Quaternary Science Reviews 319 (2023) 108307

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Invited paper

Close encounters vs. missed connections? A critical review of the evidence for Late Pleistocene hominin interactions in western Eurasia

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ARTICLE INFO

Handling Editor: Danielle Schreve

ABSTRACT

Recent advances in the study of ancient DNA recovered from fossils and cave sediments have profoundly changed our views on the biological and cultural interactions between populations and lineages of fossil *Homo* in the Later Pleistocene of Eurasia. A spatiotemporally complex picture emerges, with multiple population admixture and replacement events. Focusing on the evidence from Western Eurasia, we consider here how the mapping out of between-species interactions based on fossil and material cultural evidence is being replaced by a broader approach. Traditional narratives about human migrations and the biological and/or cultural advantages of our own species over the Neanderthals are now giving way to the study of the biological and cultural dynamics of past human populations and the nature of their interactions in time and space.

1. Introduction

In this paper we review current evidence regarding the interactions that appear to have taken place between hominins derived from different lineages (typically ascribed to Neanderthals and Modern Humans), particularly in the critical and well-studied contact areas of western Eurasia, and provide a biocultural framework for such interactions and their outcomes. In our opinion, recent advances have generated a large volume of literature from different disciplines which needs to be brought together. This paper is an attempt to provide such a synthesis.

The prevalent view holds that Modern Human-Neanderthal contact resulted in complete population replacement. Specifically, in Europe – the best-documented region, the extinction of Neanderthals and the successful colonization of the continent by Modern Humans is thought to be due to biological or ecological advantages of our own lineage (Stringer and McKie, 1996; Klein, 2001; Banks et al., 2008; Flores, 2011; Tattersall, 2012; Gilpin et al., 2016; Goldfield et al., 2018; Roberts and Bricher, 2018). Such advantages were frequently associated with differences in cognitive capacities (Tattersall, 1998; Henshilwood and Marean, 2003; Gibson, 2007; Marean, 2007), initially proposed to stem from a single genetic mutation (Klein, 2000). Later attempts to understand the nature of Neanderthal-Modern Human interactions have offered a range of alternative mechanisms (Horan et al., 2005; Bocquet-Appel and Degioanni, 2013; Serva, 2015; Wakano et al., 2018; Degioanni et al., 2019; Greenbaum et al., 2019). More recent versions have also attempted to take other factors (e.g. random events or climate fluctuations) into account, in varying degrees (Finlayson, 2004; van Andel and Davies, 2004; Finlayson, 2005; Finlayson and Carrión, 2007; Finlayson, 2008; Jennings et al., 2011; Müller et al., 2011; Sørensen, 2011; Stewart and Stringer, 2012; El Zaatari et al., 2016; Timmermann et al., 2022; Kolodny and Feldman, 2017; Shultz et al., 2019; Melchionna et al., 2018; Staubwasser et al., 2018; Wolf et al., 2018; Timmermann, 2020, Timmermann et al., 2022; Bicho and Carvalho, 2022; Vahdati et al., 2022; Zeller et al., 2023; Ruan et al., 2023; Margari et al., 2023).

Overall, these studies suggest that we likely have underestimated the spatiotemporal complexities of human range expansions and contractions. Range expansions would have been part of a continuum of varying extent (Groucutt et al., 2021), with local and regional extinctions, subsequent range expansions and even back into areas settled in previous expansions (e.g. Timmermann and Friedrich, 2016; Ruan et al., 2023)

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https://doi.org/10.1016/j.quascirev.2023.108307
Received 13 February 2023; Received in revised form 2 September 2023; Accepted 6 September 2023
Available online 29 September 2023
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and also back into source areas (Chen et al., 2020; Wang et al., 2023). In areas of contact between expanding and established populations, the outcome would have been determined by a range of variables including time and degree to which the meeting populations had been previously isolated, and hence the degree of genetic, phenetic and behavioural isolation, the densities of the two populations relative to environmental carrying capacity and the degree of ecological isolation (Finlayson, 2004; Sanchez-Quinto and Lalueza-Fox, 2015; Lalueza-Fox, 2021; Vahdati et al., 2022; Ruan et al., 2023). It is now clear that, within the same site, different populations representing different lineages of hominins occupied and re-occupied and alternated with each other. In the case of Mandrin Cave in the Rhone Valley, France, Neanderthals and Modern Humans even alternated occupation and Neanderthals were in the cave before and after Modern Humans (Slimak et al., 2022). These conclusions were derived largely from lithic evidence, with some palaeontological support. At Denisova Cave in the Altai Mountains, Neanderthal-Denisovan population turnover was inferred from analysis of ancient DNA (aDNA) in sediment, with a final layer of Modern Human occupation (Zavala et al., 2021). At Galeria de las Estatuas in Atapuerca, Spain, sediment aDNA indicated a major Neanderthal population replacement event at around 120 ka (thousand years ago) (Vernot et al., 2021).

In spite of the large number of publications on the subject of the outcome of Neanderthal-Modern Human contact, we are nowhere nearer to having a clear picture of the causes of the presumed disappearance of the Neanderthals. Models provide a range of possible scenarios, dependent on the model structure and the data used to constrain the model parameters. Scenarios range from a direct Modern Human intervention to climatic and random factors, or a mix of these (Timmermann and Friedrich, 2016; Kolodny and Feldman, 2017; Shultz et al., 2019; Melchionna et al., 2018; Staubwasser et al., 2018; Wolf et al., 2018; Timmermann, 2020; Timmermann and Friedrich, 2016; Bicho and Carvalho, 2022; Vahdati et al., 2022). The only conclusion that we can draw from this motley group of disparate schemes is that it is possible to explain the empirical pattern – namely the disappearance of the Neanderthals – with a multitude of factors and processes, both with and without the need of Modern Human interaction.

