



Evaluating the transitional mosaic: frameworks of change from Neanderthals to *Homo sapiens* in eastern Europe



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ABSTRACT

Defining varying spatial and temporal analytical scales is essential before evaluating the responses of late Neanderthals and early *Homo sapiens* to Abrupt Environmental Transitions (AETs) and environmental disasters for the period 130–25 ka. Recent advances in addressing the population histories and interactions (using both genetic and archaeological evidence) of Neanderthals and *H. sapiens* have encouraged consideration of more subtle dynamics of archaeological change. Descriptions of change based on methodologies pioneered some 160 years ago are no longer adequate to explain the patterning we now see in the record. New chronological results, using multiple dating methods, allow us to begin to unpick the spatial and temporal scales of change. Isochronic markers (such as specific volcanic eruptions) can be used to create temporal frameworks (lattices), and results from other dating techniques compared against them. A combination of chronological lattices and direct dating of diagnostic artefacts and human fossils permits us, for the first time, to have greater confidence in connecting human (recent hominin) species and their behavioural responses to environmental conditions, and in quantifying scales of change over time and space (time-transgression). The timing of innovations, particularly those in bone, antler and ivory, can be directly quantified and tested, and used to re-evaluate longstanding models of cultural change. This paper also uses these new chronologies to explore the ecologies of late Neanderthals and early *H. sapiens*: their population densities, mobilities, resources exploited and possible interactions. Environmental productivity estimates are used to generate new questions of potential population densities and mobilities, and thus the sensitivity of these groups to environmental perturbations. Scales and intensities of effect on environments from natural disasters and AETs (notably Heinrich Events and the Campanian Ignimbrite eruption) are defined as a scale from “proximal” to “distal,” with local conditions (topographic shelter or exposure) serving to intensify or mitigate those effects.

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1. Introduction

This paper sets the results obtained by Work Package 1 (henceforth “WP-1”) of the RESponse of humans to abrupt Environmental Transitions (“RESET”) into a broader Eurasian context (Lowe, 2015). It will augment the new chronological lattice (Lowe, 2015; Bronk Ramsey et al., 2015) from the RESET project with direct radiocarbon determinations on diagnostic organic artefacts, and evaluate the results in the light of time-transgressive change in hominin (late Neanderthal and early *Homo sapiens*) behaviours and landscape occupation between ~130 and 25 ka (in particular the

period 50–30 ka) (Table 1). The following themes will be addressed:

- The implications of the tephrochronological lattice for tracking Neanderthal and early *H. sapiens* occupation patterns (including population retreat and expansion).
- Differential effects in proximal versus distal eruption signatures on hominin occupation patterns and economies.
- The chronology and social contexts of innovations in organic technology.
- Time-transgressive patterning in changes seen in the archaeological record.

The limitations in the record need to be considered, in order for the major advances made by the RESET project to be developed

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further. It should be noted that, despite the best efforts of the project, no tephra records (whether visible or cryptic) have yet been identified in western Europe for the period ~130–25 ka; instead, numerous tephra records were recovered from archaeological sites in eastern Europe (Italy and further east), allowing a multi-tephra lattice to be constructed for this region. This lattice has potential for increased detail when currently-unknown tephras are identified to source and new cryptotephra occurrences found. If current models of population replacement of Neanderthals by *H. sapiens* are correct (e.g. Hublin, 2010; Stringer, 2012), then the tephrochronological lattice is of crucial importance, for it ties together sites in the part of Europe where we should expect to see the earliest *H. sapiens* occupation, and the start of Neanderthal territorial contraction. Nevertheless, the lack of tephra records in western Europe currently hampers the construction of a lattice in the areas that may contain final Neanderthal occupations.

As set out below, the ideal combination is the presence of tephra records and dateable artefacts at each site. While this co-occurrence does seem to occur at some sites, tephrochronology has yet to be augmented by direct dating of organic artefacts at a single location. Sites such as Szeleta cave, in Hungary, have yielded insufficient cryptotephra for identification, and the single Aurignacian split-based point from the site did not contain enough collagen for dating (Table S4). So far, the two dating methods seem to be mutually-exclusive at archaeological sites, though the potential for both methods to be employed (e.g. at one of the Kostenki sites) exists, and should continue as a research ambition for this key period of human prehistory.

2. Evaluating hominin demography, 130–25 ka

Before assessing the effects of environmental disasters and Abrupt Environmental Transitions (AETs) (Table 1) on Neanderthal and *H. sapiens* populations, it is necessary to establish what we know about their demographic structures and spatial extents. Neanderthal societies have often been characterised as localised and small-scale, based on raw material transport distances, limb

proportions, ancient DNA variability and energetic requirements (e.g. Féblot-Augustins, 1999; Finlayson, 2004; Verpoorte, 2006; Dalén et al., 2012). This is frequently contrasted with patterns identified for Upper Palaeolithic *H. sapiens* (see section 8), who, as a non-native European hominin species, are often presumed to be more mobile and wider-ranging, perhaps even targeting particular biome types across a region (Davies, 2001). We should remember, though, that the localised spatial patterning of Neanderthals is most apparent near the end of their existence, given additional emphasis by depleted and isolated populations (e.g. Castellano et al., 2014; Sankararaman et al., 2014). Although there is genetic evidence of long-term demographic attrition on their populations (see below), at times the Neanderthals were able to disperse and expand their ranges (Serangeli and Bolus, 2008). As discussed below (Section 3), the tephrochronological lattice for WP-1 extends back to ~130 ka, covering periods of Neanderthal range expansion and relative stability, as well as their later (post-60 ka) range contractions prior to, or penecontemporaneous with, *H. sapiens* range expansions.

Establishing the demographics (population levels, histories, structures) of *H. sapiens* and Neanderthals has proved problematic, whether one uses archaeological, climatic or genetic proxies. The issue, however, requires consideration if we are to assess the effects of volcanic eruptions and climatic shifts (environmental disasters and AETs, respectively) on hominin populations. How many hominins might have been affected, to what extent, and were patterns of landscape occupation altered? Palaeodemographic estimates are mostly restricted to the post-100 ka period; they agree that hominin populations in western Eurasia were low at about 40 ka, with archaeogenetic models of Neanderthal census metapopulation ranging between 25,000 and 200,000 individuals (Fabre et al., 2009). This metapopulation was calculated using an estimate from mitochondrial DNA (mtDNA) that effective Neanderthal populations (i.e. numbers of breeding females) represented ~25% (3125–25,000 individuals) of the total female metapopulation, and ~12.5% of the census metapopulation. Based on sizes and numbers of known archaeological sites, Bocquet-Appel et al. (2005)

Table 1
Definitions of key terms of reference.

Abrupt Environmental Transition (“AET”)	Pronounced shift from one set of prevailing environmental conditions to another, e.g. Heinrich Events (see below).
Aurignacian	Technocomplex spanning Europe and western Asia, dated ~44–32 ka, and characterised particularly by distinctive osseous (bone, antler and ivory) projectile point forms.
Bond cycle	A series of short-lived warming (interstadial) events that show progressive cooling, culminating in a severe HE (Bond et al., 1993; Lowe and Walker, 2015).
Contingency	Spatio-temporally localised hominin behavioural patterning; shifts from one state to another may have multiple social and environmental explanations.
Environmental/natural disaster	Short-term environmental perturbations, e.g. tsunamis, volcanic eruptions.
Heinrich Event (“HE”)	Rapid and massive intermittent discharges of icebergs that tracked the southern margin of the polar gyre, depositing layers of ice-rafted debris (Heinrich layers) on the floor of the North Atlantic. These reflected episodes of marked reduction of sea surface temperature during climatic episodes referred to as Heinrich Events (Bond et al., 1992; Lowe and Walker, 2015). The Campanian Ignimbrite (“CI”) appears to have occurred in the early part of one of these events, HE4 (Lowe et al., 2012).
Hominin	All hominid taxa ancestral or closely-related to <i>Homo sapiens</i> , i.e. australopithecines and members of the genus <i>Homo</i> (Wood and Richmond, 2000).
Isochron	Contemporaneous event horizons, which allow temporal correlations at a range of spatial scales (Lowe and Walker, 2015; pp. 348 & 364).
ka	Thousand years (calendric, not ¹⁴ C) BP.
Marine Oxygen Isotope Stage (“MOIS”)	Marine oxygen isotope records show characteristic fluctuations throughout the Quaternary that reflect (in the main) glacial–interglacial climatic cycles. Glacial and interglacial stages can be defined as isotopically light (interglacial) stages, which are given odd numbers, and isotopically heavy (glacial) stages (even numbers), the sequence of stages being numbered with depth from the present (Holocene) interglacial stage (MOIS-1). In total, the Quaternary comprises 103 stages (see Lisiecki and Raymo, 2005).
Technocomplex	A huge system, with an estimated range of ~1200–4800 km, encompassing connected archaeological culture groups, material cultures, assemblages and (finally) artefact-types (Clarke, 1968, p. 323, 331).
(Tephrochronological) lattice	Chronological framework of identified tephra horizons, allowing single and/or multiple markers to be connected temporally at discrete sites.
Tephra	Volcanic fragmental clasts contained in either visible and/or microscopic (cryptic) deposits.
Time-transgression	Sedimentary and archaeological event boundaries that do not start or end at the same temporal points across their spatial ranges (Lowe and Walker, 2015, p. 349–354).

estimated *H. sapiens* metapopulation sizes of 1738–28,359 for the European Aurignacian (~44–32 ka), and slightly higher populations for the Gravettian (~33–25 ka) (Table 2). However, overall metapopulation levels are of lesser concern to our analyses than the geographic distributions and regional organisation/structures of Neanderthals and *H. sapiens*, if we are to plot the distributions of marker tephras and their local environmental impacts.

Table 3 summarises regional population estimates derived from archaeological site densities. It describes varying occupations of northern and SW European regions, though it is largely dependent on known spatio-temporal archaeological site distributions. Attempts to move beyond the inherent recovery biases of the archaeological record require us to model the population levels that could have been sustained by changing climatic conditions during our study period, and these simulations can then be compared against empirical data. Sørensen (2011) used inferred temperatures from the GRIP and NGRIP ice-core records to predict Neanderthal and *H. sapiens* population levels (Table 4). His model predicted low Neanderthal populations during the interglacial conditions prevailing between 130 and 120 ka, followed by a steady, though modest, growth during the rest of Marine Oxygen Isotope Stage (“MOIS”: Table 1) 5 (120–70 ka), including increases in northern and mid-latitudinal bands of Europe. After contracting to southern Europe during the MOIS-4 stadial conditions of 70–60 ka, Neanderthal numbers were predicted to rise a little between 60 and 27 ka (MOIS-3), before increases in *H. sapiens* populations (arriving at ~45 ka) had an adverse effect. However, rather than demonstrating larger regional hominin population sizes than can be inferred from the biased archaeological record (Table 3), it would appear that Sørensen’s estimates based on temperature proxy data (Table 4) actually fall near the minima predicted by Bocquet-Appel et al. (2005). Taken at face value, minimal estimates of between 2 and 20 hominins for mid-latitudinal and northern European regions (at 90–80 ka, and 60–20 ka) raise serious questions about the viability of such small populations in these large regions. Given recent dating evidence (e.g. Higham et al., 2014), predicted Neanderthal survival beyond 40 ka (Table 4) can no longer be sustained. Sørensen’s (2011) demographic model is of interest to us because it is dynamic rather than a series of snapshots, but it seldom predicts overall population falls (e.g. 70–60 ka); instead, populations are modelled as being frequently displaced southwards from more northerly regions of Europe, resulting in higher levels in the South (or the opposite situation at 40–38 ka: see Section 4).

Direct recovery of ancient DNA from Neanderthals has allowed questions of regional hominin displacement and extinction to be tested in more detail. Regional population subdivisions among sampled Neanderthal fossils have been proposed on the basis of mtDNA variation. Fabre et al. (2009) identified three Neanderthal subpopulations in Eurasia between ~130 and 25 ka: (1) Western and (2) Southern Europe, and (3) ‘Eastern’ (i.e. Eastern Europe and western Asia), with some migration between these demes. On the basis of mtDNA variation, and genetic and demographic models, they estimated Neanderthal population decline to have started at

Table 3

Regional distributions of metapopulations in Europe during four phases of the Upper Palaeolithic (after Bocquet-Appel et al., 2005, Fig. 5). Aurignacian and Gravettian estimates for Regions 3 and 4 are of most interest to consideration of the CI and later eruptions.

	Region 1	Region 2	Region 3	Region 4	Region 5
Aurignacian	795–12,980	109–1772	388–6338		
Gravettian	877–14,271	177–2887	451–7336	81–1326	
LGM	1477–24,063		277–4511		164–2666
Lateglacial	10,778–69,021				

Note: The minimal and maximal figures account for the majority of meta-populations in each region. Region 1: southern France and northern Spain; Region 2: northern France, the Low Countries (perhaps also SE Britain) and Rhineland Germany; Region 3: Upper Danube basin and southern Poland (though latter not in the LGM); Region 4: central Russian Plain; Region 5: southern Mediterranean Iberia. In the Lateglacial period, region 1 is still the main population centre, but it has expanded to incorporate and enlarge regions 2 (into Britain and Jutland) and 3.

~40 ka, about the same time as the Campanian Ignimbrite (henceforth ‘CI’) eruption. A later Neanderthal mtDNA analysis by Dalén et al. (2012) defined two, rather than three, main population histories for Neanderthals in Eurasia; they did not identify a separate Southern European deme. Their effective population estimates were slightly lower than those of Fabre et al. (2009); they also provided more spatio-temporal analytical structure to their model than those authors. In eastern Europe, regional population continuity was identified on the basis of greater genetic diversity, contrasting with the situation in western Europe, where Neanderthal populations appear to have undergone contraction and regional extinction, followed by recolonisation from refugia, as shown by significantly reduced mtDNA variation compared to other Neanderthals. According to Dalén et al. (2012), the initial meta-population divergence of western European Neanderthals (a well-defined, but shallow, monophyletic group) from the long-established and widespread paraphyletic deme (characteristic of Neanderthals throughout Europe before 58–48 ka) occurred approximately 70–55 ka. This divergence was created by the extinction of Neanderthals in western Europe throughout much of their range, with a subsequent recolonisation of much of this region – either from eastern Europe or from a small refugium in western Europe – by ~50 ka. The most recent radiocarbon dating of Neanderthal artefacts and fossils from western Europe would seem to indicate extinction between 41 and 39 ka (Higham et al., 2014). These western European late Neanderthals are often the most “classic” in their skeletal morphology; indeed, the type specimen from Feldhofer Grotte, Neanderthal, is included in this group A (Fig. 1). Genetic evidence indicates breeding population problems in Dalén et al.’s Eastern Neanderthals, certainly at the easternmost fringes of their known distribution, in the Altai mountains. Prüfer et al. (2014) have revealed evidence of inbreeding in Neanderthals from Denisova at perhaps 60 ka: breeding networks were so restricted as to include reproduction between kin as closely-related as half-siblings or aunts/uncles and nephews/nieces. Such inbreeding not only emphasises the lack of diversity in potential

Table 2

Metapopulation estimates, based on archaeological site criteria (site numbers, sizes and densities) for four Upper Palaeolithic periods (Bocquet-Appel et al., 2005, p. 1664).

	Archaeological territory (×100 km ²)	Demographic density (per 100 km ²)			Population size		
		Average	Min. ^a	Max. ^a	Average	Min. ^a	Max. ^a
Aurignacian	26,332	0.168	0.066	1.077	4424	1738	28,359
Gravettian	22,800	0.183	0.072	1.172	4776	1879	30,589
LGM	19,200	0.257	0.101	1.646	5885	2313	37,693
Lateglacial	32,800	0.722	0.285	1.825	28,736	11,343	72,635

^a Minimal and Maximal population size estimates incorporate confidence intervals of 47.5%.

Table 4

Approximate hominin population estimates for Europe, incorporating migration between broad regions of Europe in response to climate change (if average temperature drops below -5°C) and hunting options; from Sørensen (2011, p. 24). The model does not predict Neanderthal extinction (chronological evidence from archaeological sites is not incorporated into it), and thus populations of this hominin species are allowed to continue beyond 30 ka. Ranges given in the "Total" and "Total hominins" columns represent minimal and maximal populations for the relevant period. [*Population estimates decline to zero in adverse climatic conditions, often reflecting displacements to other, less-affected, parts of Europe.]

ka	Neanderthals				<i>Homo sapiens</i>				Total hominins
	South Europe	Mid-Europe	North Europe	Total	South Europe	Mid-Europe	North Europe	Total	
130–120	210–690	92–300*	180–270*	572–870					572–870
120–110	300–550	300–490	270–410	1090–1230					1090–1230
110–100	580–1400	80–790	480–690*	1480–2360					1480–2360
100–90	880–1200	790–1100	690–1040	2360–3340					2360–3340
90–80	1200–3900	12–1600	1040–1500*	3912–4900					3912–4900
80–70	1800–5500	1700–2700*	1500–1600*	5000–7900					5000–7900
70–60	3400–5100	0	0	3400–5100					3400–5100
60–50	1600–3600	31–2000	13–510*	3413–4120					3413–4120
50–45	1500–4100	1400–2000*	20–1300*	4100–4300					4100–4300
45–40	2800–4400	600–1800	0	4600–5900	350–700	8–180*	0	530–700	5080–6600
40–37 (HE4/CI)	2100–4500	0–2000	0–230	4330–4500	500–900	0–500	0–60	700–1060	5200–5400
37–27	3800–4500	220–1300*	0	4400–4720	1000–3500	10–500*	0	1100–3500	5400–7300
27–20 (LGM)	2900–3800	2–40*	0	2900–3800	3500–9000	2–50	0	3500–9000	7390–11,900

mates, at least regionally, for Neanderthals, but accentuates the overall lack of genetic variation apparent in known genomes across their range. This restricted variation and inferred low population size (with small mating networks) might have made them more vulnerable to AETs and environmental disasters.

