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How to cite this publication

Please cite the final published version:

Riede, F., & Borre Pedersen, J. (2018). Late Glacial human dispersals in northern Europe and disequilibrium dynamics. *Human Ecology: An Interdisciplinary Journal*, 46(5), 621-632. DOI: [10.1007/s10745-017-9964-8](https://doi.org/10.1007/s10745-017-9964-8)

Publication metadata

Title:	Late Glacial human dispersals in northern Europe and disequilibrium dynamics
Author(s):	Felix Riede & Jesper Borre Pedersen
Journal:	Human Ecology: An Interdisciplinary Journal
DOI/Link:	10.1007/s10745-017-9964-8
Document version:	Accepted manuscript (post-print)

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Late Glacial human dispersals in northern Europe and disequilibrium dynamics

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Abstract   *There is mounting evidence for the non-analogue nature of Late Glacial (18.000-11.700 years BP) ecosystems. This period also witnessed several dispersal episodes of human forager groups moving, for the first time, into previously uninhabitable glacial or periglacial landscapes. In palaeartic northern Europe, these dispersals are associated with a succession of archaeological technocomplexes that are traditionally thought to reflect changing adaptation strategies synchronised with contemporaneous environmental changes. Recent investigations into ecological disequilibrium dynamics suggest, however, that there may be a greater degree of mismatch between organisms and their environments, especially in arctic-type environments and during times of rapidly changing climate. We link these climatic changes to cultural changes via demographic inference. Based on recent dating evidence, environmental analyses and preliminary*

morphometric and technological analyses of lithic material, we here develop the argument that these Late Glacial Palaeartic foragers were similarly at disequilibrium and that coupled with their very low population densities were prone to regional extinction episodes. We focus in particular on the so-called 'Hamburgian culture' and its potentially failed dispersal into southern Scandinavia.

Keywords Late Glacial; Palaeartic; Hamburgian culture; disequilibrium; artefact morphometrics

1. Introduction

Human forager groups in Europe weathered the ravages of the last Ice Age in lower-latitude refugia, most notably in the Franco-Cantabrian region. Here, small but relatively densely packed communities survived the extreme cold of that period and marked their presence by the production of astounding arrays of material culture as well as portable and parietal art (e.g. Straus, 2013; Straus et al., 1996). The transition from fully glacial conditions to the so-called Late Glacial eventually saw a warming trend that facilitated both population growth and the dispersal of forager groups belonging to the Magdalenian tradition towards the east and north (Bocquet-Appel et al., 2005; Miller, 2012; Otte, 2012; Pasda, 1998). Despite the overall warming that occurred during the Late Glacial, this period (ca. 18.000-11.700 years BP) was also marked by an exceedingly high amplitude and magnitude of climatic changes, as revealed, for instance, by ice-core records from Greenland (Rasmussen et al., 2014). In labelling this period the ‘reign of chaos’, Burroughs (2005: 13) underlines the importance of *changes* in climate rather than its mere severity as a key factor for ecological and cultural responses.

But did the rapidly changing climate really challenge contemporaneous foragers?

Recent ecological studies concerned primarily with the ways in which extant flora and fauna deal with climatic changes in the present have revealed a surprisingly high degree of disequilibrium (Normand et al., 2013; Svenning et al. 2015; Svenning & Sandel 2013), resulting in a) the absence of organisms in ecologically suitable locations as well as b) the presence of organisms in ecologically unsuitable locations. The viability of species communities under conditions of climate change also falls under the definition of disequilibrium effects. Human adaptations are fundamentally based on knowledge of biotic and abiotic resources and how they change in space and time – often