2. Paleotaxonomy and the advent of paleogenomics

The use of species concepts in paleoanthropology is notoriously difficult and has plagued the Neanderthal-human debate since its beginnings (for recent reviews, see Meneganzin and Bernardi, 2023; Nowell, 2023). The conflict that exists between species definitions and the evolutionary process of speciation (Box 1) results from the absence of time-depth in the Biological Species Concept (Mayr, 1963), but it can be dealt with if we replace the notion of species by that of lineage. Wiley's (1978) adaptation of Simpson's (1961) Evolutionary Species Concept addresses the issue of polytypic species in the fossil record while retaining the criterion of reproductive isolation (Wolf et al., 2018). Essel et al. (2023) definition states:

> "A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate"

Since the advent of paleogenomics, the focus of discussions about Neanderthal-human interactions has shifted from species competition to lineage histories and population dynamics. Recent advances in ancient DNA (aDNA) extraction and analysis reveal an intricate pattern of admixture events between human and Neanderthal lineages, and more generally with lineages of archaic *Homo* such as the "Denisovans" and hypothetical "ghost species" (Reich et al., 2010; Abi-Rached et al., 2011; Rasmussen et al., 2011; Skoglund and Jacobsson, 2011; Mendez et al., 2012, 2013; Meyer et al., 2012; Wall et al., 2013; Huerta-Sanchez et al., 2014; Prüfer et al., 2014; Fu et al., 2015; Qin and Stoneking, 2015; Sanchez-Quinto and Lalueza-Fox, 2015; Kuhlwilm et al., 2016; Posth et al., 2017; Slon et al., 2018; Wolf and Akey, 2018; Mafessoni, 2019; Petr et al., 2020).

The currently available aDNA evidence thus suggests that admixture events have been frequent among human populations in the Pleistocene, although this claim has not remained unchallenged given its dependence on underlying model assumptions (Tournebize and Chikhi, 2023).

This leads us to the next problem – how do we detect hybrids in the palaeontological and archaeological records?

3. Lineages and hybrids in the fossil and archaeological records

While the population-level outcomes of individual encounters between groups belonging to different *Homo* lineages remain unknown, the existence of first-generation hybrids within the genus *Homo* is now indisputable (Slon et al., 2018). Identifying hybrids on morphological grounds from human remains from Pleistocene sites is a different matter altogether. While palaeogenetics can study thousands of independent discrete traits (such as single-nucleotide polymorphisms) with ancestor-descendant polarity, paleo-phenetics has to content itself with comparatively few preserved skeletal traits. Moreover, most of these traits are continuous rather than discrete, they vary within paleopopulations, depend on each other through morphological integration and do not exhibit clear phyletic polarity. Many hybrids are thus likely to remain undetected on morphological grounds. What may be potentially detectable are cases where phenotypic differences between the parent lineages are clearly visible (e.g. as between Neanderthals and Modern Humans), and the hybridization event is only few generations back in time, thus preserving a sufficiently strong phenotypic signal. A number of such claims have been made for a number of specimens on the basis of morphological features regarded as intermediate, particularly between Neanderthals and Modern Humans, (Duarte et al., 1999; Soficaru et al., 2006; Rougier et al., 2007; Condemi et al., 2017; Smith et al., 2015; Hublin et al., 2017; Li et al., 2017; Harvati et al., 2019). The mandible from Peştera cu Oase is a good example of postulated admixture based on morphology (Trinkaus et al., 2003) subsequently supported by genomic data (Fu et al., 2015). Some of these cases have been disputed (e.g. Tattersall and Schwartz, 1999; Zilhao and Trinkaus, 2002), in itself a reflection of our ignorance of what a hybrid in the genus *Homo* should or could have looked like (but see Harvati and Ackermann, 2022).

Our inability to clearly define Pleistocene Modern Human fossils on the basis of morphology, or to agree on what hybrids might look like when found, creates a problem when it comes to attempting to interpret the palaeontological data. Are taxonomic attributions of specimens, based on small (often single) samples which give us practically no information of population variation (Douka et al., 2013; Benazzi et al., 2011, 2015; Gicqueau et al., 2023), robust enough to enable us to map, for example, a picture of the spread of Modern Humans and the range contraction of Neanderthals? Clearly, they are not. We may, however, contrast this difficulty with the positive effect of paleogenomics (Box 2), with even single ancient genomes providing substantial information on population size fluctuations and admixture events (Chen et al., 2019; Zhang et al., 2020).

How certain can we be that some or all of these taxonomic allocations, currently done on the premise that they must be either Neanderthal or Modern Human, might not be mistaken and that individuals that are hybrids are being overlooked? In some cases, the specimens are classified even though they may show mixed and conflicting evidence, as in the case of the Kent's Cavern maxilla which was claimed to have Modern Human and Neanderthal traits and other traits which were ambiguous, but was nevertheless reported as the earliest evidence of anatomically Modern Humans in northwestern Europe (Higham et al., 2011). We should be particularly wary of taxonomic attributions based on continuous (metrical) rather than discrete traits. For example, teeth are often characterized by morphometric traits, which reveal statistically significant differences between taxon-specific mean values (Bailey et al., 2009; Benazzi et al., 2011; Moroni et al., 2013; Zilhao et al., 2015), but overlap between taxon-specific distributions, such that single fossil specimens cannot be assigned with any certainty to one or the other taxon. Until such time as we are able to allocate specimens with certainty, and we clearly cannot do so today (although we may even be able to do so in isolated cases using evidence additional to morphology such as aDNA and palaeoproteomics) we should not use them to map past human distribution patterns and dispersals (Hublin, 2015). If we attempt to do so with the few (considering number of specimens in the timescales involved) that may be securely attributable (mostly Neanderthals), the outcome will be a highly fragmented and undoubtedly preliminary picture.

