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Impacts of palaeoclimate change 60 000–8000 years ago on humans and their environments in Europe: Integrating palaeoenvironmental and archaeological data

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ABSTRACT

Humans respond in a variety of ways to climate and environmental change. They may adapt, migrate, evolve new technologies, or experience breakdowns in their socio-cultural and economic systems. Working group 4 of the INTIMATE COST action ES0907 aims to summarise and synthesise the effects of climate changes from 60 000–8000 years ago on ecosystems, including animals and humans. The study of ecosystem and human responses and their causes requires close collaboration between archaeologists, zoologists, palaeoecologists, and geomorphologists. An INTIMATE workshop in Ghent, Belgium (November 6–7, 2012) focused on stimulating the integration of archaeological and palaeoecological approaches and methodology to improve reconstructions of ecosystem and human responses to climate changes in the full- and late-glacial and early-Holocene periods in Europe. Six main topics were delimited. High quality chronological control and accurate correlation is crucial for precisely relating ecosystem responses to climate changes and the ensuing human responses. The palaeoecological toolbox should contain both biotic proxies and physical proxies that can be applied flexibly to data collection during this period. Geomorphological and palynological studies reveal direct or indirect climate impacts and environmental changes at regional-scales. The geographical scale of human response will depend on the questions being asked. Humans depend almost exclusively on their local environment, so the impacts of climate changes on both terrestrial and wetland habitats need to be reconstructed at local ecosystem scales in relation to habitation sites. An array of high quality local data-sets across Europe that integrate palaeoenvironmental and archaeological records can be synthesised and examined for causal relationships in time and space. Emerging geographical patterns of climate and environmental change will give an overview of patterns of resilience and vulnerability of human societies to these changes. Gaps in knowledge will become apparent. Humans are a top predator and thus changes affecting the food chain, particularly in keystone prey composition, will be important to their survival. Integrative studies carried out at a variety of spatial and temporal scales encourage a development towards a better understanding of the varying resilience and sensitivity of ecosystems and human societies to palaeoclimate changes.

1. Introduction

Over the last decade refinements of archaeological and palaeoenvironmental records have highlighted the complexity of ecosystem and human responses to both abrupt and gradual palaeoclimate changes. No longer is it automatically assumed that where there is evidence for palaeoclimate change there will be correlating evidence for major ecosystem changes and subsequent human adaptations. Various palaeoclimate changes once thought to have negative global-scale impacts on ecosystems and human societies are now often seen to have had geographically confined

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impacts on ecosystems and/or human societies in particular areas of the globe, whereas in other areas there appear to be no impacts (Meltzer and Holliday, 2010; Straus and Goebel, 2011; Eren, 2012; Meltzer and Bar-Yosef, 2012). Thus, in recent years there has been a turn toward less deterministic approaches to the investigation of palaeoclimate-ecosystem-human interactions that takes into account the disturbance of equilibrium and the dynamics and variability between different proxy records and scales of analysis (e.g. Dearing et al., 2006a, 2006b, 2008). This opens up exciting research prospects that promise to enrich our understanding of the sheer complexity and diversity of ecosystem and human responses to a range of palaeoclimate changes that had different causes, onsets, durations, and magnitudes in different areas of the world (e.g. Van der Leeuw et al., 2011; Costanza et al., 2012).

In the past 50 years, the theoretical concept of "the balance of nature" has been rejected by palaeoecologists in favour of a more dynamic, holistic view, in which ecosystem development is defined as an interaction between climatological, ecological, and also human processes (Fig. 1) (including non-linear change, feedback processes, and even regime shifts; e.g. Scheffer et al., 2001; Folke et al., 2004; Crumley, 2006; Dearing, 2006a,b, 2008). This approach is promoted by the increasing interaction between environmental and archaeological scientists as demonstrated by Bell and Walker (2005).

Archaeological evidence has accumulated for human-induced landscape modifications showing that Palaeolithic societies were capable of shaping nature for millennia prior to European Neolithic settlement (Briggs et al., 2006). Hunter-gatherer activities would have affected their habitat at local scales, such as by burning or over-hunting large animals, or by allowing growth of anthropochorous weeds, or encouraging food plants such as hazel (e.g. Bos and Urz, 2003). Overall, a more integrated and quantitative interdisciplinary approach needs to be developed for understanding past climate–ecosystem–human interactions (Dearing, 2006a,b, 2008; Dearing et al., 2006a, 2006b; Oldfield, 2006). The critical challenge is to juxtapose palaeoenvironmental records against archaeological findings at the same temporal and spatial resolution (Caseldine and Turney, 2010; Meltzer and Holliday, 2010; Bell, 2012; Eren, 2012; Gronenborn, 2012; Meltzer and Bar-Yosef, 2012; Gelorini and Verschuren, 2013; Robinson et al., 2013).

Modern humans have lived in Europe since they arrived ca. 45 000 years ago. What was their world like and how did they survive, adapt to, and interact with the changing conditions of the Weichselian glacial period and the dramatic climate shifts and environmental changes at the start of the Holocene? To investigate these questions we can integrate evidence derived from the people themselves and the traces they left behind with evidence of the palaeoenvironment in which they lived. Over the last decade there has been an increase in high-resolution multi-proxy palaeoclimate and palaeoenvironmental data associated with advances in chronometric methods. This has resulted in an increase in studies that focus on the problems and prospects for integrating palaeoenvironmental data-sets with archaeological data in order to investigate climate–ecosystem–human interactions over multiple spatial and temporal scales (e.g. McIntosh et al., 2000; Blockley et al., 2006; Dearing, 2006a,b, 2008; Dearing et al., 2008; Maher et al., 2010; Meltzer and Holliday, 2010; Bell, 2012; Eren, 2012; Gronenborn, 2012; Meltzer and Bar-Yosef, 2012; Pillatt, 2012; Wilkinson, 2012; Robinson et al., 2013). Their aim is to understand if, where, and how ecosystems and human societies responded to these climatic events and to characterize the processes by which humans mitigated the impact of these events upon them. Our aim here is to further facilitate interdisciplinary collaboration between archaeologists and palaeoecologists by outlining some areas where better communication could be concentrated in the future.

