PERSPECTIVE

Middle Pleistocene fire use: The first signal of widespread cultural diffusion in human evolution

Katharine MacDonald[a], Fulco Scherjon[a], Eva van Veen[a], Krist Vaesen[a,b], and Wil Roebroeks[a,1]

Edited by Polly W. Wiessner, The University of Utah, Salt Lake City, UT, and approved June 22, 2021 (received for review February 5, 2021)

Control of fire is one of the most important technological innovations within the evolution of humankind. The archaeological signal of fire use becomes very visible from around 400,000 y ago onward. Interestingly, this occurs at a geologically similar time over major parts of the Old World, in Africa, as well as in western Eurasia, and in different subpopulations of the wider hominin metapopulation. We interpret this spatiotemporal pattern as the result of cultural diffusion, and as representing the earliest clear-cut case of widespread cultural change resulting from diffusion in human evolution. This fire-use pattern is followed slightly later by a similar spatiotemporal distribution of Levallois technology, at the beginning of the African Middle Stone Age and the western Eurasian Middle Paleolithic. These archaeological data, as well as studies of ancient genomes, lead us to hypothesize that at the latest by 400,000 y ago, hominin subpopulations encountered one another often enough and were sufficiently tolerant toward one another to transmit ideas and techniques over large regions within relatively short time periods. Furthermore, it is likely that the large-scale social networks necessary to transmit complicated skills were also in place. Most importantly, this suggests a form of cultural behavior significantly more similar to that of extant *Homo sapiens* than to our great ape relatives.

fire use | cultural behavior | Middle Pleistocene | Middle Stone Age | Middle Paleolithic

Interaction with fire, including enhanced maintenance and production (1), is generally considered one of the most important processes within the cultural evolution of humankind. Fire afforded hominins protection against predators and cold, broadened the range of edible foods and the amount of energy that could be extracted from them through cooking (2), allowed manipulation of materials (3), extended the length of day, and impacted the character of social interactions (4). Fire gave hominins a means to increase the productivity of their habitats, over time significantly transforming natural landscapes (5, 6). Fire also came with costs (7–9), as fire-using hominins had to collect fuel to be brought to a central place, calling for cooperation within a group (10). Given the impact pyrotechnology must have had, understanding the origins and development of fire use is relevant for our understanding of the development of the niche of hominin species through time, including—as we argue here—the importance of cultural behavior. Indeed, we hypothesize that the increasing evidence for the appearance of regular fire use within a (relatively) restricted time window (400 to 350 thousand y ago, ka) and across an extremely wide geographic region can be best explained by cultural diffusion of skills related to fire use. In fact, the fire record might provide the first clear evidence of the emergence of cultural diffusion in the evolution of humankind, indicating that a distinctive characteristic of the cultural behavior of *Homo sapiens* was in place at this time.

The importance of cultural behavior is clear for our own species today: on a daily basis we use technology that we could not invent ourselves, and contemporary human cultures produce unique material and symbolic artifacts from complex technologies to languages to money and symbolic mathematics. Cultural behavior changed the nature of human evolution, and some argue it played a role in the evolution of large-scale cooperation between nonfamily members (11), and of aspects of cognition (12). Several authors see cultural

[a]Faculty of Archaeology, Leiden University, 2300 RA Leiden, The Netherlands; and [b]School of Innovation Sciences, Eindhoven University of Technology, 5600 MB Eindhoven, The Netherlands

Author contributions: K.M., F.S., and W.R. designed research; K.M., F.S., E.v.V., K.V., and W.R. performed research; and K.M., F.S., E.v.V., K.V., and W.R. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence may be addressed. Email: w.roebroeks@arch.leidenuniv.nl.

Published July 23, 2021.

behavior as the explanation for the near-global distribution and success of *H. sapiens* (e.g., refs. 13 and 14). However, it is not clear when key characteristics of cultural behavior present in *H. sapiens* today emerged and it is possible that some characteristics first appeared earlier than others. These characteristics include its often adaptive or inherent value, regional traditions, which are present in a number of species (15, 16), and the accumulation of elements, or "ratcheting," which is rare in nonhuman animals (17), and may also include the rapid spread of socially learned behaviors over large distances.