encapsulated by the term traditional and local ecological knowledge (TLEK; Berkes et al., 2000; Reyes-García et al., 2016) – plus the available technology serving as an extra-somatic means of adaption (Binford, 1962: 218, following White, 1959) that modulates carrying capacity. The notion of ‘landscape learning’ has been put forward as a process-oriented approach to the build-up of ecological knowledge, especially in relation to how pioneering dispersers need to acquire ecological place-based *locally specific* knowledge over some period of time (Rockman, 2001, 2003). The evolutionary corollary of this landscape learning perspective is that ecological knowledge and the adaptations it underwrites are imperfect at any given time (Rockman, 2009) – there is disequilibrium. In this paper, we explore one such disequilibrium scenario from the northern European Palaeartic. We focus on the late so-called Havelte phase of the Hamburgian culture, which is a northern variant of the pan-European Late Magdalenian. The Hamburgian culture (ca. 12.700-12.000 BC) is a Late Glacial hunter-gatherer culture, which represents the first colonization of northern-central Europe and, by extension, southern Scandinavia at the end of the last Ice Age. It is traditionally divided into an earlier and more eastern ‘classic’ and a later and more north-western ‘Havelte’ phase. The main difference between the two phases is to be found in their diagnostic projectile points rather than in any other aspects of their lithic repertoire or economy (Weber, 2008). Also, the two overlap chronologically and spatially (Grimm and Weber, 2008). Based on sparse faunal remains and the placing of locales high in the landscape, the Hamburgian culture on the whole is interpreted as focused on reindeer hunting, albeit this economy was likely also supplemented with small game, fish and available plant resources (Kabacinski and Sobkowiak-Tabaka, 2009).

These hunter-gatherers were part of the meta-population that reclaimed the previously glaciated landscapes of northern Europe in the period sandwiched between the last glacial maximum and the onset of the Holocene. We begin by reviewing the evidence for climatic and environmental changes during the initial Late Glacial warming, the so-called Bølling warming phase with particular emphasis on the mounting evidence for non-analogue and hence non-equilibrium environments. We then link these climatic and environmental changes to changes in past Hamburgian demography, and then use a detailed qualitative and quantitative shape analysis of Hamburgian stone tools to argue for very small populations characterised by classic meta-population processes of colonisation-extinction-re-colonisation along the edges of their possible range. By linking tool variants to specific sub-populations/communities of practice, we make the case for a more Gleasonian, i.e. individualistic response to the Late Glacial climatic amelioration where the choices of small groups – perhaps even of individuals – leave specific archaeological signatures. The corollary of this perspective is that the abrupt disappearance of these specific signatures in the archaeological record marks the regional extinction (cultural/biological) of their bearers. We note from the outset, however, that our approach is exploratory and aimed at formulating rather than testing hypotheses. The evidence marshalled here is indirect, i.e. we rely entirely on proxy evidence allowing us infer past demography rather than to study it directly (see Riede, 2009).

2. Rapid climate change and non-analogue environments in the Late Glacial Palaeartic of northern Europe

The Late Glacial, sometimes also referred to as the Last Glacial-Interglacial Transition (LGIT), was a period of temporally and spatially transgressive rapid climatic oscillations and attendant environmental responses (Lowe, 2001; Walker, 2001). Proxy data from the Greenland ice-cores show rapid oscillations in temperature, precipitation, and wind of at times considerable magnitude (Rasmussen et al., 2014) resulting a to-and-fro of colder stadial and warmer interstadials (Table 1). Across terrestrial, lacustrine and marine archives in Europe, there is a general correspondence with these patterns, but both leads and lags occur (Lane et al., 2013; Lowe et al., 2008). Palaeoecological studies focusing on comparing different regions reveal decadal-to-centennial-scale variation in these environmental changes and the associated floral successions, most parsimoniously explained by the need for soils to sufficiently evolve before any vegetation can be established (Feurdean et al., 2014). In southern Scandinavia, the eponymous site of Lake Bølling has in fact provided evidence of this late soil development. Here, lake productivity remained low and soils unstable until late in the Allerød (Bennike et al., 2004). What is important in the context of this paper is that although during warmer phases of the LGIT temperatures rose to near-Holocene levels, climatic variability was much greater (Fig. 1).

Table 1. *A schematic for climatic, environmental, demographic and cultural changes.*

Adapted from Gamble et al. (2005).

Figure 1. *The 20-year interval measure of climatic variance (black) derived δO^{18} temperature proxy record of the GISP2 ice-core and its long-term trend (white line). This measure, calculated by taking the square of the difference between the δO^{18} values*

themselves and their 21-term binomial running mean, aims to capture the intensity of climatic changes observable within a single generational timeframe. Note how this variance increases during the Last Glacial-Interglacial Transition despite the overall warming trend following the end of the Last Glacial Maximum. Modified from Burroughs (2005).