4. Lithics, culture and hominin lineage attribution

When archaeologists attempt to map human distribution in the Palaeolithic, they organize their observations about the lithic evidence in terms of stone tool industries (Shea and Bar-Yosef, 2005). This is largely because of the paucity of fossil material available compared to the much richer lithic record. Lithics are used as proxies for hominin taxa. The most commonly-cited stone tool industries group together stone (and sometimes bone) artefacts excavated assemblages from multiple sites. Some less-well-known industries appear at one site only. In an odd practice that assumes correlation between culture change and sedimentation, archaeologists assign stone tools from a single sedimentary deposit to a single industry only. Practices for defining new industries vary, but in principle they require those proposing new ones to identify artefact-types and toolmaking strategies that differ from industries already recognized in the same region and/or time period. In practice, a newly-identified industry's recognition, acceptance, and use depends on appeals to authority and various national research traditions.

Named stone tool industries first appear in 19th century archaeological writing as universal stages of human cultural evolution, but their number increased dramatically as 20th century archaeologists increasingly sought entities with which to describe histories of prehistoric culture change, or “prehistory” (Shea and Bar-Yosef, 2005). When industries appear in prehistory, they do so as proxies, or “stand ins” for groups of people, the functional equivalent of ethnographic cultures. Many archaeologists dispute such equations, of course, either for specific industries or in general, but this is how students use industries in current debates about replacement versus continuity among Late Pleistocene hominins. Descriptions of excavated Pleistocene-age European and western Asian stone tool assemblages that do not assign those assemblages to one or another prehistoric industry remain uncommon.

Archaeologists customarily identify Late Pleistocene industries from Europe, western Asia and North Africa as either Upper Palaeolithic (UP), Middle Palaeolithic (MP) or MP/UP Transitional age-stages (papers in Bar-Yosef and Pilbeam, 2000). Most of the differences between MP, UP, and MP/UP industries reflect greater or lesser proportions of fracture products detached from “Levallois” cores (bifacial hierarchical cores) or from “prismatic blade cores” (elongated unifacial hierarchical cores). Levallois products are more common in MP assemblages, prismatic blades more common in UP assemblages. MP/UP Transitional industries vary widely in this respect. Archaeologists consider retouched artefacts more culturally diagnostic than unretouched ones. Short oval “sidescrapers” and thick triangular “points” characterize MP assemblages, while narrower “end scrapers” and backed/truncated pieces more commonly appear in UP assemblages. MP/UP Transitional assemblages may combine such artefacts, due either to stratigraphic mixing or to actual variation in stone working. Long core-tools (“handaxes” and allied tool forms) appear in some MP assemblages, while thin “foliate” (leaf-shaped) points in some MP/UP Transitional and UP assemblages. Carved bone, antler, and ivory artefacts including perforated beads occur in many UP assemblages, but such artefacts rarely appear in MP ones. Whereas archaeologists often assign assemblages from vast areas to either MP or UP industries, those they assign to MP/UP Transitional assemblages have more restricted regional distributions. In spite of these major problems of taxonomic attribution, the reality is that the presumed pattern of replacement of Neanderthals by Modern Humans in Europe, in the absence of sites with human remains, has been largely inferred from archaeological sites (Bar-Yosef and Pilbeam, 2000; Hublin, 2015).

In many cases, the evidence linking human taxon with technology is supported by a small number of sites where human remains attributed to either Neanderthals or Modern Humans have been associated with a particular stone tool technology. This is a dangerous practice which is flawed as it assumes that particular human taxa are exclusively linked to particular technologies, which they are not (Shea, 2016). There is no *de facto* reason why different human taxa should not be able to produce the same technology, especially if cultural exchanges occurred at times of genetic exchange and technologies were the product of ecological circumstances (Finlayson and Carrión, 2007). The problem is compounded by our absence of knowledge of which technologies were associated with hybrids.

In Table 1 and Fig. 1 we illustrate the current panorama that sets out the Middle to Upper Palaeolithic transition in Europe and the Middle East, which is generally equated to the replacement of Neanderthals (associated with Middle Palaeolithic industries) by Modern Humans (associated with Upper Palaeolithic industries). The process of replacement is assumed to commence in the Middle East, with populations of Modern Humans of presumed African origin, with a subsequent east-west spread across Europe (Bar-Yosef and Pilbeam, 2000; Hublin, 2015). The narrative is typically displayed as maps of spread with arrows pointing the direction of movement. Such maps, based on stone tool industries as proxies for human taxa, are generally inaccurate as they assume that each industry equates to a specific sort of hominin. The degree of certainty of attribution is, at best, based on few sites in which the hominin-industry link has been established or is claimed to have been established (Table 1).

In the majority of cases the links themselves are tenuous as they rely on single or very few specimens or sites, juvenile specimens, teeth (which we have seen are susceptible to unexpected variation in primate hybrids), artefacts made from bone or teeth (Essel et al., 2023), sites of questioned stratigraphy and dating (Table 1 and references therein). The recent case of Bacho Kiro in Bulgaria (Hublin et al., 2017) would have appeared to have pinned this particular, and localized, Initial Upper Palaeolithic Industry firmly to Modern Humans but even these have now been shown to have had Neanderthal ancestors a few generations back in their family history (Hajdinjak et al., 2021, Box 2). Evidence linking the Protoaurignacian to Modern Humans has been provided by Benazzi et al. (2015) but, though suggestive, it does not guarantee that this industry was made exclusively by Modern Humans (Box 3).

How do these industries help us understand Neanderthal and Modern Human interactions? Not very well. No prior theory suggests that they correspond to self-conscious social groups such as ethnographic “cultures.” That some of them persist, minimally variable for thousands of years and across thousands of kilometres suggests named stone tool industries are virtually the *opposite* of actual ethnographic cultures. Actual cultures change rapidly and vary widely over time and space (e.g. Flegontov et al., 2019). Dividing hominins into conjectural social groups based on their lithic litter makes no more sense than dividing and grouping living humans based on the kinds of pens and pencils that appear in their trash cans.