1.1. *The human-related ecosystem*

The base of any ecosystem is the landscape which supports micro-organisms, plants and vegetation, and invertebrate and vertebrate animals which, under constant climatic conditions and associated geomorphological processes, co-exist in a dynamic equilibrium. Abrupt changes at a regional scale can be caused by rapid widespread extrinsic change such as climate change (Williams et al., 2011). However, the magnitude, timing, and direction of impact may be different in various regions or ecosystems. Changes in an ecosystem can also be brought about through gradual climate change and through intrinsic factors, such as succession, immigration, and abiotic processes affecting biotic interactions that pass thresholds and tipping points (Williams et al., 2011). Such changes may be abrupt if stochastic processes such as

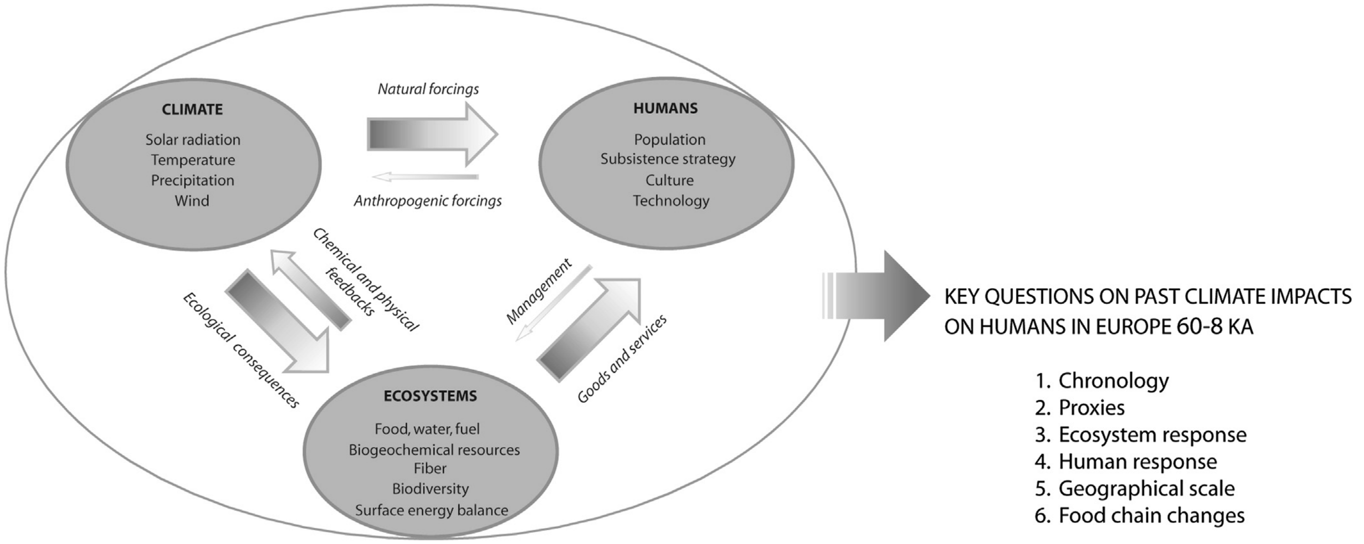

Fig. 1. Climate-ecosystem-human interactions in Europe 60 000–8000 cal BP. The width of the arrows indicates the size of the impacts and feedbacks. In order to understand the interactions better, 6 questions, discussed in the text, were pinpointed where future collaborative understanding and research may be stimulated.

fire, disease, or other disturbance events occur, but these changes are likely to be localised. In either case the result could be a mosaic of changes both in space and in time depending on the structure of an ecosystem and its resilience or sensitivity to change (Williams et al., 2011).

Palaeolithic and Mesolithic societies were an integral part of dynamic ecosystem networks. Humans were a top predator and therefore a keystone species. Humans are not passive within their habitats but possess qualities of group behaviour and leadership, inventiveness, curiosity, and communication. These qualities can endow them with great adaptability that allows them to be resilient to environmental changes, so that they can choose to move away or to modify their social organization and economic or technological strategies and thus to adapt to new conditions. They will rarely become locally extinct unless the environment changes beyond their limits of tolerance (e.g. extended drought, sea-level rise), if a sudden natural disaster strikes, or, in the case of Neanderthals, they are acculturated or out-competed by neighbouring hunter-gatherers (Stiner and Kuhn, 2006). While human culture can facilitate resilience to certain kinds of environmental change, certain socio-ecological systems are less flexible and therefore more vulnerable to particular kinds of palaeoenvironmental change. The central contribution to our general understanding of climate–ecosystem–human interactions that can be made by the different palaeo-sciences is the development of our knowledge about how specific kinds of environmental change impact particular aspects of human socio-ecological systems, and what specific adaptive strategies are carried out by humans to mitigate particular kinds of environmental challenges.