Numerous recent analyses have highlighted the non-analogue nature of Late Glacial plant communities. Willerslev et al. (2014), for instance, use soil-genetic methods to investigate community composition and stability in the Arctic and demonstrate that northern plant communities around the Last Glacial Maximum (25,000-15,000 BP) were significantly less diverse than both before and after. In this study, the LGIT is lumped together with the Holocene, but it is precisely here – in the period between the end of fully glacial regimes and the onset of the Holocene interglacial, that environments were subject to a major regime change. Such large-scale processes find their local expressions at sites such as Slotseng in south-western Denmark, where archaeological remains from the Hamburgian culture are found near a kettle hole that has also yielded robust environmental data (Holm, 1991; Noe-Nygaard et al., 2007). Mortensen et al. (2011) present a non-analogue floral community from this site as well as providing general environmental envelopes for the period in question.

Subfossil beetles provide additional insights into Late Glacial environments. Coope and Lemdahl (1995) and Coope et al. (1998) provide large-scale but regionally differentiated climate temperature reconstructions for northern Europe. These data show convincingly that both latitude and continentality have an impact on temperature

and that temperatures were rather variable from region to region (Fig. 2). Again, the Slotseng locale has provided direct evidence for such temperatures in southern Scandinavia (Table 2)

Table 2. *Minimum and maximum temperature (in °C) envelopes for southern Denmark during the Bølling chronozone as reconstructed from subfossil beetles and their ecological tolerances, from Lemdahl et al. (2014). Also given are the calculated population densities (persons/km²) as calculated by $e=(0.163 \times \text{AMT} + 1.840)/100$ (Binford, 2001).*

Figure 2. *Late Glacial maximum summer temperature reconstructions based on coleopteran beetle assemblages from four regions in northern Europe. From Coope and Lemdahl (1995).*

Of most direct relevance to Late Glacial hunter-gatherers probably were the responses of large mammals to these climatic and environmental changes, especially reindeer (*Rangifer tarandus*), which also was the preferred prey of the initial pioneers in southern Scandinavia. Stewart and Lister (2001) reviewed evidence from both plant and animal taxa across from the Last Glacial Maximum to the Holocene. They argue that non-analogue communities were common during the LGIT, reflecting the individualistic responses of species rather than previously established and coherent communities to the turbulent climatic and environmental changes of this period. Sommer et al. (2014) offer a synthetic study of reindeer range dynamics over the last 25,000 years and articulate this with parallel dynamics in other species (Sommer et al., 2011). They

clearly demonstrate that species whose ecological preferences are thought to be quite different co-occur during the Late Glacial. Aaris-Sørensen (2009) and Riede et al. (2010) provide the detailed view of the mammalian ecological succession in southern Scandinavia and nearby regions. They also stress the non-analogue nature of Late Glacial faunal communities, whilst also emphasising the general poverty of these communities during the very first part of the LGIT.

Lack of diversity does not, however, translate into lack of biomass. *Rangifer* thrives in such early successional landscapes and can quickly grow to enormous herd sizes (Geist, 1999; Spiess, 1979). At the same time, this species is notorious for its demographic fluctuations that can throw human populations reliant on them in great subsistence crises – even under the rather stable conditions of the late Holocene across the Arctic (e.g., Binford, 1991; Burch, 1972; Minc and Smith, 1989; Stenton, 1991). In well-controlled actualistic studies of reindeer populations and their fluctuations, Aanes et al. (2000: 437) note that ‘population fluctuations of arctic ungulates are strongly influenced by stochastic variation in climate’; with these variations having been more pronounced during the LGIT, the fluctuations in *Rangifer* herd sizes may also been more extreme still than those documented in the more recent past. A further dimension of environmental change in this period are the potentially dramatic palaeogeographic changes. Sea-level appears to have risen substantially and rapidly at during the Bølling (Deschamps et al., 2012). The Baltic Ice Lake, too, formed at this time (Björck, 1995). These changes in the palaeogeographic and hydrological conditions framing the study area are likely to have further impacted the livelihoods of these Late Glacial foragers.

