Rapid ecological turnover and its impact on Neanderthal and other human populations

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The latter part of the last glaciation, 50 000–12 000 years ago (kya), was characterized by a rapidly changing climate, cold conditions and corresponding vegetation and faunal turnover. It also coincided with the extinction of the Neanderthals and the expansion of modern human populations. Established views of modern human superiority over Neanderthals as the cause of their extinction are under attack as recent work shows that Neanderthals were capable of behaviour that is regarded as modern. As we discuss here, the exact nature of biological and cultural interactions between Neanderthals and other human groups between 50 kya and 30 kya is currently hotly contested. The extinction of the Neanderthals, and other modern human lineages, now appears to have been a drawn-out, climate-related affair.

The Palaearctic 50–12 kya

The period 50–12 thousand years ago (kya) was of huge significance for humans. At 50 kya, the only humans living across a wide belt of the southern Palaearctic, excluding North Africa (Figure 1), were Neanderthals [1]. By 30 kya, most humans occupying the Palaearctic, including areas not previously occupied, were anatomically modern [1], the last Neanderthals surviving only in remote pockets [2]. At the height of the last glaciation, ~18 kya, humans were confined to southern strongholds [3], which were areas of continuous occupation. With deglaciation, these populations re-colonized the north [4]. However, the situation during the intervening period (50–30 kya), coinciding with a significant period of cooling and variable climate [5], still remains unclear.

The ecological fluctuations of this crucial period of transition and their impact on humans have come under increasing scrutiny in recent years [5,6]. The relative impact of climate-driven ecological change and the arrival of anatomically modern humans (AMHs) in Europe on the existing local populations of Neanderthals is hotly debated [7–9], as is the degree to which the incoming populations interacted with local Neanderthals [5], whether they exchanged genes [10,11], technology or ideas [12,13]. Here, we review the latest evidence of climate and ecological change in the period 50–12 kya, in relation to human

geography. We propose that an understanding of the ecological, human biological and cultural mosaic of the period 50–30 kya, will overtake the simplistic Neanderthal–AMH dichotomy that has dominated the debate. We pay special attention to Europe for which we have the greatest volume of available information.

Were Neanderthals behaviourally modern?

The identification of 34 kya-old human fossils at the French site of Arcy-sur-Cure as Neanderthal in 1996 [14] opened a heated debate. It is generally accepted that the Arcy Neanderthals were associated with an industry known as Châtelperronian (Box 1), which apparently emerged from local Middle Palaeolithic industries also made by Neanderthals. The importance of the Châtelperronian results from the presence of Upper Palaeolithic elements, generally ascribed to AMHs, such as blades and artefacts made from bone and ivory. By contrast, the contemporary Aurignacian culture (Box 1), associated with AMHs, was fully Upper Palaeolithic and is widely accepted as representing their arrival into western Europe [15]. The similarity of the Arcy personal ornaments with those found nearby in contemporary Aurignacian sites was taken to indicate either trading between Neanderthals and AMHs or technical imitation of AMH technology by Neanderthals.

Not everyone accepted this conclusion, considering instead that Neanderthals were capable of independent and parallel technological innovation [16]. At the root of the debate lies the central question of what constitutes behavioural modernity, when and where this arose and whether it was the exclusive domain of AMHs [17,18]. Were Neanderthals inferior in some way to the AMHs and was their extinction the direct result of AMH arrival [5]? Although the debate appears to have reached an impasse [12,13], it is becoming increasingly clear that an understanding of the ecology of the various human populations living in the crucial period between 50 kya and the Last Glacial Maximum (LGM), ~18 kya, might provide a way forward [5].

Climate and ecological change in the Palaearctic 50–12 kya

The climatic changes that Europe experienced during the Late Pleistocene, particularly during 50–30 kya, were
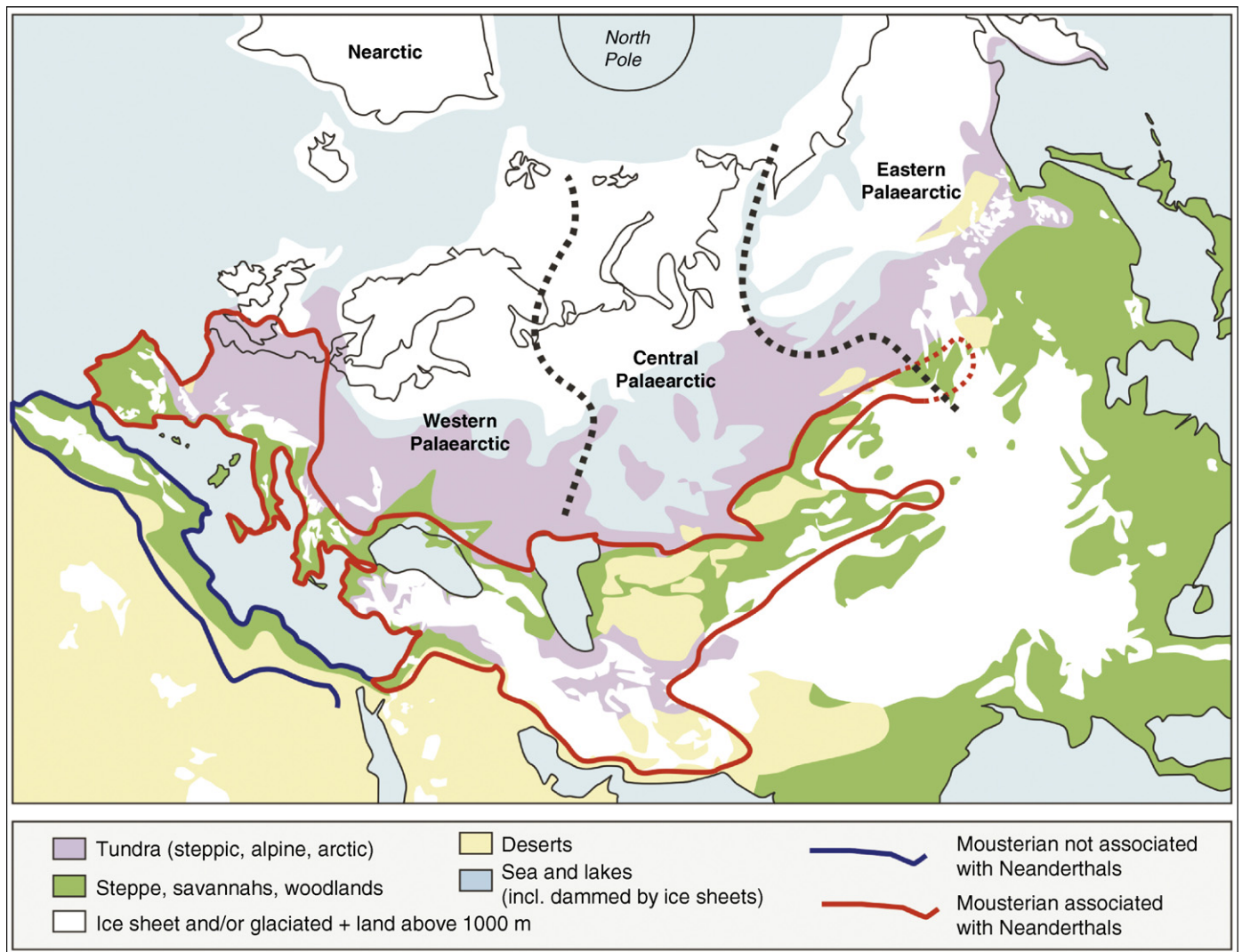
Figure 1. Major physiographical features of the Palaearctic at the LGM. Vegetation has been simplified into non-wooded (tundra) and wooded or semi-wooded (steppe with scattered trees, savannah and woodland). The central corridor provided by the Eurasian Plain, dominated by steppe–tundra communities, is visible between the ice sheets and ice-dammed lakes in the north and the MLB, deserts and Mediterranean in the south. The MLB is the belt of topographically heterogeneous, largely mountainous, land that stretches from the Atlas (Morocco) and Betic (Spain) ranges in the west to the Altai (Siberia) in the east. North Africa is relatively isolated by the Mediterranean in the north and the expanded Sahara in the south. The distribution of Aurignacian-family industries (not shown) closely matches the maximum geographical area occupied by the Neanderthals in Eurasia (area bound by red line), which, in turn, matches the MLB. In North Africa, the Mousterian industries are associated with AMHs, there being no known Neanderthal fossils from that region. Palaearctic sub-regions are separated by dotted lines. Based on Refs [69,70].