Genomic data furthermore suggest that Neanderthal population numbers had been depleted not only during their final 20,000 years, but through much of their earlier history in Eurasia. Using a high quality genome recovered from a foot bone from Denisova Cave, Altai, Sankararaman et al. (2014) were able to compare the reconstructed demographic history of this Neanderthal female individual with those of the Denisovan female, and a series of contemporary humans. The resultant patterns suggested a relentless decline in inferred historical population size (and genome diversity) from both the Neanderthal and Denisovan individuals, following the separation of their ancestors from those of the

modern humans (*H. sapiens*). This attrition might reflect the greater challenges of Eurasian climates and their marked instability, compared with those endured by the ancestral *H. sapiens* population in Africa. This interpretation is supported by the fact that the modern non-African genomes show much more severe signs of demographic erosion around and after the time of the inferred Neanderthal and Denisovan extinctions, presumably because their ancestors were by now also in Eurasia, and therefore suffering from similar millennial scale fluctuations (and the Last Glacial Maximum), until their Holocene recoveries. The recently-analysed *H. sapiens* femur from Ust'-Ishim (western Siberia) contains longer chunks of Neanderthal DNA than in modern populations, implying that this individual lived relatively soon after the (local) interbreeding with Neanderthals: perhaps 232–430 generations of 29 years each (Fu et al., 2014). This bone is dated to ~48–42.5 ka (Table 6a), placing the interbreeding between ~50 and 60 ka (Fu

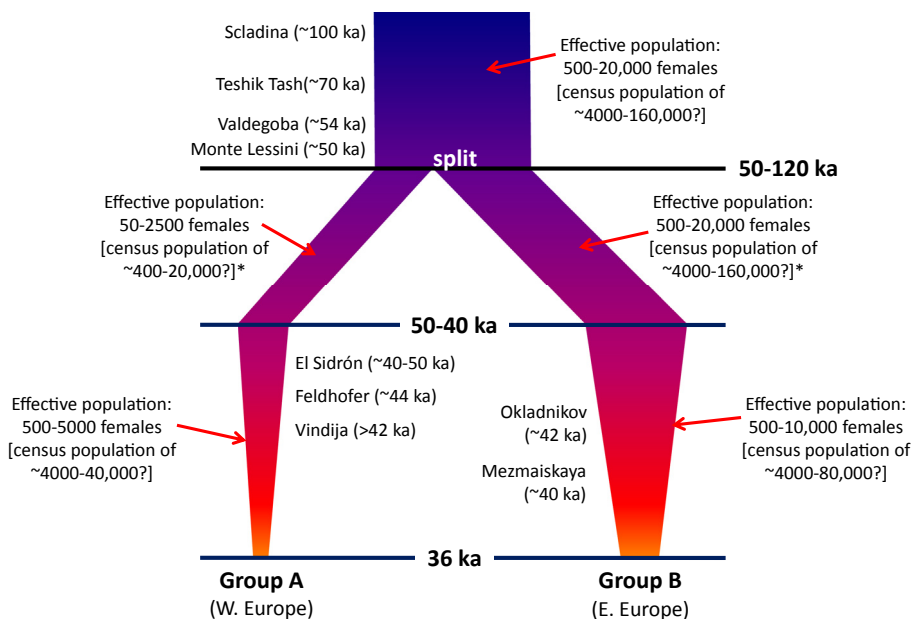


Fig. 1. Timings of split and effective population estimates (from Dalén et al., 2012, Fig. S2). Census metapopulations have been calculated by multiplying mtDNA effective populations by 8 (see Fabre et al., 2009 for explanation). *Effective population estimates from Dalén et al. (2012, Table S3) differ slightly from those in their Fig. S2; between ~55 and 70 ka, effective population size for group A (western Europe) is given as ~300 [= census population of ~2400?], while that for group B (eastern Europe) is ~2000 [= effective population of ~16,000?].

Table 5a

WP-1 sampling sites (~130–25 ka).

Site	Country	Site type	Assemblage(s)	Status	Tephra(s)
Azokh 1	Armenia	Cave	Middle Palaeolithic	Complete	1
Beregovo	Ukraine	Open-air	Early Upper Palaeolithic	Complete	
Blaz	Albania	Cave	Upper Palaeolithic	Complete	
Bohunice-Brno 2002	Czech Rep.	Open-air	Early Upper Palaeolithic	Complete	
Bondi	Georgia	Cave	Late Middle-Upper Palaeolithic	Complete	
Coșava II	Romania	Open-air	Early Upper Palaeolithic	Complete	
Cueva Antón	Spain	Rock shelter	Middle Palaeolithic	Complete	
Golema Pešt	Macedonia	Cave	Middle-early Upper Palaeolithic	Complete	1
Grotta di Santa Croce	Italy	Cave ^a	Middle Palaeolithic	In progress	1+
Grotte Mandrin	France	Cave	early Upper Palaeolithic	Complete	
Grub-Kranawetberg	Austria	Open-air	Upper Palaeolithic	Complete	
Kabazii II	Crimea	Rock shelter	Middle Palaeolithic	Complete	
Karabai II	Crimea	Rock Shelter	late Middle Palaeolithic	Unanalysed	
Kebara	Israel	Cave	Middle-Upper Palaeolithic	In progress	1+
Klissoura 1	Greece	Rock shelter	Middle-Upper Palaeolithic	In progress	3 (4?)
Kostenki XIV	Russia	Open-air	early Upper Palaeolithic	Complete	1
Kozarnika	Bulgaria	Cave	Middle-Upper Palaeolithic	Complete	2
Kůlna	Czech Rep.	Cave	Middle-Upper Palaeolithic	Complete	
Lakonis I	Greece	Rock shelter	Middle-early Upper Palaeolithic	Complete	
L'Arbreda	Spain	Rock shelter	Middle-Upper Palaeolithic	Complete	
Les Cottés	France	Cave ^a	Late Middle-early Upper Palaeolithic	Complete	
Moravský Krumlov IV	Czech Rep.	Open-air	Early Upper Palaeolithic	Complete	
Mujina pećina	Croatia	Cave	Late Middle Palaeolithic	Complete	
Redaka II	Bulgaria	Cave	Late Middle-Upper Palaeolithic	Complete	
Riparo l'Oscurusciuto	Italy	Rock shelter	Late Middle Palaeolithic	In progress	1+
Romanești-Dumbravita I	Romania	Open-air	Early Upper Palaeolithic	Complete	1
Romualdova pećina	Croatia	Cave	Late Middle-Upper Palaeolithic	Complete	
Siuren I	Crimea	Rock shelter	Early Upper Palaeolithic	Complete	
Szeleta	Hungary	Cave	Late Middle-early Upper Palaeolithic	Complete	
Tabula Traiana	Serbia	Cave	Late Middle-early Upper Palaeolithic	Complete	2
Theopetra	Greece	Cave	Middle-Upper Palaeolithic	Complete	3
Tincova	Romania	Open-air	Early Upper Palaeolithic	Complete	
Üçağızlı I	Turkey	Rock shelter	Early Upper Palaeolithic	Complete	
Undo	Georgia	Rock shelter	Middle Palaeolithic	Complete	
Vedrovice V	Czech Rep.	Open-air	Early Upper Palaeolithic	Complete	
Velika pećina in Kličevica	Croatia	Cave	Late Middle Palaeolithic	Complete	
Zaskalnaya V	Crimea	Rock shelter	Late Middle Palaeolithic	Unanalysed	
Želeč/Ondratice I	Czech Rep.	Open-air	Early Upper Palaeolithic	Complete	

^a Sampling profiles located outside the cave, and site type classed as rock shelter in Table 5b.

et al., 2014); subsequent loss and diminution of Neanderthal DNA in *H. sapiens* can be attributed to a variety of factors, including local extinction.

Castellano et al. (2014) used exomic data from three Neanderthal individuals (El Sidrón, Vindija and Altai) to reconstruct their within- and between-group variation, and infer population sizes. Their average heterozygosity was significantly smaller than in humans today, even within Europe or Asia, and they each had much longer runs of homozygosity, suggesting that mating among related individuals was more common in Neanderthals than in present-day humans, as already observed in the Altai Neanderthal. However, at the same time, the genetic differentiation among individuals, as measured by the pairwise fixation index (FST), was greater among the Neanderthals than among the recent African, European and Asian samples, suggesting that mating within small and relatively isolated populations probably caused Neanderthal populations to

be more differentiated from one another than is typical for present-day humans.

3. Sampling and the identification of key tephra isochrons

As highlighted throughout this issue, one of the key aims of the RESET project has been the development of a novel methodological approach that utilises cryptotephra (microscopic tephra shards) as physical time markers co-registered within sedimentary archives. As each volcanic eruption potentially produces a chemically distinct signature, far-travelled cryptotephra have the potential to be more widespread than their visible counterparts, and their potential recovery in secure stratigraphic contexts enables an expanded geographic area over which 'ash time-lines' (isochrons) can be traced. Prior to RESET, cryptotephra occurrence in Palaeolithic sites, and its preservation in meaningful archaeological contexts, remained largely untested. This lack of an extensive database of cryptotephra records made it especially difficult to move beyond the proximal fallout zones into the distal ones (see later).

Patterns of cryptotephra distribution and preservation are influenced by several key factors, including study location relative to volcanic sources/fall-out, prevailing atmospheric circulation at time of eruption, age-range and completeness of distal site records, and post-depositional sedimentary processes, to name a few. To test the potential geographic range of the method across Europe and the circum-Mediterranean, WP-1, working with a network of

Table 5b

Summary of WP-1 sampled sites (~130–25 ka).

Site type	With tephra	No tephra	Total
Open-air	2 20%	8 80%	10
Rock shelter	3 27%	8 73%	11 ^a
Cave	6 40%	9 60%	15
Total number of sites processed	11 31%	25 69%	36

^a Two sites (Zaskalnaya V and Karabai II) were not analysed, and are not included in totals.

Table 6a

Pre-Cl directly-dated hominins. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULLU} curve (two-sigma (95%) calibrated ranges) (Weninger and Jöris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range). Indirectly-dated hominin specimens (through association with dated archaeological assemblages) that might be seen as pre-Cl in age are predominantly **Neanderthal**: Jarama VI and Zafarraya, Spain (Wood et al., 2013); possibly Devil's Tower, Gibraltar (Vogel and Waterbolk, 1964, p.350); Baume Moula-Guercy, Abri de La Ferrassie, La Chapelle-aux-Saints, France (Grün and Stringer, 1991; Defleur et al., 1999); Grotta di Fumane (Benazzi et al., 2014) and Grotta Guattari, Italy (Grün and Stringer, 1991); Krapina (Rink et al., 1995); Dederiyeh Cave and Umm el-Tlel*, Syria (Griggo, 2004); Tabūn (see Table entry for problematic direct date), Kebara and Amud caves, Israel (Millard, 2008; Grün, 2006; Mercier and Valladas, 2003; McDermott et al., 1993; Grün and Stringer, 1991; Schwarcz et al., 1989); Shanidar Cave, Iraq (Vogel and Waterbolk, 1963); Teshik Tash, Uzbekistan (Krause et al., 2007); Denisova Cave (Prüfer et al., 2014). **Homo sapiens** specimens, whether directly or indirectly dated, are rare in Eurasian archaeological contexts, and mostly concentrated in the Levant: Qafzeh and Skhul (individuals IX and V, at least), Israel (Millard, 2008; Grün, 2006; Grün et al., 2005; McDermott et al., 1993; Grün and Stringer, 1991; Stringer et al., 1989); possibly the teeth from the earliest Initial Upper Palaeolithic of Uççağızlı Cave, Syria (layers H and G) (Kuhn et al., 2009); Ksar 'Akil, level XXV (partial maxilla), Lebanon (Douka et al., 2013); a possibly-diagnostic deciduous incisor from the Mousterian level A9I at Grotta di Fumane (Benazzi et al., 2014), the two deciduous teeth from the Uluzzian levels EIII and EII-I (both below the visible Cl layer) of Grotta del Cavallo, Italy (Palma di Cesnola and Messeri, 1967; Benazzi et al., 2011). The cranial fragments from the lower Aurignacian ("Delta") layer at Cueva de El Castillo are lost, and it is not possible to say if they are Neanderthal or *H. sapiens* (Garralda, 2006). Other *H. sapiens* attributed to very early Aurignacian assemblages, e.g. Riparo Bombrini, layer III (Formicola, 1989), have no associated dates at all. The Kent's Cavern 4 maxilla would date to the pre-Cl if the oldest stratigraphically-associated fauna is correctly correlated, but research on this issue is ongoing.

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
43.386°N, 5.733°W	El Sidrón (Spain)	Guardia Civil excavation (Mousterian)	<i>H. neand.</i>	Bone (SID-00 00/46) (amino-acid)	GifA-99167	48,500 ± 2600	58,910–45,630 58,502–44,182	De Torres et al., 2010; Wood et al., 2013
					GifA-99704	49,200 ± 2500	59,620–46,380 58,458–45,014	
					OxA-21776	48,400 ± 3200	59,730–44,570 63,282–43,489	
		Ossuary Gallery section, level III (Mousterian)	<i>H. neand.</i>	Bone (no. 441; SID-2A)	GX-30241	11,289 ± 79	13,346–13,022 13,303–13,025	
					GX-30242	10,340 ± 70	12,614–11,894 12,518–11,841	
						Beta-89644	34,940 ± 680	41,966–38,010 41,197–38,245
					Beta-192065	40,840 ± 1200	46,394–42,330 47,045–42,601	
						Beta-192066	37,300 ± 830	43,066–41,014 43,025–40,295
					Beta-192067	38,240 ± 890	43,696–41,436 44,080–41,180	
[ANU ESR: EU] [ANU ESR: LU] [AAR]	(37,000 ± 3000) (40,000 ± 3000) (44,400 ± 8500, average)							
41.2218°N, 1.7715°E	Cova del Gegant (Spain)	GL1; level XVa (Mousterian)	<i>H. neand.</i>	Mandible	[JD52a+b (U-Th, average)]	(54,600–50,000)	Daura et al., 2010	
36.95116°N, 4.12142°W	Cueva del Boquete de Zafarraya (Spain)	Sala del Entrada 193–198 (UE34), Q18, Mousterian]	<i>H. neand.</i>	Mandible 2	[U-series (γ); EU] [U-series (γ); LU] [U/Pa (γ); EU] [U/Pa (γ); LU] [Th/Th (γ); EU]	(23,000 ± 5000) (49,000 ± 11,000) (15,000 ± 7000) (33,000 +17,000 –14,000) (86,000 +73,000 –44,000)	Wood et al. 2013, SI table 2	
42.1068°N, 2.7678°E	Banyoles* (Spain)	~4 m depth below surface, in travertine	<i>H. neand.</i>	Mandible, embedded in travertine (latter has been dated)	[U-series/ESR] UCLA-930	(66,000 ± 7000) 23,560–18,720 23,937–19,056	Grün et al., 2006; Berger and Libby, 1966	
46.415°N, 0.741°E	Les Rochers-de- Villeneuve (France)	level J, sq. H8 (Mousterian)	<i>H. neand.</i>	Femur (individual 1)	OxA-15257	45,200 ± 1100	51,465–45,313 [>50,000]–46,704	Beauval et al., 2006
44.95176°N, 0.937903°E	Grand Abri de La Ferrassie (France)	La Ferrassie 1 burial, base bed C (Mousterian)	<i>H. neand.</i>	Distal right tibia from individual 1 (23645, 1953–25)	OxA-X-2294-25 [amino-acid] OxA-X-2395-25 [ultrafiltered] OxA-X-2403-18 [amino-acid]	11,540 ± 55 12,910 ± 90 12,950 ± 130	13,608–13,276 13,475–13,275 15,688–15,276 15,737–15,159 16,336–15,092 15,900–15,123	Higham et al., 2014, p. S32

				Distal left tibia from individual 1	OxA-X-2294-14 [amino-acid]	32,750 ± 450	38,814–35,406 38,263–35,851	
					OxA-X-2395-26 [ultrafiltered]	35,700 ± 1500	43,242–36,970 43,296–36,986	
					OxA-X-2403-14 [amino-acid]	32,100 ± 1800	41,379–32,687 41,590–33,370	
50.4803°N, 4.6743°E	Grotte de la Betche- aux-Rotches, Spy (Belgium)	"Second ossiferous level", layer C ("Lincombian-Ranisian- Jerzmanowician" industry?), or possibly "Third ossiferous level", layer E (Mousterian)	<i>H. neand.?</i>	Right scapula fragment (Spy 572a; Spy I/II?)	OxA-8912	23,880 ± 240	29,620–27,984 28,491–27,590	Toussaint and Pirson 2006; Semal et al., 2009; Crevecoeur et al., 2010
					OxA-8913	24,730 ± 240	30,111–29,227 29,376–28,261	
					GrA-21546	31,810 ± 250	36,310–35,006 36,249–35,132	
			<i>H. neand.</i>	Bone from maxilla fragment attached to molar (right M3) (Spy 94a; Spy I/II)	GrA-32623	35,810 +260, –240	42,277–39,401 41,086–39,841	
					<i>H. neand.</i>	Incisor (left I1) (Spy 92b; Spy I/II)	GrA-32626	
			<i>H. neand.</i>	Right middle third manual phalange (Spy 430a; Spy II) Spy 40a (ultrafiltered)			GrA-32630	
					<i>H. neand.</i>	Right hemi-mandible (Spy 646a; Spy VI infant) Upper right incisor (di1) (Spy 589a; Spy VI infant) (ultrafiltered)	OxA-17916	
			GrA-32627	32,970 +200, –190			38,721–35,801 37,849–36,393	
			OxA-17977	34,700 ± 550	41,720–38,040 40,653–38,179			
			OxA-21610	33,950 ± 550	41,776–36,468 39,732–36,795			
	[Spoil] from slope below the cave	<i>H. neand.</i>	Vertebra fragment (Spy 737a; Spy I/II?) (ultrafiltered)	OxA-10560	36,250 ± 500	42,299–40,587 41,813–39,884		
51.2206°N, 6.9363°E	Kleine Feldhöfer Grotte, Neandertal (Germany)	In clay matrix ~60 cm below surface of cave deposits (Middle Palaeolithic)	<i>H. neand.</i>	Humerus (individual 1)	ETH-20981	39,900 ± 620	44,752–42,400 44,745–42,671	Schmitz et al., 2002
				Tibia fragment (NN4 [=individ. 1])	ETH-19661	40,360 ± 760	45,340–42,500 45,367–42,819	
				Humerus (NN1; individual 2)	ETH-19660	39,240 ± 670	44,271–42,043 44,343–42,194	
46.305°N, 16.088°E	Vindija cave (Croatia)	Layer G ₃	<i>H. neand.</i>	Bone fragment (Vi-75-G3/h-203)	Ua-13873	>42,000	Krings et al., 2000; Serre et al., 2004; Zilhão 2009	
				Tibia fragment (Vi-33.16 [aka Vi-80])	Ua-19009	38,310 ± 2130		45,886–38,802 48,180–39,235
44.2217°N, 40.0034°E	Mezmaiskaya (Russia)	Layer 3d (Middle Palaeolithic)	<i>H. neand.</i>	Rib fragment of neonate (Mez 1)	Ua-14512	29,195 ± 965	35,106–31,834 35,207–31,281	Ovchinnikov et al., 2000; Pinhasi et al., 2011; Golovanova et al., 2010 ; Higham et al., 2014, p.S108
		Pit (Quad. N19) from layer 2 into layers 2A, 2B-1 [tephra] and 2B-2 (Middle Palaeolithic)	<i>H. neand.</i>	Infant bone (Mez 2) : cranial fragment 13 (ultrafiltered)	OxA-21839	39,700 ± 1100	45,228–41,884 45,631–42,039	
32.6702°N, 34.96596°E	Et Tabūn cave Israel)	Layer C (or possibly B), near back of cave (Mousterian)	<i>H. neand.</i>	Mandible of C1 individual (adult female)	[U-series (γ) (weighted average min.)]	(34,000 ± 5000)	Schwarcz et al., 1998; Millard 2008; Grün and Stringer, 2000, p.610	
				C1 left lower M1, enamel fragment	[U-series (γ age range)]	(63,000 +27,000, –22,000)		
					[ESR (EU)]	(112,000 ± 29,000)		
Femur of C1 individual)	[ESR (LU)]	(143,000 ± 37,000)						
				[U-series (γ) (weighted average EU)]	(19,000 ± 2000)			
32.6713°N, 34.9660°E	Es Skhūl cave (Israel)	2.15 m below the surface, in hard breccia [B1?] (Mousterian)	<i>H. sapiens</i>	Skhūl IX individual: small (171 mg) surface sample	[U-series (TIMS)]	(131,000 ± 2000)	Grün et al., 2005	

(continued on next page)

Table 6a (continued)

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
58.03° N, 68.86° E	Baigara locality* (Russia)	Base of a late Pleistocene outcrop (re-deposited on bank of R. Irtysh)	<i>H. sapiens</i>	Adult (male?) left talus (some carnivore damage?)	AA-61831	>40,300		Kuzmin et al., 2009
57.701° N, 71.165° E	Ust'-Ishim* (Russia)	Sand and gravel layers on bank of R. Irtysh.	<i>H. sapiens</i>	Adult male left femur (diaphysis) (ultrafiltered)	OxA-25516 OxA-30190	41,400 ± 1300 41,400 ± 1400	47,100–42,500 48,014–42,870 47,270–42,390 48,314–42,794	Fu et al., 2014
51.7319° N, 84.0337° E	Okladnikov cave (Russia)	Layer 3 [Middle Pal.]	<i>H. neand.</i>	Sub-adult humerus (OK1)	KIA-27011 Beta-186881 OxA-15481	29,990 ± 500 34,860 ± 360 37,800 ± 450	35,039–33,363 35,026–33,165 41,744–38,292 40,222–38,622 43,045–41,561 42,746–41,489	Krause et al., 2007; Skoglund et al., 2014; Akimova et al., 2010
		Layer 2 [Middle Pal.]	<i>H. neand./sapiens</i>	Adult humerus fragment	KIA-27010	24,260 ± 180	29,868–28,376 28,690–27,891	

international collaborators, adopted a west-east and south-north transect approach spanning the Iberian Peninsula to the southern Caucasus, and the Levant to Moravia, respectively. Site selection was restricted to those under active excavation, or those in which sampling of accessible preserved sections was granted. Cryptotephra samples were collected in high-resolution (2 cm or 5 cm) continuous intervals spanning the complete stratigraphic sequence of interest. Our focus in this paper is on RESET's European cryptotephra record, specifically on sites ranging in age from ~130 to 25 ka that contain key Middle and/or Early Upper Palaeolithic contexts.