Together, these different lines of environmental evidence suggest that although LGIT environmental changes did not correspond in a lock-step fashion to the climatic fluctuations recorded in the Greenland ice-cores, these environments were fluctuating dramatically during this period. They transitioned from the cold but relatively stable conditions of the preceding glacial towards the full and again stable interglacial (Holocene). Detailed studies of present-day Arctic vegetation show how even relatively moderate changes in climate can unbalance ecological communities and so drive changes community composition, diversity and spatial extent (Schmidt et al., 2016). Returning to the notion of landscape learning and TLEK, such disequilibrium and the attendant difficulty of scheduling economic activities may have posed major challenges for pioneering foragers entering southern Scandinavia.

3. Reconstructing Hamburgian demography

Demography is the summary result of individual life-history decisions, which take their cues from the socio-ecological environment, and chance events that impact birth and death rates. Numerous recent studies have attempted to link past hunter-gatherer population dynamics to environmental variables such as reconstructed temperatures, productivity or biodiversity. Binford (2001) has provided an extensive dataset for recent hunter-gatherers that allows the statistical linkage between subsistence strategies, recorded population densities and climate as well as environmental variables. Subsequently, these data have been used to extrapolate past hunter-gatherer populations under Holocene conditions as well as back to the Last Glacial Maximum (Tallavaara and Seppä, 2012; Tallavaara et al., 2015). Working with just a small, source-critically evaluated subset of Binford's data (Table 3), Kretschmer (2015) has recently

placed this demographic envelope into an analytical framework (see also Schlummer et al.; Zimmermann et al., 2009) that also takes account of the density and volume of archaeological finds in a given area, namely Late Glacial Europe. She notes that the resulting population densities extrapolated for the Hamburgian culture are at the very low end or even below those known from the ethnographic record, and suggests, in passing, that these may have been below a viability threshold.

Table 3. *The 16 hunter-gatherer groups selected by Kretschmer (2015) for her reconstruction of European Late and Final Palaeolithic forager population densities, including the Hamburgian culture. Also listed are climatic variables (Binford, 2001) that can be reconstructed from proxy records or modelled using simulation studies.*

Following a related track, Morin (2008) first established a correlation between mammalian diversity and forager population density and then calculated past population densities based on available faunal records from French Upper Palaeolithic locales. Extending this approach, Riede (2009, 2014) used aggregated faunal data for southern Scandinavia to show how also this method indicates population densities that are below those known from recent hunter-gatherers (Fig. 3). So, whilst many local temperature reconstructions for southern Scandinavia during the LGIT indicate climatic boundary conditions not too different from those of terrestrial hunter-gatherer populations known from the ethnographic record, non-climatic variables do indicate environments more rapidly changing and hence more challenging than those of the Holocene. Lemdahl et al. (2014), for instance, present temperature estimates for the

Slotseng locale in southern Denmark that are comparable to those known from ethnographic cases. Yet, Bennike and colleagues' (2004) reconstruction for the Lake Bølling locale in central Denmark paints a rather inhospitable picture. Such gradients are also strongly reflected in simulations for the early part of the LGIT that flag up marked mean temperature differences between, for instance, the southern part of the Hamburgian range and its northern periphery in southern Scandinavia (Fig. 4).

Figure 3. *Large terrestrial mammalian species diversity plotted (on a log-log scale) against population density data of 27 North American terrestrial hunter-gatherer groups (from Morin 2008). Open diamonds denote those groups living in cold and open landscapes; closed circles denote those in forested northern/temperate groups. There is a strong correlation between mammalian species diversity and forager population density in this data set: $r_s=0.62$, $p<0.002$ for the whole data set; $r_s=0.82$, $p<0.001$ for cold/open country groups; $r_s=0.81$, $p<0.07$ for temperate grassland groups. Linear fit lines have been added for the whole dataset (wide stippled), the cold/open (narrow stippled) and temperate/northern forested (solid line) groups. Added to this figure is the species diversity for the period of the Hamburgian culture in southern Scandinavia (Aaris-Sørensen, 1999), which does not intersect with the regression lines based on the ethnographic dataset suggesting a very low population density.*