abrupt and severe [19]. These rapid climatic changes are detected from significant oscillations in pollen sequences, indicating major changes in vegetation composition and structure from forest to open environments and back at the scale of centuries [20,21]. Such changes are also observable in the distribution of mammals, including humans.

Vegetation change
Recent attempts have been made, as part of a major interdisciplinary project studying this period [6], to map pan-European biomes during cold and warm events [22]. However, the interpretation of maps, in terms of vegetation units, is in doubt [23]. These, for example, indicate a cover of boreal forest over much of mid-latitude Europe [24], a result that has been difficult to reconcile with the dominance of open grassland mammal species at the time [25]. Another point of controversy arises from the dissimilarities between simulated and inferred biomes [26]. Vegetation diversity in the topographically

heterogeneous southern European peninsulas, which acted as glacial strongholds for many species [27], has been seriously underestimated.

In spite of the inherent difficulties, it is possible to understand the nature of vegetation responses in different contexts (Figure 2, Box 2). Localized areas in southerly latitudes maintained a significant cover of humid and warmth-loving woody vegetation throughout the entire period [28,29]. The further north and east in Europe, the greater the impact of continental and arctic climates and the greater the expected reduction in tree cover, a pattern that was locally interrupted in favourable localities [30,31]. The situation at the height of the LGM is relatively better known when compared with the earlier stages and relatively detailed vegetation maps are available [32]. The LGM situation enables us to observe one extreme (cold climatic stage; the coldest conditions) in a continuum that has the wooded thermal optimum (warmest conditions) at the other. It also enables us to detect significant

boundaries between major vegetation types, infer boundary zones where the changes would have been most rapid and abrupt, and demarcate important tree strongholds (Figures 1,2).

The expansion of treeless vegetation across Europe from east to west, and the persistence of tree populations mainly in the south, caused major shifts in the geographical distribution of many animals, the best documented being the mammals [5].

Mammalian faunal change

The mammals of Late Pleistocene Europe largely represented the remnants of the Middle Pleistocene (∼780–125 kya) fauna, recognizable by the presence of large species, such as straight-tusked elephant *Elephas antiquus* and narrow-nosed rhinoceros *Stephanorhinus hemitoechus* [33]. This fauna was significantly impoverished by the start of the Last Interglacial (∼125 kya), probably as a result of increasingly long periods of hostile and variable climate [34]. Major demographic and distribution swings in response to climate-driven changes in vegetation typified many mammal species, the survivors of the Middle Pleistocene 'warm' fauna (e.g. straight-tusked elephant and narrow-nosed rhinoceros) disappearing before the Glacial Maximum, with most of the 'cold' fauna (e.g. woolly rhinoceros *Coelodonta antiquitatis*) barely reaching the end of the Pleistocene

[35]. The woolly mammoth, *Mammuthus primigenius*, and the giant deer *Megaloceros giganteus* survived into the Holocene [36].

The shifting distribution patterns of Late Pleistocene mammals reflect the expansion and contraction of habitats in response to climate change [37,38]. There is a clear separation between the mid-latitude belt (MLB) of mountains that stretch across the Palaearctic, the plains to the north and the deserts to the south (Figure 1) [5]. The MLB is characterized throughout by the presence of 'warm' faunas, including the Middle Pleistocene survivors. The plains, however (Figures 1,2), were dominated by 'cold' and steppe faunas. A generalized carnivore suite of species, including spotted hyaena *Crocuta crocuta* and wolf *Canis lupus*, was widespread [39]. Zones of contact between MLB and plains were particularly rich and show repeated changes in faunal composition depending on climatic conditions [40]. The southern peninsulas, however, maintained a constant suite of species and the 'cold' fauna never reached these latitudes (Figure 2).

Open woodland (e.g. red deer *Cervus elaphus*) and rocky habitat (e.g. ibex *Capra ibex*) mammalian herbivores offered opportunities for human ambush hunters [5]. Humans with projectile technology and long-range mobility, which enabled the following of the large herds, were best suited to exploiting plains mammals (e.g. horse,

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Box 1. Characterization of cultural groups

It is possible to characterize the cultural groups referred to in the main text (see also Box 3) by geographical region, time period (Figure I) and, in some cases, human taxon (Table I; Figure I).