In total, 38 Middle and/or Early Upper Palaeolithic sites across Europe were sampled under RESET (Table 5a and b; Fig. 2). These included 15 cave, 13 rock shelter and 10 open-air sites. Of the 36 sites processed to date, 31% contain significant levels of cryptotephra, including 40% of the sampled caves, 27% of rock shelters, and 20% of open-air sites (Table 5b), all of which are located in eastern Europe (Italy and further east). While our main analytical focus initially was documenting the occurrence of the Campanian Ignimbrite (Lowe et al., 2012), dated by $^{40}\text{Ar}/^{39}\text{Ar}$ at $39,395 \pm 51$ BP (de Vivo et al., 2001), a number of other important tephra were also identified (e.g., Karkanas et al., 2015). Significantly, more than half of the sites which yielded tephra preserve more than one chemically distinct cryptotephra layer. These results demonstrate the wide geographic distribution of cryptotephra in Palaeolithic sites in eastern Europe, and confirm its potential as an important dating and correlation technique in interdisciplinary archaeological research.

Key to tephra's use as an isochron, however, is the ability to document these discrete event horizons within very complex stratigraphic and archaeological deposits. Site formation processes will vary both within and between localities, and so too will the stratigraphic resolution of identified tephra isochrons. These inherent differences in site depositional and post-depositional patterns will impact upon confidence levels in correlating cryptotephra layers to distinct archaeological contexts. Therefore, a detailed understanding of a site's formation processes and stratigraphy is paramount for establishing secure links between cryptotephra horizons and specific archaeological industries.

It is also clear that cryptotephra presence at sites is localised, particularly for sites in the distal fallout zones. Szeleta (Bükk mountains, Hungary), for example, demonstrated very low concentrations of tephra shards in the excavated sections sampled for WP-1, but it has potentially higher concentrations in the unexcavated, extensive talus deposits at the front of the cave (also likely to have stronger evidence for hominin activities, given the south-facing aspect and sheltered position of that talus). Our work at Kostenki XIV has shown differential vertical concentrations of CI tephra in different sectors of the site. Additional sampling is not only needed within sites, but the number of sampled sites needs to be increased, both within and beyond hypothesised fallout zones. Fallout zones are often characterised by visible tephra, and the possibility of marker tephra beyond known spatial envelopes requires further testing, using cryptotephra. Some of the cryptotephra found at sites in WP-1 have not yet been identified to source, but their data (and the samples themselves) have been archived, so that identifications may be possible in future.

4. Evaluating spatial and temporal scales of change

The tephrochronological lattice enables us to evaluate appropriate spatio-temporal scales for analysing change. Assessing similarities/differences in cultural records connected by the same tephrochronological marker allows us to establish how "universal" or localised/contingent changes in human behaviour were across continents and their varied biomes. For example, was there more

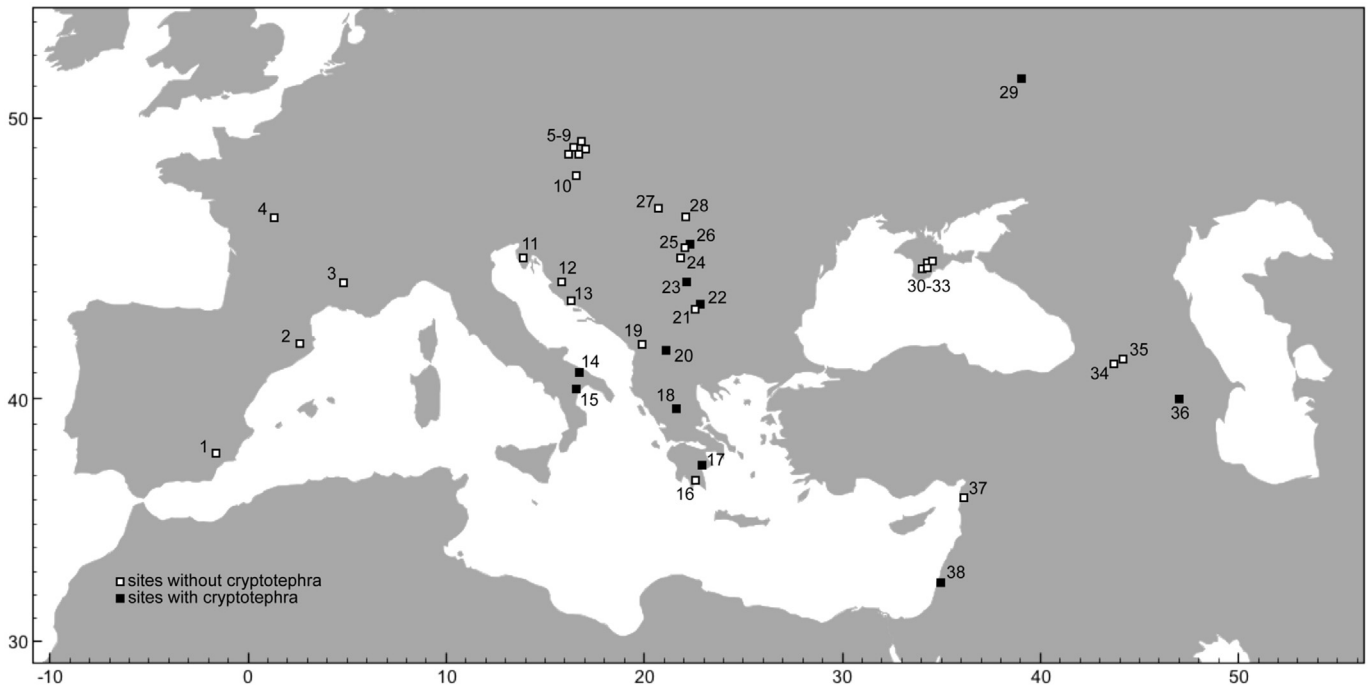


Fig. 2. Map of RESET WP-1 sampling sites. [1 = Cueva Antón (Spain), 2 = L'Arbreda (Spain), 3 = Grotte Mandrin (France), 4 = Les Cottés (France), 5 = Bohunice-Brno 2002 (Czech Rep.), 6 = Želeč/Ondratice I (Czech Rep.), 7 = Vedrovice V (Czech Rep.), 8 = Moravský Krumlov IV (Czech Rep.), 9 = Kůlna (Czech Rep.), 10 = Grub-Kranawetberg (Austria), 11 = Romualdova pečina (Croatia), 12 = Velika pečina in Kličevica (Croatia), 13 = Mujina pečina (Croatia), 14 = Grotta di Santa Croce (Italy), 15 = Riparo l'Oscurusciuto (Italy), 16 = Lakonis I (Greece), 17 = Klissoura I (Greece), 18 = Theopetra (Greece), 19 = Blaz (Albania), 20 = Golema Pešt (Macedonia), 21 = Redaka II (Bulgaria), 22 = Kozarnika (Bulgaria), 23 = Tabula Traiana (Serbia), 24 = Tincova (Romania), 25 = Coșava II (Romania), 26 = Romanești-Dumbravita I (Romania), 27 = Szeleta (Hungary), 28 = Beregovo (Ukraine), 29 = Kostenki XIV (Russia), 30 = Karabai II (Crimea), 31 = Zaskalnaya V (Crimea), 32 = Kabazii II (Crimea), 33 = Siuren I (Crimea), 34 = Undo (Georgia), 35 = Bondi (Georgia), 36 = Azokh 1 (Armenia), 37 = Üçağızlı I (Turkey), 38 = Kebara (Israel)].

cultural or economic variability in a particular part of Europe at a given time than elsewhere? What was the contemporary response to abrupt change on the northern and southern shores of the eastern Mediterranean? How far were population movements driven by AETs, and how can they be recognised through archaeological evidence? The ability to match tephrochronological lattices to increased precision in the dating of diagnostic archaeological artefacts enables us to assess the degree of environmental cause and effect in the instigation of cultural change. Among records of environmental disasters, tephras have distinct advantages: the principal one being that visible and cryptic tephras can be found in archaeological contexts. This evidence of major environmental events within or between archaeological assemblages allows much easier consideration of hominin responses to them than when we try to infer the effects of Heinrich Events (“HE”; see Table 1), for example, on patterns of behaviour and regional occupation. Sørensen (2011), for example, has modelled the combined effects of HE4 and the CI (spanning ~40–37 ka) on hominin population levels and spatio-temporal distributions (Table 4): Neanderthal and *H. sapiens* groups in southern Europe continued to increase in size immediately after 40 ka, but crashed by 38 ka to ~2100 (Neanderthals) and ~500 (*H. sapiens*) individuals, with contemporary more northerly regions showing corresponding demic influxes (having previously been uninhabited at ~40–38 ka).

The spatial position of hominin groups in relation to a major environmental perturbation/change should be considered a key factor when modelling the responses of the former to the latter: were humans close to (“proximal”) or distant from (“distal”) that event? As a working hypothesis, we here define “proximal” as significantly disrupting hominin occupation patterns: termination or extinction, displacement, and/or forcing cultural change. “Distal” sites would be those where effects on occupation organisation and

density were at worst temporarily-disruptive (short-term displacement), and might often have had no discernible effects at all on hominin populations.

Displacement and replacement have been key assumptions of Palaeolithic archaeology for a long time: phases of behavioural stability ruptured by sudden changes, and perhaps caused by replacement or interactions with new groups. Since the mid-nineteenth century, Palaeolithic archaeologists have identified cultural ‘phases’ at key sites and extrapolated these sequences to all other sites dug subsequently. Thus, the stratigraphic sequence of Aurignacian assemblages at La Ferrassie (SW France) has been taken as the diagnostic developmental sequence for that technocomplex, for example, despite the absence of some of those ‘phases’ anywhere else (e.g. Aurignacian IV) (Peyrony, 1933, p. 559; Djindjian, 1986, p. 101).

Fig. 3a depicts a schematic rendering of a hypothetical cultural sequence within a region, whose sites have been geographically-ordered by longitude. Three out of the five sites have the same four archaeological industries in the same stratigraphic order, while the remaining two show the absence of one or two industries in their sequences. The provision of absolute dates for many archaeological assemblages has encouraged archaeologists to search for proof of penecontemporaneous phasing of industries over large areas, with each phase being treated as a diagnostic fossil assemblage: each archaeological assemblage is seen as sharing essential traits with those attributed to the same phase found elsewhere (essentialism). There is assumed to be no change in artefactual morphologies and combinations between the initiation and extinction of a phase, and little consideration of parallel/independent evolution. Fig. 3b is the result of such assumptions: each industrial ‘phase’ can be fitted into a discrete period (A, B, C or D), even if some sites have apparently ‘incomplete’ occupation sequences.

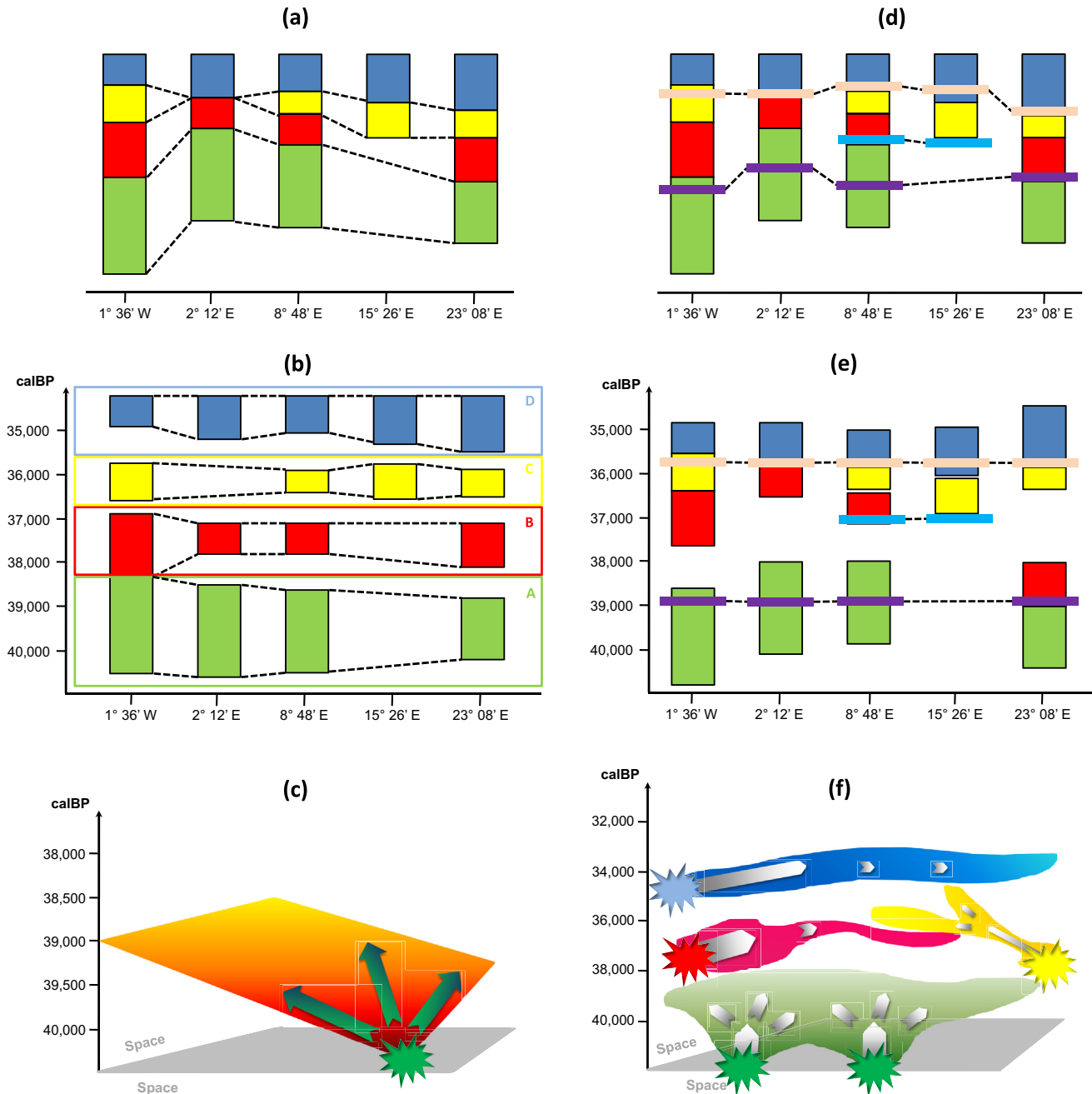


Fig. 3. Schematic depiction of archaeological approaches to behavioural change over time and space. a–c: 'epochal' views of archaeological cultural successions. d–f: dynamic and time-transgressive views of cultural change and diversity in the archaeological record.

The latter 'gaps' at these sites are explained as occupational hiatuses, with a 'missing' industry failing to utilise these locations during its epoch. Each archaeological industrial phase is assumed to have spread consistently across space from its source (Fig. 3c) in a spatio-temporal gradient, and it is thought to be homogeneous in its composition, with no discernible change in its essential aspects (tool types, morphologies and combinations). Transitional change only occurs when one industrial phase is replaced by another. These essentialist views of change assume landscapes of uniform affordances and resistances ('table-top models') for industries to spread rapidly across; little attention is given to environmental variation (topography, biomass and ecotones), and the role it might have played in facilitating or impeding hominin mobility.

Isochronic markers within a chronological lattice allow us to evaluate these universalist and essentialist models of change with more confidence. We cannot assume that cultural successions happened as universal phases across large areas, and lattices enable us to identify the spatio-temporal scales of hominin behavioural mosaics with more confidence. Unravelling the variation in hominin behavioural patterns across time and space enables us to ask the more interesting questions about what might explain such patterning (environmental affordances? social choices? movements of individuals and groups?). Fig. 3d shows how isochronic markers can connect together archaeological sites at different spatial and temporal scales. Sites containing just one such isochron can be connected to others with more than one tephrochronological

marker, and cryptotephra vastly increase the spatial coverage and detail of our comparisons by augmenting the number of locations with such records. In addition, artefacts diagnostic of particular archaeological industries can be fitted into this lattice, ideally using direct (radiocarbon) dates, and their morphological variation over space and time measured to test dynamic (rather than essentialist) hypotheses about hominin responses to environmental conditions. Isochronic markers encourage the re-evaluation of hypotheses of dynamic change in the archaeological record, rather than the pre-supposition of essentialist and universal phases/epochs of hominin behaviour. Such ideas can be further tested by incorporating morphometric studies of directly-dated diagnostic artefact types, to identify any spatio-temporal patterning in behavioural changes and hominin responses to environmental conditions. Not only can independent invention of similar artefact types in different places at different times be addressed, but the nature of technological

variation across assemblages from the 'same' industries can be evaluated, allowing us the opportunity of dating morphological variation in diagnostic tool types. Ideas of localism and contingency in hominin behaviour, rather than generalising and universalist ones, can be made the main focus of our analyses.

Fig. 3e clarifies the different durations and timings of hominin industries at different sites, showing how the spatio-temporal scales of behavioural mosaics might be identified. Reasons other than AETs and environmental disasters must be sought to explain 'universal' changes and transitions in Palaeolithic societies and hominin species. Thus, we are evaluating different spatio-temporal behavioural mosaics, with different lead and lag times in their patterns of change (Fig. 3f). More subtle and inflected conceptualisations of mobility in Palaeolithic populations are thus needed, ranging from daily migrations to trans-generational dispersals (Baker, 1978, p. 23; Davies, 2012). The reconstruction of

Table 6b

Directly-dated hominins penecontemporary with the CI. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULLU} curve (two-sigma (95%) calibrated ranges) (Weninger and Joris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range). ESR results indicate that Skhül II is significantly older (>66 ka) than the apparent U-series age estimate on the dentine (~32 ka); the best age estimate is given by the combined U-series-ESR result of $116 \pm 24 + 43$ ka (Grün et al., 2005). Indirectly-dated homin specimens (through association with dated archaeological assemblages) that might be seen as pre-CI in age are predominantly *H. sapiens*: Isturitz, Brassempouy, Tarté, Blanchard, Castanet and La Combe (France) teeth (some perforated) (MacCurdy, 1914; Petit-Maire et al., 1971; Henry-Gambier et al., 2004; Normand et al., 2007; Bailey et al., 2009); La Quina-Aval (France) two mandibles and teeth (Verna et al., 2012); the Les Rois (France) teeth and mandible A (Ramirez Rozzi et al., 2009); the Les Cottés (possibly Aurignacian) skull and postcrania (Patte, 1954); a scapular fragment from the Aurignacian level E of Grotta del Fossellone, Italy (Mallegni and Segre-Naldini, 1992); teeth from the Aurignacian of Hohlenstein-Stadel, Schelklingen, Kleine Ofnethöhle, Schafstall, Sirgenstein and Geissenklösterle (Germany) (references in Street et al., 2006); Dzeravá skala (Slovakia) molar tooth (Svoboda, 2001; Bailey et al., 2009); the Aurignacian Istállós-kő (Hungary) molar (Thoma and Vértes, 1971); cranial and mandibular fragments from Bacho Kiro, level 11, Bulgaria (Gleñ and Kaczanowski, 1982; Churchill and Smith, 2000); the Aurignacian teeth from Siuren' I (Crimea) (Klein et al., 1971); the Initial Upper Palaeolithic skull and postcrania ('Egbert') from Ksar 'Akil (Lebanon) (Douka et al., 2013) and teeth from Üçağızlı cave (Kuhn et al., 2009). The cut-marked child mandible (B) from the Aurignacian of Les Rois is claimed to be Neanderthal, perhaps implying consumption or symbolic use of a Neanderthal child (Ramirez Rozzi et al., 2009, p.174). Another late Neanderthal might be the Le Moustier specimen (Grün and Stringer, 1991).

