uncertain than when
654 standard deviation is smaller.

655
656 Supplementary figure 2. Null model test of the summed probability distribution (SPD) of
657 radiocarbon dates. The black curve is the observed SPD, grey band is the 95% envelope of the
658 exponential null model envelope, and blue and red bands indicate statistically significant negative
659 and positive deviations from the null model. Monte Carlo null model test is based on 1000
660 iterations.

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Figures

Figure 1

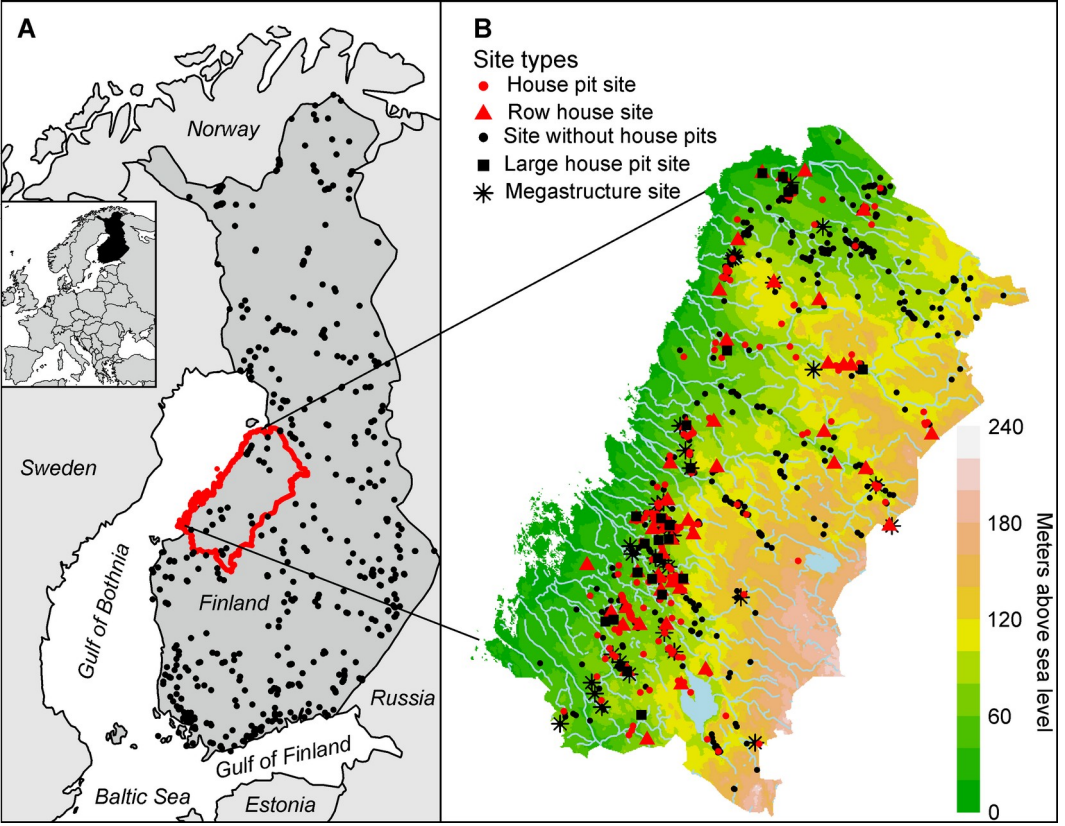


Figure 2

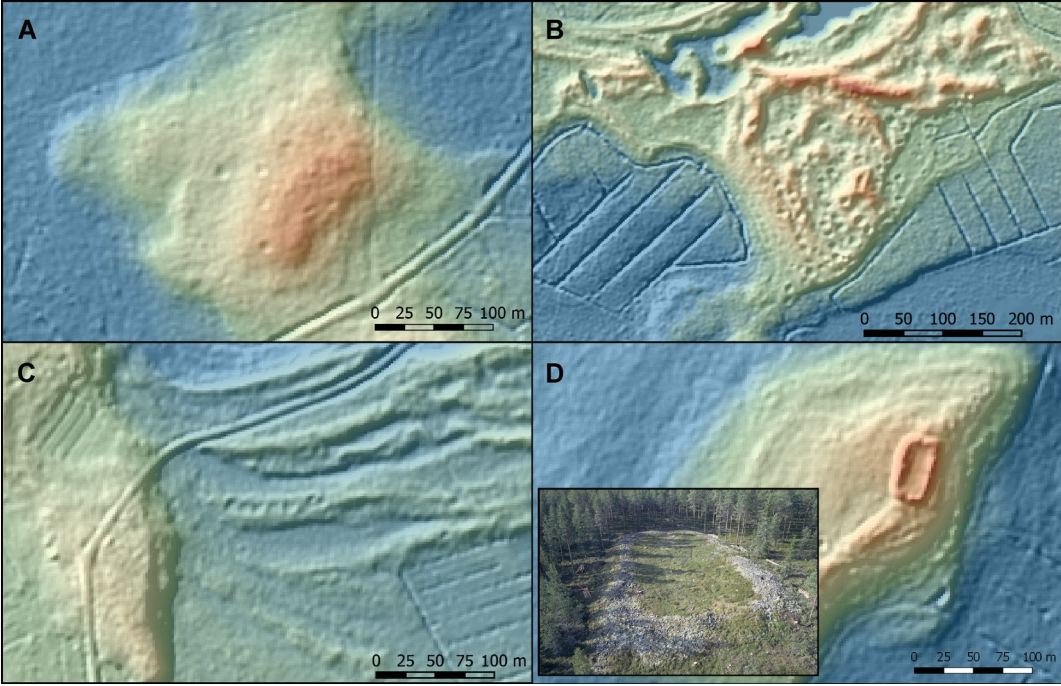


Figure 3

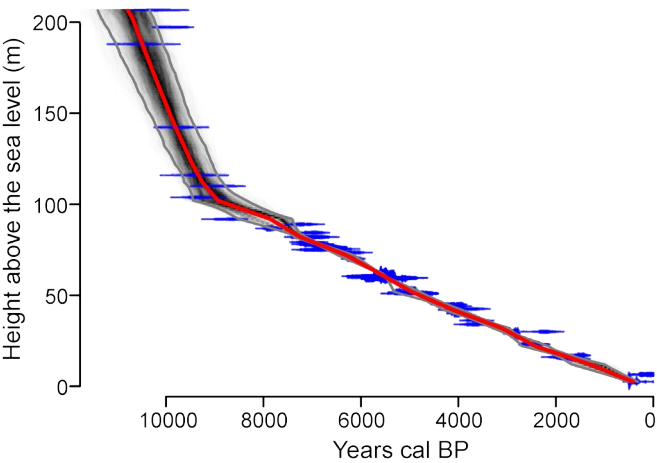


Figure 4