Table I. Main cultural groups and taxonomic affiliations occupying the western Palaearctic in the period 50–10 kya

Cultural group	Cultural mode[a]	Biological affinity[b]	Characterization
Mousterian	MP	NEA/AMH	Widespread flake-based technology with a variety of retouched implement types; bifacial tools (e.g. hand axes) rare or absent. In Europe, and probably much of Asia, it is exclusively associated with the Neanderthals. In the Middle East and North Africa, it is also associated with early AMHs
Aterian	MP	AMH	Flake-based technology, found from Morocco to Libya and south to Chad; diagnostic features are the bifacially worked leaf-shaped and tanged projectile points
Transitional	MP/UP	NEA/AMH?	Characterized by the appearance of blade-based UP technology on a flake-based MP substrate; localized (e.g. Châtelperronian in France and northern Spain). Only the Châtelperronian has associated human fossils, which are Neanderthal
Ahmarian	UP	AMH?	Early UP (EUP) blade-dominated industries first appear in the Middle East ∼45 kya. Bone tools and marine shells used for decoration appear as innovations. The Ahmarian tradition follows directly from the EUP and persists to the LGM
Dabban	UP	AMH?	A localized blade-based technology known mostly from the site of Haua Fteah in Libya
Aurignacian	UP	Unknown	The first European UP technology; characterized by blade-based tools that show a high degree of standardization, antler, ivory and bone projectile points, body ornamentation and cave art
Gravettian	UP	AMH	The first technology of the steppes; characterized by small pointed bladelets with blunt but straight backs. This culture is associated with Venus figurines, construction of large skin tents on mammoth bone frames in Eastern Europe, the first large and semi-permanent camps, and the first spear throwers and eyed needles
Iberomaurusian	UP	AMH	The first North African UP technology, found from Morocco to Libya, characterized by the presence of small bladelets
Solutrean	UP	AMH	An advanced UP technology of south-western Europe with associated cave art and body ornamentation. A characteristic is the production of fine bifacial leaf points made by a high pressure flaking technique, light projectiles, tanged and barbed arrowheads. The bow-and-arrow probably originates with this culture. The Magdalenian culture, characteristic of post-glacial western Europe, emerges from the Solutrean
Epigravettian	UP	AMH	Evolved from the Gravettian and characterized by the reduction (microlithization) of stone tools. The use of bone is rare
Kebaran	UP	AMH	Characterized by a variety of small tools (i.e. geometric microliths), in keeping with a highly mobile nomadic existence; separated from the contemporary Iberomaurusian by the Sahara Desert

[a]MP, Middle Palaeolithic; UP, Upper Palaeolithic.
[b]AMH, anatomically modern human; NEA, Neanderthal.
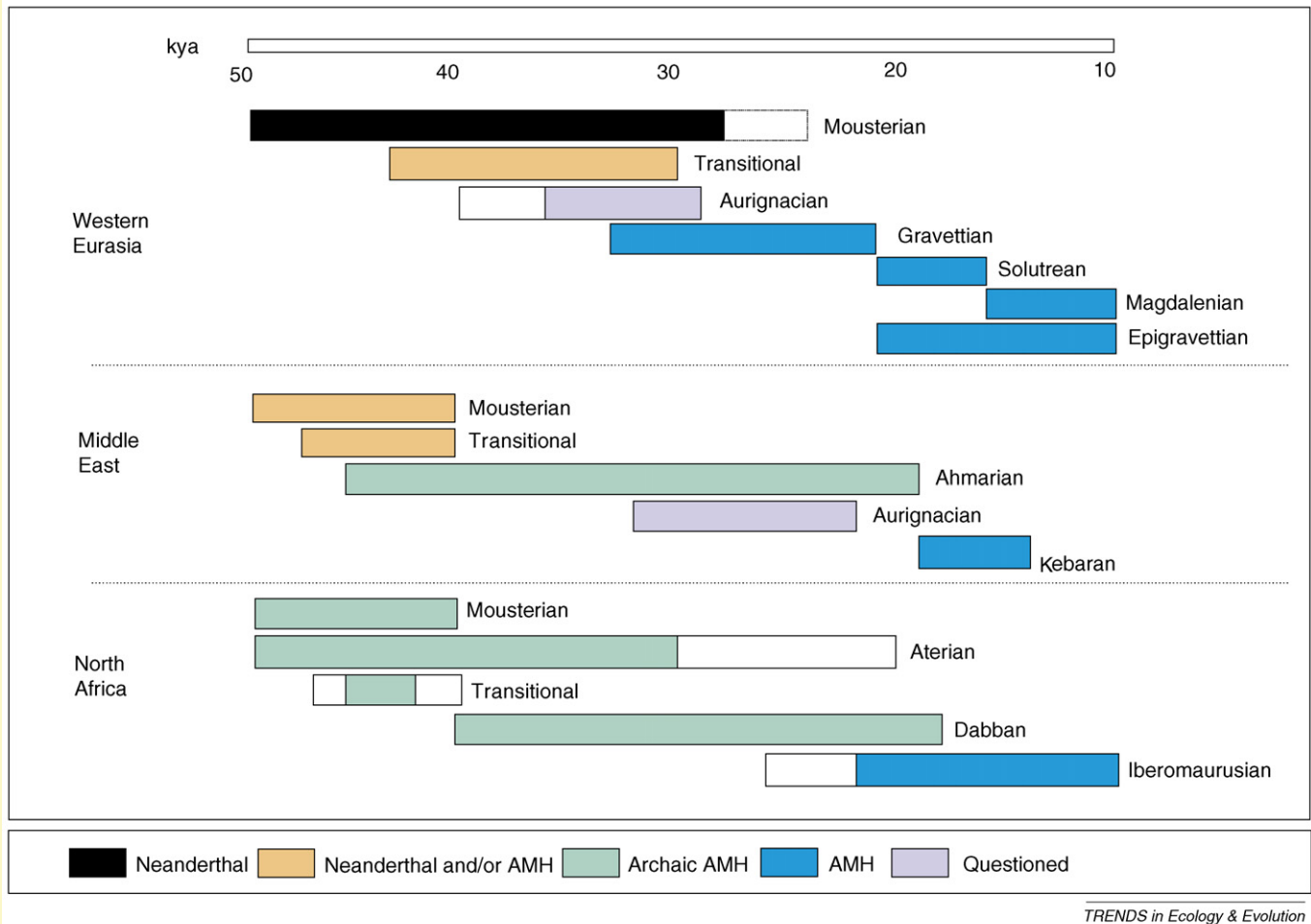
Box 1 cont'd.