Cultural transmission is one of several processes by which elements of cultural behavior (ideas, behavior, and artifacts) can spread. It refers to the process of passing on, through social learning, cultural traits from one individual to another. Cultural transmission may give rise to several patterns: local traditions, cumulative culture, and the focus of the present paper, the wide distribution of cultural traits. Here, we use the term "cultural diffusion" to describe the spread of cultural traits from one population to the next, through processes of cultural transmission. Studies of the diffusion of cultural traits have focused on major innovations. Classic studies of the diffusion of innovation address farming, hunting, pottery, architectural technology and the adoption of architectural styles [reviewed in Amati et al. (18)]. Cultural diffusion can be responsible for the geographically wide distribution of innovations and other cultural traits and their presence in different populations and societies. In other species, widespread behaviors are generally explained in terms of processes of genetic evolution. Large-scale cultural diffusion is an important, distinctive characteristic of modern human culture, and we investigate a possible first appearance of it in the archaeological record.

The Spatiotemporal Pattern of Fire Use

A full review of the record for early fire use is beyond the scope of this perspective paper; our goal is to describe a pattern, focusing on contrasts between the record before and after 400 ka, to propose an explanation and to stimulate debate and further research. Tracking the development of early fire use in time and space has proven to be challenging, as identifying traces of fire as anthropogenic is not straightforward. One reason for this is the widely distributed, transient nature of its use by mobile hunter-gatherers, who rarely invest in structures around fires. Hence, common proxies for their fires consist of materials exposed to heating, and include charcoal, heated lithics, charred bone, and the heat-altered sediments on which a fire was built (19, 20). In the open air, many of these fragile traces are easily removed by natural processes (21), while natural fires can create a range of proxies that mimic anthropogenic ones (22). To deal with these issues, new analytical methods have been developed (for two recent reviews, see refs. 23 and 24), with experimental studies testing the effects of heat on wood, bone, and various types of artifacts, as well as on sediments underlying fireplaces (25–27). As such methods have still not been widely applied, one could assume that earlier cases of fire use have gone undetected thus far. However, despite the evidentiary constraints of the archaeological record, a review by Roebroeks and Villa (20) identified a clear pattern for Europe: there the record strongly suggests that anthropogenic fire use was very rare to nonexistent during the first half of the Middle Pleistocene, as exemplified by the absence—bar a few dispersed charcoal particles—of fire proxies in deeply stratified archaeological karstic sequences, such as the Atapuerca site complex in Spain or the Caune de l'Arago at Tautavel (France), as well as from such prolific open-air sites as Boxgrove in the United Kingdom. In contrast, the record from 400 ka onward is characterized by an increasing number of sites with multiple fire proxies (e.g., charcoal, heated lithics, charred bone, heat-altered sediments) within a primary archaeological context (19, 20, 28).

Studies published following this review have strengthened this pattern and identified its existence beyond Europe. In the Gruta da Aroeira cave site (Portugal), for example, fire proxies in the form of heated bones start to appear in layers dated to 400 ka (29). At Bolomor Cave (Spain), 14 hearths associated with heated materials have been excavated from multiple levels dating from 350 to 100 ka (30). Fire proxies are present at open-air as well as rock-shelter sites, and there are open-air sites at which such fire evidence is repeated many times, over long periods, such as at Biache-Saint-Vaast (France) dating to 240 to 170 ka (31). Fire was used to gain access to deep caves (32), for production of pitches (3), and processes such as cooking, which are documented for late Neandertals (33) but may have been relevant earlier too. Importantly, for the Levant, Shimelmitz et al. (34) estimate the emergence of habitual fire use at 350 to 320 ka, a date based on the long and well-dated sequence of Tabun Cave (Israel), as well as on a review of the evidence from a range of other sites in the Levant. At Qesem Cave (Israel), in addition to evidence for extensive burning throughout the occupation history of the site, 400 to 200 ka (35, 36), a very large and repeatedly used central hearth was found, dating to around 300 ka (37). Beyond its western parts, there is thus far very limited evidence for fire use in the Middle Pleistocene of Asia (38). The putative fire evidence from Zhoukoudian (China) has been much debated (e.g., ref. 39), with recent work identifying traces of anthropogenic fires in a layer for which the age estimates obtained vary per dating technique but all point to the 500- to 250-ka range (40) (i.e., to the same period in which we see fire use emerge in western Eurasia).