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
45.75087°N, 0.50586°W	Abri de la Roche à Pierrot (Saint-Césaire) (France)	SP 28 (Châtel-perronian)	<i>H. neand.</i>	Bone (ultrafiltered)	OxA-18099	$36,200 \pm 750$	42,963–38,679 42,142–39,347	Hublin et al., 2012
50.5924°N, 5.4089°E	Grotte Schmerling, Engis (Belgium)	At base of cave deposits (Layer B) (Mousterian)	<i>H. neand.</i>	Juvenile cranium (calotte): parietal (Engis 2)	OxA-8827 GrA-21545	$26,820 \pm 340$ $30,460 \pm 210$	32,122–31,006 31,400–30,405 35,013–34,173 34,826–34,035	Toussaint and Pirson, 2006
46.305°N, 16.088°E	Vindija cave (Croatia)	Layer G ₁	<i>H. neand.</i>	Bone (Vi-207)	OxA-8296	$29,080 \pm 400$	34,366–32,638 34,026–32,069 34,336–32,728 34,005–32,263	Smith et al., 1999; Higham et al., 2006a; Karvanić et al., 1998, p. 139
				Vi-207 (ultrafiltered)	OxA-X-2082-10	$29,100 \pm 360$	41,842–32,878 41,680–33,674 (51,000 ± 8000)	
			<i>H. neand.</i>	Bone (Vi-208)	OxA-8295	$28,020 \pm 360$	33,272–31,808 32,905–31,201	
				Vi-208 (ultrafiltered)	OxA-X-2082-09	$29,200 \pm 360$	34,390–32,826 34,086–32,460	
					OxA-X-2089-07	$32,400 \pm 1800$	39,147–34,563 38,581–34,861	
					OxA-X-2094-10	$31,390 \pm 220$	35,929–34,653 35,792–34,785	
45.0177°N, 21.91°E	Peștera cu Oase (Romania)	At head of Panta Strămoșilor slope, in Sala Mandibulei (surface)	<i>H. sapiens</i>	Mandible (Oase 1) (ultrafiltered)	OxA-11711	>35,200		Trinkaus et al., 2003, 2006
				Mandible (Oase 1)	GrA-22810	$34,290 +970, -870$	42,105–36,173 40,969–36,533	
				Mandible (Oase 1) (combined date)	OxA/GrA	$34,950 +990, -890$	42,193–37,533 41,700–37,461 36,375–35,530	
32.6713°N, 34.9660°E	Es Skhül cave (Israel)	1.40 m beneath the surface, in partly-hardened earth [B1?] (Mousterian)	<i>H. sapiens</i>	Skhül II dentine fragment	[U-series (TIMS)]		(32,100 ± 800)	Grün et al., 2005

different scales of mobility (from return migrations or movements radiating from a central base to long-distance displacements) allows us to model the likely effects of varying scales of environmental change (e.g. the proximal and distal effects of volcanic eruptions) on hominin movements. Mobility scales for each region need to be identified, which can then be scaled chronologically within our lattices, and related to assemblage characteristics and resources exploited. This increased spatio-temporal confidence in identifying localised characteristics will allow us to restore perspectives of contingency to our analyses of the archaeological record, rather than in assuming large-scale, universalist 'phases.'

5. Neanderthals, *H. sapiens* and the tephrochronological lattice

Several tephra marker horizons have been identified by RESET at WP-1-sampled sites. While the CI is the best-defined and most extensive of these (and thus the focus of this paper), other eruptions are well-represented in the WP-1 database. The Pantellerian P-11 (~133 ka) and Y-6 (Green Tuff; ~45–50 ka), together with the Nisyros Upper Pumice (>50.4 ka), occur in the Middle Palaeolithic sequence of Theopetra cave (Karkanias et al., 2015), while the Y-7 tephra of the Monte Epomeo/San Angelo complex (~51–59 ka) is found in the late Middle Palaeolithic sequences of Kozarnika and Klissoura 1 caves (C. Lane, pers. comm.). These WP-1 sites are all east of the Bay of Naples; despite sampling trips to France and Spain, no tephtras were recovered from sites sampled. This is not to say that there are no known tephtras from Middle and Early Upper Palaeolithic sites in western Europe; level VI at the site of La Baume Moula-Guercy in SE France comprised 2–3 cm of tephra (most likely to have derived from either Le Ray-Pic or Le Pic de l'Étoile volcanoes in the Massif Central), whose quartz is dated somewhat imprecisely to 72 ± 12 ka (two-sigma) by R-TL (Defleur et al., 1999; Sanzelle et al., 2000). This date provides a *terminus ante quem* age estimate for the lower level XV (possibly 100–120 ka), which contains a Mousterian industry and numerous Neanderthal bones showing evidence of defleshing and possible marrow extraction (Valensi et al., 2012). However, La Baume Moula-Guercy was dated using a visible tephra horizon; it remains to be seen whether identification of cryptotephra horizons will lead to more precise isochronic dates in western Europe. In eastern Europe, the upper Neanderthal from Mezmaiskaya (Mez 2: 24 infant cranial fragments) has been dated directly (Table 6a), and related to two volcanic tephtras of local origin (Golovanova et al., 2010). It was found in a pit dug down from layer 2, underneath tephra layer 1D (provisionally attributed to an eruption from Mt. Kazbek (~40 ka?) on the basis of chemical composition (Golovanova et al., 2010, p. 668)), and which cut into layers 2A, 2B-1 (a tephra attributed to the Tash Tebe volcano, and dated between 45.3 ± 2.8 ka and 43.4 ± 9.3 ka using ESR on quartz in lava (Golovanova et al., 2010; pp. 659–660)) and 2B-2 (Pinhasi et al., 2011).

As stated above, the CI is the most widely-represented identified tephra in the WP-1 database, allowing evaluation of chronology in central and eastern Europe at a key period of behavioural change. A small number of hominin remains has been related to visible tephra occurrences of the CI: the identified *H. sapiens* from Grotta del Cavallo (Benazzi et al., 2011) and Kostenki XIV (Marom et al., 2012) (Table 6b). Neanderthals at the site of Vindija might, in theory, have been within the CI distal distribution zone, but it is uncertain whether any cryptotephra that might be recovered from the surviving sediments could be related to the G₁ layer containing the hominin remains (Wolpoff et al., 1981; Karavanić, 1995; Karavanić and Smith, 1998). The ultrafiltered direct AMS radiocarbon determinations on Neanderthal bones from Vindija were regarded by their authors as minimal estimates (Higham et al., 2006a); they lie

at about 32,000 ¹⁴C BP (~35–39 ka when calibrated; Table 6b), ostensibly indicating a post-CI Neanderthal occupation of the site. Dalén et al. (2012) incorporated the Vindija Neanderthals into their population A (the well-defined, shallow, monophyletic Neanderthal group; Fig. 1), implying demic links between them and more westerly late Neanderthals. The remainder of the region covered by tephtras identified or drawn from the literature by WP-1 falls within Dalén et al.'s (2012) population B (Fig. 1), and the spatio-temporal distributions of these Neanderthals suggest that they would not have been affected by the CI (either too distant, or too early). At present, the results of WP-1 do not allow us to refine the regional chronology of Neanderthal extinctions: our successful tephra identifications are restricted to Italy and further east, and only at Kebara did WP-1 find cryptotephtras that, while still at an early stage of research, might be potentially associated with Neanderthal skeletal remains. While cryptotephra markers (Y-7 complex (~51–59 ka) tephra at Klissoura 1 and Kozarnika caves, and P-11 (~133 ka), Nisyros Upper Pumice (>50.4 ka) and Y-6 (~45–50 ka) markers in Theopetra cave) have been found associated with the European Middle Palaeolithic, we have no evidence that such eruptions caused the demise of those industries and, by widely-assumed association, Neanderthals.

A similar number of early *H. sapiens* sites contain traces of tephra, one in Italy (Grotta del Cavallo) and the other further east (Kostenki XIV). Direct radiocarbon dates for European early *H. sapiens* are given in Tables 6b and c, and shown in Fig. 4. Current results suggest that the presence of *H. sapiens* in eastern Europe precedes the CI eruption (Lowe et al., 2012). The Romanian site of Peștera cu Oase has yielded human remains dated to ~35,000 ¹⁴C BP (OxA/GrA; ~42–37 ka when calibrated: Table 6b), but depositional circumstances (redeposition by running water) of the skeletal material discouraged any attempt to sample the site for cryptotephra markers. If the Grotta del Cavallo hominin deciduous teeth are attributable to *H. sapiens*, as recently argued (Benazzi et al., 2011), then they might well be pre-CI. The contexts (layers EIII and EII-1) in which they were found were overlain by a visible occurrence of the CI (Giaccio et al., 2006); between layer EII-1 and the CI is layer D, which has been argued to contain a mixture of Uluzzian and Aurignacian cultural elements (Gioia, 1990).

Other directly-dated specimens of early *H. sapiens* should be seen as post-CI (Table 6c). The burial from Kostenki XIV (Markina Gora) is dated by single amino-acid AMS dating to $33,250 \pm 500$ ¹⁴C BP (OxA-X-2395–15; ~39.6–35.6 ka when calibrated: Table 6c), and was cut through the CI layer at the site without disturbing cultural layer III. This information suggested to the excavators that inhumation took place between the deposition of the CI and the third cultural layer. The CI was present in the walls of the burial pit, but was not visible in the burial fill (Marom et al., 2012, p. 6879). Ancient mtDNA recovered from this *H. sapiens* burial (Krause et al., 2010) matches haplogroup U2, connecting this individual to the earliest-known mitochondrial lineage in Europe today.

As can be seen from Tables 6a and b, most directly-dated Neanderthals precede the CI, implying that they have largely disappeared by 40 ka. It is thus difficult to plot the chronology of Neanderthal and *H. sapiens* interactions on the basis of direct dates, making claims of acculturation and interactions between the two hominin groups (e.g. d'Errico et al., 1998) difficult to pinpoint in any given region. Traditionally, archaeological technocomplexes have been used as proxies for hominin species to give a finer-grained record of Neanderthal and *H. sapiens* behaviours and landscape occupation patterning, though this approach is not unproblematic, especially given the lack of certainty in authorship of some industries (e.g. the Bohunician of central Europe). The Aurignacian (~44–32 ka) seems to have been made by *H. sapiens*, though its

Table 6c

Post-Cl directly-dated hominins. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULLU} curve (two-sigma (95%) calibrated ranges) (Weninger and Jöris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range). Many indirectly-dated late Aurignacian and Gravettian *H. sapiens* remains fall within this phase, probably including the well-known burial site of Abri Crô-Magnon in SW France (Henry-Gambier, 2002). Some of the teeth are not always attributed to *H. sapiens* with confidence, for example the Aurignacian teeth from level 6/7 of Bacho Kiro (Bulgaria) (Glen and Kaczanowski, 1982; Churchill and Smith, 2000).

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
45.6894°N, 0.4197°E	Les Garennes (Grotte de Vilhonneur) (France)	Chamber 2, dispersed across lime-stone scree surface; concreted bones (long bones gnawed by carnivores)	<i>H. sapiens</i>	Young adult male; rib no. 18 (Vilhonneur 1)	Beta-216141	27,110 ± 210	32,097–31,557 31,376–30,841	Henry-Gambier et al., 2007
				Young adult male; rib no. 19 (Vilhonneur 1)	Beta-216142	26,790 ± 190	31,921–31,353 31,195–30,685	
44.84°N, 0.85°E	Grotte de Cussac (France)	locus 1: human remains (on cave floor) locus 2: human remains (on cave floor)	<i>H. sapiens</i>	Left-hand rib fragment	Beta-156643	25,120 ± 120	30,287–29,743 29,501–28,836	Aujoulat et al., 2002
				Left-hand rib fragment	Beta-156644	15,750 ± 50	18,907–18,723 19,157–18,865	
45.0158°N, 1.1016°E	La Rochette (France)	layers 3–5 [but from the Gravettian layer 2, sector A?]	<i>H. sapiens</i>	Right ulna fragment (La Rochette 1)	OxA-11053	23,630 ± 130	28,593–28,069 27,963–27,517	Orscheidt, 2002
43.1313°N, 3.0905°E	La Crouzade (France)	layer F (Aurignacian)	<i>H. sapiens</i>	Maxilla fragment (La Crouzade VI)	ERL-9415	30,640 ± 640	35,888–33,776 36,021–33,656	Henry-Gambier and Sacchi, 2008
50.4676°N, 3.502°W	Kent's Cavern (UK)	cave earth [-3.2m]	<i>H. sapiens</i>	Maxilla fragment (KC4)	OxA-1621	30,900 ± 900	36,718–33,538 37,432–33,408	Hedges et al., 1989, p.209
51.5499°N, 4.2555°W	Paviland Cave [Goat's Hole] (UK)	"Red Lady" burial [Gravettian]	<i>H. sapiens</i>	Left femur and tibiae (Paviland I) (conventional date)	BM-374	18,460 ± 340	23,021–21,261 23,137–21,497	Oakley, 1968; Barker et al., 1969, p.289; Hedges et al., 1989, p.209; Aldhouse-Green and Pettitt, 1998; Jacobi and Higham, 2008
				Tibia (Paviland I)	OxA-1815	26,350 ± 550	32,112–30,076 31,349–29,356	
				Rib (Paviland I)	OxA-8025	25,840 ± 280	31,540–30,012 30,748–29,399	
				Ochre-stained rib fragment (Paviland I; Q1/29) (ultrafiltered)	OxA-16412	28,870 ± 180	33,965–32,789 33,587–32,514	
					OxA-16502	28,400 ± 320	33,635–32,071 33,275–31,491	
				Ochre-stained scapula fragment (Paviland I; Q1/30) (ultrafiltered)	OxA-16413	29,490 ± 210	34,420–33,328 34,075–33,246	
					OxA-16503	28,820 ± 340	34,135–32,463 33,725–31,875	
51.643°N, 4.704°W	Eel Point, Caldey Island (UK)?	<i>H. sapiens</i> humerus (coll. 1839)	<i>H. sapiens</i>	Humerus (ultrafiltered)	OxA-11015	24,000 ± 140	29,571–28,187 28,409–27,747	Schulting et al., 2005
					OxA-11543	23,370 ± 110	28,315–27,967 27,772–27,387	
					OxA-14164	24,470 ± 110	29,858–29,126 28,782–28,225	
40.7359°N, 17.5566°E	Grotta di Santa Maria di Agnano (Italy)	Burial in "principal cavern" (Gravettian)	<i>H. sapiens</i>	Human bone (skeleton 1)	Gif-9247	24,410 ± 410	30,188–28,164 29,352–27,732	Coppola, 1992, p.220
43.78362°N, 7.53534°E	Barma Grande (Italy)	Burial; from innermost part of cave, at 6.4 m depth (Gravettian)	<i>H. sapiens</i>	Metatarsal (Barma Grande 6)	OxA-10093	24,800 ± 800	31,366–27,822 30,733–27,653	Formicola et al., 2004
44.1701°N, 8.3464°E	Arene Candide (Italy)	Burial ('Il Principe') (Gravettian)	<i>H. sapiens</i>	Femur (Arene Candide 1)	OxA-10700	23,440 ± 190	28,479–27,923 27,900–27,339	Pettitt et al., 2003
49.707°N, 17.0167°E	Mladeč cave (Czech republic)	(Aurignacian)	<i>H. sapiens</i>	Ulna (Mladeč 25c)	VERA-2736	26,330 ± 170	31,762–30,634 30,981–30,234	Wild et al., 2005
				Right M2, distal half of the crown (Mladeč 1)	VERA-3073	31,190 +400, -390	35,954–34,378 35,996–34,397	
				Left M3, distal half of the crown (Mladeč 2)	VERA-3074	31,320 +410, -390	36,064–34,444 36,111–34,533	

(continued on next page)

Table 6c (continued)