Figure I.

Equus ferus, reindeer *Rangifer tarandus* and steppe bison *Bison priscus*) [5]. The expansion of plains mammals across the Palaearctic as treeless vegetation spread [37,39] was a crucial factor in the fate of human populations. It favoured the AMHs and constrained the Neanderthals [5].

Humans between 50 and 12 kya
In spite of over a century of research in Europe, our knowledge of human taxa and their distribution during the crucial period that included the Neanderthal extinction and the expansion of AMHs, is still poor.

Fossil evidence
There is no doubt, based on a large number of fossil discoveries, that the taxon that occupied most of Europe during the late Middle Pleistocene and the early Late Pleistocene until ~35 kya, and even later in refugia [2], was the Neanderthal [5]. The range of the Neanderthals extended significantly eastwards well into the central Palaearctic, probably reaching the Altai Mountains and into Transbaikal in southern Siberia [41] (Figure 1).

The humans that occupied much of central and western Europe after 30 kya were anatomically modern [42],

Box 2. Latitudinal trends in vegetation change across western Europe (50–12 kya)
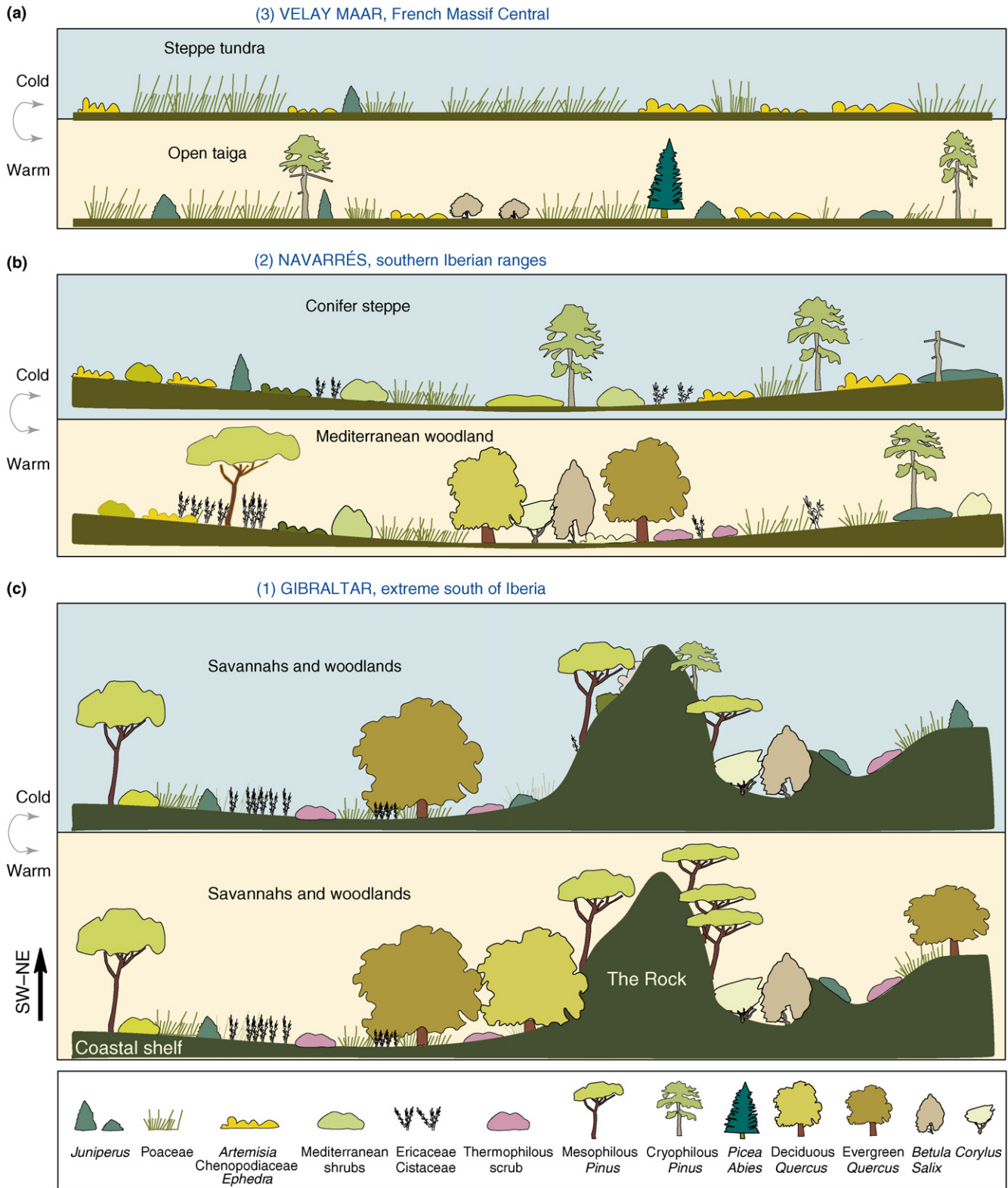
A latitudinal pattern in vegetation development across the European continent, for the period c. 50–12 kya, is shown in Figure I. The Velay pollen sequences in the French Massif Central (Figure Ia; see Figure 2, main text, for location) show the succession of several short temperate episodes of tree colonization (open boreal forest) alternating with complex cold phases that are characterized by shrubby tundra [66].

In the Navarrés pollen record, eastern Spain [67], woodlands dominated by oaks and pines, occur between ~31 and 27 kya (Figure Ib). After ~27 kya, the landscape shows a return to glacial conditions, with high percentages of steppics. Pines, however, continue to be abundant and eventually reach high proportions.