To discover humans' place in their ecosystem, we need diverse sources of evidence, provided by experts in archaeology, chronology, geomorphology, sedimentology, and plant and animal palaeoecology (Oldfield, 2006). Archaeologists provide evidence of distributions of cultures in space and time, societal behaviour, food sources, population sizes, and adaptations (or lack thereof) in response to climate and environmental changes, and most importantly, the ways in which these processes defined long-term cultural evolution during the Late Pleistocene and early Holocene. Zoologists can provide evidence revealed by invertebrate remains such as terrestrial beetles and a range of aquatic organisms such as chironomids, ostracods, and cladocerans. Bone and teeth remains witness the composition of vertebrate populations, both in general and in those ecological systems exploited by human societies. Small rodents and insectivores like marmots and shrews tell much about habitat conditions, such as the openness or dryness of the vegetation. Large grazers are ecosystem engineers and may hold an ecosystem such as the mammoth steppe in a constant state although it may be in disequilibrium with climate (e.g. Zimov et al., 2012). Carnivores hold the grazers in balance. Humans can use their intelligence, coordinated activity, and tools to hunt large prey, butcher it, and cook it for consumption. Additionally, the record of specific fungal remains may provide information on herbivores (e.g. Bos et al., 2006) although caution is necessary until the interpretation of fungal spores is more closely defined (e.g. Baker et al., 2013). Palaeoecologists can provide evidence of vegetation and ecosystem changes through time, most importantly in terrestrial ecosystems but also in aquatic ecosystems from where their evidence is often derived, such as lake sediments or wet frozen ground (permafrost). Geomorphologists can provide evidence of changes in the abiotic landscapes, which provide the environmental settings for the ecosystems.

To coordinate the diverse evidence of past ecosystems, dating and chronology are of paramount importance. Radiocarbon dating, in association with Uranium Series and Optically Stimulated Luminescence in older sites and non-organic deposits are routinely used. Correlation methods using time-stratigraphic marker horizons such as tephras and the relative positions of multiple proxies in single records can provide additional age control, which is especially important when considering synchronicity of climate, environment, and cultural change (Blockley et al., 2006; Riede, 2008; Lowe et al., 2012). It is essential, although it can be difficult, to correlate the ages of the archaeological sites with the records of environmental change from bone deposits and organic sediments, or other sources such as loess deposits. We must be able to place the archaeological assemblages of human societies from 60 000–8000 ka BP precisely in their habitats.

1.2. Climate and chronology

The overall driver of environmental change is climate. The two most important components are temperature and precipitation. Palaeo-records and ice-core records have shown how these vary continuously in time and in space. The NGRIP ice-core holds the current standard record of climate events, stadials and interstadials, as defined in Greenland ice (Blockley et al., 2012). Besides containing a climate record, the Greenland ice cores provide a precise chronology for the changes registered in them, standardised as the Greenland Ice Core Chronology 2005 (GICC05) (Rasmussen et al., 2006). The calibrated radiocarbon chronology can be correlated with GICC05 and thus we can correlate Greenland climate events with terrestrial chronologies (e.g. Lohne et al., 2013). However, we also have independent climate records derived from palaeo-data. Although there is broad agreement between the chronologies within the bounds of their error envelopes, it is becoming clear that the climate responses recognised throughout Europe are not always synchronous. Temperature and precipitation changes themselves may show gradients and tipping points may not be synchronous or even experienced at all at the continental scale. We have to read our data critically and interpret them independently of ice-core or other paradigms. Only then will we be able to reconstruct ecosystem responses fully. Biological responses may be initiated by a climatic shift, but the consequences and following interactions will take time to play out, over decades, centuries, or even millennia. The magnitude of response by the ecosystem being impacted depends on both the magnitude of the driving change and the sensitivity, adaptability, and resilience of the ecosystem conferred by the traits of its components.

1.3. Background setting

Here we restrict ourselves to Europe in the time range 60 000–8000 calendar years before present (cal BP) (Present = 1950 AD). Through this period up to about 11 650 years ago, conditions were typical of a glacial period, during which the Scandinavian Ice Sheet fluctuated with associated changes in the North Atlantic Meridional Overturning Circulation and variations in sea-ice extent, all of which affected atmospheric circulation and temperature and precipitation. Although cold and hostile near the ice-sheet during glacial advances, climate in southern Europe was more temperate and steppe or lightly forested landscapes were occupied by Pleistocene megafauna and humans. Around 48 000–45 000 years ago, anatomically modern human populations entered and spread across Europe and Neanderthals gradually became extinct, the timing depending on the geographical region considered (e.g. Stiner and Kuhn, 2006; Svendsen et al., 2010; Müller et al., 2011; Bradtmüller et al., 2012; Davies, 2012; Lowe et al., 2012). As archaeological knowledge of the local and regional complexities of these changes increases, the questions of the correlation and potential causality between climate and cultural change becomes an increasingly complex challenge to overcome for future research.

The climate warming at the onset of the late-glacial interstadial around 14 640 cal BP, initiated ice-sheet melting, reorganisation of the ocean and atmospheric circulation patterns, and caused melting of permafrost south of mainland Scandinavia. These processes were intensified at the rapid and large warming at the start of the Holocene (11 650 cal BP). Virgin land became available for colonisation by plants and animals, while in the periglacial areas the distribution of permafrost decreased considerably, thereby influencing the local hydrology and soil formation leading overall to stabilisation of the abiotic landscape. Forest species spread from their southern refugia and from isolated more northerly refugia (e.g. Willis and van Andel, 2004; Tzedakis et al., 2013) into former tundra and steppe and into the newly deglaciated areas. During the Holocene, forest trees spread across northern Europe and into Scandinavia (Huntley and Birks, 1983). The composition of the forests and their associated ecosystems altered as thermophilous trees, such as *Corylus, Ulmus, Quercus,* and *Tilia*, invaded and spread, replacing pioneer species, like *Betula* and *Pinus* in northern Europe (Iversen, 1973; Birks and Birks, 2004). Thus the Holocene warming had dramatic and long-lasting impacts on the previously treeless tundra of northern Europe and the steppe of central and southern Europe extending into Asia, both on the flora and on the fauna. Many mega-herbivores became extinct (Koch and Barnosky, 2006) and were replaced by forest taxa. The impact on humans was great. However, there is good evidence for a continuity of microlithic technologies and thus cultural traditions through the late glacial into the early Holocene. The lines are being increasingly blurred between Final Palaeolithic and Mesolithic societies. Mesolithic societies are merely hunter-gatherers adapted to living in warmer climates often at the margins of forest, as at the sea shore or the tree line. Thus northern Europe was colonized by hunter–gatherer societies that would establish the cultural and ecological foundations for subsequent human settlements throughout the Holocene, culminating in the present ‘Anthropocene’.