Figure 4. *Reconstructed mean (1) summer and (2) winter temperature gradients (black) for Europe (Renssen and Isarin, 2001) superimposed on a site-based reconstruction of hunter-gatherer metapopulation densities (Bocquet-Appel et al., 2005).*

In sum, these different ways in which population density can be estimated for the Hamburgian culture point to very small groups operating over very long distances at the periphery of their range. As Hamburgian groups expanded northwards, they met ever-colder temperatures and shorter growing seasons. While reindeer may have been abundant in certain years, the intrinsic instability of these herds and the immaturity of these landscapes that had either been recently deglaciated or otherwise were heavily affected by periglacial processes made anything other than the most ephemeral settlement possible. In southern Scandinavia, only a very small number of sites and single finds are known. In the following, we look closer at the archaeological material itself in order to evaluate the duration and intensity of habitation, and to estimate the number of people.

4. Morphometric and technological analyses as additional proxies for population density

During excavation of a typical Havelte-group site at Krogsbølle on the eastern Danish Island of Lolland in 2012 (Westen, 2007) an observation was made regarding the lithic material of the site, more specifically, the projectile points. Here, two rather distinct morphologies are represented. Variant A is relatively short with alternately retouched tang tapers towards the base, whereas variant B is long with a broad tang with an angular base (Fig. 5). Both variants have close parallels in other Havelte group assemblages, especially those of southern Scandinavia. In contrast, the projectile point of the classic Hamburgian is rather diverse, in spite of the fact that the remainder of the lithic inventory is rather standardized (Grimm et al., 2012). Riede et al. (in press)

suggested on the basis of the material from Krogsbølle that these projectile variants may most parsimoniously be interpreted as the work of only a few individual flint-workers active at all these sites, or perhaps the material expressions of micro-traditions with practitioners that were only minimally separated in time (cf. Tehrani and Riede, 2008). Individual flint-knappers have been identified through close technological analysis elsewhere (e.g. Stapert, 2007; Whittaker, 1987) and our individualised interpretation of the lithic point variability within the Hamburgian culture is supported by the observation that classic and Havelte type points regularly occur together within Hamburgian assemblages (e.g. at Ahrenshöft LA73 – see Clausen, 1998), but that – at least in southern Scandinavia – classic type points do not occur.

An inter-assemblage analysis of Hamburgian projectile point shapes using geometric morphometric techniques further supports the notion of extensive versus restricted variability in the classic and Havelte phases of this culture respectively. Analyses of shape variability among classic and Havelte projectile points using qualitative assessments or linear measurements have been conducted before (Burdukiewicz and Schmider, 2000; Grimm et al. 2012). As alluded to earlier, the main difference between the lithic inventories of the classic Hamburgian and Havelte groups is found in the shape of the projectile points, with classic points having a wide variety of point shapes while Havelte points being somewhat more restricted shape-wise. A geometric morphometric approach is ideally suited for analysing such variability as it offers the possibility to capture and treat the entire outline of each point and to then compare them visually in an abstract morphospace that captures the main axes of variability.

The data used in the present analysis consists of illustrations of 123 projectile points from different sites across the Hamburgian range (Table 4). Illustrations are chosen as the source of data because they represent accurate descriptions of the original artefacts as well as being easily accessible, thereby facilitating the inclusion of a rather large dataset (cf. Shott and Trail, 2010). Here we focus exclusively on the 2D outline shape of the projectile points. Prior to analysis each illustration is extracted as a single image file and then oriented according to its axis of maximal symmetry using the GIMP image-editing program (Costa, 2010; Serwatka, 2014). When oriented, one TPS file was made consisting of all the 123 images using the program *TpsUtility* (Rohlf, 2006). Then *TpsDig* (Rohlf 2004) was used to place 40 equidistant semilandmarks that trace the outlines of the projectile points; these semilandmarks were then converted into XY coordinates. Finally, the programme PAST was used for processing and analysing these data (Hammer et al., 2001). The coordinate data are Procrustes-transformed and so standardized for size, orientation and position. Principal component analysis (PCA) is used to visualise the underlying patterns with PC1 and PC2 explaining 39.5% and 26.1% of the overall variance respectively.