Pollen in cave sediment and coprolites, and charcoal analysis, from Gorhaḿs Cave, Gibraltar, reveal a highly diversified landscape, including oak, pine and juniper savannahs, forests, wetlands, grasslands with heaths and xerothermic coastal scrub (Figure Ic) [68]. Little change is observed in the palaeo-landscapes in the period ~32–12 kya, which demonstrates that the Strait of Gibraltar was a reservoir of woody species during the OIS3 and LGM. This north–south pattern of vegetation change is similarly observed in the Italian and Balkan peninsulas, although with lower incidence of thermophilous sclerophylls and an increased abundance of broad-leaf trees. In the southernmost regions of Mediterranean Europe, many site-specific deviations to this pattern occur, caused by physiographical heterogeneity. In addition, processes of resilience, even inertia, can provoke important delays or even a lack of response of vegetation to climate change [66–68].

Box 2 cont'd.

(a)   (3) VELAY MAAR, French Massif Central

(b)   (2) NAVARRÉS, southern Iberian ranges

(c)   (1) GIBRALTAR, extreme south of Iberia

Figure I.

although evidence of their presence in Europe before 30 kya is scant. In 2002, a robust modern human mandible discovered at Peştera cu Oase (south-west Romania) and dated to 34–36 kya [43], is currently the oldest European AMH [42]. Recently, attempts have also been made to date fossils directly in collections, with mixed results. For example, five AMH fossils from the Mladeč Caves (Moravia, Czech Republic) produced approximate ages of
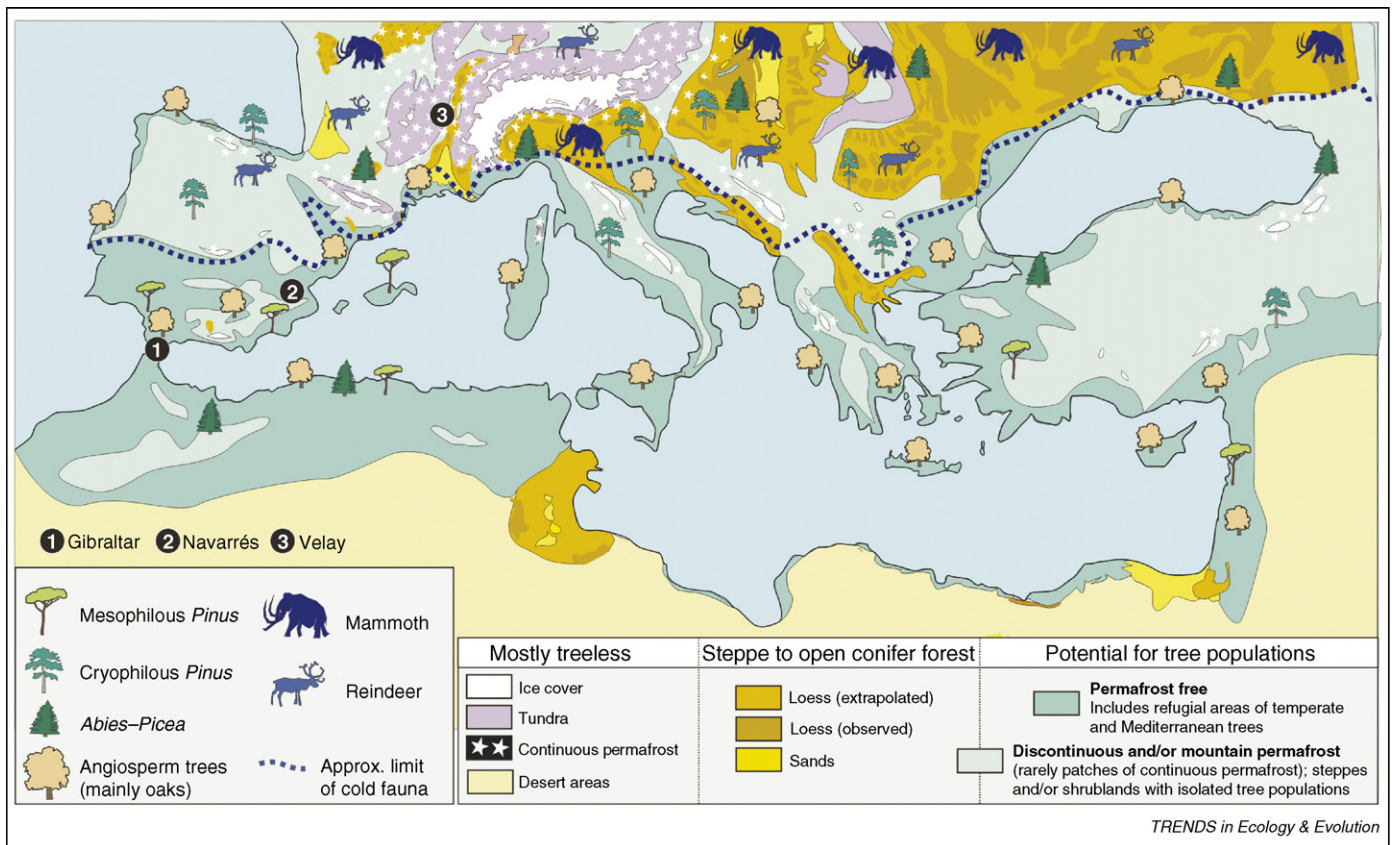
Figure 2. LGM physical setting in the south-western Palaearctic. The LGM physical setting [32,69,70] serves as a model system for one of the extreme cold climatic stages that embraced the period 50–12 kya. Whereas ice sheets, continuous permafrost, loess sandy deposits and tundra-like vegetation covered high-latitude and high-elevation regions, and the Sahara desert expanded northwards, steppic environments with sparse trees patched with heliophytic woodlands and savannahs prevailed in the Mediterranean Basin. Thus, temperate tree populations survived in North Africa, the Near East and up to 46°N, reaching even further north in western Europe. Populations of conifers and angiosperms (*Pinus, Picea, Larix, Betula, Taxus, Salix* and *Juniperus* spp.) occurred throughout the Mediterranean peninsulas, whereas sclerophylls, such as evergreen *Quercus, Olea, Pistacia, Phillyrea, Buxus, Arbutus* and *Myrtus* spp. were largely confined to southernmost territories. This is also the case for mesophilous broadleaf trees such as *Corylus, Alnus, Carpinus, Ilex, Castanea, Ulmus, Fraxinus* and *Acer* spp., which survived in humid biotopes in montane valleys. During the LGM, the complexity of vegetation mosaics increases southwards in Europe and northwards from the Saharan to the Mediterranean Region in North Africa. Numbered places refer to sites discussed in Box 2. Based on Refs [20,26–28,32].