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
				Left M2, mesial-buccal root (Mladeč 8)	VERA-3075	30,680 +380, –360	35,541–34,113 35,381–33,980	
				Right maxillary canine (Mladeč 9a); lingual half of the root (white-coloured collagen)	VERA-3076A	31,500 +420, –400	36,258–34,526 36,251–34,657	
				Right maxillary canine (Mladeč 9a); lingual half of the root (brown-coloured collagen)	VERA-3076B	27,370 ± 230	32,343–31,643 31,588–30,951	
48.0746°N, 20.7484°E	Görömböly-tapolca (Hungary)	Yellowish-brown clay (Gravettian?)	<i>H. sapiens</i>	Occipital bone (ultrafiltered)	OxA-15080	30,300 ± 300	34,979–34,011 34,833–33,831	This paper (Table S1); Thoma and Vértes, 1971; Tillier et al., 2006
48.3216°N, 15.4037°E	Willendorf I* (Austria)	Gravettian	<i>H. sapiens</i>	Femoral diaphysis fragment	ETH-20690	24,250 ± 180	29,858–28,366 28,682–27,885	Teschler-Nicola and Trinkaus, 2001
48.8805°N, 16.6686°E	Dolní Věstonice I* (Czech republic)	Burial (Gravettian)	<i>H. sapiens</i>	Femur (Dolni Vestonice 35)	OxA-8292	22,840 ± 200	28,273–26,769 27,538–26,638	Trinkaus et al., 1999
49.202°N, 16.621°E	Brno-Francouzská Street* (Czech republic)	Burial (late Gravettian)	<i>H. sapiens</i>	Human bone (Brno 2)	OxA-8293	23,680 ± 200	29,181–27,909 28,195–27,464	Pettitt and Trinkaus, 2000
49.443°N, 20.1563°E	Obłazowa 1 cave (Poland)	layer VIII (Aurignacian)	<i>H. sapiens</i>	Distal left phalange (OBC6)	OxA-4586	31,000 ± 550	36,018–34,126 36,105–34,017	Housley, 2003
45.1895°N, 23.755°E	Peștera Mueirilor [Mueirii], Baia de Fier (Romania)	sector A, "Mousterian gallery"	<i>H. sapiens</i>	Scapula + tibia (Mueirii 1)	LuA-5228	30,150 ± 800	35,793–32,893 36,081–32,655	Paunescu, 2001, p.231; Soficaru et al., 2006
			<i>H. sapiens</i>	Cranium (Mueirii 1) (ultrafiltered)	OxA-15529	29,930 ± 170	34,580–33,896 34,357–33,708	
			<i>H. sapiens</i>	Temporal bone (Mueirii 2) (ultrafiltered)	OxA-16252	29,110 ± 190	34,184–32,980 33,756–32,842	
45.5862°N, 23.1296°E	Peștera Cioclovina Uscată (Romania)	Sector 1 (1952); ~2 m depth, under "coaja de apa" stalagmitic crust (Aurignacian?)	<i>H. sapiens</i>	Temporal bone (Cioclovina 1)	LuA-5229	29,000 ± 700	34,652–32,052 34,809–31,262	Paunescu, 2001, p.231; Soficaru et al., 2007
				Occipital bone (Cioclovina 1) (ultrafiltered)	OxA-15527	28,510 ± 170	33,500–32,384 33,086–31,789	
51.4036°N, 39.0488°E	Kostenki I* (Russia)	Cultural layer III (Aurignacian)	<i>H. sapiens</i>	Femur (Kostenki 1)	OxA-7073	32,600 ± 1100	40,217–34,253 39,678–34,641	Richards et al., 2001; Higham et al., 2006b
				Kostenki 1 (ultrafiltered)	OxA-15055	32,070 ± 190	36,658–35,310 36,375–35,530	
51.3742°N, 39.0733°E	Kostenki VIII* (Russia)	Cultural layer II (Eastern Gravettian)	<i>H. sapiens</i>	Burnt skull fragment	OxA-7109	23,020 ± 320	28,516–26,732 27,795–26,589	Sinitsyn, 2004
51.3975°N, 39.0417°E	Kostenki XIV* (Russia)	Under cultural layer III; burial pit cut through Campanian Ignimbrite layer (Aurignacian).	<i>H. sapiens</i>	Tibia	OxA-7126	4750 ± 40	5658–5290 5590–5328	Sinitsyn, 2004; Hoffecker, 2011; Marom et al., 2012
					GrA-9303	3730 ± 40	4211–3947 4231–3935	
					SR-7366/ UCIAMS-61666	13,610 ± 40	16,960–16,792 16,612–16,218	
				Tibia (amino-acid – hydroxyproline – repeat measurement)	OxA-X-2395-15	33,250 ± 500	39,599–35,611 38,685–36,263	
51.4067°N, 39.0535°E	Kostenki XVIII* (Russia)	Burial pit in sand; depth of 40 cm; covered by 3 layers of mammoth bones (Eastern Gravettian)	<i>H. sapiens</i>	Child (~9–10 years) vertebra	GrA-9304	19,830 ± 120	23,934–23,410 24,187–23,542	Sinitsyn, 2004
					OxA-7128	21,020 ± 180	25,426–24,630 25,791–24,866	
56.134°N, 40.479°E	Sungir* (Russia)	Burial 1 (Eastern Gravettian)	<i>H. sapiens</i>	Human bone	OxA-9036	22,930 ± 200	28,345–26,849 27,624–26,753	Pettitt and Bader, 2000; Kuzmin et al., 2004;
				Vertebra fragment	AA-36473	19,160 ± 270	23,562–22,466 23,732–22,477	Dobrovolskaya et al., 2012; Marom et al., 2012

				Human bone	KIA-27006	27,050 ± 210	32,063–31,523 31,341–30,811	
		Burial 2 (Eastern Gravettian)	<i>H. sapiens</i>	Human bone	OxA-9037	23,830 ± 220	29,535–27,959 28,412–27,569	
				Right-hand ribs	AA-36474	27,210 ± 710	33,187–30,563 33,149–29,920	
				Left-hand ribs	AA-36475	26,200 ± 640	32,126–29,826 31,363–28,997	
				Human bone (ultrafiltered)	OxA-15753	25,020 ± 120	30,183–29,703 29,414–28,741	
				Human bone (Hydroxyproline (amino-acid) fraction of (ultrafiltered) sample)	OxA-X-2395-06	30,100 ± 550	35,242–33,382 35,284–33,186	
		Burial 3 (Eastern Gravettian)	<i>H. sapiens</i>	Human bone	OxA-9038	24,100 ± 240	29,784–28,172 28,646–27,736	
				Rib fragments	AA-36476	26,190 ± 640	32,119–29,819 31,354–28,991	
				Human bone (ultrafiltered)	OxA-15751	25,430 ± 160	30,634–29,858 30,077–29,054	
				Human bone (ultrafiltered)	OxA-15754	24,830 ± 110	29,972–29,632 29,176–28,576	
				Human bone (ultrafiltered)	KIA-27007	26,000 ± 410	31,783–29,991 30,986–29,335	
				Human bone (Hydroxyproline (amino-acid) fraction of (ultrafiltered) sample)	OxA-X-2395-07	30,000 ± 550	35,140–33,264 35,155–33,032	
45.16°N, 34.396°E	Buran-Kaya III (Ukraine)	layer 6–1	<i>H. sapiens</i> (Gravettian)	Parietal bone fragment	GrA-37938	31,900 +240, –220	36,366–35,150 36,297–35,263	Prat et al., 2011 ; Higham et al., 2007 , p. S8
				Bone (“sample 3”) (ultrafiltered)	OxA-13302	32,790 ± 280	38,670–35,598 37,867–36,129	
55.3295°N, 92.4469°E	Pokrovka (Russia)		<i>H. sapiens</i>	Frontal bone of young adult [ultrafiltered]	OxA-19850	27,740 ± 150	32,634–31,858 31,823–31,183	Akimova et al., 2010

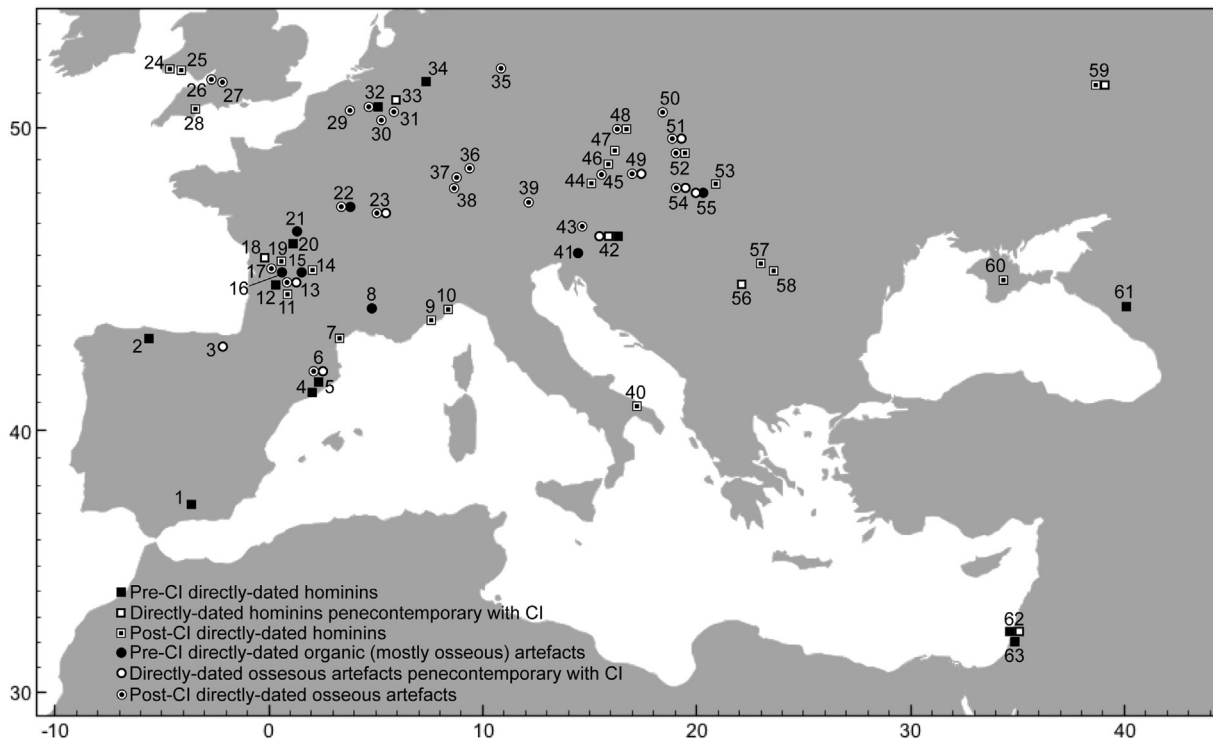


Fig. 4. Map of sites listed in Tables 6a–c and 8a–c. [1 = Cueva del Boquete de Zafarraya (Spain), 2 = El Sidrón (Spain), 3 = Labeko Koba (Spain), 4 = Cova del Gegant (Spain), 5 = Banyoles (Spain), 6 = L'Arbreda (Spain), 7 = La Crouzade (France), 8 = Grotte Mandrin (France), 9 = Barma Grande (Italy), 10 = Arene Candide (Italy), 11 = Grotte de Cussac (France), 12 = La Ferrassie (France), 13 = Abri Pataud (France), 14 = La Rochette (France), 15 = Le Moustier (France), 16 = La Quina (France), 17 = Les Rois cave (France), 18 = Abri de la Roche à Pierrot (Saint-Césaire) (France), 19 = Les Garennes (Grotte de Vilhonneur) (France), 20 = Les Rochers-de-Villeneuve (France), 21 = Les Cottés (France), 22 = Grotte du Renne (France), 23 = Trou de la Mère Clochette (France), 24 = Eel Point, Caldey Island (UK), 25 = Paviland Cave [Goat's Hole] (UK), 26 = Uphill Quarry cave 8 (UK), 27 = Hyaena Den cave (UK), 28 = Kent's Cavern (UK), 29 = Maisières-Canal (Belgium), 30 = Trou Magrite (Belgium), 31 = Trou al'Wesse (Belgium), 32 = Grotte de la Betche-aux-Rotches, Spy (Belgium), 33 = Grotte Schmerling, Engis (Belgium), 34 = Kleine Feldhöfer Grotte, Neandertal (Germany), 35 = Hermannshöhle (Germany), 36 = Vogelherd cave (Germany), 37 = Brillenhöhle (Germany), 38 = Sirgenstein cave (Germany), 39 = Tischoferhöhle (Austria), 40 = Grotta di Santa Maria di Agnano (Italy), 41 = Ljublansko Barje (Slovenia), 42 = Vindija cave (Croatia), 43 = Potočka zijalka (Slovenia), 44 = Willendorf I (Austria), 45 = Alberndorf (Austria), 46 = Dolní Věstonice I (Czech republic), 47 = Brno-Francouzská Street (Czech republic), 48 = Mladeč cave (Czech republic), 49 = Dzeravá skala (Slovakia), 50 = Borsuka cave (Poland), 51 = Mamutowa cave (Poland), 52 = Obłazowa cave (Poland), 53 = Görömböly-tapolca (Hungary), 54 = Istállóskő cave (Hungary), 55 = Pes-kő cave (Hungary), 56 = Peștera cu Oase (Romania), 57 = Peștera Cioclovina Uscată (Romania), 58 = Peștera Mueirilor [Muierii], Baia de Fier (Romania), 59 = Kostenki I, VIII, XIV, XVIII (Russia), 60 = Buran-Kaya III (Crimea), 61 = Mezmaiskaya (Russia), 62 = Es Skhul cave (Israel), 63 = Et Tabun cave (Israel). Sites not indicated: Sungir' (Russia), Pokrovka (Russia), Baigara locality (Russia), Okladnikov cave (Russia)].

earliest phases contain little or no associated hominin skeletal material, and much is fragmentary (often teeth). The captions for Tables 6a–c list the main *H. sapiens* specimens indirectly dated through association with dated archaeological assemblages. Such an approach is problematic for a number of reasons: intrusion of hominin skeletal elements into assemblages (through taphonomic processes or intentional funerary practices such as burial), imprecise archaeological recovery techniques (especially for excavations conducted many decades ago), or undiagnostic associated archaeological assemblages; in some cases, the hominin specimens are not even associated with any archaeology. In the European Aurignacian, there appear to be some spatially-restricted funerary practices, such as possible deposition in unoccupied caves (Mladeč), and the fragmentation of bodies and transformation of human teeth into pendants in multiple SW French Aurignacian phases (Isturitz, Tarté, La Combe, Brassempouy) (MacCurdy, 1914, p. 179; White et al., 2003; Henry-Gambier et al., 2004; Normand et al., 2007; Bailey et al., 2009). There appear to be no complete inhumations in the Aurignacian (unlike the succeeding Gravettian), which perhaps reflects more mobile and territorial lifestyles. Very little skeletal material has been recovered from the very earliest phases of the Aurignacian, and what there is, is fragmentary. The earliest-known directly-dated *H. sapiens* individual in Europe, Peștera cu Oase, indicates that our species was present from at least 40 ka, making it penecontemporaneous with the early Aurignacian

in Europe, but with little clear overlap with Neanderthals. A juvenile mandible fragment was recovered from level 11 (Bachokirian/archaic Aurignacian) of Bacho Kiro, Bulgaria, AMS ^{14}C -dated to between $38,500 \pm 1700$ ^{14}C BP (OxA-3213) and $34,800 \pm 1150$ ^{14}C BP (OxA-3212) (calibrating to ~ 45 – 36.7 ka (95% confidence); see Table 6b), while teeth were found in level 6/7, more clearly post-dating the CI (Evin et al., 1978; Mook, 1982; Hedges et al., 1994; Churchill and Smith, 2000). The El Castillo mandible and teeth from the early Aurignacian (old and new excavations) are unfortunately not diagnostic enough to define as either Neanderthal or *H. sapiens*; however, they may well precede the CI (Garralda, 2006). As suggested by a new dating programme on faunal remains, the Kent's Cavern 4 *H. sapiens* maxilla may be considerably older than its non-ultrafiltered direct date of $30,900 \pm 900$ ^{14}C BP (Proctor et al., 2013), but unfortunately a further direct date is not feasible, due to the fragmentary condition of the specimen.

It has been proposed (Müller et al., 2011) that the main demic change among European Neanderthals occurred at $\sim 48,000$ [^{14}C] BP. Müller et al. (2011) also propose that the Levant served as a refugium for *H. sapiens* until ~ 47 ka, when changing climatic conditions facilitated the appearance in central Europe of the Bohunician (thought to be made by *H. sapiens* on the basis of technological similarities with the Levantine Emiran industry (Richter et al., 2008)) in Greenland Interstadials (henceforth "GI") 14–13 (~ 55 – 48 ka). The main *H. sapiens* incursion into Europe, with the earliest Aurignacian,

Table 7a

Population estimates for CI proximal and distal fallout zones, based on modelled NPP (Huntley and Allen, 2003) and harvestable NPP (Belovsky, 1988) values (grammes of carbon/m²/year) for 42 ka. The low population estimates attributed to Belovsky (1988) derive from scaling-down of the densities of 2–3 people per 100 km² (for 100 g of harvestable primary biomass per square metre); the larger population estimates derive largely from ethnographic data published in Kelly (2013, Tables 3–1 and 7–3) and Binford (2001, Table 5.01). More details are given in Table S2 and Figs. S1a and S1b.

	Proximal fallout zone ^a		Distal fallout zone ^b	
	NPP	hNPP	NPP	hNPP
Average	245.48	4.91	283.42	5.67
Standard Deviation (St Dev)	128.49	2.57	110.15	2.2
Median	256	5.12	296	5.92
Range	19–624	0.38–12.48	3–580	0.06–11.6
N terrestrial cells	31		981	
Terrestrial area covered (km ²)	111,600		3,531,600	
Belovsky pop. estimates	110–164 people		4004–6005 people	
Kelly/Binford pop. estimates	904–2365 people		27,846–84,722 people	

^a CI proximal fallout zone: within 300 km radius of Campi Flegrei (~40.82°N, 13.13°E).

^b CI distal fallout zone (estimated): terrestrial cells between 33.9°N–52°N and 9.1°E–50°E have been included.

was identified by Müller et al. (2011) in GI-12 (~47–45 ka), and thought to be facilitated by expansion of open-forest biomes in the Balkans at the expense of desert-steppe. It would appear that *H. sapiens* could also exploit cold steppic environments before the CI, as has been recently argued by Nigst et al. (2014), based on the early Aurignacian occupation of Willendorf II at ~43.5 ka (GI-11). While the attribution of the western European Châtelperronian to Neanderthals is seldom contested (e.g. Leroi-Gourhan, 1961; Lévêque and Vandermeersch, 1980; Hublin et al., 1996; cf.; Bar-Yosef and Bordes, 2010), the authorship of the Italian Uluzzian is much more difficult to demonstrate. Benazzi et al. (2011) believe that the two deciduous teeth from the Uluzzian levels EIII and EII-I at Grotta del Cavallo are from *H. sapiens*, though the higher one (in level EII-I) was sufficiently robust for the original authors (Palma di Cesnola and Messeri, 1967) to claim it was Neanderthal; both papers agree that the lower tooth (in level EIII) was modern human. While the Italian Uluzzian might

have some association with early (pre-CI) European *H. sapiens*, the Greek Uluzzian (notably from Klissoura Cave 1) has no hominin fossils (Kaczanowska et al., 2010).

The central European Szeletian technocomplex, whose technological connections with the preceding Middle Palaeolithic is frequently highlighted in the literature (e.g. Allsworth-Jones, 1986, 1990; Kaminská et al., 2011), is almost devoid of associated hominin fossils. The best-known site with associated hominin material is Remete Felső, attributed to the Jankovichian/Transdanubian Szeletian on the basis of a dozen artefacts (Svoboda, 2001; Tillier et al., 2006). However, the three hominin teeth (two incisors and a canine) that accompany this assemblage are too worn and non-characteristic to be able to attribute either to Neanderthals or *H. sapiens* (Tillier et al., 2006). Thus we cannot yet attribute the Szeletian (*sensu lato*) to Neanderthals, though recent re-evaluation of the chronological and technological patterning of this technocomplex hints at the possibility that the Early and Late phases might have been made by different hominin species: Neanderthals for the Early Szeletian, and possibly *H. sapiens* for the Late phase (Kaminská et al., 2011, p. 45). Early Szeletian assemblages are mostly recovered from the eastern Czech republic and are dated to at least ~43–42 ka (GI-11 and GI-10). They appear to be technologically and chronologically separated from Late Szeletian assemblages (Austria, Czech republic and Slovakia), which appear to post-date HE4 and the CI (Kaminská et al., 2011; pp. 42–46). If HE4 and the CI did create an occupation hiatus within the Szeletian region (Kaminská et al., 2011, p. 46; cf. Table 4), then we do not have any identifiable record so far of cryptotephra in Szeletian sites sampled by WP-1 (Table 5a: Moravský Krumlov IV, Vedrovice V and Szeleta). The central European Bohunician, found so far only in open-air contexts (represented in Table 5a by the site of Bohunice), has no associated hominin fossils. The open-air site of Ondratice I/Želeč (Table 5a) appears to contain diagnostic elements of Szeletian, Bohunician and Aurignacian assemblages, and may represent occupations by different groups (Mlejnek et al., 2012); it has yielded no cryptotephra, and remains undated.