The PCA shows a clear difference between the shape and shape variation of classic Hamburgian- and Havelte-type projectile points, but also an overlap between them (Fig. 6). This overlap supports the notion that classic and Havelte elements cannot be separated at the level of culture or even facies but that individuals making these distinct variants occupied the same sites at the same time at some sites. This is further supported by how the Havelte material seems to represent a distinct cluster within the overall shape spectrum of the Hamburgian projectile points. The current division between the classic and Havelte phases, and the associated change in point morphology,

is commonly understood in connection with environmental change (cf. Grimm et al. 2012). However, there are at present no datasets indicating significant environmental shifts at that time. It also seems questionable that a change in floral or faunal composition would change the morphology of just one tool class. The shift in point morphology could instead reflect much more strict norms for projectile production and thereby indicate a production reserved to a single group or at least a few groups closely related in time. Further indications of this are found near the Havelte site of Slotseng in Denmark, where at least 12 reindeer have been excavated from a kettle hole. These have all been dated to the same hunting (and hence deposition) event in the latest phase of the Bølling warming period, contemporary with the nearby Havelte site (Mortensen et al. 2012). This archaeological evidence indicates that the Slotseng site reflects a single occupation event and supports the notion of the Havelte sites in general as being of an ephemeral character, as a rule reflecting single occupation events. Refitting between locales can demonstrate such strict contemporaneity, but succeeds rarely (Scheer, 1986). Future refitting work targeting the nearby locales in eastern and western Denmark might yet be able to provide such proof.

Table 4. *The sample of Hamburgian projectile points used in this study.*

Figure 5. *The proposed projectile variants based on the Krogsbølle assemblage. These variants can be identified again in all northern Havelte-phase inventories.*

Figure 6. *Results of the principal components analysis of the shape variation among the studied Hamburgian points.*

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5. Disequilibrium in prehistoric hunter-gatherers

Recent studies of Arctic ecosystems stress that, as a rule, there is a lack of equilibrium between species' adaptation and the environments they inhabit. Arctic – and perhaps even more so Palearctic – foragers may be no exception. Although we often think of hunter-gatherers as perfectly in tune with their environment and of being able to flexibly respond to climatic and environmental changes using their cultural repertoire, also these means of adaptation have their limits (e.g. Laughlin and Brady 1978; Minc and Smith 1989; Mandryk 1993). They constrained by limited traditional ecological (landscape) knowledge under conditions of pioneering colonisation, of limited foresight under conditions of rapid climate change as well as perhaps by cultural norms that direct and limit adaptive change (cf. Dugmore et al., 2012; Willerslev, 2009). We have here presented a case study from the very first part of the Late Glacial-Interglacial Transition in southern Scandinavia. Numerous data derived from temperature proxies and simulations, from the faunal record and from archaeological site distribution data point to a short-lived, ephemeral and ultimately unsuccessful occupation of this region by the specialised reindeer hunters of the so-called Hamburgian culture. Numerous uncertainties remain, however.

Our morphometric and technological study must be considered preliminary and exploratory. An obvious next step is to include even more material and it is likely that by more strictly defining landmarks we may be able to find even closer matches of projectile point variants across sites. Furthermore, no modelling studies that attempt to reconstruct past hunter-gatherer populations densities take into account ethnographic

reports of forager population collapse (Grønnow and Meldgaard, 1991; Keckler, 1997; Laughlin and Brady, 1978). With groups of 0 population density not represented in the dataset used to reconstruct past hunter-gatherer population densities, the lower boundary conditions for these reconstructions remain inadequately represented. Very few of our proxy datasets are highly resolved, which limits our ability to reconstruct not just static population estimates for a given period but demographic dynamics from generation to generation. Our hypothesis of marked disequilibrium in early Late Glacial forager adaptation thus remains difficult to test. Improved modelling efforts that more adequately take account of ethnographic hunter-gatherer extinctions/population collapses and efforts to model environmental stress, risk and resilience (Barton et al., 2017; Brothwell, 1998; Stringer et al., 2004) rather than simply changing temperatures may provide productive avenues ahead. In addition, studies trying to refine the dating of the northern Hamburgian sites – including refitting aimed at establishing strict contemporaneity – could provide further evidence for the timing of occupation. Once this timing is better constrained, the relationship between human presence and climatic and environmental changes around this time can be investigated.