1.4. *Integration and synthesis*

Together, archaeologists, palaeoecologists, and geomorphologists need to face the incredibly daunting challenge of integrating extremely diverse palaeoenvironmental and archaeological data-sets over an enormous period of time. Existing datasets have variable composition and resolution and were designed to address a wide range of questions. Their diversity makes their integration difficult. Specific investigations are local, but they need to be put into a regional or global context to see the bigger picture (Dearing, 2006a,b). If a way can be found to integrate different datasets, this will be a first step in the way forward to providing a basic foundation from which further work with specific aims will stem (Van der Leeuw et al., 2011; Costanza et al., 2012). From a synthesis, further questions will become apparent, for example the designing of focused investigations to characterise gradients and locate tipping points or ecotones. New approaches to address such questions will contribute to the refinement of the overall pattern.

To realise successfully the potential for understanding responses to climate changes it is crucial that archaeologists and palaeoecologists should engage in informed dialogue on theoretical, conceptual, and methodological matters. For this reason, a workshop was organized by INTIMATE Working group 4 in Ghent, Belgium (6–7 November 2012) (Hoek et al., 2014 this issue) on the integration of palaeoenvironmental and archaeological data-sets across Europe between 60 000 and 8000 years ago. In this workshop archaeologists, palaeoecologists (animal and plant specialists), and geomorphologists considered six main questions and problems that could be addressed. This paper focuses on these six questions, in order to provide points for discussion and to encourage communication between diverse researchers. Hopefully this will stimulate improved understanding and development of theoretical and methodological frameworks for the integration of archaeological and palaeoenvironmental data to improve the investigation of ecosystem and human responses to palaeoclimate changes. Much is already known, but synthesis of existing data and new directions of multi-proxy investigation and collaboration will enlarge our current knowledge and highlight new avenues for research.

2. Six questions that might advance archaeological and palaeoecological integration

We summarise and enlarge on the discussions at the Ghent workshop and present some concepts that might advance understanding and collaboration between archaeologists and palaeoecologists, setting them out as a series of questions. The importance of precise chronologies is paramount in all investigations and is discussed under question 1. An understanding of the availability and the potentials and pitfalls of proxy data is an important methodological consideration and is discussed under question 2. The impacts of climate changes on ecosystems and human societies and technologies are discussed in question 3, the responses of humans to climate change in question 4, the scales of response in question 5, and impacts on food chains in question 6.

2.1. *How can we improve dating and correlation?*

We should use the radiocarbon chronology or calibrated year chronology when discussing events rather than the imprecise Blytt–Sernander climate periods, such as Boreal, Atlantic, etc. Radiocarbon chronology can be calibrated and matched against the GICC05 events if required for broader correlation. Our interpretations should always take account of the zone of uncertainty associated with reconstructed time scales, which limits the precision of correlation both within the radiocarbon timescale and between it and GICC05 (Lohne et al., 2013). Correlations between the $\delta^{18}O$ curve in Greenland ice and in the radiocarbon calibration curve should be made with caution. All age-depth models should be evaluated carefully when making correlations (Blaauw and Heegard, 2012). They reveal any irregularities in sedimentation rates, which could be important, especially in archaeological contexts.

To improve chronology we should be aware of the various pitfalls associated with radiocarbon and other types of dating and try to avoid them. Errors associated with radiocarbon dates do not only consist of the 2σ 95% measurement uncertainty. There may be reservoir effects associated with the origin of the carbon in the sample, fractionation by preferential uptake, imprecision of sampling, and possibilities of contamination, both during sampling and during the deposition and preservation of the sample (Walker, 2005). All these provisos can make it difficult to identify response times precisely by dating. In addition, our period extends to the limit of the radiocarbon-dating method so other types of dating are useful. Greater precision is possible in certain depositional situations such as when a marker horizon like a tephra is present, or when the relative position in time is known, as in parallel records of various proxies within one sedimentary sequence or core.

Investigations of ecosystem and human responses to abrupt climate changes require palaeoenvironmental and archaeological records with high precision chronologies (Blockley et al., 2006; Caseldine and Turney, 2010; Maher et al., 2010; Meltzer and Holliday, 2010; Bell, 2012; Davies, 2012; Eren, 2012; Gronenborn, 2012; Meltzer and Bar-Yosef, 2012; Wilkinson, 2012; Robinson et al., 2013). High precision chronologies depend on the adequate preservation of sufficient dateable materials throughout the palaeoenvironmental and archaeological records. High precision and resolution might be impossible to obtain in some regions and for particular climate-change events between 60 000 and 8000 years ago. Preservation of dateable materials depends on local and regional geomorphological and taphonomic processes that might yield high-resolution chronologies over long periods of time, cause gaps in sequences especially at archaeological sites, or obliterate entire records for long periods of time. The potential to test for contemporaneity and possible causality between climate and cultural change will depend on the stratigraphic integrity of the site or sites considered. This changed through time; Pleistocene archaeological sites are often located in cave and rock-shelter contexts with stratified deposits, whereas Holocene sites are most often found in open-air contexts that are much more susceptible to post-depositional disturbance and lack stratified deposits. Usually temporal variability in the archaeological record is found across regions. One would not necessarily expect simultaneous responses over wide geographical areas. Contemporaneity and causality between climate and cultural change will always have to be ground-checked by careful stratigraphic studies (Brown, 2008; Bradtmöller et al., 2012). A further challenge comes from problems of scale incongruity caused by a site or groups of neighbouring sites that indicate localized patterns of change that are unconnected with larger regional transitions in cultural techno-complexes (Kuhn, 2013). It is therefore of utmost importance that integrative archaeological-palaeoecological studies are carried out in spatially and temporally flexible ways that enable researchers to zoom-in and zoom-out of different scales in order to highlight particular scale incongruities and direct research forward to the scales with the best relative resolution and highest potential for yielding relevant answers to the questions of interest.