Given that so many Early Upper Palaeolithic industries are highly localised in time and space, it is correspondingly difficult to

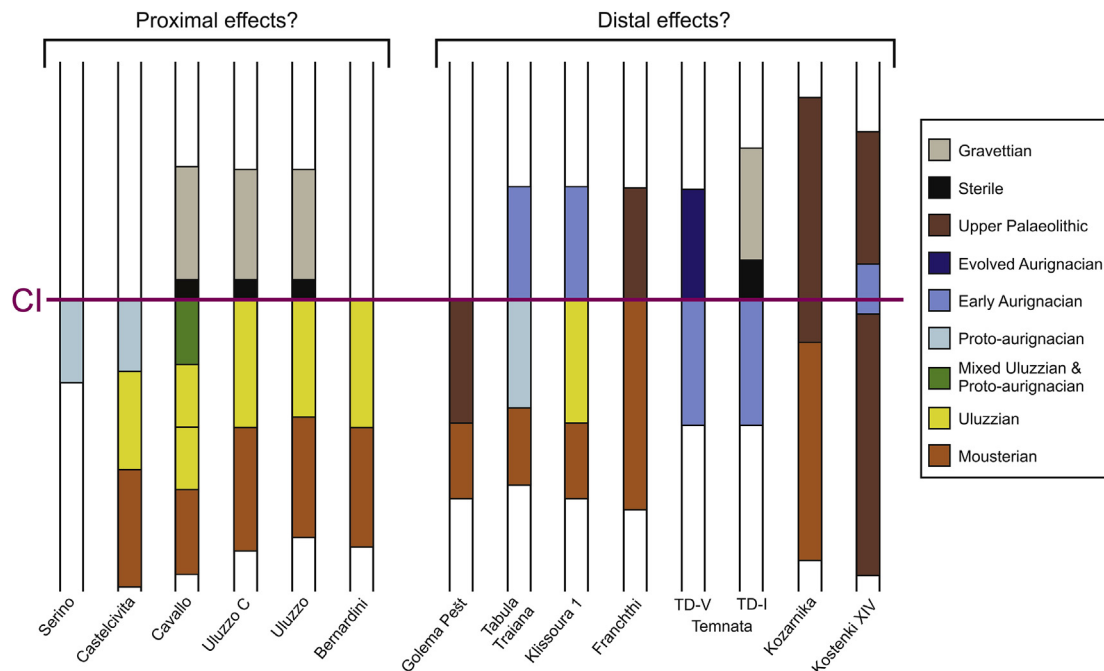


Fig. 5. Cultural heterogeneity at the time of the CI eruption. Archaeological sites are broadly organised by longitude: left (western) to right (eastern).

Table 7b

Changing distributions of modelled NPP (Huntley and Allen, 2003) and harvestable NPP (Belovsky, 1988) values for Europe at 42 ka (“warm phase”), 30 ka (“cooler phase”) and 21 ka (“LGM”), and resulting estimates of hunter–gatherer populations that could be sustained by such primary biomass. The Binford and Kelly data are summarised in Table S2.

	Terrestrial cell <i>N</i> (each 3600 km ²) ^a	NPP (g/C/m ² /yr)				Harvestable NPP (2% of NPP)				Population estimates	
		Average	St Dev	Median	Range	Average	St Dev	Median	Range	Range 1 (Belovsky)	Range 2 (Kelly; Binford)
42 ka	2424	245.21	118.88	248	2–624	4.9	2.38	4.96	0.04–12.48	8139–12,209	59,084–184,514
30 ka	2293	231.5	92.18	237	1–595	4.63	1.84	4.74	0.02–11.9	7244–10,866	53,223–166,140
21 ka	1792	215.72	99.85	216.5	1–731	4.31	2	4.33	0.02–14.62	5256–7884	40,572–125,370

^a Only cells with NPP values above 0 g/C/m²/yr have been counted in this table (see also Figs. S2a and b).

attribute them to specific hominin species. The remainder of this paper will assess these uncertain attributions in the light of wider tephrochronological, behavioural and demographic questions.

6. Proximal versus distal effects of volcanic eruptions on hominin occupation patterns and economies

The stratigraphic evidence shows varying potential effects of volcanic eruptions on hominin occupation patterns at different distances from the epicentre. Taking the Campanian Ignimbrite as the main example for discussion allows us to define what the terms “proximal” and “distal” might mean with reference to effects on hominin occupation strategies and densities (see Section 4 for working definitions). Cultural change forced by sudden environmental shifts is difficult to demonstrate with current chronological evidence; the presence of such an event at the base of a cultural layer does not necessarily demonstrate a causal effect. Results from WP-1 have not lent support to this AET-forcing option; it remains to be proved using future research. At present, local population extinction or displacement are the likeliest outcomes for sites located in the proximal eruption zone. Away from the proximal zone, we should expect a reduction in the effective intensity of an environmental change, declining with increasing distance from, and reduced exposure to, the fallout.

Using patterning from the southern Italian Palaeolithic record as a guide, we hypothesise that a rough boundary between proximal and distal effects might lie between 250 and 300 km radius from the Campi Flegrei (near Naples, where the CI originated) (Table 7a). Archaeological sites within this radius show evidence of extinguished (within a radius of about 100 km) or interrupted (radii between 100 and 300 km) hominin occupations (Fig. 5), which serve us here as an heuristic model for testing ecologically. In addition, sites (Serino, Castelcivita) within the inner (100 km-radius) proximal zone show evidence of having received the full CI pyroclastic sequence (basal pumice and overlying ignimbrite units), suggesting that people would have had minimal chances to escape the eruption, and were probably extinguished. Those in the outer (100–300 km radius) zone (e.g. Cavallo, Uluzzo, Uluzzo C and Bernardini), hypothetically had more opportunities for avoiding the full effects of the CI, and indeed occupations here tend to be interrupted, rather than extinguished (Fig. 5).

Table 7a outlines population levels, predicted from terrestrial plant productivity estimates (see below), for this proximal zone (300 km radius from the CI source). These productivities would suggest hominin populations of somewhere between 110 and 164 (a conservative estimate, based on densities of 0.2–0.3 people per 100 km² that were scaled down from Belovsky (1988, p. 343)) and 904–2365 people. The higher population estimate range is derived from data on mid-to-high latitude hunter–fisher–gatherers collected in Binford (2001) and Kelly (2013). We might hypothesise that up to 1000 people were directly affected by the maximal proximal effects of the CI eruption. This can be contrasted with the higher populations in the distal zone (Table 7a), who were spread

over a much wider area, and whose experience of the CI ash was much more variable.

Predictions have already been made in the literature for population and ecological effects on human populations from the CI, and we here focus upon two recent ones. Golovanova et al. (2010, p. 673) propose an effect akin to a “nuclear winter” caused by the CI: catastrophic and disruptive environmental change between 42 and ~37 ka (p. 657) that might have caused the disappearance of Neanderthals from the Caucasus region (and perhaps elsewhere in eastern Europe). However, they do not really articulate a model of how these effects might have operated on hominin populations around 40 ka, and it falls to Fedele et al. (2008) to define processes and correlations that are potentially testable in the archaeological record. They clearly articulate possible effects, linkages and feedback mechanisms for the CI upon hominin ecologies, behaviours and mobilities, and argue that the rapidity of change “would have created conditions for selectively transforming the human circulation patterns and subsistence strategies” (p. 845). Their central hypothesis is that the combination of HE4 with the CI and the Bond cooling trend (Table 1) destabilised already-sensitive environmental systems and ecologies for a considerable period (centennial scales), making their model more AET than (relatively short-lived) environmental disaster. They predict that these environmental perturbations affected the distribution of biotic resources and water very rapidly, as well as the interplay between altered hominin resource bases, population ecologies, distribution/mobility in the landscape and social configurations. They contend that displaced populations would have created “an entirely new mosaic of depopulation and crowding” (p. 849), the latter focussed on areas less affected by the CI. However, given the population estimates for Europe discussed above (Section 2), and in Tables 2–4, 7a and b, it is difficult to know what “crowding” meant in an Early Upper Palaeolithic context.

At present, the results of WP-1 and other researchers provide no evidence to support suggestions (Fedele et al., 2008) that the Balkans formed part of the CI proximal zone, or that the effects of the CI were (northern) hemispheric in scale. Based on the results of WP-1, we instead include Balkans sites within the distal zone sites; there is not yet evidence in these zones that the CI interrupted site occupations. Nevertheless, the model of Fedele et al. contains useful propositions and feedback mechanisms that deserve closer consideration (see Sections 7 and 8, below). We agree with them that effects on hominin and herbivore populations were likely to have been most intense in the direct-impact (inner proximal) zone. There is little doubt that the CI (and other eruptions) created “landscapes of stress as well as opportunity” (Fedele et al., 2008, p. 845), but the question rests on the modelled duration of their direct effects: years, decades, or centuries? Table 7a would suggest that relatively few people – perhaps 1000 – were directly affected by the CI.

Consideration of direct (proximal) versus indirect (distal) effects of eruptions on hominins requires examination of ecological systems and human adaptations. There is evidence that *H. sapiens* withstood apparently “unattractive” climatic conditions if

Table 8a

Pre-Cl directly-dated organic (mostly osseous) artefacts. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULU} curve (two-sigma (95%) calibrated ranges) (Weninger and Jöris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range). Middle Palaeolithic (Neanderthal) examples of osseous technology include small numbers of bone points made from mammoth ribs from Salzgitter-Lebenstedt (Germany) (Gaudzinski, 1999), and *lissoirs* [bone polishers] from the French sites of Pech-de-l'Azé I and Abri Peyrony (Soressi et al., 2013). Overall, Neanderthal bone technology prior to the Cl marker is small-scale and patchy in its distribution/preservation.

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
47.5909°N, 3.7636°E	Grotte du Renne (France)	Level XII (Mousterian)	<i>H. neand.</i>	Reindeer bone awl (ultrafiltered)	OxA-21594	37,000 ± 1000	43,127–40,411 43,147–39,673	Higham et al., 2010
				Horse bone awl (ultrafiltered)	OxA-21557	38,100 ± 1300	44,133–40,873 44,997–40,278	
		Level X (Châtelperronian)	<i>H. neand.</i>	Reindeer bone retouchoir (ultrafiltered)	OxA-X-2222-21	23,120 ± 190	28,265–27,641 27,717–27,087	
				Horse bone awl (ultrafiltered)	OxA-21590	21,150 ± 160	25,721–24,693 25,825–25,143	
				Reindeer bone awl (ultrafiltered)	OxA-21592	36,200 ± 1100	43,254–38,070 42,670–38,723	
46.6927°N, 0.8415°E	Les Cottés (France)	Layer 08, sq. Y5 (Mousterian)	[Bone] retouchoir (ultrafiltered)	EVA-18	42,200 ± 350	46,730–43,810 46,198–44,870	Talamo et al., 2012	
				MAMS-10829	41,780 ± 600	46,510–43,390 46,335–44,150		
				OxA-V-2382-49	42,690 ± 750	47,660–43,820 47,764–44,699		
45.50704°N, 0.29305°E	La Quina Amont (France)	Loc. 2 (Mousterian)		Retouchoir on <i>Equus ferus</i> metatarsal (F965-327) (ultrafiltered)	OxA-22154	46,900 ± 2700	57,236–44,072 57,674–42,459	Higham et al., 2014, p. S23
44.99417°N, 1.05973°E	Le Moustier, lower shelter (France)	Level H (Mousterian)		Retouchoir on large mammal limb bone (ultrafiltered)	OxA-21750	50,000 ± 3900	66,203–44,463 70,427–44,755	Higham et al., 2014, p. S17-S18
				Retouchoir on large mammal limb bone (ultrafiltered)	OxA-21751	44,100 ± 1900	51,744–43,264 [>50,000]- 45,075	
		Level J (Mousterian)	<i>H. neand.</i>	Retouchoir on large mammal limb bone (ultrafiltered)	OxA-21754	45,100 ± 2300	53,891–43,415 [>50,000]- 45,443	
				Retouchoir on large mammal limb bone (ultrafiltered)	OxA-X-2300-21	40,700 ± 1300	43,308–41,096 43,437–40,420	
44.47207°N, 4.77214°E	Grotte Mandrin (France)	Layer F, testpit (Mousterian)		Retouchoir on mandibular fragment [bovid or horse sized mammal] (ultrafiltered)	OxA-21695	>48,200		Higham et al., 2014, p. S36-S37
				Layer E, level 7 (Middle Palaeolithic)	Retouchoir on horse tibia (ultrafiltered)	OxA-21692	>47,300	
		Layer D, testpit (Mousterian)		Retouchoir on horse tibia (ultrafiltered)	OxA-21693	>48,600		
				Retouchoir, cf. reindeer femur (ultrafiltered)	OxA-21694	>47,100		
48.0468°N, 20.4264°E	Pes-kő cave (Hungary)	[lowest layer; clay] (Aurignacian)		Planoconvex-sectioned bone point (Pb.933) (ultrafiltered)	OxA-17967	38,300 ± 1500	44,604–40,684 45,796–40,110	This paper (Table S3)
				[Split-based?] antler point (Pb.930) (ultrafiltered)	OxA-17964	33,500 ± 450	41,345–35,313 38,836–36,511	
				Cut-marked bone [rib]: decorative markings? (Pb.929) (ultrafiltered)	OxA-17965	37,300 ± 1600	44,419–38,303 45,165–38,862	
				Antler split-based point (Pb.927) (ultrafiltered)	OxA-17966	36,400 ± 800	43,042–38,986 42,356–39,473	
				Yew (<i>Taxus</i> sp.) wood point; blackened surface suggests fire-hardening.	Beta-252943 OxA-19866	>43,970 38,490 ± 330	43,350–41,970 43,013–42,083	

preferred resources were present (Davies and Gollop, 2003), and such findings encourage us to examine models of hominin adaptations further. Potts (e.g. 1996, 1998) has developed the idea of variability selection, exploring concepts of adaptive versatility in responding to environmental dynamics themselves. This idea allows us to augment our terminology of adaptations; instead of

trying to decide if Neanderthal or *H. sapiens* groups were either environmental specialists or generalists, and thus how seriously their dietary requirements might have been disrupted by the impacts of volcanic eruptions, we can assess behavioural flexibility (versatilism) over time as well. In theory, versatile and/or generalist species might have better chances of surviving environmental

Table 8b

Directly-dated osseous artefacts penecontemporary with the CI. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULLU} curve (two-sigma (95%) calibrated ranges) (Weninger and Jöris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range).

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
42.1607°N, 2.74401°E	L'Arbreda (Spain)	Level H (Proto-aurignacian)		[Bone] Spatula (E3 CE108) (ultrafiltered)	OxA-21784	36,000 ± 700	42,808–38,552 41,931–39,216	Wood et al., 2014
				Spatula on indet. rib fragment (B2 BB104 1427, 75, 37, –517.5) (ultrafiltered)	OxA-21674	33,800 ± 550	41,937–35,681 39,532–36,628	
43.06102°N, 2.4908°W	Labeko Koba (Spain)	Level VII (Proto-aurignacian)		Retouchoir on <i>Capra pyrenaica</i> tibia diaphyseal fragment (LK.11D.-242.142) (ultrafiltered)	OxA-21766	36,850 ± 800	42,828–40,700 42,651–39,936	Wood et al., 2014
				Chisel on diaphyseal fragment from a large species (LK. 15G.-237.177) (ultrafiltered)	OxA-X-2314-43	36,500 ± 750	42,708–40,192 42,342–39,677	
		Level VI (Early Aurignacian)		Retouchoir on diaphyseal fragment from a small-sized taxon (LK.13H.-204.330) (ultrafiltered)	OxA-21778	35,100 ± 600	42,041–38,181 41,060–38,517	
				Possible retouchoir on diaphyseal fragment from a large taxon (LK.13G.-203.129) (ultrafiltered)	OxA-21794	32,200 ± 450	38,570–34,718 37,533–35,101	
				OxA-21841	32,150 ± 450	38,507–34,667 37,438–35,046		
		Level V (Early Aurignacian)		Retouchoir on radius diaphyseal fragment from large taxon (LK.13F.-207.255) (ultrafiltered)	OxA-21767	34,750 ± 600	41,785–38,005 40,853–38,125	
				Retouchoir on tibia diaphyseal fragment from large taxon (LK.13J.-175.139) (ultrafiltered)	OxA-21779	34,650 ± 600	41,728–37,932 40,745–37,901	
				Retouchoir on diaphyseal fragment (LK.13H.-159.232) (ultrafiltered)	OxA-21780	33,550 ± 550	41,771–35,203 39,161–36,386	
		Retouchoir on diaphyseal fragment from a medium-sized taxon (LK.13J.-160.100) (ultrafiltered)	OxA-21768	33,600 ± 500	41,841–35,281 39,095–36,499			
44.93837°N, 1.0117°E	Abri Pataud (France)	Level 12; trench II/III, sq. B (Early Aurignacian) Level 11; Trench III, sq. B (Early Aurignacian) Level 11; Trench IV, sq. C (Early Aurignacian) Level 11; Trench III, sq. A (Early Aurignacian)		Retouchoir on reindeer femur fragment (12F6290 BII/III) (ultrafiltered)	OxA-21671	34,300 ± 600	41,631–37,503 40,286–37,140	Higham et al., 2011
				Retouchoir on horse metapodial III fragment (11F1813) (ultrafiltered)	OxA-21580	33,550 ± 550	41,771–35,203 39,161–36,386	
				Retouchoir on horse metatarsal III fragment (11F1768) (ultrafiltered)	OxA-21602	33,500 ± 500	41,527–35,235 38,951–36,424	
				Retouchoir on <i>Bos/Bison</i> humerus fragment (11F702) (ultrafiltered)	OxA-21601	34,150 ± 550	41,605–37,325 39,981–37,037	
47.138°N, 5.571°E	Trou de la Mère Clochette (France)	Unit B; yellow, brecciated middle layer, comprising clay and blocks; 0.1–1.0 m thick (Aurignacian) <i>Couche ferrugineuse</i> (1906): 10 m ² surface, near southern entrance, in unit B; 0.15 m thick on average. (Aurignacian)		Antler split-based point wing (ultrafiltered)	OxA-19621	33,750 ± 350	41,836–36,008 38,963–36,967	Szmids et al., 2010
				Antler split-based point wing (ultrafiltered)	OxA-19622	35,460 ± 250	42,145–38,821 40,721–39,441	
50.16944°N, 19.80723°E	Mamutowa cave (Poland)	Centre/rear of cave deposits (1880s excavations) (Aurignacian)		Ivory (Mladeč) point (Kraków Museum 14–17) (ultrafiltered)	OxA-14436	33,640 ± 250	41,824–35,616 38,671–37,126	This paper (Table S3)
				Ivory (Mladeč) point (Kraków Museum 14–67) (ultrafiltered)	OxA-14434	32,280 ± 220	38,389–35,009 36,685–35,656	
48.4922°N, 17.295°E	Dzeravá skála (Slovakia)	1913 Hillebrand excavations [=modern layers 4a'/5a?'] (Aurignacian)		[Antler] "chisel"/broken Mladeč point (Pb.580) (ultrafiltered)	OxA-17963	35,600 ± 400	42,306–38,758 41,178–39,321	This paper (Table S3); Kaminská et al., 2005, pp. 37–8
46.305°N, 16.088°E	Vindija cave (Croatia)	Layer G ₁	<i>H. neand.?</i>	"Split-based point" (U-series)	[U-Th (γ)] [U-Pa (γ)]		(45,000 ± 6000) (30,000 ± 3000)	Karavanić et al., 1998, p. 139
48.0654°N, 20.4108°E	Istállós-kő cave (Hungary)	Pre-WW2 excavations [if by Saád and Megay (1927), then from "lower layer" (7); or dug by Mottl (1938?)] [Aurignacian] "Lower layer" (Vértes, 1950): trench I, 1.6 m depth (Aurignacian)		Antler projectile point (Herman Otto Museum, 6306; 53.37.8) (ultrafiltered)	OxA-X-2170-18	33,600 ± 900	41,987–34,991 40,203–35,917	This paper (Table S3); Dobosi, 2002
				<i>H. sapiens</i> Bone/antler medial point fragment (Pb.50/34) (ultrafiltered)	OxA-X-2244-32	34,890 ± 250	41,742–38,370 40,033–38,795	

disasters or AETs, as they would have more freedom to adjust their dietary sources to avoid increased competition with other displaced species.