Arctic hunter-gatherer adaptations have a deep antiquity (Hoffecker, 2005), but they did not come into existence fully developed. Instead, selection sorted those behavioural and technological elements into eventually stable combinations – the ones we know from the ethnographic record. Against this background, the Hamburgian culture can perhaps be considered as an early form of mid-to-high latitude Arctic adaptation that involved extremely high mobility in the absence of dogs, of boats and of other means of non-pedestrian transport.

The expansion of these prehistoric hunter-gatherers into the very northern periphery of the Hamburgian range may eventually have led to a bottleneck. hunter-gatherers have limited means of buffering against environmental risk with mobility being one of the prime options (Halstead and O'Shea, 1989). The high mobility of Hamburgian individuals may have been an attempt to adapt to the unstable climate of the Bølling warming period or the subsequent cooling of the Older Dryas. With their focus on reindeer as a key resource, such increases in mobility are likely to have been driven by changes in herd sizes, movement patterns and distances. This, we argue, must have afflicted some degree of economic and social pressure upon such a group. The notion of disequilibrium in arctic ecosystems – here extended to include Late Pleistocene palaeartic foragers – provokes such models of punctuated colonisation and local extinction as a process underlying changes observed in the archaeological record.

More research is needed. Most pressingly, existing demographic models for hunter-gatherers should include those known instances, where populations have gone extinct. The resulting models would provide a better demographic envelope for extrapolation into the past. In addition, more detailed technological and morphometric studies of Hamburgian projectile points and other technological elements would also contribute to an increased understanding of individual vs. collective flint-knapping signatures. Refitting within and – boldly - between sites may be able to resolve to what degree the preserved tools represent the works of few or many individuals and what kind of occupation span the sites we know of represent. Refitting between sites is a risky endeavour, but one that can conclusively demonstrate contemporaneity (cf. Scheer 1986). Finally, specific models using the tools of species distribution modelling or similar approaches (e.g. Franklin et al., 2015; Svenning et al., 2011) could be used to

further quantify and hence clarify the relationships between Late Glacial foragers and different biotic and abiotic parameters. Studies applying such methods to past hunter-gatherers are emerging now (Barton et al., 2017; Benito et al., 2017; Nielsen et al., 2017) and hold great promise for unravelling these complex relations. Finally, genetic inference methods as well as ancient DNA analyses would no doubt facilitate additional insights into these volatile demographic processes. Human remains from the Late Pleistocene are scarce, however, and there are none available from our study area. At any rate, such analyses would yield the most robust results if they are grounded in clearly formulated a priori hypotheses concerning demographic continuity and discontinuity. We have here provided one such hypothesis for the earliest re-colonisation of southern Scandinavia after the last Ice Age.

Funding: This study was in part funded through a Post-Ph.D. Research Grant 8456 awarded by the Wenner-Gren Foundation for Anthropological Research, successive grants by the Beckett Foundation, and by Dronning Margrethe II's Arkæologiske Fond.

Conflict of Interest: The authors declare that they have no conflict of interest.

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Variant A

0
2
cm

Variant B

EVENT STRATIGRAPHY	ICE CORE APPROX. YEARS OF ONSET (BP)	CHRONOZONES	POPULATION EVENTS	TECHNO- COMPLEXES
Holocene	11,500			
GS-1		Younger Dryas	Contraction	<i>Ahrensburgian?</i>
GI-1a	12,650	Late Allerød	Isolation	<i>Brommean?</i>
LAACHER SEE ERUPTION				
GI-1b	12,900	Gerzensee Oscillation	Decline	<i>Federmesser- gruppen</i>
GI-1c	13,150	Early Allerød	Resettlement	
GI-1d	13,900	Older Dryas	Abandonment	<i>Hamburgian</i>
GI-1e	14,500	Bølling	First settlement	
GS-2a	16,900		First expansions	S Scandinavia not settled
GS-2b	19,500		into C Europe	
GS-2c	21,200			
	21,800			
GI-2		Last Glacial Maximum	Refugium phase	