2.2. What are the most appropriate proxies to illustrate environmental response to climate change?

Palaeoenvironmental proxies are powerful tools that help elucidate impacts of past climate change on ecosystems. Although each proxy *per se* can contribute to an understanding of ecosystem response to past climate change, a multi-proxy approach takes advantage of the information provided by different proxies in parallel, both biotic and abiotic. The changes in abundance of fossil organisms or trends in abiotic components and their sensitivity to climate variability will depend on factors of local and regional climate (e.g. temperature and rainfall regimes), landscape (e.g. soil, topography, hydrology) and habitat (e.g. plants, animals, and their interactions). The sediment archives in which these proxies are recorded may vary greatly according to differences in age, origin, biotic composition, preservation, chemistry, and sedimentology (Battarbee, 2000). At present, multi-proxy approaches, using records of two or more proxies from preferably the same sediment sequence (Birks and Birks, 2006), are widely adopted to reconstruct environmental responses to climatic change through time. However, these approaches sometimes lead to contradictory reconstructions, so the characteristics of each proxy together with their strengths and weaknesses should be considered during interpretation (Birks and Birks, 2006; Huntley, 2012). Circular arguments should be avoided by testing an interpretation against an independent proxy (e.g. Birks and Birks, 2013). Aspects of the abiotic component (e.g. climate, soil, topography, water chemistry, water temperature) in past ecosystems can be regarded as a set of predictors or forcing functions within the past ecological system under study, whereas biotic components of the system (e.g. species, populations, communities, biotic interaction) can be typically viewed as response variables (Lotter and Birks, 2003; Birks et al., 2010; Lotter and Anderson, 2012).

For the interpretation of biological proxies it is important to integrate quantitative, region-specific calibration and reconstruction exercises (such as already established for pollen (e.g. Seppä et al., 2004), chironomids (e.g. Eggermont and Heiri, 2012), and diatoms (e.g. Bigler and Hall, 2002) to reconstruct more accurately biotic responses to past climate change through space-for-time substitution (*sensu* Jackson and Williams, 2004). Transfer-function techniques should be used with caution and assessed for unreliable and misleading reconstructions (Birks et al., 2010; Juggins and Birks, 2012; Juggins, 2013).

Traditional terrestrial proxies, such as pollen, plant macroremains, loss-on-ignition, and charcoal, may provide complementary insights into climate-driven soil and hydrological processes (e.g. moisture-balance, erosion, etc.), and vegetation shifts (e.g. forest invasion, fire frequency etc.). Aquatic proxies, such as diatoms, macrophyte macrofossils, chironomids, and cladocerans, document changes in the aquatic ecosystem (e.g. Birks and Wright, 2000; Birks et al., 2000), and may also be used to reconstruct changes in temperature (Heiri and Lotter, 2005) and salinity (Fritz et al., 1991). Novel temperature and hydrological proxies, such as organic biomarkers (e.g. TEX86, BIT, MBT/CBT, see Blaga et al., 2013), stable isotopes, and other geochemical components determined by XRF scanning (e.g. Arnaud et al., 2012), are now increasingly applied to sediment archives, particularly those from lakes. The use of ancient animal DNA to study range fluctuations and population dynamics is advancing rapidly (e.g. Hofreiter and Stewart, 2009; Shapiro and Hofreiter, 2014)).

Certain proxies are directly related to the reconstruction of human adaptation to habitats and their lifestyle during prehistoric times. For example, well-dated shell middens containing mollusc shells and fish otoliths illustrate diets and provide good preservation of accretionary calcium carbonate remains, stable isotopes, and fish ages and growth rates (Gutiérrez-Zugasti et al., 2011). While faunal and macrobotanical information on archaeological sites can offer direct evidence of modified human subsistence practices during periods of climate and environmental change, it is important to acknowledge that the assemblages can be biased by taphonomic processes or that the specific nature of activities undertaken at one site may not be typical of an entire economic system. Artefacts themselves such as tools and associated production debitage provide indirect evidence of human interaction with their environment, thus allowing inferences about adaptations to climate and ecosystem changes. These inferences have the potential to provide key information on changes in mobility, social and technological organization, and/or social exchange networks. Furthermore, anthropogenic hearths from hunter–gatherer camp-sites may yield valuable data on the palaeoenvironment and chronology, obtained from charcoal and other biotic remains such as plant macrofossils and animal and human bones (Crombé et al., 2013b; Robinson et al., 2013). Skeletal features can often yield indications of events survived during life and possible causes of death. These human-related archives are a source of proxy records of past climate and environmental conditions and may provide detailed pictures of human–environment interaction (Andrus, 2011). However, linking direct proxies of human adaptations to specific environmental or social conditions with the interpretation of less direct proxies such as the stone tool industries which make up the largest portion of the archaeological record throughout the Palaeolithic and Mesolithic periods is not easy. The correlation between changes in stone tool industries and potential resource imbalances could be tested by using local floral and faunal assemblages to reconstruct habitat changes to see if tool development is an independent process or has been driven as a response to ecological changes (Meltzer and Holliday, 2010; Dillehay, 2012.