This pattern is not limited to Eurasia, however. At the site of Jebel Irhoud (Morocco), a clear fire signal is visible at 300 ka, with abundant evidence for anthropogenic fire use, including heated lithics and heated faunal remains (41). The Jebel Irhoud evidence fits very well with other evidence from the African Middle Stone Age (MSA), a period broadly spanning ∼350 to 35 ka, roughly contemporary with the western Eurasian Middle Paleolithic. Bentsen's (42) review of the various kinds of fire evidence suggests that pyrotechnology was very important in the early part of the MSA in sub-Saharan Africa, although the number of sites is small and dominated by cave sites in South Africa, reflecting the amount of fieldwork done there. At Border Cave, hearths and ash layers have been excavated from multiple levels dating from 230 ka to 1000 CE (43, 44). Fire was used to modify the properties of stone raw material (45), for cleaning and possibly pest control (44), and to cook starchy rhizomes (46).

That there is, from 400 ka onward, such a marked, geographically widely distributed pattern of regular fire use (24) does not imply that hominins might not have used fire before 400 ka. Indeed, it has been suggested that traces of anthropogenic fire might be around 0.8 Ma old in Spain (47, 48) and Israel (49, 50), 1 Ma old in South Africa (51–54), or even older in East Africa (19, 55–57). Furthermore, based on paleoanthropological evidence for anatomic changes, Wrangham and Carmody (58) have argued that fire was first used by *Homo erectus* 1.8 Ma ago. However, the anthropogenic status of most of the pre–400-ka traces remains controversial (see, e.g., refs. 19, 29 and 59–62): as an example, the origin of 1.5-Ma-old reddened patches of sediments at the FxJj20, Koobi Fora, Kenya, has been debated from initial publication four decades ago to the present day (56, 57, 59, 63, 64).

An in-depth review of the pre–400-ka evidence is beyond the remit of our paper, but the record from several distinctive landscapes illustrates the isolated and problematic nature of the early fire record. A case in point is Wonderwerk Cave (South Africa), which is located on the eastern slopes of the Kuruman Hills. If the heated materials recovered at this site, dated at 1 Ma, were indeed the result of anthropogenic fire [52; but see Goldberg et al. (60) for results of new samples], it is striking that, among the millions of roughly contemporary stone tools recovered at the western slopes of the hills, not a single heated lithic has been found (1). In Chazan's view, this situation is difficult to reconcile with an important role of fire in this period, as inferred by Wrangham's cooking hypothesis (1, 2). Another interesting fire signal comes from the Melka Kunturé open-air site complex, situated in the Upper Awash valley in the northern Ethiopian highlands and located at about 2,000 m above sea level. The sites document hominin adaptations to high-altitude environments over a very long period, from ∼1.7 Ma to the Late Stone Age (LSA). In the Pleistocene, these high altitudes witnessed severe cold periods, probably too cold for a continuous hominin presence there, as suggested for the occupation signal from the 850- to 700-ka sequence of Gombore II (65). Apart from one possibly heated pebble from Garba 1, a late Acheulian site (66), there is no evidence for the presence of fire use until the LSA throughout the whole of the spatially extensive Melka Kunturé complex.

While one needs to interpret the lack of solid evidence for the pre–400-ka period with caution, given the taphonomic issues with fire proxies (55) and the limited sampling in time and space of early sites in general, nothing substantiates a pattern like the one observed after 400 ka, with fire use recorded by multiple proxies at multiple sites from each region and recurring within sites. The current data for early fire use in Africa and Eurasia, described elsewhere as "sketchy…to say the least" (67), not only show that the dispersal of early hominins into Eurasia, at around 2 Ma ago, was not associated with any type of archaeologically visible fire use, but also strongly suggest that fire use as a regular component of the hominin technological repertoire was a much later phenomenon, dating to the second half of the Middle Pleistocene. Around that time Africa and Eurasia were home to a variety of hominin (sub)populations, including early *H. sapiens* and *Homo naledi* in Africa, Neandertals in western Eurasia and Denisovans, and *H. erectus* populations further east, many interacting and exchanging genes repeatedly with neighboring subpopulations of the wider hominin metapopulation [in the sense of Pääbo (68); see also refs. 69–71].