Table 1. *A schematic for climatic, environmental, demographic and cultural changes. Adapted from Gamble et al. (2005). GI= Greenland Interstadial, GS= Greenland Stadial.*

Table 2. *Minimum and maximum temperature (in °C) envelopes for southern Denmark during the Bølling chronozone as reconstructed from subfossil beetles and their ecological tolerances, from Lemdahl et al. (2014). Also given are the calculated population densities (persons/km²) as calculated by $e=(0.163 \times \text{AMT} + 1.840)/100$ (Binford, 2001).*

Slotseng basin – extreme negatives			
	Bølling	Older Dryas	Early Allerød
t _{min}	-17	-17	-23
t _{max}	11	9	15
ET	10.2	9.8	10.9
MEAN	-3	-4	-4
Population density (persons/km ²)	0.014	0.012	0.012

Slotseng basin – extreme positives			
	Bølling	Older Dryas	Early Allerød
t _{min}	-3	-3	-8
t _{max}	16	13	18
ET	11.8	11.0	11.9
MEAN	6.5	5	5
Population density (persons/km ²)	0.029	0.027	0.027

Table 3. *The 16 hunter-gatherer groups selected by Kretschmer (2015) for her reconstruction of European Late and Final Palaeolithic forager population densities, including the Hamburgian culture. Also listed are climatic variables (Binford, 2001) that can be reconstructed from proxy records or modelled using simulation studies.*

Group name	Long	Lat	Region	ET	t _{min}	t _{max}
Ona	-68.62	-53.90	Tierra del Fuego	9.8	1.1	9.5
Rainy River Ojibwa	-85.1	45.21	Ontario	11.7	-15.7	19.4
North Sauteaux	-96.78	52.28	Ontario	11.7	-18.2	20.0
Round Lake Ojibwa	-90.62	52.71	Ontario	11.3	-21.2	17.6
Mistassini Cree	-72.66	51.75	Labrador peninsula	11.2	-18.0	16.5
Sekani	-120.00	56.14	Alberta	11.1	-13.3	14.8
Slave	-119.5	61.15	Northwest Territories	11.0	-25.7	16.3
Kaska	-125.00	59.73	British Columbia	11.0	-23.3	15.9
Tahltan	-127.85	57.66	British Columbia	11.0	-14.5	14.4
Mountain	-125.37	63.68	Northwest Territories	10.9	-28.1	15.7
Hare	-125	67.47	Northwest Territories	10.9	-29.0	15.6
Chippewyan	-106.19	59.47	Saskatchewan	10.8	-26.4	15.2
Satudene	-122.89	65.75	Northwest Territories	10.7	-27.7	14.6
Naskapi	-68.92	56.19	Quebec	10.3	-22.0	11.7
Noatak Inuit	-160.00	68.09	Alaska	10.1	-25.5	10.3
Nunamiut Inuit	-151.71	68.18	Alaska	9.9	-25.4	9.3
MEAN				10.8	-20.8	14.8
MIN				9.8	-29.0	9.3
MAX				11.7	1.1	20.0

Table 4. *The sample of Hamburgian projectile points used in this study.*

Country	Site	Classic	Havelte	Reference
Germany	AhrenshöftLA58a	3	1	Hartz (1987)
	Borneck	10	-	Rust (1958)
	Hasewisch	13	-	Rust (1958)
	Meiendorf	6	-	Tromnau (1975)
	Poggenwisch	27	-	Rust (1958)
	Teltwisch 1	18	-	Tromnau (1975)
	AhrenshöftLA58d	-	1	Hartz (1987)
	AhrenshöftLA58e	-	3	Hartz (1987)
	AhrenshöftLA73	-	4	Clausen (1988)
	Dörgener Moor	-	4	Schwabedissen (1937)
The Netherlands	Havelte Holtingerzand	-	6	Holm & Rieck (1992)
	Oldeholtwolde	-	8	Johansen & Stapert (2004)
Denmark	Slotseng C	-	3	Holm & Rieck (1992)
	Jels 2	-	13	Holm & Rieck (1992)
	Sølbjerg 2	-	3	Petersen & Johansen (1994)