In recent years, models of environmental Net Primary Productivity (NPP) for MOIS-3 and MOIS-2 have been created, based on pollen evidence and simulated palaeoclimatic regimes (Huntley and Allen, 2003; Allen et al., 2010). These models are for characteristic time-slices: 42 ka (“stable warm” conditions), 30 ka (less stable and cooling conditions) and 21 ka (Last Glacial Maximum conditions); they do not reflect the known climatic instability or impacts of environmental disasters and AETs in the period between 60 and 20 ka. Nevertheless, in the absence of more dynamic models, we can use such reconstructions to identify regions of higher NPP. For example, the Huntley and Allen (2003) 42 ka simulation estimates up to 600 g of carbon/m²/yr in northern Italy and the northern fringes of the Black Sea, swathes of up to 500 g of carbon/m²/yr in the Pannonian basin and southern Russian Plain, and patches of up to 400 g of carbon/m²/yr in the Ardennes, the Rhône-Saône corridor and SW France.¹ According to Belovsky (1988, p. 338), about 2% of such NPP estimates can be seen as harvestable by humans (fruits, tubers and seeds; perhaps also inner bark of certain trees (Sandgathe and Hayden, 2003)), and annual meat yields per square metre of herbivore-harvestable primary productivity are very small: 1–3 g/m²/yr (Belovsky, 1988, p. 339). MOIS-3 (42 ka) environments might thus be predicted to have yielded about 5–15 g of edible resources per square metre per year for hominin groups, perhaps creating minimal population densities of 0.2–0.3 people per 100 km² (Belovsky, 1988, p. 343). Ethnographic data published by Kelly (2013, Tables 3.1 and 7.3) suggest population densities of 0.5–1.0 people per 100 km² for mid-to-high latitude hunter-fisher-gatherer densities living in environments producing up to 100 g of carbon/m²/yr; those in areas of the same latitudes with higher NPP can have hunter-fisher-densities of between 0.1 and, rarely, over 86 people per 100 km² (Table S2). Table 7b gives us an idea of possible numbers of hunter-gatherers that could have been sustained by reconstructed NPP and harvestable NPP values across Europe for warm (42 ka), fluctuating/cooling (30 ka) and LGM (21 ka) conditions, and provides a useful comparison to population estimates made using ancient DNA (see above), archaeological sites (Tables 2 and 3) and palaeoclimate proxies (Table 4). The true population sizes in Europe in MOIS-3 probably lay above the minimal (Belovsky-derived) estimates of 0.2 people per 100 km² (Table 7b, Range 1), but more robust testing of such possibilities is needed. The NPP-derived population estimates decline over time, as the amount of productive land decreases towards the LGM. This pattern seems to contradict the archaeological record, which – notwithstanding its imperfect preservation and recovery – appears to show increasing hominin activity and populations over time (Tables 2 and 3). Thus, human occupations might have been increasingly focussed on areas of persistent/increased productivity over time. The initial *H. sapiens* dispersal into Europe, at/prior to 42 ka would thus represent low population numbers within generally productive terrestrial environments; any competition with native Neanderthal groups would vary greatly in time and space (see below).

We should bear in mind, though, that these coarse-scale productivity estimates (each grid cell is 60 × 60 km in size) do not reflect cycles of environmental productivity, incorporate aquatic resources or small-scale resource patches, or account for the probable existence of animal and plant communities for which we

have no modern analogues (Stewart et al., 2003, p. 126). Thus these productivity estimates serve only as guidance. The concept of environmental carrying capacities is largely meaningless for our analyses of late Middle and early Upper Palaeolithic demographies, especially given the frequent lack of stability in MOIS-3 environments. Instead, future research should focus on dynamic relationships between hominin and prey population densities, individual energetic efficiencies and reproduction rates (Boone, 2002, p. 22), and scales of social connections (exchange of ideas and artefacts) between scattered groups.

It is difficult to predict the extent of direct competition for resources between Neanderthals and *H. sapiens*, given the state of current knowledge. As mentioned earlier, we are not even sure if they co-existed in many of the same Eurasian regions, and population densities appear to have been relatively low overall (see also Sørensen, 2011, p. 23). While *H. sapiens* shared many terrestrial food-sources with Neanderthals, on the basis of processed faunal remains found at sites and on isotopic modelling (Fabre et al., 2011; Bocherens et al., 2014), we cannot yet quantify levels of possible food competition between the two species. Earlier suggestions that *H. sapiens* ate higher quantities of aquatic resources in comparison to Neanderthals (Richards et al., 2001; Richards and Trinkaus, 2009) might alternatively be explained as equivalent or co-varying consumption of species with similar isotopic values to fish, such as mammoths (Fabre et al., 2011). In other words, isotopic values can tell us something about the qualities of Neanderthal and *H. sapiens* diets, but not their exact components and relative proportions. Proportionality of dietary components is key here: Neanderthals and *H. sapiens* may well have consumed the same resource types, but we do not currently know if they obtained them in the same proportions. If they did eat similar quantities of the same resources, then competition would have been more direct, particularly if one or both hominin groups were specialising in particular plants or animals. Competition would have been more indirect if exploitation percentages and range of exploited species (broad versus narrow spectrum) varied.

Bocherens et al. (2014) recently raised the question of increased aridification in SW France between 31,000 and 35,000 ¹⁴C BP (~35–40 ka), which might have elevated δ¹⁵N levels in hominin and animal remains from the period. In other words, hominins might not have switched to aquatic resources, but carried on consuming terrestrial prey, which reflected changing isotopic values in the broader environment. Bocherens et al. (2014, p. 40) hypothesise that this period, around the time of the CI, might evidence a major environmental disturbance (AET, in our terminology) that benefited *H. sapiens* at the expense of Neanderthals in SW France. Contingency and localisation of effects need to be borne in mind, however, as Sepulchre et al. (2007) identify penecontemporaneous aridity in Iberia during HE4, but there is so far no evidence of clear replacement of Neanderthals by *H. sapiens* throughout that peninsula in this period (Higham et al., 2014). Müller et al. (2011, p. 278) see the rapid onset and intensity of HE5 (starting ~48 ka) as marking a turning-point in competition between Neanderthals and *H. sapiens*, but they identify different effects in particular regions: mid-latitude Europe cooled, while Mediterranean Europe became drier. These reconstructions of hominin food preferences and behavioural flexibility enable us to ask many interesting questions, but more information is needed before we can answer them satisfactorily and at relevant spatio-temporal scales.

7. Chronology and social context of innovations in organic technology

A key theme raised by many authors (e.g. Fedele et al., 2002, 2003, 2008; Bradtmöller et al., 2012) is the impact of

¹ Modelled NPP data and plots from the Stage 3 Project can be found at: <http://www.esc.cam.ac.uk/research/research-groups/oistage3/stage-three-project-databases> (accessed November 2014).

Table 8c
 Post-Cl directly-dated osseous artefacts. *Asterisked site names are open-air. Radiocarbon dates are calibrated using the CalPal2007_{HULLU} curve (two-sigma (95%) calibrated ranges) (Weninger and Jöris, 2008) – normal text – and OxCal 4.2, using the IntCal13 curve (Bronk Ramsey, 2009; Reimer et al., 2013) – italic text (95.4% confidence range).

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
42.1607°N, 2.74401°E	L'Arbreda (Spain)	Level G (later Aurignacian)		Lozangic point (B4 DB28643) (ultra-filtered)	OxA-21783	32,100 ± 450	38,447–34,603 37,332–34,991	Wood et al., 2014
51.3204°N, 2.9781°W	Uphill Quarry cave 8 (UK)	(Aurignacian)		Antler oval-sectioned point distal fragment	OxA-8408	28,080 ± 360	33,332–31,840 32,971–31,231	Jacobi and Pettitt, 2000; Jacobi et al., 2006
				Antler oval-sectioned point distal fragment (ultrafiltered)	OxA-13716	31,730 ± 250	36,240–34,908 36,184–35,056	
51.2263°N, 2.6761°W	Hyaena Den cave (UK)	(Aurignacian)		Bone/antler point	OxA-3451	24,600 ± 300	30,215–28,539 29,333–27,981	Hedges et al., 1996; Jacobi et al., 2006
				Bone/antler point (ultrafiltered)	OxA-13554	33,200 ± 1600	42,278–33,862 41,588–34,598	
					OxA-13323	30,240 ± 380	35,053–33,865 34,936–33,691	
					OxA-13803	31,550 ± 340	36,200–34,636 36,165–34,785	
44.93837°N, 1.0117°E	Abri Pataud (France)	Level 7; Trench III, sq. D (later Aurignacian)		Retouchoir on bovini femur fragment (7F6779 DIII) (ultrafiltered)	OxA-21680	32,850 ± 500	38,957–35,437 38,413–35,887	Higham et al., 2011
		Level 7; Trench III, sq. E (later Aurignacian)		Retouchoir on <i>Bos/Equus</i> femur/humerus fragment (7F6641) (ultrafiltered)	OxA-21583	32,400 ± 450	38,666–34,998 37,877–35,361	
		Level 5; rear lower, I1; trench III, sq. D (early Gravettian)		Retouchoir on medium-sized herbivore long Bone fragment (AP5FR15090) (ultrafiltered)	OxA-21585	28,180 ± 270	33,284–31,992 32,862–31,389	
45.5391°N, 0.1449°E	Les Rois cave (France)	Stratum B (evolved Aurignacian)	<i>H. sapiens</i>	Bone shaft fragment used as retouchoir	KIA-25247	28,960 ± 210	34,100–32,820 33,689–32,580	Ramirez Rozzi et al., 2009
47.5909°N, 3.7636°E	Grotte du Renne (France)	Level V (Gravettian)		Reindeer antler <i>bâton percé</i> (ultra-filtered)	OxA-21567	23,070 ± 210	28,310–27,386 27,731–26,986	Higham et al., 2010
				Reindeer antler awl (ultrafiltered)	OxA-21568	23,180 ± 210	28,316–27,676 27,769–27,107	
47.138°N, 5.571°E	Trou de la Mère Clochette (France)	Unit B: yellow, brecciated middle layer, comprising clay and blocks; 0.1–1.0 m thick (Aurignacian)		Reindeer antler split-based point wing (ochred) (ultrafiltered)	Beta-150312	29,490 ± 190	34,404–33,360 34,049–33,308	Szmidt et al., 2010
				Ochred bone awl (ultrafiltered)	Beta-150311	29,920 ± 220	34,616–33,828 34,443–33,655	
50.4781°N, 4.679°E	Grotte de la Betche-aux-Rotches, Spy (Belgium)	(Aurignacian)		Flat & triangular antler[?] [split-based?] point [may be cave bear bone] (Spy SP2, Spy 1954)	GrA-32619	32,830 +200, –190	38,630–35,694 37,621–36,276	Semal et al., 2009
50.4812°N, 3.97768°E	Maisières-Canal* (Belgium)	Champ de Fouilles, K10 (Early Gravettian)		Mammoth ivory artefact (ultrafiltered)	OxA-17962	29,060 ± 170	34,135–32,955 33,697–32,827	Jacobi et al., 2010
50.2243°N, 4.926°E	Trou Magrite (Belgium)	(Aurignacian)		Fragment of a [lozangic?] reindeer antler point	OxA-6564	25,080 ± 320	30,551–29,515 30,025–28,466	Charles et al., 2003
50.421°N, 5.294°E	Trou al'Wesse (Belgium)	From late 19 th /early 20 th century excavation spoil (Aurignacian)		Ivory Mladec point	OxA-7496 (Lyon-592)	30,750 ± 850	36,385–33,517 36,908–33,263	Otte et al., 1998
48.5603°N, 10.1913°E	Vogelherd cave (Germany)	Layer VI [Middle Pal.]		Massive-based bone point	KIA-19541	31,310 +240, –230	35,877–34,589 35,733–34,710	Bolus and Conard, 2006
48.4089°N, 9.772°E	Brillenhöhle (Germany)	Layer XIV (Aurignacian)		Massive-based bone point	KIA-19551	32,470 +270, –260	38,556–35,224 37,254–35,736	Bolus and Conard, 2006
				Split-based? point	KIA-19550[a]	30,400 +240, –230	34,982–34,126 34,814–33,967	

				Split-based? point ("rest fraction")	KIA-19550[b]	32,110 +480 –450	38,485–34,597 37,420–34,985	
51.7594°N, 10.8608°E	Hermannshöhle (Germany)	Saal: Site III		Bone/red deer antler Mladeč point (HK 63:145) [ultrafiltered]	OxA-13048	29,210 ± 210	34,265–33,045 33,849–32,907	Grünberg, 2006
48.3842°N, 9.7614°E	Sirgenstein cave (Germany)	Layer VI (Aurignacian)		Bone awl	KIA-13083	30,360 +230, –220	34,928–34,116 34,771–33,953	Bolus and Conard, 2006
		Layer V (Aurignacian)		Bone point distal fragment	KIA-13082	26,730 +170, –160	31,875–31,331 31,148–30,674	
		Layer IV (Aurignacian)		Mammoth rib tool (bone burnisher)	KIA-13081	28,400 ± 200	33,416–32,232 32,971–31,627	
		Layer III (Aurignacian/ Gravettian)		Bone burnisher	KIA-13080	30,210 ± 220	34,797–34,041 34,661–33,861	
		Layer II (Gravettian)		Bone tool (point)	KIA-13079	27,250 +180, –170	32,178–31,634 31,422–30,947	
47.5924°N, 12.197°E	Tischoferhöhle (Austria)	T 139 (Aurignacian)		Bone point distal fragment	KIA-19543[a]	32,010 +510, –480	38,393–34,433 37,347–34,850	Bolus and Conard, 2006
				Bone point distal fragment ("rest fraction")	KIA-19543[b]	31,220 +400, –380	35,971–34,399 36,016–34,445	
		T 143 (Aurignacian)		Split-based point	KIA-19544[a]	31,530 +210, –200	36,035–34,763 35,932–34,927	
				Split-based point ("rest fraction")	KIA-19544[b]	30,250 +360, –340	35,009–33,917 34,883–33,738	
		T 137 (Aurignacian)		Antler (massive-based?) point	KIA-19545	29,500 ± 200	34,417–33,357 34,071–32,293	
46.4493°N, 14.6691°E	Potočka zijalka (Slovenia)	W Section, layer 7 (Aurignacian)		Massive-based point proximal fragment; PZ 128	VERA-2526	29,560 ± 270	34,501–33,313 34,221–33,163	Rabeder and Pohar, 2004
				Massive-based point proximal fragment; PZ 126	VERA-2525	29,740 +330, –310	34,627–33,447 34,518–33,319	
				Massive-based point proximal fragment; PZ 121	VERA-2524	29,760 +330, –310	34,635–33,475 34,532–33,350	
				Massive-based point proximal fragment; PZ 112	VERA-2523	31,490 +350, –340	36,151–34,591 36,125–34,735	
		NW section, back of cave, layer 5 (Aurignacian)		Massive-based point; PZ 59	VERA-2522	30,140 +340, –330	34,887–33,855 34,778–33,688	
				Bone point distal fragment; PZ 54	VERA-2521	31,080 +370, –360	35,837–34,345 35,806–34,307	
48.6818°N, 16.1121°E	Alberndorf* (Austria)	1994 excavations: sector 1 (profile); Lfm=20/21; datum=197 (Aurignacian)		Reindeer antler "handle" (no. 1935) (ultrafiltered)	OxA-X-2191-43	30,600 ± 1300	37,693–32,321 38,441–32,039	This paper (Table S3)
					OxA-18523	28,950 ± 400	34,298–32,494 33,897–31,897	
49.707°N, 17.0167°E	Mladeč cave (Czech republic)	(Aurignacian)	<i>H. sapiens</i>	Pierced elk incisor pendant (Vienna NHM No. 72188) (ultrafiltered)	OxA-X-2185-21	>30,100		This paper (Table S3)
48.4922°N, 17.295°E	Dzeravá skala (Slovakia)	Prošek 1950 excavations (Aurignacian)		Antler [Mladeč] projectile point (ultrafiltered)	OxA-15334	31,600 ± 900	38,624–33,640 38,152–34,053	This paper (Table S3)
					OxA-15335	31,000 ± 1100	37,894–33,082 38,316–33,226	
50.16944°N, 19.80723°E	Mamutowa cave (Poland)	[1873–1881] Zawisza excavation [=levels X/ IX of Kowalski] (Gravettian)		Bone polisher (Kraków Museum 13–5) (ultrafiltered)	OxA-14435	25,560 ± 150	30,781–29,965 30,248–29,277	This paper (Table S3)
		Kowalski [1957–1974] excavations: level X or IX [Gravettian]		Worked ivory plaquette (Kraków Museum MAK/PM/ 149/1) (ultrafiltered)	OxA-14412	27,040 ± 140	32,001–31,577 31,274–30,861	
50.15397°N, 19.70503°E	Borsuka cave (Poland)	Layer VI: fresh limestone rubble within a greyish-yellow loam-	<i>H. sapiens</i>	Pendant (<i>Alces alces</i> / <i>Bison priscus</i> / <i>Bos primigenius</i> tooth) fragment	Poz-38236	25,150 ± 160	30,367–29,727 29,589–28,796	Wilczyński et al., 2012, 2015

(continued on next page)

Table 8c (continued)

Position	Site	Context	Species	Sample	Lab. no.	Date	CalBP (95%)	References
		loess matrix; 150 cm depth to bedrock. Child burial with 112 large herbivore tooth pendants at 160–220 cm (Gravettian).		Pendant (<i>Alces alces</i> / <i>Bison priscus</i> / <i>Bos primigenius</i> tooth) fragment	Poz-32394	27,350 ± 450	32,744–31,356 32,503–30,711	
49.443° N, 20.1563° E	Oblazowa cave (Poland)	Layer VIII, sector B2	<i>H. sapiens</i>	Mammoth tusk "boomerang"	OxA-3694	18,160 ± 260	22,621–21,141 22,547–21,326	Housley, 2003
		Pit XXII, sector A1		Antler point (157/88)	OxA-3695	23,420 ± 380	29,291–27,419 28,431–26,990	
		Layer VIII, sector C1	<i>H. sapiens</i>	Red deer antler wedge (222/85)	OxA-4584	32,400 ± 650	38,896–34,768 38,324–35,101	
				Bone perforator/awl (197/85)	OxA-4585	30,600 ± 550	35,726–33,870 35,731–33,726	

environmental change on technology and innovation, encouraging us to ask: to what extent is technology dictated, or even selected, by environmental fluctuations? Tables 8a, b and c bring together all direct dates on organic artefacts (wood, antler, bone and ivory) for the late Middle and early Upper Palaeolithic that are known to us. As can be seen from those tables, the application of new methods of pretreatment, such as ultrafiltration of bone/antler/dentine samples to remove more contaminants (Bronk Ramsey et al., 2004), has pushed back the ages for innovations and use of osseous tools towards 40,000 ¹⁴C BP (Fig. 6b). Fedele et al. (2008, p. 851) have argued that increased formalisation and expansion of osseous tools was seen in the period after the CI. To some extent this pattern can be seen in Fig. 6b, but that graph also demonstrates that antler projectile tip forms associated with the Aurignacian pre-dated the CI eruption. The earliest such projectiles appear to be found in eastern Europe (Pes-kő cave: Table 8a; Fig. 4), but are found in western Europe by the time of the CI (Table 8b; Fig. 4), and continue and diversify in form in the post-CI period (Table 8c; Fig. 4).