Cultural Diffusion of Fire Use?

A striking characteristic of the fire signal that emerges from the archaeological record is the strong increase in evidence for fire use across a wide geographic area and in (geologically speaking) the same period and in different hominin subpopulations. We suggest that this represents the first clear instance of widespread cultural diffusion in human evolution documented in the archaeological record. Cultural diffusion played an important role in the fast spread of innovations in skills and technology over large regions in prehistory. As discussed above, we consider this to be one of several distinguishing characteristics of present-day *H. sapiens*' culture, which also include cumulative cultural evolution and the existence of regional traditions. Our hypothesis implies that knowledge and techniques were transmitted across hominin social networks, interacting within the wider metapopulation inhabiting major parts of the Old World. Below we will counter alternative explanations for the observed pattern and discuss evidence supporting our hypothesis of cultural diffusion. We also point to archaeological data that, independent of the fire record and somewhat younger, strongly supports the interpretation of the existence of cultural diffusion in the later part of the Middle Pleistocene, particularly the archaeological record of a specific stone-working technology (namely, the Levallois technique). Finally, we will explain why we interpret this as the first clear-cut case of widespread cultural diffusion evidenced by the archaeological record.

Arguments against: Independent Innovation, or Genetic or Demic Explanations. The spatiotemporal pattern of the appearance in the archaeological record of an innovation provides evidence relevant for identifying how the innovation came to be widely distributed: that is, through independent innovation, demic processes, cultural diffusion, or genetic processes. The fact that regular fire use appeared relatively quickly across the Old World and in different hominin subpopulations strongly suggests that the behavior diffused or spread from a point of origin rather than that it was repeatedly and independently invented. Additional evidence comes from environmental data. If the product of convergent evolution, fire use would be expected to correlate with environmental pressures. So a scenario could be suggested in which hominin subpopulations developed similar technology in different places in response to similar challenges in their environments. In such a scenario we would expect the change in the fire record to correspond to or follow a change that had comparable effects on regional environments over the whole geographical area, most likely a global change in climate. We might also expect to see fire use appear and disappear depending on environmental conditions, until hominins displayed adaptations to regular fire use. Fire use has several benefits that may be particularly advantageous in cooler conditions; at the same time, the costs of fire use, specifically fuel collection, are considered to be higher in open conditions (8).

Two environmental hypotheses are possible regarding increasing use of fire by hominins: this occurred 1) in cooler conditions driven by necessity or 2) in wooded conditions when costs were lower. By 500 ka ago, the 100-ka-long glacial–interglacial cycle characteristic for the later part of the Pleistocene was firmly established, associated with a high global volume of ice. This pattern became dominant following the mid-Pleistocene transition (∼1.25 to 0.7 Ma ago), which had a profound effect on biota and landscapes and was complete about 300 ka before the prominent change in the fire record (72). The very severe glaciation of Marine Isotope Stage (MIS) 12, which was associated with cooler and more arid conditions worldwide, had ended before the fire record picked up. Sites at which convincing evidence for fire has been recovered from the period 400 to 300 ka are associated with both cool and warm conditions (73). In addition, relatively wooded periods recurred throughout the Pleistocene. Environmental change therefore does not seem to be in keeping with a scenario of convergent evolution.

Furthermore, the spatiotemporal pattern tells us something about the underlying processes. In general terms, the diffusion of a new technology over a large region can be explained in genetic, demic, or cultural terms, or combinations thereof (18, 74, 75). Of these, *ceteris paribus*, genetic diffusion (across subpopulations or an entire species) is the slowest process, demic diffusion is somewhat faster, and cultural diffusion leads to the fastest spread of a novel behavior (76, 77). In genetic diffusion, heritable traits (including behaviors) become more frequent within a (sub)population as a result of natural selection or drift. Depending on, among other things, the size of the subpopulations and the strength of the selective pressures, this process will minimally take a couple of generations (77). If the trait is to be genetically diffused across multiple subpopulations—recall that regular fire use did travel across a high number of subpopulations—many more generations are needed. Rapid, genetic spread of behavior is only feasible within a local population or when genetic diffusion is accompanied by processes of strong demic diffusion. In demic diffusion, the diffusion of traits is driven by demographic and range expansions, the fusion of subpopulations, and the replacement of local populations by other populations. Such demographic and migratory processes might take place at timescales of a couple of decades rather than generations. Finally, cultural diffusion can work at even shorter timescales (years rather than decades). Here the transmission of behavioral traits is driven by cultural learning, that is, learning of traits by observing others, or by being instructed by them. As long as contacts among individuals or subpopulations are friendly and sufficiently frequent, behavioral traits might travel great distances even in 1 single year (77).