~31 kya (range ~26–32 kya) [44]. Other results, however, have come as a shock. Human skeletal remains from the German site of Vogelherd had traditionally been regarded as providing the best evidence of association between AMHs and the Aurignacian culture (Box 1), considered to represent the expansion of the first AMHs into Europe. In 2004, it was revealed that all the key Vogelherd fossils dated to 3.9–5.0 kya, representing subsequent intrusive Neolithic burials into the Aurignacian levels [45]. Overall, it is clear that diagnostic and well-dated AMH fossils are not found west of the Iron Gates of the Danube before 32 kya [42], implying a relatively recent entry into western Europe.

In the Middle East, AMH fossils are found at the sites of Qafzeh and Skhul dating to ~90–100 kya [46]. There is then no trace of AMHs until after 40 kya, an AMH from Nazlet Khater 1 (Egypt) at 37.57 kya and an AMH child from Ksar 'Akil rock shelter (Lebanon) at ~35 kya [46]. Between 90 and 40 kya, the Middle East was occupied by Neanderthals, a southward range expansion from Europe apparently associated with climatic cooling [46]. Thus, the early appearance of AMHs ~90–100 kya and their subsequent absence of ~50 kya could represent a failed northward expansion. Importantly these early AMHs in the Levant are associated with the Mousterian industries

(Box 1), which were the hallmark of the Neanderthals. Also associated with Mousterian are late-Middle Pleistocene AMHs in the Maghreb, which show affinities to the Skhul-Qafzeh specimens [47]. There appears to be biological continuity with later AMHs that produce the Aterian culture (Box 1), a possibly more recent Middle Palaeolithic alternative to the Mousterian. The situation for the rest of the Palaearctic is even worse, owing to a poor fossil record and we are left with the archaeological study of cultures as proxies for biological taxa, something that is proving to be increasingly inadequate [42,45].

Cultural evidence

The apparent coincidence between the timing of observed cultural changes occurring in the European Middle–Upper Palaeolithic transition and the 'generally agreed timing of the dispersal of anatomically and genetically modern human populations across the continent' [18] is now the main claim in support of the cultural invasion of Europe by AMHs (see Box 1 and 3 for contrasted evidence). The alternative (parallel development of cultures among separate lineages of hominins) is dismissed as too unlikely [18], even though we have evidence of parallel cultural developments in humans [48] and even among chimpanzees [49].
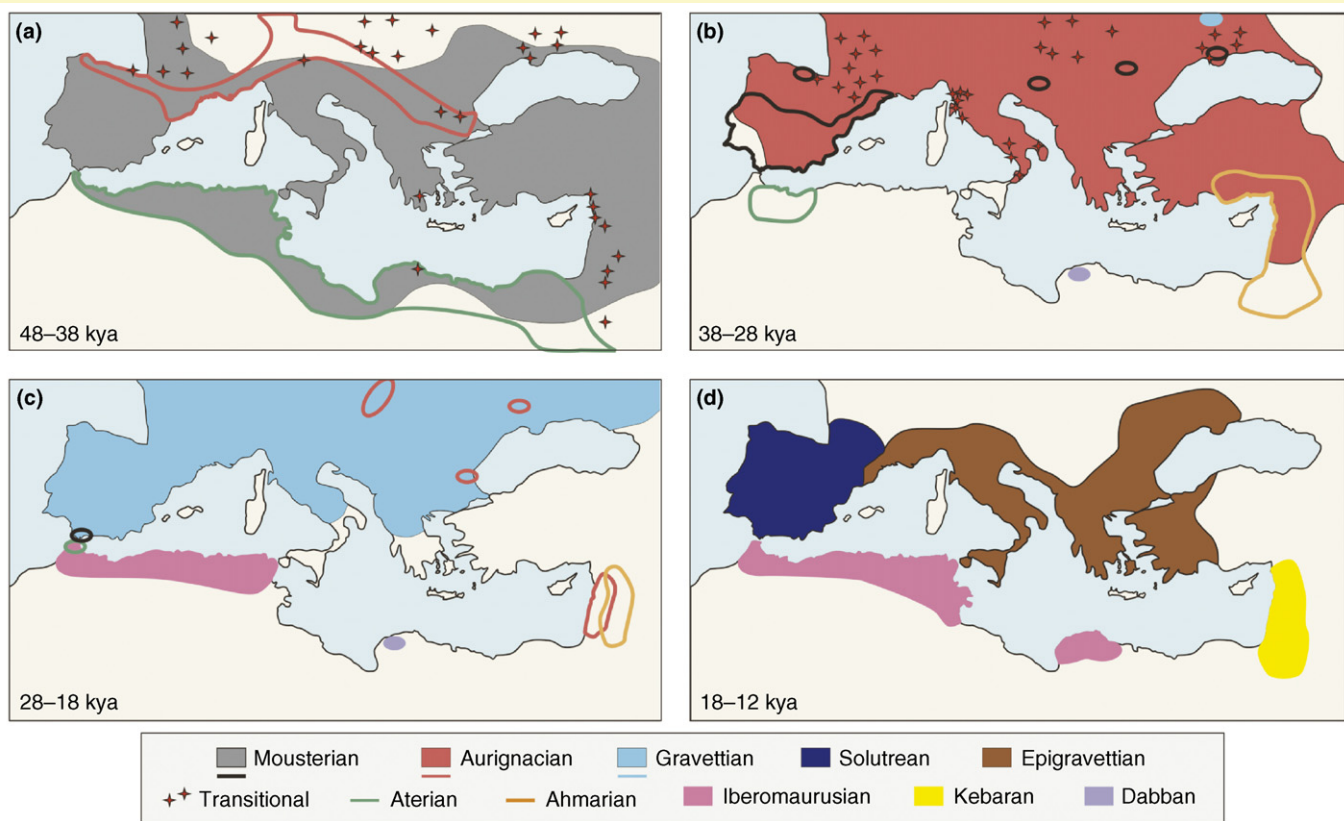
Box 3. Distribution of main technological cultures across southwestern Eurasia between 48 and 12 kya