2.3. What is the impact of climate changes on the ecosystems and humans living in them?

Climate impact on individuals and populations may operate either directly through physiology (metabolic and reproductive processes) or indirectly through the ecosystem, including prey, predators, and competitors (Stenseth et al., 2002). The linkage between climate change and its impact on ecosystems and humans is complex, including responses to natural and anthropogenic forcings, ecological consequences, and chemical and physical feedbacks (Julius et al., 2003; Dearing, 2006a,b). Broad-scale conclusions can be synthesised from numerous studies made at the local ecosystem scale (Crumley, 2006; Dearing, 2006a,b; Oldfield, 2006).

Climate changes will have a proportional impact on ecosystems depending on local site characteristics, the resilience of the system, and the tolerance limits of its components. For example, the amplitude of the climate oscillations registered in sea-surface temperature reconstructions differs considerably between the more extreme Heinrich Events and the less intense Dansgaard—Oeschger stadials. But in Portuguese marine pollen sequences both types of events appear to have resulted in similar tree-pollen reductions (Roucoux et al., 2001). In Greece, the pollen records of Tenaghi Philippon and Kopais show that even moderate climate changes during the last glacial had major impacts on temperate tree populations (Tzedakis et al., 2004). This is because ecosystems positioned at an ecotone are more vulnerable to climate impacts and are more easily tipped into a different stable state (e.g. Mayer and Khalyani, 2011; Williams et al., 2011). Resilience and inertia of the ecosystem and its components will determine whether thresholds are crossed or not and whether changes are so large that they could be considered as a regime shift. Small changes in climate can trigger major, irreversible responses in ecosystems once a threshold is passed. For example, today we can observe a strong response in Arctic ecosystems to recent climate warming (ACIA, 2004; CCSP, 2009; Post et al., 2013). Although fossil records are often hampered by limited taxonomic resolution, resulting in incomplete biogeographical information (Comes and Kadereit, 1998), large temporal changes in species distribution can be mapped at a continental scale, as shown by isopollen maps of European tree taxa through time (Huntley and Birks, 1983) and isochrone maps of North American tree taxa (Davis, 1984) suggesting that taxa may respond individualistically to environmental perturbations. Lorenzen et al. (2011) indicated that species of megafauna responded differently to climate change, redistribution of habitats, and human encroachment during the Late Pleistocene. Climate change alone may explain the extinction of European musk ox and woolly rhinoceros, whereas both climate change and human exploitation can explain the extinctions of steppe bison and wild horse (Lorenzen et al., 2011). Furthermore, a taxon may be impacted differently by climate changes between different regions. For example, subfossil reindeer records ceased at different times in northern Central Europe and in southern Scandinavia, corresponding to the timing of transitions from light open birch/pine forests to closed pine/deciduous forests in these regions (Sommer et al., 2013).

Biotic responses initiated by climate changes will always continue after the climate forcing event through small to considerable amounts of time, depending on the magnitude of the driving change and the adaptive traits and distributions of the organisms concerned. For example, the warming at the start of the Holocene initiated vegetation successions that continued for millennia, such as the spread of forest trees across Europe (Huntley and Birks, 1983). Forest succession would have had strong local impacts on a resident human population as the plant and animal assemblages changed in the ecosystem. The impact of climate change on prehistoric communities acted through climate-induced alterations of food, fuel and timber resources, and water supply.

Climate changes had both negative and positive influences for human societies, depending on the specific local ecosystem responses and the relative flexibility afforded by different human cultural systems. The thresholds at which climate changes have positive or negative impacts changed through time and were dependent on the social and environmental factors faced by humans in specific times and places (Minc and Smith, 1989). This can be illustrated by two examples within the INTIMATE timeframe.

First, the period from 48 000 to 36 000 years ago (GS-13-GS-8) encompasses the extinction of Neanderthal populations and the entry and spread of Anatomically Modern Human (AMH) populations throughout Europe. The relationships between this long complex transition and the abrupt climate changes associated with the cold Heinrich Events (HE) 5 and 4 are uncertain. The environmental record from Tenaghi Philippon (Tzedakis et al., 2004) in northern Greece is pivotal in the debate because it spans the period of the entry of AMHs into Europe and lies along its route. Müller et al. (2011: 278) proposed a model in which the climatic deterioration of HE5 caused a ‘demographic vacuum’ for Neanderthal populations in northern Europe, just as AMH populations were poised at the gateway to Europe. The ecosystem changes at the start of GI-12 from desert-steppe to open forest biomes facilitated the rapid expansion of AMH populations into central and northern Europe before the more sedentary Neanderthal populations were able to reoccupy these former territories, which resulted in ‘competitive exclusion’. Thus this climate change had positive impacts for one hominid group and negative impacts for another.

The cause of the final demise of Neanderthals in southern Europe has been proposed to be related to climate changes caused by HE4 and the Campanian Ignimbrite (CI) volcanic eruption. To test this hypothesis, Lowe et al. (2012) examined well-stratified archaeological sites in southeast Europe containing both Middle and Upper Palaeolithic cultural deposits and also the Tenaghi Philippon record to pinpoint the location of the CI tephra in relation to the stratigraphy. They found that the extinction of Neanderthals in southeast Europe preceded HE4 and the CI eruption, so it was unrelated to the impacts of the HE4 climate change on ecosystems. On the other hand, in southwest Europe Bradtmöller et al. (2012) critically assessed the stratigraphy of sites where very late Neanderthal survival had been proposed and found that Neanderthal extinction in Iberia was related to climate changes during HE4, coinciding approximately with GS-5. Their stratigraphic assessment, coupled with the integration of the chronological changes in certain cultural techno-complexes and the evaluation of key environmental records, refuted the evidence for late Neanderthal survival and linked their extinction to ‘widespread desertification’ caused by HE4. Thus not only will hominid populations be impacted by climate and ecosystem changes in different ways, but most importantly, their responses will be related to the particular impacts made by climate change in the regions where they were living.