Using industries to investigate Neanderthal versus Modern Human evolutionary relationships may actually create more problems than it solves. Archaeologists refer industries to one or another hominin based on fossils found in the same sediments with the stone artefacts assigned to them. Some of these fossils appear to be deliberate burials, but many more are isolated teeth, maxillary and mandibular fragments, and finger or toe bones. Whether or not one can credibly assign such isolated fragments to one hominin or another depends on the bone in question

Table 1
Distribution of stone tool industries, their association with hominin taxa, chronology and geographic distribution for Europe and the Middle East in the period 50–30 ka. Stone Tool Industry and Age-stage follow Shea (2016).

Stone Tool Industry	Age-stage	Hominin	Date (ka)	Geography	Remarks
Neronian	IUPal	Modern	52–57	France (Mandrin Cave).	Slimak, et al. (2022) Neronian layers between otherwise Mousterian ones.
Late Levantine Mousterian	MPal	Uncertain. Assumed Neanderthal	43–42	Levant (Ksar Akil)	Dates have been presented at one standard error (Douka et al., 2013).
Late European Mousterian	MPal	Probably Certain. Assumed all Neanderthal	41-39 (37)	Western Europe	Higham et al. (2014). Extended to 37 ka for Iberia (Zilhao et al., 2017). Late dates of 32 ka at Gibraltar (Finlayson et al., 2006) are currently under re-examination.
Bohuncian	IUPal	Uncertain. Assumed "Modern"	50–46	Czech Republic	Retains MPal features but not considered transitional (Kuhn, 2003). (Richter et al., 2009).
Bachokiran	IUPal	Modern	47–44	Bulgaria	Fewlass et al. (2020); Hublin et al., 2017
Initial Upper Palaeolithic, Turkey	IUPal	Uncertain. Assumed "Modern"	45–39	Turkey	Hominin attributions few and unclear (Ewing, 1963; Gleń and Kaczanowski, 1982; Metni, 1999; Yazbeck, 2004; Kuhn et al., 2009). Dates have stratigraphic issues (Kuhn et al., 2009) or have been presented at one standard error (Douka et al., 2013). 50 k estimate, from TL dates of 48.2 ± 1.9 ka for Bohunice (Richter et al., 2009).
Emiran	IUPal	Uncertain. Assumed "Modern"	(50)45-36	Levant	Dates (Marks, 1983) require revision (Hublin, 2015). Dates 45–36 ka from Stutz et al. (2015).
Szeletian	"Transitional" MPal/UPal	Uncertain.	48–44	Czech Republic, Hungary	Gábori-Csánk (1983); Kaminská et al. (2004). Nigst (2012).
Uluzzian	"Transitional" MPal/UPal	Uncertain. Now Assumed "Modern"	45–40	Italy, Greece	Palma di Cesnola and Messeri (1967); Churchill and Smith (2000); Benazzi et al. (2011), 2014; Banks et al. (2013); Ronchitelli et al., 2014 Douka et al. (2014)
Châtelperronian	"Transitional" MPal/UPal	Uncertain. Assumed Neanderthal	44–40	Spanish Basque Pyrenees, southwest and central France	Leroi-Gourhan (1958); Hublin et al. (1996), 2006; Bailey and Hublin, 2006 a & b; Bailey et al. (2009); Bar-Yosef and Bordes (2010). Higham et al. (2010); Hublin et al. (2012).
Lincombian-Ranisian-Jerzmanowician (LRJ)	"Transitional" MPal/UPal	Uncertain	43–40	Southern United Kingdom, Belgium, Germany, Poland	Hublin (2015). Kozlowski (2002); Cooper et al. (2012); Flas (2011)
Ahmarian	UPal	Uncertain. Assumed "Modern"	48–40	Levant, Turkey	Juvenile ("Egbert") lost but claimed to be "Modern" (Bergman and Stringer, 1989). Rebollo et al. (2011); Douka et al. (2013) (dates have been presented at one standard error)
Kozarnikian	UPal	Uncertain	43–41	Bulgaria	Guadelli et al. (2005).
ProtoAurignacian	UPal	Possibly Certain. Assumed all "Modern"	42–38	N. Italy, S. France, N. Spain	Benazzi et al. (2015). Szmidt et al. (2010); Douka et al. (2012).
Early Aurignacian	UPal	"Modern" and Uncertain	44–35	Austria, Germany, Italy, France, Slovakia, Russia, Portugal	Hublin (2015). Haesaerts et al. (1996); Higham et al. (2012) (dates have been presented at one standard error); Nigst and Haesaerts (2012); Nigst et al. (2014).
Levantine Aurignacian	UPal	Uncertain	38–34	Middle East	Alex et al. (2017)
Later Aurignacian	UPal	"Modern" and Uncertain[21]	35–31	Czech Republic, Germany, Romania, Poland, Hungary, France, Spain	Hublin (2015).

and the criteria used. However, even if one can make such identifications, one cannot necessarily take the stratigraphic associations between these fossils and stone tools at face value. Teeth, mandibles, and phalanges are among the densest bones in the human body. Stone tools are nearly indestructible. All of these things can and do move around in sedimentary deposits, such as the surfaces of caves. Excavating consolidated cave sediments can create the illusion that, once deposited, fossils and stone tools remain in place. Sinking up to one's ankles in the unconsolidated surface sediments of a modern-day cave offers a valuable corrective to this assumption.

Industry-hominin attributions based on burials seem unassailable, but they are actually quite the opposite. Burials are intrusive features. The only thing one can say about them with confidence is that the buried individuals are younger than the sediments surrounding them. Even if one can tell how much younger, no consensus exists among archaeologists about how much of a temporal offset is sufficient to sever the hypothetical link between the fossils and the stone tools. Much can change in a century or two.