While cultural and demic diffusion processes can in principle be distinguished based on diffusion rates calculated from the archaeological record (e.g., ref. 78), this is significantly more challenging for the Paleolithic period, due to the limitations of the dating methods (76, 79). The large margins of error associated with radiometric dates for the Middle Pleistocene make it impossible to quantitatively distinguish between demic and cultural diffusion. However, in qualitative terms, the phenomenon that we observe, involving the appearance of fire use in a relatively small time frame and widely dispersed areas, suggests a rapid process. Additionally, the genetic and fossil evidence undermines explanations in terms of genetic and demic diffusion. Fossil evidence [reviewed by Hublin (80)] supports the hypothesis of population divergence of Neandertals and *H. sapiens* before this period, between 500 and 400 ka, while genetic studies suggest a much earlier divergence, situating the last common ancestor of the *H. sapiens* and the Neandertal/Denisovan branches at 550 and 765 ka (70). A recent study of dental evolution suggests an age before 800 ka (81). In line with these age estimates, genetic studies of a fossil population from Sima de los Huesos, Spain, suggest a date of >430 ka for the Neandertal/Denisovan divergence (70). These hominin subpopulations diverged genetically and phylogenetically before the period in which we are interested and were present in different continents throughout. Since multiple hominin subpopulations persisted and left evidence of fire use, it is unlikely that practices associated with fire use were transported by a single dispersing hominin subpopulation. Furthermore, as we have indicated above, it is unlikely that "genes for fire use" developed repeatedly, in different hominin populations, and in response to environmental change.

Arguments for a Cultural Explanation. We turn now to our arguments for cultural diffusion of skills related to fire use. Middle Pleistocene hominins are often characterized as "thin on the ground" (82), and the world of hominins in the later Middle Pleistocene featured multiple subpopulations (68) and major geographical barriers. However, genetic evidence suggests that populations encountered one another sufficiently for cultural diffusion to occur: specifically, recent genetic studies demonstrate direct contact between subpopulations with a repetitive exchange of genes within the hominin metapopulation, including introgression from ancient *H. sapiens* into Neandertals occurring 200 to 300 ka (69–71). Members of these subpopulations therefore encountered each other, repeatedly and over very long timespans, providing a canvas for cultural diffusion. Even though individuals may have lived in relatively isolated and small populations most of the time, as suggested for Late Pleistocene Neandertals in Siberia (83), the genetic record shows that interactions between individuals from different regional populations did occur repeatedly.

There are several reasons to believe that the social structure of hominins in the period of interest would, at a minimum, have supported adequate levels of intergroup tolerance necessary for the transmission of fire skills, discussed below. First, the skills associated with using and making fire would have included knowledge of the properties and location of materials (e.g., flint, pyrite, tinder, fuel), and might also have included techniques for starting a fire. These could be passed on quickly, easily, even from a distance (within a matter of days, without much effort by a learner, with or without instruction). Second, there is little specialization in relation to fire skills: in a survey of fire use practices among 93 recent hunter-gatherer groups, McCauley et al. (9) found only 5 that mentioned fire production as a task for males and 10 that mentioned fire maintenance as a task for females. Because it requires little specialization, group members could easily pick up the required knowledge for starting and maintaining a fire by observation. Third, analyses of nonhuman primates indicate that the last common ancestor of humans and chimpanzees probably already had a degree of social tolerance supporting this level of learning between individuals in different groups. For example, tolerant intergroup encounters in nonhuman primates have been documented for reasons of increased foraging returns, extragroup mating, and inspecting a new group before transferring (84), while bonobos have recently been observed sharing meat outside their group (85). Such nonhuman primate encounters last from a matter of hours to a few days, which is long enough for the diffusion of fire-related skills by observation. In addition, the chances of tolerant encounters and learning opportunities are higher in the context of resources like fire, for which the costs of defending the resource outweigh the benefits of exclusive access (especially since the benefits of using a fire are not diminished when extra people use it) (84).