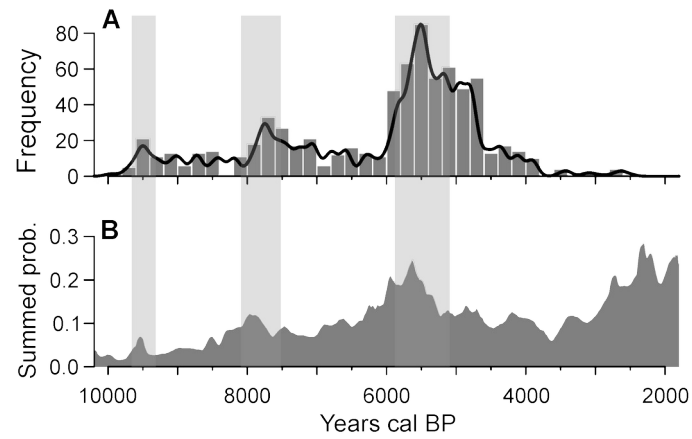


Figure 5

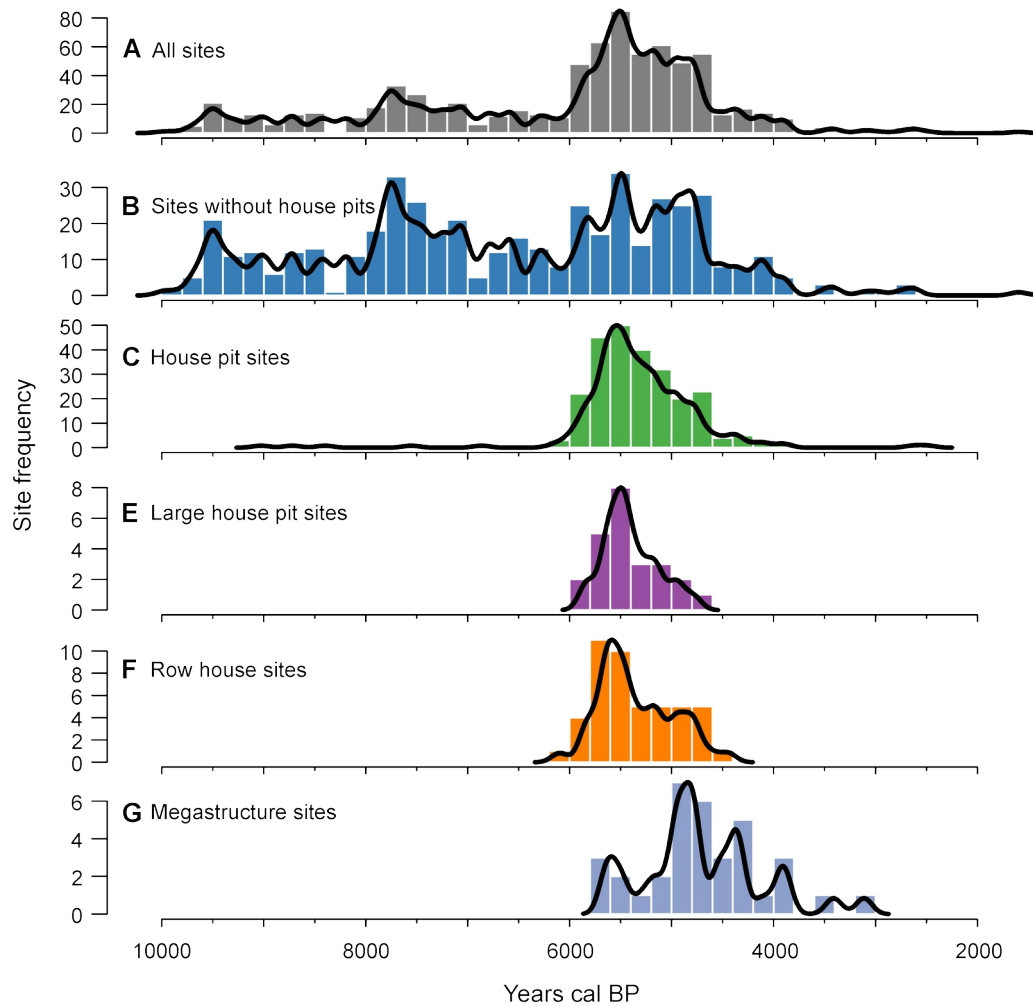
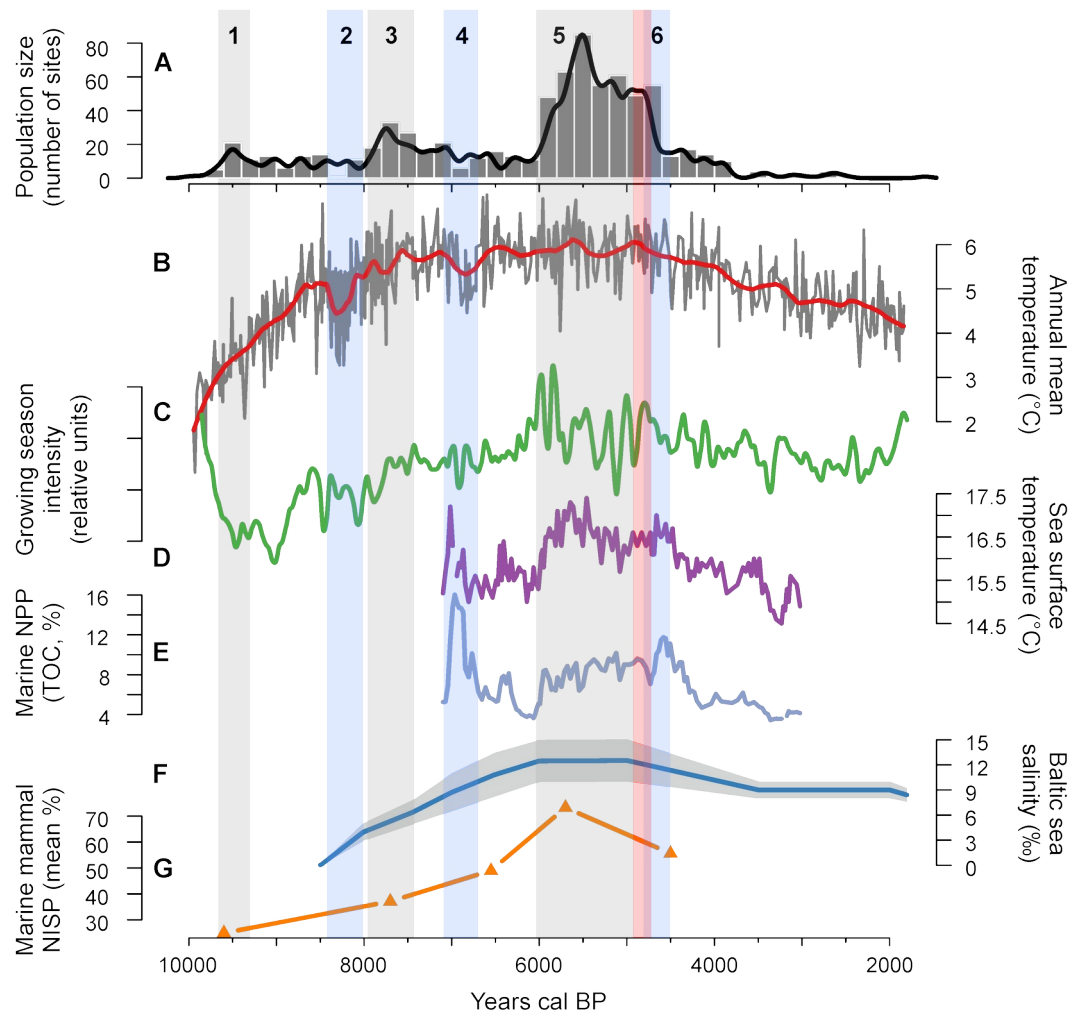
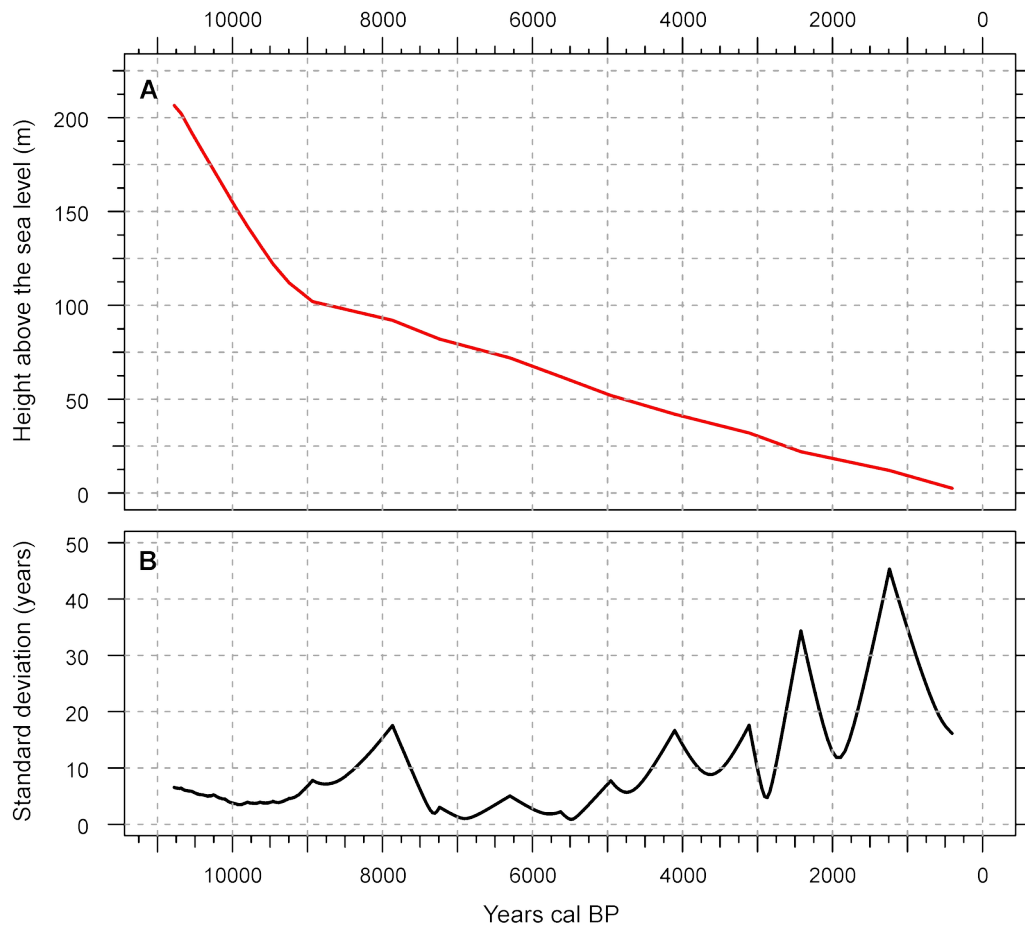


Figure 6



Supplementary figure 1



Supplementary figure 2