In evaluating burial-based attributions, one also has to guard against prematurely rejecting alternative explanations for them. Some may be burials like those recent humans create in funeral rituals. Some may be natural deaths rapidly buried (Gargett, 1989), or burials for hygienic reasons. Some might even be concealed homicides. If prehistoric homicides invited fear of retribution, as recent homicides usually do, caves might have offered guilty parties concealed locations in which to dispose of a body unobserved.

The assumption that "Middle Palaeolithic/Mousterian equals Neanderthals" is so well-entrenched in European prehistory that one can easily forget that this hypothesis is *demonstrably false* in North Africa and the East Mediterranean Levant, the two regions most often proposed as sources for Europe's Modern Human populations. Middle Palaeolithic "Mousterian" tools appear in North African sites dating between 45 and

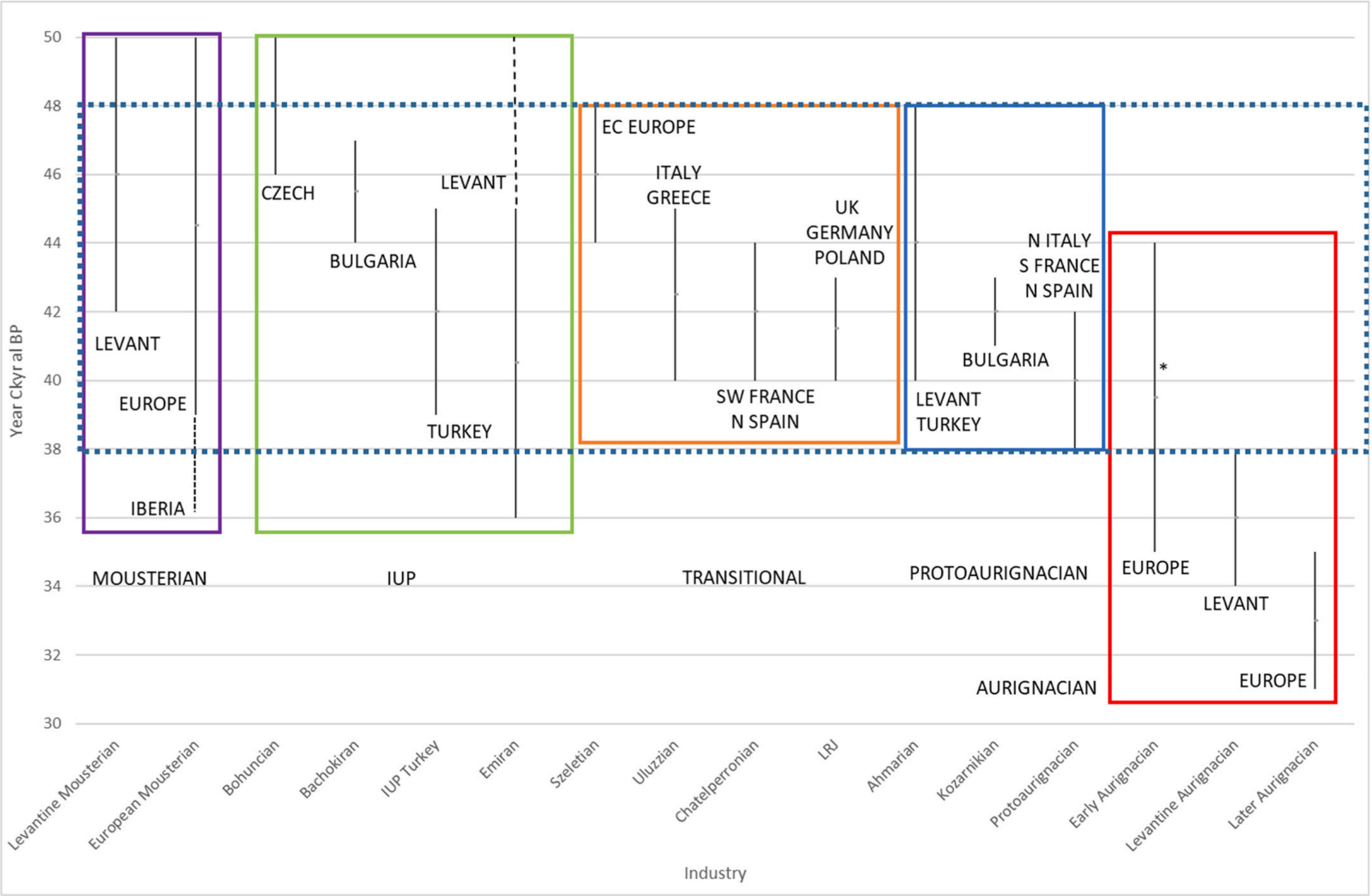

Fig. 1. Geographical and chronological distribution of stone tool industries between 50 and 30 ka in Europe and the Middle East. Asterisk marks the temporal position of the earliest Aurignacian in Central Portugal.

300 Ka and together with Modern Human fossils only (Scerri, 2017). Neanderthal remains appear at a handful of sites in the Levant together with Mousterian artefacts, but so, too, do Modern Human fossils (Shea and Bar-Yosef, 2005; Hershkovitz et al., 2018). Most Levantine MP, MP/UP, and UP sites lack *any* hominin fossil remains. Who made them is anybody's guess. This being the case, perhaps we ought to ask why we bother guessing?