Technological cultures [3] are represented in Figure I (see also Figure 2 and main text for explanation). There are several main elements of the human population dynamics of this period: (i) a progressive retreat of Neanderthals towards the periphery (48–28 kya; Figure Ia,b) and, finally, the extreme south-west; (ii) the appearance of the Aurignacian along a middle band from northern Spain to Bulgaria (48–38 kya; Figure Ia, followed by a latitudinal expansion (38–28 kya; Figure Ib) and a retreat towards peripheral, eastern areas (28–18 kya; Figure Ic); (iii) the appearance of transitional industries along a middle band that is similar to the Aurignacians (48–38 kya; Figure Ia), with little indication of subsequent expansion [with the exception of an appearance in Italy (Uluzzian, 38–28 kya)] and absence ~28–18 kya (Figure Ic); (iv) prolonged existence of Upper Palaeolithic industries in the Middle East (i.e. Ahmarian and Kebaran, 38–12 kya; Figure Ib–d); (v) persistence of Middle Palaeolithic Mousterian and Aterian industries in the Maghreb and the late appearance of the Upper Palaeolithic (Iberomaurusian, 28–18 kya; Figure Ic); (vi) the dominance of the Gravettian 28–18 kya (Figure Ic; and (vii) the distribution of Upper Palaeolithic industries (i.e. Solutrean and Epigravettian) in southern refugia (18–12 kya; Figure Id).

Overall, the observed patterns are: (i) the Neanderthal retreat into refugia (38–28 kya) followed by extinction (28–18 kya; Figure Ic); (ii) latitudinal pulses of expansion and contraction among Aurignacian and transitional cultures (48–28 kya; Figure Ia,b), followed by retreat into refugia and extinction (38–18 kya; Figure Ib,c); (iii) an east–west expansion of Gravettians (28–18 kya; Figure Ic), followed by retreat into refugia (18–12 kya; Figure Id). These populations did not go extinct.

The Neanderthal, Aurignacian and transitional patterns appear similar (i.e. occupation of a wide area followed by contraction and extinction) but not in temporal phase. The Gravettian expansion is unique, in that it was not followed by extinction, although the subsequent retreat to refugia resembles that experienced by other hominins.

Most recently [71], a distinctive Upper Palaeolithic industry has been reported from Kostenki on the Russian Plain. It is ~40 kya, the earliest known, and is unrelated to the Middle Palaeolithic or the Aurignacian. It might correspond to pioneer exploitation of the plains, presumably by AMHs, and reinforces the view expressed here that the entry of AMHs into Europe was by plains-adapted people from the east.

(a) 48–38 kya
(b) 38–28 kya
(c) 28–18 kya
(d) 18–12 kya

Legend: Mousterian · Aurignacian · Gravettian · Solutrean · Epigravettian · Transitional · Aterian · Ahmarian · Iberomaurusian · Kebaran · Dabban

TRENDS in Ecology & Evolution

Figure I.

In addition, although it has now become clear that we can have no certainty regarding the identity of the humans that produced the Aurignacian culture [45], the presumed westward spread of AMHs across Europe is still based on the controversial first dates of the Aurignacian [50,51]. Uncertainty as to the makers of the various transitional industries adds to the confusion (Box 1). It is only after 30 kya that the situation again becomes clearer as Gravettian AMHs occupy much of the continent (Box 3). Part of the existing confusion is due an excessively Eurocentric focus to the problem.

Widening the horizon

Several recent Y-chromosome and mtDNA genetic studies, using molecular clocks, give a clear picture of the timing and expansion of AMHs from north-east Africa [52–56]. A population expansion within Africa ~80–60 kya led to the first, and only, successful AMH dispersal out of Africa by no later than 54 ± 8 kya [52,56]. The coastal route towards south-east Asia and Australia was the fastest but the expansion into Eurasia took longer, probably owing to the harshness of the conditions, the presence of

Neanderthals, the seasons and the rapidly changing climatic conditions [56]. Before 30 kya, AMHs reaching Eurasian mid-latitudes for the first time only gained tenuous footholds [56]. In keeping with the fossil evidence, the genetic data only provide limited evidence of AMHs in Europe before the appearance of the Gravettian culture ~30 kya [56].

With the climatic stabilization ~30 kya towards the cold conditions of the LGM, there is clear evidence of population growth among local AMH populations. All major non-tropical expansion clusters from this time period are eastern, southern and central Asian [52]. This evidence is supported by the high Y-chromosome diversity found among Central Asian populations, indicating the region to have been the source of at least three major waves of migration into Europe, the Americas and India [55], that into Europe being dated to ~30 kya [53]. By contrast, the evidence for an earlier entry into Europe via the Balkans from the Middle East, the traditional view of the arrival of the presumed AMH Aurignacians [50,51], is weak [54,56] and, if such an entry did occur, the genetic signature appears to have been almost wiped out by the later Central Asian dispersal [53].

The Aurignacian and the transitional industries in context

An examination of the distribution of Aurignacian and transitional industries (Box 1) across Europe during the crucial time frame between 45 and 30 kya (Figure 3) reveals a striking correspondence between location and the presence of sharp physiographical boundaries. This suggests that these industries, some made by Neanderthals (Châtelperronian) and others perhaps by AMHs (Aurignacian?), were independent regional responses to rapidly fluctuating ecological conditions. Their absence from more stable regions, such as south-western Iberia, supports this view. The changing circumstances and stresses experienced by human populations across the Palaearctic, most notably between the MLB and the plains (Figures 1,3), created a template for innovation [5]. Many of the trends are towards light and portable technology, which can be carried over long distances, as a means of reducing risk in the unpredictable new world of the plains [5,57] (Box 1). The fluctuating world between 45 and 30 kya meant varying circumstances for these frontier humans (established Neanderthals and pioneer AMHs) as they alternated technology between the heavy weaponry of the Mousterian designed for a wooded Middle Pleistocene world of megafauna and the lighter, portable, projectile technology of the new Late Pleistocene world of vast open spaces. Information exchange, strategic planning, social and trading networks, and symbolism entered the risk-reduction melting pot [57], giving the illusion of a cognitive revolution [15]. These innovations appear, instead, to be responses to living in vast open spaces rather than to changes in brain wiring [5].