Second, in the Younger Dryas (YD, GS-1) northern Europe experienced considerable environmental changes from light forest or shrub communities to grasslands and tundra in the YD, whereas central Europe witnessed the continuity of earlier pine-dominated forests (e.g. Weber et al., 2011). These regional differences appear to have had little impact on most human populations during this time (Weber et al., 2011). However, in the circum-Baltic region it is likely that YD conditions were more favourable to hunter-gatherers than the earlier warmer forested period (Allerød) (Burdukiewicz, 2011). Human societies only showed adaptations during the YD in Europe at ecotones (Weber et al., 2011), which, as noted earlier, are the most susceptible to the impacts of climate change. Populations that had developed specific ecosystem-related sociocultural and ecological traditions either would have to move with these same ecosystems, or adapt their subsistence, mobility, and social network systems. As human populations increased, so did their density. This might have impeded free population movements across territorial barriers, thereby enforcing societies to adapt to the changing local conditions (Crombé et al., 2011).

2.4. How did people respond to ecosystem changes?

Humans are masters of adaptation to adverse conditions, often responding by cultural evolution. A currently emerging hypothesis suggests that extreme climate variability shaped human nature, allowing us to survive in all sorts of environments through our property of adaptability (Gibbons, 2013). The ecosystem controls the social economy, which will be adapted to environmental changes to maximise survival. This may involve adaptation *in situ* or adaptation during migration (an example of hunter-gatherer response in the mid Holocene in Finland is given by Tallavaara and Seppä, 2012; Manninen and Tallavaara, 2014). All the cultural changes, typified usually by changes in tool design and production techniques, will lead to increased chances of survival and prosperity in the new environment. Therefore the functional purpose of stone and bone tools and their evolution should be considered in addition to their identification and typification in different cultures.

Humans are affected by their local environment and therefore their responses are local. However, a widespread climate change could result in regional and continental scale impacts affecting many ecosystems in parallel (Berglund, 2003, 2006). The research question determines the scale to be considered.

People need to live on dry land but near fresh water such as a river or lake. Many palaeoecological studies from wetland or aquatic sites have provided ecosystem contexts for archaeological sites near freshwater. The lives and economy of the people are closely linked to the freshwater environment and any change in this will have large effects on the population. Because the people were not living directly on the wetland site, the local palaeoecological reconstruction has to be closely related to the archaeology. There are several late-glacial examples. The period of suitable environment for people to hunt reindeer in Jutland (Denmark) was documented from a small shallow lake site which must have been near their campsite (Mortensen et al., 2011). The integration of late-Palaeolithic people in a cover-sand environment in northeast Belgium, living on a sand ridge and hunting in shrubs and reed-swamps, and fishing in lakes, was reconstructed by Bos et al. (2013). Although outside Europe, the response of people to late-glacial climate changes in northwest Iran is an excellent example of integrated archaeology and palaeoecology. The palaeolimnology of Lake Zeribar reconstructed the environmental development and indicated that cereal cultivation was stimulated by the arid climate during Younger Dryas time (Wasylikowa and Witkowski, 2008).

The close relationship of Mesolithic people with fresh water has been shown in several studies. Bos and Urz (2003) used pollen, macrofossil, and geomorphological evidence to show how Mesolithic people in a riverine ecosystem in N Germany lived on a river terrace where they had a small impact upon the vegetation and hunted and fished in the floodplain marshes. It is long known that Mesolithic people were widespread across the low-lying and marshy exposed floor of the North Sea, utilising both the terrestrial and aquatic habitats (e.g. Gaffney et al., 2007; Spinney, 2008). The mid-Holocene sea-level rise forced them to evacuate this area. Settlements were not always terrestrial; some settlements were made on platforms over water, possibly to be safer from attack by wild animals or other humans. A well-known Mesolithic example is the lake dwelling at Star Carr (UK) (Mellars and Dark, 1998). There are many Neolithic and later examples in the Alpine area (e.g. Jacomet, 2009). A good example of integrated archaeology and multi-proxy palaeoecology by Godłowska et al. (1987) demonstrated how successive Neolithic cultures living on a terrace of the Vistula River in Poland related to their varying environments that were reconstructed from sediments in an oxbow of the river below the terrace. On-going projects are demonstrating the importance of the proximity of freshwater and reed marshes, both as a water supply and for hunting, to Mesolithic people (e.g. at Moerbeke (Belgium), see Crombé et al., 2013a; Gelorini et al., 2014 this issue, and at the Rotterdam Yangtze harbour (The Netherlands) (Weerts et al., 2012)).

2.5. What were the broad scale geographical patterns of responses to climate changes?

Species can move, adapt, shift habitat, or become extinct, or in some cases, evolve in response to climate change (Dawson et al., 2011). Total extinction of plants during our period is unknown in Europe, but mammal extinctions are numerous, and those of the mega-herbivores and carnivores are spectacular (e.g. Barnosky et al., 2004). Near the start of our period, our human cousins the Neanderthals, died out (e.g. Svendsen et al., 2010; Stringer, 2012). Range and abundance changes are often rapid (within 1000 years) and can occur at local and regional scales (Blois and Hadley, 2009). Such changes are commonplace and can be illustrated by maps of fossil distributions within suitable time slices if there are sufficient reliable records.