Archaeologists' answers to "who questions" about extinct hominins hinge on accepting arguments about stone tool "authorship." Proving these arguments right or wrong, would require one to observe extinct hominins. So, unless or until someone invents a time machine capable of two-way travel (something nearly all physicists consider impossible), perhaps students of human evolution should set "who questions" aside and focus instead on answering "how questions," questions about prehistoric human activities (Shea and Bar-Yosef, 2005). Early Modern Humans, and at least some Neanderthals and Denisovans, became our ancestors by overcoming obstacles to their survival. Not because of who they were, but because of what they did. If researchers still want to continue to play "Pin the Tail on the Donkey" (match hominins to stone tool industries), then they should focus on identifying species-specific behaviours, chart those behaviours' distributions in time and space, and then propose hypotheses about how different kinds of interactions among various hominins ought to affect change and variability in those behaviours.

As we have seen, it is very likely that Europe and the Middle East were occupied by populations of hominins which were, in all probability, hybrids. We have virtually no knowledge of the phenotypes of these hybrids and even less their extended phenotypes (Dawkins, 1982). In spite of this, it is clear from Table 1 that uncertainty in the attribution of stone tool industries to hominin taxa is pervasive. We cannot, therefore, place any credence on maps and narratives of the spread of Modern Humans across Europe (or indeed anywhere else) in the critical period between 50 and 30 thousand years ago (ka) (Finlayson and Carrión, 2007).

In cases where Neanderthals have been linked to technologies akin to the Upper Palaeolithic of Modern Humans, e.g. the Châtelperronian at Grotte du Renne, Arcy-Sur-Cure, France (Hublin et al., 1996), supporters of Modern Human cognitive superiority over Neanderthals, wrongly imputing unverifiable behavioural qualities of "primitiveness" or "modernity" (Shea, 2016), have been quick to interpret these as the product of the acculturation of Neanderthals by newly arrived Modern Humans (Mellars, 1999; Gravina et al., 2005; Mellars et al., 2007a,b). Others have argued for an independent origin of these stone tool industries (d'Errico et al., 1998; Zilhao and d'Errico, 1999; Zilhao et al., 2006), giving the Neanderthals comparable cognitive abilities to Modern Humans (Finlayson et al., 2016) and reflecting the degree of flexibility between the types of technology adopted by Modern Humans and "Archaic Humans" across the world (Finlayson et al., 2000). The acculturation interpretation has two major problems. On the one hand the archaeology is unable to demonstrate who acculturated whom but, more importantly, the acceptance of such acculturation in interstratified archaeological levels implies a long period of coexistence and therefore runs contrary to population replacement by competitive exclusion or the notion of Modern Human advantages, other than originality of thought. Had that been the case, it clearly did not have an immediate or tangible demographic or competitive impact given the long period of overlap. It is also relevant that, although the stratigraphic position of the Neanderthal remains at the Grotte du Renne have been questioned (Bar-Yosef and Bordes, 2010; but see Higham et al., 2010; Welker et al., 2016), statistically validated evidence for Modern Human remains from this site is still weak (Gicqueau et al., 2023), given the probabilistic nature of metric traits mentioned above. The entire acculturation discussion has been based on Neanderthal remains, whose stratigraphy is questioned, versus Aurignacian stone tools and related artefacts which are attributed to Modern Humans. Given our comments above on the dangers of attributing stone tool industries to hominin taxa, the entire acculturation question must be viewed with scepticism (see also Gravina et al., 2022).

As this section has argued, archaeologists' efforts to develop and test hypotheses about Late Pleistocene "cultural geography" in the northern and eastern Mediterranean Basin rely on a complex patchwork of equations between specific stone tool industries and specific hominins. A full exegesis of the complexities underlying these equations, a review of their historical bases, and critical analysis of their relative strengths and weaknesses vastly exceeds the space available for this journal paper. Nevertheless, such a study, indeed several of them, must be priorities of Pleistocene archaeology. In the meantime, we must retain multiple working hypotheses about any and all such equations' validity.

5. Timing neanderthal disappearance and Modern Human arrival

A very short period of interaction between Modern Humans and archaic humans (including the Neanderthals) when they met, the Modern Human advantage leading to a rapid replacement, is predicted by proponents of replacement. The argument for the involvement of Modern Humans in the Neanderthal extinction has been almost universal: "But it *is* evident that the days of the Neanderthal era in Europe were numbered when the Cro-Magnons first arrived" (Stringer and Gamble, 1993; see also Hublin, 2015). The alternative, that the late entry of Modern Humans into Europe compared to other regions was due to the Neanderthal presence (Finlayson, 2009, 2014) has received less attention. In actual fact, it is impossible to identify Modern Humans as the main cause of the Neanderthal extinction or Neanderthals as the main cause of the Modern Human delay, simply from an archaeological stratigraphy. From an archaeological perspective the two are indistinguishable.

A range of scenarios have been discussed for the disappearance of the Neanderthals: from "Blitzkrieg" models, through stochastic processes, to competition (Graves, 1991; Pettitt, 1999; Kolodny and Feldman, 2017). The case for competitive exclusion (Banks et al., 2008) suffers fundamentally by its inability to demonstrate causality. The opposite, in fact, is what seems to have occurred: rather than a rapid replacement, Neanderthals and Modern Humans are thought to have overlapped for thousands of years (see also Rabett, 2018). Based on radiocarbon data the duration of this overlap has been estimated to between 2600 and 5400 years (Higham et al., 2014), but combined palaeogenetic and archaeological data suggests a more extended time period (Hajdinjak et al., 2021; Prüfer et al., 2021; Vallini et al., 2022) and the presence of Early Modern Humans north of the Alps 43,500 years ago has also been used to argue in favour of an extended period of contact in Europe (Nigst et al., 2014). These claims must, nevertheless, be treated with caution as they rely to a large extent on stone tool industries as proxies for human taxa. Additionally, last recorded dates of human material at a site (e.g. Deviese et al., 2021) should not be taken to mean the last presence of that human taxon at the site but rather when the population was substantial to have been picked up in fossil material. Actual disappearance is expected to follow a protracted process after the last date of observation (Bradshaw et al., 2012). Similarly, earliest dates at a site (e.g. Sun et al., 2021) need not represent first arrival dates either. So, questions of temporal overlap need to be treated with great caution. The genetic evidence, on the other hand, confirms that there must have been significant, widespread and prolonged overlap (Reich et al., 2010; Abi-Rached et al., 2011; Rasmussen et al., 2011; Skoglund and Jacobsson, 2011; Mendez et al., 2012, 2013; Meyer et al., 2012; Wall et al., 2013; Huerta-Sanchez et al., 2014; Prüfer et al., 2014; Fu et al., 2015; Qin and Stoneking, 2015; Kuhlwilm et al., 2016; Posth et al., 2017; Slon et al., 2018; Petr et al., 2020).