Reaching the Far West

One or more AMH populations, exposed for the longest to these divisions between woodland and open plain, found ways of living permanently away from trees and caves,
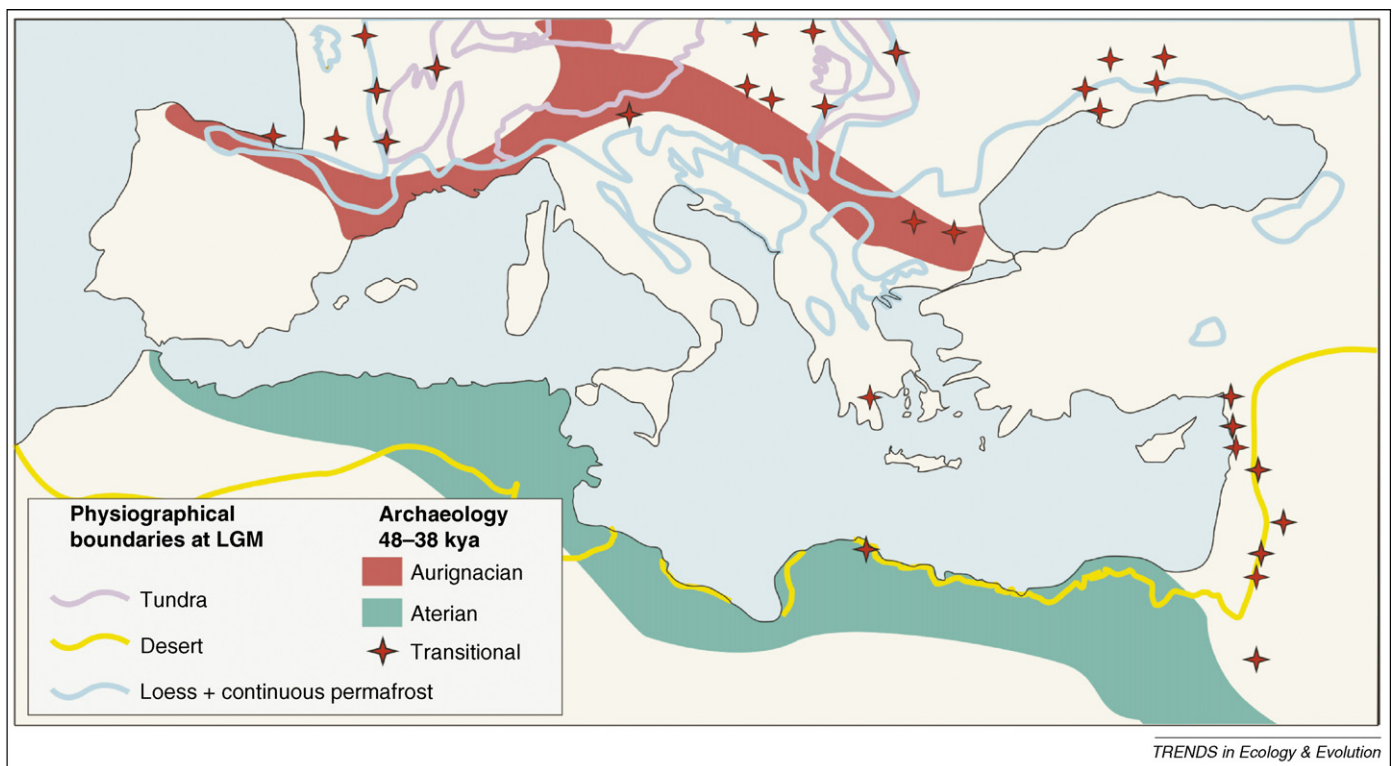

Figure 3. Distribution of Aurignacian, Aterian and Transitional industries in relation to physiographical boundaries. The map represents the period 48–38 kyr (Box 3) and the physiographical boundaries from Figure 2. The association between these industries and ecotonal areas is clear and suggests that the Aurignacian and transitional industries were responses to situations of rapidly changing ecological conditions across sharp boundaries. Interestingly, the North African Middle Palaeolithic Aterian industry might also fall in the same response category. Industry distribution based on Ref. [3].

even constructing dwellings out of the remains of the mammoths [58] (Box 1). Pioneers reached the European Arctic by ~36 kya, but could not establish a foothold [59]. By ~30 kya, as the Gravettians, they had reached the European Plains, the 'Far West', to become the 'Hunters of the Golden Age' [60]. In the other direction, they reached the Russian Arctic at 71°N by 27 kya [61] and the stage was set for the first colonization of the Nearctic.

The crux of the matter: biological identity and cultural affinities of Late Pleistocene Palaearctic humans

Issues of genetic admixture between Neanderthals and AMHs have recently come to the fore with new discoveries of AMH fossils, claimed to have Neanderthal-type features [11]. It now appears that the microcephalin gene (*MCPH1*), which regulates brain size during development, might have been introduced into AMHs ~37 kya, through admixture with Neanderthals [62]. The genetic distinctiveness between Neanderthals and AMHs [63] has been taken to mean that there was no genetic admixture between them [10], although the most recent evidence from Neanderthal genomic DNA does not exclude this possibility [64,65]. This apparent paradox might be resolved if we take the Gravettians to be the AMHs that contributed to the post-30 kya Eurasian genetic pool. As Neanderthals and Gravettians would have rarely met, we would not expect to find Neanderthal genes among these AMH populations or their descendants. If Neanderthals interacted with other populations, which might have been anatomically modern, before 30 kya and these vanished along with the Neanderthals, then any trace of such interaction would have been lost among present populations but might survive in fossils. If indeed there was interbreeding, trading or imitation [12,13] between Neanderthals and the Aurignacians, we are left with the uncertainty of who imitated whom.

Conclusion

Rapid climate-driven ecological turnover was of paramount importance to the fate of humans that lived in the northern hemisphere throughout the period 50–30 kya. Instead of the simple delimitation of the human taxa into Neanderthal or AMH, here we adopt a population approach that views the human biological and cultural mosaic in relation to ecological change. An examination of the distribution of Aurignacian and transitional industries across Europe and North Africa at this time reveals a striking correspondence between location and the presence of sharp physiographical boundaries. Alternatively, technological innovations of the so-called Upper Palaeolithic can be understood as responses to living in vast open spaces rather than to the consequence of a cognitive revolution associated with an evolutionary change. Future research should focus on the biological identity of the cultural groups that lived across the entire Palaearctic, not just Europe, 50–30 kya.

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