As ecotones moved in response to climate changes, areas became sensitive at different times, so changes from tundra and steppe to forest in the early Holocene for example are geographically time-transgressive. Suitable climates and environments for trees shifted northwards (e.g. Huntley and Birks, 1983) or upwards (e.g. Eide et al., 2006) or spread geographically (e.g. Willis and van Andel, 2004). Trees spread as a consequence, but usually did not keep pace with habitat availability, showing lags in arrival (e.g. Huntley and Birks, 1983). Therefore, we should not expect the apparent consequences of climate-driven changes to be synchronous across the European continent. As outlined in the Introduction, we would be wise to identify sensitive areas (hinge regions) for study from where we will obtain the most useful information about the impacts of climate changes. To study these impact patterns, we have to synthesise local-scale studies. A broad-scale pattern is only as detailed as the precision and distribution of its local components. So we need as many detailed local studies as possible. For example, we can use sedimentological information from lake basins to reconstruct the impacts on abiotic landscape-forming processes. The effects of these changes can then be investigated with biotic data to reveal the impacts of both climate variability and landscape alterations on the organisms and people inhabiting the area (e.g. Berglund, 1991, 2006). A synthesis can then be compiled by assembling all the data, thereby revealing changes in the geographical patterns of biological responses to climate forcings and pinpointing areas where more data are required.

Geomorphological changes can be reconstructed not only in local detail, but also over relatively large areas, particularly because most of the geomorphological features are well preserved. An example is the northeast European Sand Belt (Kasse, 2002; Kaiser et al., 2009) that extends from Belgium into NW Russia. The evolution of this periglacial landscape has been reconstructed from climatic, geomorphological, vegetational, faunal, and archaeological evidence (e.g. Hoek and Bohncke, 2002; Bos et al., 2013). Broad-scale active aeolian processes occurred particularly during the colder and drier phases of GS-2 and GS-1. In the interstadial between, GI-1, aeolian processes ceased and organic soils under open birch or birch-pine forests could develop (Hoek and Bohncke, 2002). The geographical changes between tundra (GS-2), open birch-pine forest (GI-1), and return to tundra conditions (GS-1) determined the distributions of reindeer and reindeer hunters which are clearly reflected in the different cultures: Hamburg, Ahrensburg, Federmesser etc. in this area, and also in Denmark (Mortensen et al., 2011; Sommer et al., 2013).

Another important issue is the scale on which palaeoenvironmental reconstructions can be interpreted. Regional vegetation reconstructions are generally inferred from fossil pollen. Because of the abundance and relatively wide distribution of many pollen grain types, macro-scale reconstructions of vegetation types (such as "an open birch-pine forest") can be obtained for example, from the late-glacial period in the Netherlands (Hoek, 2000), where a large number of pollen data-sets are available. Complementary to pollen, the use of plant macrofossils provides more precise and nuanced reconstructions of local vegetation (Birks and Birks, 2000). Most faunal remains, both from vertebrates and invertebrates, are also of local origin, reflecting site-specific environmental conditions.

2.6. *How are food chains affected by climate change?*

A stable ecosystem is an interlocking network of causes, effects, and feedbacks in balance. Pre-Neolithic humans lived in dynamic equilibrium with their environment. Climate controlled the overall character of the vegetation, which supported small and large animal grazers, preyed upon by carnivores, including people. If climate change results in a dislocation of a link in the network it will result in a shift in the biodiversity ecosystem function, which may lead to a regime shift in community structure (e.g. Ripple et al., 2013). Such a shift may include the formation of novel ecosystems by the invasion of new pioneer species forcing the modification of previous biotic interactions (e.g. Blois et al., 2013). The net result is a loss of biodiversity through local extinction of species unable to adapt to the new conditions. The extreme case is the extinction of the Pleistocene mega-herbivore fauna near the end of the glacial period in Europe, mediated through habitat change and hunting (Barnosky et al., 2004). The decrease in biodiversity resulting from climate change affects human lifestyles and makes ecosystems more sensitive to further climate changes and other impacts, particularly human feedbacks (Cardinale et al., 2012).

3. Conclusions; a way forward

Human responses to climate and environmental change 60 000–8000 years ago in Europe include resilience, adaptation, migration, local extinctions, and behavioural and cultural evolution. During the last 50 years, techniques of archaeological, palaeoecological, and chronological analyses have greatly advanced and now the interpretation of data is often approached through modern calibration studies, modelling and statistical methods, and multi-proxy research. Taking an overview of the parallel efforts of many individual researchers, the participants at the Ghent workshop outlined six main areas that could be explored more thoroughly to determine the impacts of palaeoclimate changes on humans and their environments. The six key questions addressed in this paper focus on cutting-edge issues regarding chronology, availability of proxies, ecosystem and human responses, geographical scale, and food-chain changes. We conclude that dialogue, discussion, and collaboration between archaeologists, zoologists, geomorphologists, palaeoclimatologists, and palaeoecologists are vital to help disentangle more precisely the relationships between climate, ecosystems, and humans through time. In this paper, it is certainly not our intention to establish a novel comprehensive research strategy which will close all knowledge gaps left by traditional palaeoenvironmental and archaeological research disciplines. Rather, we hope that by pinpointing some concepts where disciplines have different approaches, researchers in the different fields may be stimulated to appreciate other points of view and learn from their colleagues and thus be able to tackle the research challenges in the most productive way. Improved inter-disciplinary communication and research should inspire renewed efforts and promote multidisciplinary perspectives in unraveling the exact timing and relative magnitude of ecosystem and human responses to climate impacts. An informed conceptual framework for palaeo-related research can offer consistent tools to assess properly the resilience and sustainability of natural ecosystems to climatic and human impacts and the adaptability of humans to their changing ecosystem services.

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