It is also a prevalent misconception that all archaeological sites represent equivalent human presence. Sink populations are maintained only by immigration from a source population so conditions need not be optimal where such sink populations survive (Brown and Kodric-Brown, 1977; Dytham, 2000). Differences in ecological quality of sites occupied by Neanderthals have been shown in at least one case (Finlayson et al., 2016). At the same time colonization-extinction models predict that at any point in time there will be a proportion of habitable patches that will remain empty as a consequence of demographic stochastic extinctions (Hanski and Gilpin, 1997; Tilman and Karieva, 1997; Hutchings et al. 2000). This means that absence of human presence at a site need not signify that the site was unsuitable. A model of range expansion and contraction cannot therefore use archaeological sites as proxies for range changes without first determining the quality and metapopulation features of each site.

6. Life in the fluctuating world of europe and the Middle East between 50 and 30 ka

The main conclusion that we derive from our analysis of presently available data is that there is a great deal of uncertainty regarding the patterns and processes of dispersion of populations of *Homo* in Europe and the Middle East during the long, twenty thousand-year, period between 50 and 30 ka. Did Modern Humans enter Europe some time between 45 and 40 ka? If we assume that Europe, prior to 50 ka, was occupied solely by Neanderthals, then it would be logical to accept that the later presence of other, non-Neanderthal, *Homo* populations must have come from outside. If so, the most parsimonious explanation would advocate a geographical expansion from the Middle East, either directly into Europe or circuitously via Central Asia, passage across the Strait of Gibraltar not having been proven (Finlayson, 2004).

But could populations of *Homo,* attributed to Modern Humans, have been present in Europe earlier? The presence of populations with morphology claimed to be associated with Modern Humans in Jebel Irhoud, Morocco, at >300 ka (Hublin et al., 2017), in the Middle East at 194–177 ka (Hershkovitz et al., 2018) and in Greece at >210 ka (Harvati et al., 2019) suggests that this might well have been the case. The best evidence so far is of recent introgression of Modern Human Y chromosomes into Neanderthals at ~370–~100 ka (Petr et al., 2020) which indicates that contacts between these hominin taxa were taking place well before 50 ka. This makes it very likely that populations of *Homo* present in Europe prior to 50 ka were not exclusively Neanderthal and also included hybrids and, very probably, Modern Humans.

Evidence of a ~45 ka entry of Modern Humans from the Middle East would then rest on a clear chronological demonstration of this dispersion spatially from east to west. The Initial Upper Palaeolithic Industries (IUP) are lumped together (Kuhn et al., 2009) but there is no evidence, other than techno-typological similitude, suggesting that they were all made by the same hominin (Kuhn, 2003; Kuhn et al., 2009; Hublin, 2015; Hublin et al., 2017). In fact, a comparison of date ranges for the different IUP Industries (Table 1; Fig. 1) could be equally interpreted to mean a dispersal from south-eastern Europe into the Middle East. This would not be dissimilar to the Levantine Aurignacian which is considered to represent a "back migration" from Europe to the Middle East (Table 1; Fig. 1; Alex et al., 2017). Others have proposed that the IUP represents a partially successful Modern Human expansion which did not reach western Europe (Müller et al., 2011).

A further alternative could be that the IUP represents ways in which hominins were coping to changing environmentally-driven conditions in south-eastern Europe, Turkey and the Levant at 48–38 ka (Table 1). It would be seen as a geographical alternative to similar responses at the same time across Europe (north-west Europe, East-Central Europe, Italy, the Balkans, south-west France and northern Spain) and represented by the transitional industries (Hublin, 2015). The Protoaurignacian "family" of industries would represent alternative responses within the same time frame, but concentrated in the southern parts of the geographical area (Ahmarian in the Levant and Turkey; Kozarnikian following the Bachokiran in Bulgaria; and the Protoaurignacian in northern Italy, southern France and northern Spain) (Table 1; Fig. 1). The Mousterian and Aurignacian would appear as partially, temporally and geographically, overlapping industries. This scenario cannot, by any stretch of the imagination, be seen as a clear signal of an east-west geographic Modern Human expansion at the expense of the Neanderthals.

A regional adaptation by European and Middle Eastern hominins (Neanderthals, Modern Humans and hybrids) to changing environmental conditions, accentuated along physiographic boundaries as proposed by Finlayson and Carrión (2007), is a more parsimonious and biologically meaningful interpretation. Broadly, it would appear to correspond to an increase in the use of lightweight, long-distance, projectile technology as a response to the need to adapt to the exploitation of open tundra-steppe-desert habitats and habitat mosaics which were overrunning much of Europe and the Middle East during Marine Isotope Stage (MIS) 3 (Van Andel and Davies, 2004). Such industries may be seen as examples of "technological intensification in the service of improved energy capture/conservation" (Shea, 2016).