While some of the projectiles discussed in this section were made in ivory, e.g. those from Mamutowa, Maisières-Canal and Oblazowa (Tables 8b and 8c), none of those is among the earliest osseous technology (i.e. those in Table 8a), so it cannot be argued that use of sub-fossil ivory is artificially inflating the ages of these artefact-types. The single directly-dated wooden point, from Ljublansko Barje (Table 8a), was made from apparently fire-hardened yew wood (*Taxus* sp.), so it is possible that its age might be a *terminus post quem* if one assumes an old-wood effect for this long-lived tree species. Because this wooden point was found redeposited in a river bed (Gaspari et al., 2011), we cannot be sure of its original archaeological context: it might have been made by Neanderthals or *H. sapiens*. There are wooden artefacts from Mousterian (Neanderthal) sites such as Abri Romaní and Krapina (Carbonell and Castro-Curel, 1992), and Lehringen (e.g. d'Errico, 2003), probably representing a tiny fraction of the original number and formal variety of such objects, and such technology doubtless persisted into the Early Upper Palaeolithic. Aurignacian split-based point manufacture, for example, appears to have transferred techniques derived from shaping and cleaving wood to antler. Antler is a fine-grained osseous material with some capacity for flexion while being shaped (Tartar and White, 2013). Scanty evidence for the working of bone is also present in pre-CI, Neanderthal contexts, such as Salzitter-Lebenstedt, where some 30 worked bones include a single small bone point with a notched base (Gaudzinski, 1999); the assemblage is dated to between 58,000 and 48,000 ¹⁴C BP (i.e. late MOIS-4 to early MOIS-3). Small numbers of claimed bone points have been found in other Middle Palaeolithic contexts (Villa and d'Errico, 2001), but few of them show signs of extensive working, and might instead be seen as awls rather than carefully-shaped and standardised projectile tips.

Traditionally, archaeologists have used different osseous point forms to define successive essentialist epochs (see Section 4) of the Aurignacian (e.g. Peyrony, 1933), starting with the split-based (antler) forms characteristic of the "Aurignacian I", and continuing with lozangic, massive-based/Mladeč-type forms in later phases. However, it has been clear for some time that Peyrony's "type-site" for the Aurignacian succession contained combinations of different osseous point forms in some of its key layers (de Sonneville-Bordes, 1960), and thus alternative explanations for differences in osseous points were required (Davies, 2001; Szmidi et al., 2010). Direct dating of osseous points (Tables 8a–c) reveals chronological overlap between split-based and other point forms in western and eastern Europe. Thus, a modelled diachronic succession of forms (Fig. 3) needs replacement by more subtle models

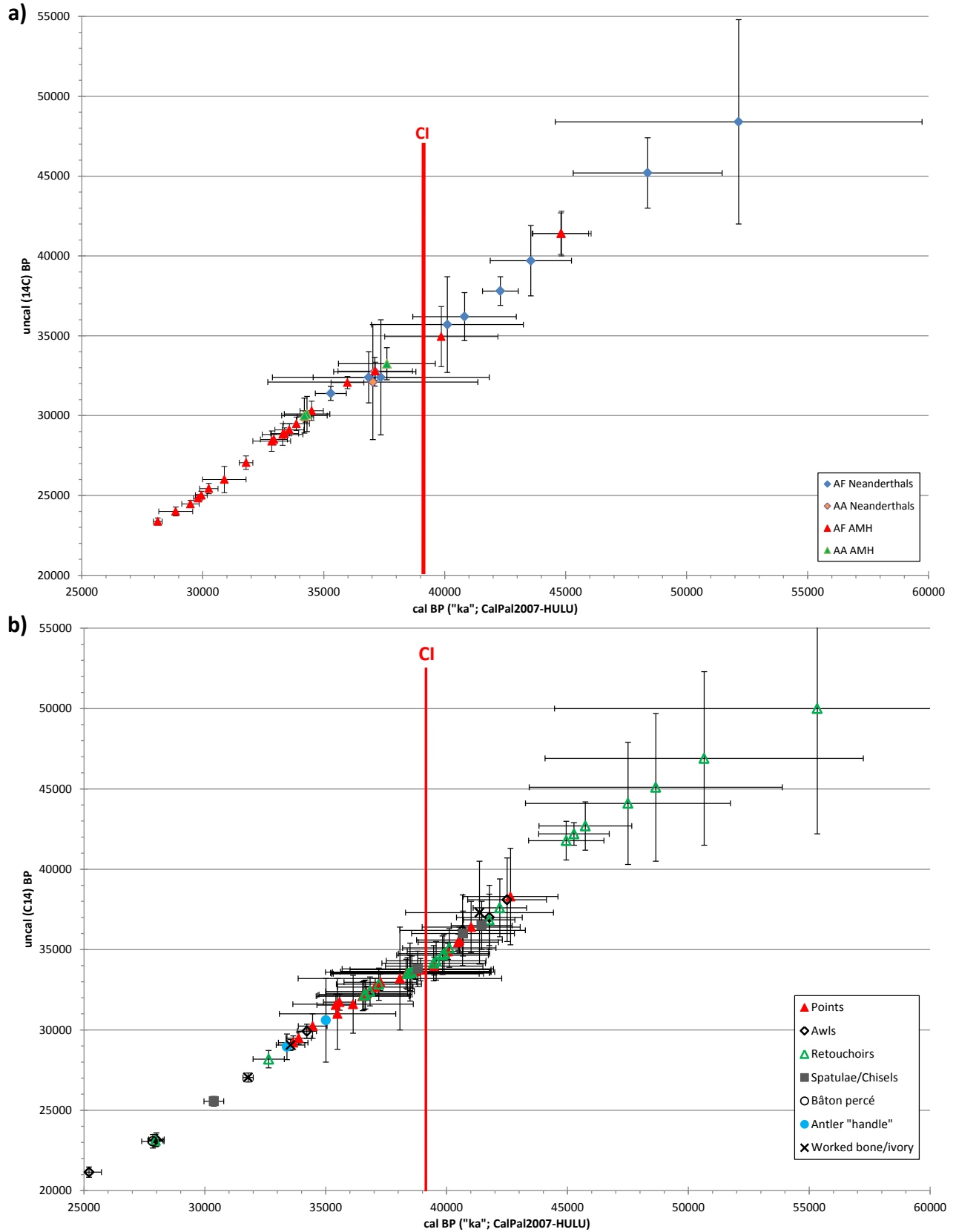


Fig. 6. **a:** Ultrafiltered ('AF') and single amino acid ('AA') AMS radiocarbon determinations on Neanderthal and *H. sapiens* ('AMH') bones and teeth. Errors (x- and y-axes) given at 95% confidence (2-sigma). Dates calibrated using the CalPal_{HULU} curve (Weninger and Jöris, 2008). **b:** Ultrafiltered ('AF') AMS radiocarbon determinations on osseous artefacts. Errors (x- and y-axes) given at 95% confidence (2-sigma). Dates calibrated using the CalPal_{HULU} curve (Weninger and Jöris, 2008).

of human responses to different raw material types (antler versus ivory) and functional requirements.

Tartar and White (2013) have sought to explain why carefully-shaped osseous points might have gained popularity in the Aurignacian, and thus evaluate the idea that lighter projectile weapons allowed, or even favoured, individual hunting practices among Aurignacian people (*H. sapiens*), rather than the close-encounter (group-dependent?) killing permitted by the heavy-duty thrusting spears of the Middle Palaeolithic (Neanderthals and *H. sapiens*). Standardisation of osseous point forms in the Aurignacian permits a variety of economic approaches to hunting, though probably most focussed on specialism (expression of active ecological preferences, and prey selection) and versatility (flexible ecological preferences expressed across environmental cycles; technology adaptable enough to be used for a range of medium-to large-sized prey taxa) (cf. Potts, 1996, 1998). This hypothesis requires further experimental testing, using replica artefacts to measure efficiency in different contexts.

Direct dating of diagnostic artefacts has allowed us to re-assess the validity of archaeological “assemblages” first constructed in the 1860s by archaeologists that had no other means of analysing chronology in the Palaeolithic. When the Mladeč *H. sapiens* remains were directly dated to between ~34 and 36 ka (Table 6c), it was not certain that the associated perforated animal teeth were chronologically associated with them, particularly as they included taxa from a variety of habitats. While it was not possible to extract enough collagen from the dentine of perforated beaver and bear teeth, one perforated tooth (cf. *Alces* sp.) yielded enough collagen from its dentine to give an age of >30,100 ¹⁴C BP (OxA-X-2185-21) (Table 8c and S3), implying it was penecontemporaneous with the dated hominin teeth (Table 6c), and thus likely to be associated. Results such as these allow us to re-combine directly-dated organic elements into new associations, if necessary, and give us more confidence in identifying, measuring and testing Upper Palaeolithic innovative responses to environmental change. Not all organic tools are as widespread as the various osseous point forms; some osseous artefacts appear to have been temporally and regionally specific, e.g. the antlers modified as handles (for holding lithic tools?) from the sites of Alberndorf (Table 8c) and Willendorf II. Direct dating of organic artefacts thus permits linkage and testing of different scales of spatio-temporal patterning in traces of human behaviour to the broader tephrochronological lattice.

8. Time-transgressive patterning in changes seen in the archaeological record

It is clear that the tephra deposits that rained down on eastern Europe and the Levant were not falling on a homogeneous hominin world (Fig. 5). The WP-1 tephrochronological lattice has revealed no clear demarcation of human species or cultural epochs; instead, a mosaic pattern of cultural heterogeneity, of varying spatial extents at a given isochron, has been demonstrated. The challenge of this section is to set out ways we can quantify and qualify this mosaic. Direct dates on organic artefacts tend to tell us most about smaller-scale changes in behaviour (Davies, 2012), especially when combined with technological and morphometric analyses of the dated artefacts. We can identify modifications of established forms (and raw material economisation, through the re-working/recycling of organic artefacts), as well as the replacement of one specific artefact form with another, but it is difficult, if not impossible, to demonstrate wholesale replacement of an entire toolkit with another using direct dating alone (most Palaeolithic tools are difficult to date directly). Archaeologists need to analyse assemblages at all available scales, from individual tool morphologies and manufacturing techniques to patterns across wide geographic

areas, and our chronometric techniques need to be able to allow us to do that.

Multiple chronological methods (used comparatively) are required to plot hominin responses over time and space to AETs and environmental disasters. Direct dates on diagnostic organic artefacts give us insights into changes in preferred forms and manufacturing techniques (innovations and inventions), but these need to be nested within broader environmental chronological lattices (such as those from tephra), for which direct evidence has been found in both archaeological sites and palaeoenvironmental records. As can be seen from Fig. 6b, several bone point dates (plus those on less diagnostic tools, such as retouchoirs and awls) long precede the CI. Some manifestations of osseous technology, such as eyed needles, have not been directly dated. Nevertheless, on tephrochronological evidence (Golovanova et al., 2010 (including comments by Hoffecker)), the earliest such tools are found in parts of eastern Europe (Kostenki and Mezmaiskaya) between 40 and 35 ka (using a tephra lattice). We have no evidence for needles further west in Europe at this date, but instead other artefact types are (locally) typical, e.g. the antler “handles” from two Austrian open-air sites. It must be noted that many direct dates on osseous artefacts derive from regions with conditions conducive to preservation of collagen, and this means that our chronological analyses of organic artefacts in, for example, southern Italy (the proximal zone of the CI) are unable to combine tephrochronology with other dating methods. These biases cannot be avoided at present, and should ensure that we do not generalise beyond the available spatio-temporal scales of our evidence.

The occurrences of dated behaviours and preferences that we can identify encourage us to consider mobility and regionality in the later Palaeolithic. Insights derived from proximal and distal impacts of volcanic eruptions can help us to define possible hominin responses to such disasters. White and Pettitt (2011, pp. 77–82) have developed the concept of Local Operational Areas to evaluate the presence or absence of apparent connections between clusters of contemporaneous sites. Many of their Middle Palaeolithic British Local Operational Areas are between 100 and 140 km apart. These distances/radii are similar to the distances discussed in Section 6, above: it might therefore be conceivable that some hominin groups were able to move ~150 km away from the maximum-impact proximal zone of the CI, but much would depend on how widespread the impact was on environments in the intermediate zone between proximal and distal ones. Habitat tracking would have been practised anyway by hominin groups, as MOIS-3 environments would not have remained exactly consistent over decades or centuries. Impact on groups fortunate enough to be in a position to escape the direct dangers of an eruption would depend on (1) their knowledge of landscapes beyond their main ranges and (2) their social connections to groups in those more distant regions. Groups with long-distance networks would have increased chances of knowing where to retreat in the landscape, as long as their connections were in the distal, rather than proximal, zone of the environmental disaster.

The ability to be versatile and flexible (see above) in diet (as well as in modes of response to the environment), rather than specialist, would confer an advantage on hominin groups outside the immediate (proximal) impact zone of environmental disasters; a reliance on preferred species would not prevent them from knowing how to exploit a broad range of (secondary) species. Several researchers have argued that dispersing *H. sapiens* would have adopted a versatile approach to resources, targeting a variety of species (O’Connell, 2006), and perhaps focussing on biomes with the most diversity (Davies, 2001). The main ecological effect of AETs and environmental disasters would have been to obscure or rearrange spatial patterning of biomes, with only those most sheltered being

able to remain *in situ*. In or near the proximal zone, any environmental spatial structure would be obliterated, at least in the case of large volcanic eruptions, and even outside this zone the mosaic structure of the environment is likely to have become more homogeneous, with only the more tolerant species surviving.

It is essential to consider how long-lasting the effects of AETs and environmental disasters might have been. Fedele et al. (2008, p. 848) preferred centennial scales for these environmental perturbations, meaning that in their model the CI was an AET rather than an environmental disaster (which would have lasted for years or decades before its effects were reversed). Hominins might have been able to tolerate even major environmental perturbations as long as they had the means to sustain themselves (surviving resource species and social support networks that extended into less-affected regions), and as long as the major impact was short-lived. Effects that persisted for more than a few years might require re-evaluation of responses. If such conditions cannot be met, the regional extinctions of vulnerable hominin populations are the likeliest outcome (Hublin and Roebroeks, 2009; Bradtmöller et al., 2012).

Much recent research has revealed essentially localised movements of Neanderthal groups, based on resources collected and also on their likely energy budgets. Physiologically, Neanderthals are likely to have had higher Daily Energy Expenditures than *H. sapiens*: 3500–5000 kcal per day, as opposed to 3000–4000 kcal per day for modern circumpolar male fisher–hunter–gatherers (Hublin and Roebroeks, 2009, p. 505). In addition to this higher basal metabolic rate, Neanderthal physiology rendered mobility round the landscape more costly (Verpoorte, 2006), perhaps explaining why many persistent Neanderthal occupation regions were in dissected terrain, with fine-grained mosaics of different biomes close together. By placing themselves at the intersections of many biome types (i.e. on the ecotones), Neanderthals would have been able to minimise their mobility and resource transport costs. The apparent ability of *H. sapiens* to move longer distances more efficiently, together with the increased ability for long-distance social networks that could bestow, would have enabled them to be more versatile in resource exploitation. They would also have been less susceptible to isolation of groups (implied in Neanderthals by evidence for inbreeding and low genetic diversity). Development of lightweight hunting equipment, such as osseous projectile tips, would have allowed greater flexibility in hunting strategies.

The model developed by Fedele et al. (2008) allows us to address many of the above issues, but it is clear that it needs more explicit theoretical definition of impacts on ecosystems and biogeography before the CI can be clearly connected to hominin ecologies. We are a long way from being able to define, let alone test, the “mal-adaptive solutions” they discuss (p. 850), and more biogeographical modelling is required before we can assess what “crowding” might mean in generally low hunter-gatherer population levels and densities. AETs and environmental disasters need to be seen in a more dynamic sense, as Fedele et al. (2008) emphasise, but they also need to be set in a broader context of environmental cyclicality (many of these cycles operating at different spatial and temporal scales).

9. Conclusions

There are no clear correlations between either turnover of hominin species or organic tool-type innovations and AETs/environmental disasters. The effects of AETs and environmental disasters are easiest to define and identify in proximal zones, as their impacts are strongest and relatively homogeneous. In distal zones, however, their effects are more heterogeneous and less clearly-

defined, with topography and local conditions exerting strong mitigating or cancelling effects in many locations. Our challenge is to define the boundaries between proximal (consistent, graded) and distal (inconsistent, mosaic) effects (Table 7a), as well as to find extensive evidence of volcanic eruptions in Europe west of Italy (the apparent lack of CI tephra across the whole of Europe dictates how the impact of AETs and environmental disasters can be measured in different regions). It is clear that necessity was not the mother of invention, as far as organic projectile technology was concerned; such technology arose before the CI environmental disaster, and developed in the period immediately afterwards (Tables 8a–c; Fig. 6b), while directly-dated Neanderthals imply that their population decline had begun long before the CI. Population levels of both Neanderthals and *H. sapiens* appear to have been low during our chosen study period (Tables 2–4, 7a and b), but the genetic diversity patterning of Neanderthals implies that they were operating within even more restricted social and mating systems than our ancestors. Archaeologists might well explore concepts of continuous variation in the production of artefact forms; using direct dating (where possible), technological and morphometric analyses to test whether selection (social, ecological, or both) operated on this variation to generate preferred morphologies (Davies, 2012).

This paper has combined the results of RESET WP-1 with other recent chronological data on hominin species and organic artefact forms, to evaluate the possible contributions that multiple strands of dating evidence can make to Palaeolithic archaeology, particularly in the sphere of hominin responses to environmental change. At present, the recovery of visible and cryptic tephra by WP-1 has only met success in the eastern Mediterranean and inland eastern Europe; our tephrochronological lattice therefore does not cover the whole of Europe. Any conclusions drawn must therefore be tentative and show awareness that a widespread tephra marker horizon is not yet available in western Europe (Fig. 2). Detailed chronology for the latter region is currently only possible using direct radiocarbon dating of diagnostic artefacts and hominin skeletal remains. It is thus difficult to attribute Neanderthal extinction in western Europe to a clear AET or environmental disaster at present. Tephra isochrons, where present, allow the correlation of environmental proxy records with archaeological assemblages, as they can appear in both, while direct dates on organic artefacts give indications of shifts in technology and technique within that broader framework. However, we are only just beginning to be able to make such correlations; not only do we need to integrate our chronometric and technological analyses more closely (rather like directly dating bones sampled for ancient DNA), we also need to have firmer conceptions of palaeoecology.

Palaeoecological modelling should include not only presence/absence of species and their spatio-temporal combination in Pleistocene sites, but where they might have come from in the landscape. Concepts such as nutriscares (Brown et al., 2013), evaluating where key food types might be found in a given landscape, could help us bridge the gap between reconstructed Net Primary Productivity values for the late Pleistocene (e.g. Huntley and Allen, 2003; Allen et al., 2010; Huntley et al., 2013) and the animal and plant resources found on Palaeolithic sites. How does the latter evidence match our modelled predictions of what was available in the surrounding landscape, and at what distances? Reconstructing hominin occupation densities in the landscape, and metapopulation levels more generally, using environmental productivity indicators can give a sense of how many people a biome might have sustained, but we need other lines of evidence to evaluate *how* human groups exploited those resource capacities, and at what levels of intensity. In addition to matching types of exploited fauna and flora found at archaeological sites to simulations of NPP, we also need to have a

better understanding of Upper Pleistocene ecologies (species combinations and distributions in time and space). Such an understanding is a prerequisite for modelling the impact that AETs and environmental disasters had on Upper Pleistocene ecologies (e.g. Huntley et al., 2013), let alone on the contemporary hominin behavioural responses (e.g. Fedele et al., 2008; Bradtmöller et al., 2012). Isotopic studies of teeth and bones from dated hominins and their prey species would help us to address questions of mobility and resource patterning in environments inhabited by late Neanderthals and early *H. sapiens*. Such analyses (e.g. laser-ablation on teeth to track fine-grained movements of animals/hominins during the growth of the teeth) are in their infancy, and we should not delude ourselves that our methodologies can be transformed overnight. Nevertheless, the combination of these isotopic techniques, designed to address questions of mobility and possible dietary sources, will help archaeologists to develop new methods of palaeoecological analysis when combined with chronological lattices and directly-dated hominins and organic artefacts.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2014.12.003>.

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