Rapidly and stochastically fluctuating environments would also be expected to facilitate coexistence (Hening and Nguyen, 2020) and promote hybridization and hybrid zones (Anderson, 1948; Hubbs, 1955; Harrison, 1993; Arnold, 2016) with consequent adaptive advantages to colonisers of new environments or to those locally keeping up with rapid ecological change (Arnold and Kunte, 2017). It is therefore very probable that what we are observing in the tumultuously fluctuating conditions of Europe and the Middle East between 50 and 30 ka, is extensive biological and cultural interchange leading to experimentation. It would include successes (in the form of demographic and geographical expansion) and failures (demographic and geographical contraction and extinction). The apparent Neanderthal-Modern Human-Neanderthal turnover in Mandrin Cave, France (Slimak et al., 2022, 2023), as indeed the long-established dynamics in the Middle East (e.g. Tchernov, 1992) would seem to bear this out. In this scenario, hybridization and cultural exchanges can be seen as contributors to a common fitness currency, providing quick fixes as alternatives to the slower processes of natural selection of novel mutations or of independent invention.

The flip side to the story is provided by the Iberian Peninsula. The absence of all IUP, transitional and Protoaurignacian family industries from the Iberian Peninsula), other than the Eurosiberian zone in the extreme north (Straus, 2018), stands out in contrast to the rest of Europe and the Middle East. Here, coastal areas of the Mediterranean and Atlantic seaboards, least affected anywhere in Europe by the vicissitudes of the MIS 3 climate (Carrión et al., 2008, 2018; Jennings et al., 2011; Ochando et al., 2020; Vidal-Cordasco, 2022), were occupied by remaining makers of the Mousterian, a stone tool industry linked with the exploitation of forested and semi-forested habitats and ambush hunting strategies (Finlayson, 2004, 2009; Finlayson et al., 2006; Zilhao et al., 2017; Carrión and Walker, 2019; Zilhao, 2021; Ochando et al., 2022). A comparable situation seems to have occurred in southern and eastern Asia prior to 50 ka, where warm and humid habitats did not challenge dispersing humans who show no major shifts in stone tools used, contrasting with the situation in northern Eurasia (Shea, 2016).

The cold and arid central Iberian tablelands (meseta), which at times became an extension of the Eurosiberian zone (Finlayson, 2011) and which the mammalian cold fauna penetrated during MIS 3 (Álvarez-Lao and Garcia, 2010), were, on the other hand, largely uninhabited at this time (Straus, 2018; Haws et al., 2020). The few hominins occupying the edges of this vast meseta not unsurprisingly appear to have made the Aurignacian industry (Haws et al., 2020). This sporadic presence, dated to 41.1–38.1 ka, has been interpreted as evidence of a rapid westward expansion of Modern Humans into Central Iberia, even though the hominin attribution is only inferred. An alternative, and equally plausible explanation is that it is yet another example of hominin adaptation to changing environments on the edge of a changing MIS 3 world. The Levantine Aurignacian, which first appears at a later date than this Iberian Aurignacian (Alex et al., 2017) could also be interpreted as a local adaptation to changing circumstances instead of a movement of people from Europe.

Current discussion on the late survival of Neanderthals in southern Iberia (Finlayson et al., 2006) remains an open question. The dating of late Neanderthals in southern Iberia by Higham et al. (2014) is limited to a single site in a mountainous area which was only occupied sporadically by Neanderthals (Finlayson et al., 2016), and therefore insufficient to have any level of certainty as to the wider regional picture. The presumed early presence of Aurignacian at another Iberian site, this time in the extreme south of the peninsula at Bajondillo, Málaga, has been taken as evidence of a correspondingly early Neanderthal extinction (Cortés-Sanchez et al., 2019). This evidence has been discredited as a result of a mixed stratigraphy and non-diagnostic technology (Anderson et al., 2019; de la Peña, 2019). The additional error is in presuming that the presence of the Aurignacian (equated to Modern Humans) at one location must signify the disappearance of the Mousterian (equated to Neanderthals) over an entire region. There is enough evidence, as reviewed in this paper, to show that this persistent angle of region-wide population replacement is untenable. Instead, the currently available evidence indicates that cultural, as well as genetic, contacts and exchanges between Middle Pleistocene *Homo* and Modern Humans (equated to *H. sapiens*) were already taking place in the Middle East as far back as 140,000–120,000 years ago (Zaidner et al., 2021).

7. Concluding remarks

The two competing models of human origins, which dominated the literature for several decades, are now defunct. Advances in the methods for extracting and studying ancient DNA in fossils and cave sediment, especially in the last decade, have allowed us to scratch the surface of the complex relations between human (genus *Homo*) populations and lineages in the Late Pleistocene of western Eurasia and beyond. These pioneering studies are revealing, *inter alia*, the high degree and frequency of admixture that took place between different populations and lineages. The inescapable conclusion is the realization that human populations in the Late Pleistocene of Eurasia were highly admixed. It follows that attempts to map out "human species" interactions based on a small number of fossils, fossil sites or a larger number of archaeological sites (dominated by lithics) – the standard procedure for over three decades – can no longer be viewed with any degree of confidence. We are seeing a clear paradigm shift (Kuhn, 1962) in the study of human origins. Historical narratives of the timing and extent of human species migrations, of Modern Human advantages over others, and indeed on the timing of extinctions, that probably did not happen, are finally giving way as the focus moves towards looking at the biology and culture of human populations and the nature of their interactions in time and space. We must now not only accept the reality of the "Neanderthal inside us" (Saraiva, 2022), but also that of "us inside the Neanderthals" (Petr et al., 2020).

Author contribution

All authors contributed to the manuscript. CF and GF coordinated the work.

The following were primarily responsible for these disciplines:

Ecology and Evolution CF, GF, JC, SF, Paleogenomics, CZ, MPdL, Archaeology, JS, FGG.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data were used for the research described in the article.

Acknowledgements

C. Finlayson, G Finlayson, S Finlayson and F Giles-Guzman, acknowledge the support of HM Government of Gibraltar. J. S. Carrión acknowledges funding by Project of Spanish Ministry of Science - FEDER: PID 2019-1049449 GB-I00.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2023.108307.

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