Above, we described a minimal scenario for intergroup interaction, requiring nothing more than tolerance among individuals of different groups. However, a less minimal scenario involving more intricate cultural and cooperative interactions between large numbers of individuals, similar to those of recent hunter-gatherers, is also plausible. By 400 ka, brain size and corresponding energy needs had increased substantially in the (at least) 6 Ma of evolution since the last common ancestor with chimpanzees and bonobos existed (86). Enhanced intergroup cooperation might have been a strategy to manage increasing risks of shortfalls associated with high energy requirements by maintaining access to and information about distant resources (84).

Another factor that strengthens our cultural diffusion explanation relates to changing views of the fluidity and scale of past hunter-gatherer social organization. A growing body of ethnographic studies emphasizes this characteristic, with individuals being part of larger social networks than commonly acknowledged. In the words of Bird and colleagues, "If small-scale social organization characterized ancestral hominin communities, such communities have no clear analogue in contemporary mobile hunter-gatherers. This general disconnect between traditional views of hunter-gatherer social organization and quantitative ethnographic evidence highlights an important weakness in current paleoanthropological/neurological models of the co-evolutionary relationships between human cognition, pro-sociality, and hunter-gatherer group size and organization" (87). Hominin group sizes or "distributed communities" estimated based on primate trends increase after 600 ka, although the largest level of grouping is argued to be restricted to *H. sapiens* (88–91). Migliano et al. (92) suggest that a fluid social structure with multiple levels of clustering in social networks was already characteristic for late Middle Pleistocene hunter-gatherers, at around 330 ka. As these authors point out, raw materials were transported over long distances in the early MSA (93), suggesting changes in mobility and social connections. We find parallels for these new extended distances in the Middle Paleolithic record (94, 95). If individuals were indeed members of much larger and more fluid groups in the Middle Pleistocene, if not much earlier (96), the changes in the archaeological record of the Old World discussed above, occurring at geologically similar times over vast areas, might very well be the result of occasional friendly contact between individuals from different groups, which over time supported cultural transmission over widespread areas and over long periods. In addition to skills relating to fire, this social structure may have been important in the transmission of other relatively complex cultural artifacts and skills (13), as discussed further below.

Note that increasing cooperative interactions might, but need not, be correlated with increasing hominin population sizes. The best available evidence suggests that hominin populations only started to grow at the end of the Pleistocene (97–100). Still, given that population size estimates are notoriously difficult to make, the data might misrepresent Pleistocene demographic patterns. In any case, demography is not the only mechanism that might prompt more intricate cooperative networks. These might just as well be the result of increasing mobility and changes in social organization (101).

Intensified Intergroup Interactions

There is another feature that becomes prominent in the Middle Pleistocene archaeological record, ∼100 ka later than the fire phenomenon: the so-called Levallois technique of stone knapping, which entails a very specific way of preparing a core for the production of one or more large and thin flakes. The chronology of the appearance of the Levallois technique has been reviewed extensively (e.g., refs. 102–105). If properly differentiated from simple forms of prepared-core technology (102–104), its appearance can be assigned to a narrow time slot around 300 ka (104). Levallois was used by different hominin groups, including early *H. sapiens* (e.g., at Jebel Irhoud) and Neandertals, and over major parts of the Old World, in Africa (41, 106, 107), western Asia (108, 109), and Europe (102, 110). Levallois technology has not been recovered in the Middle Pleistocene record of East Asia thus far, with a claim for its possible occurrence at 170 ka in southwest China (111) at best presenting products of the simple prepared-core techniques referred to above (104). In a recent study, Hérisson and Soriano (110) situate the transition of the Lower to Middle Paleolithic, exemplified by the full adoption of Levallois technology, between 280 and 250 ka, in northwestern Europe as well as in the Near East. The spatiotemporal distribution of the Levallois technique is thus similar in geographic area and yet more sharply constrained in time than regular fire use. Accordingly, early Levallois technologies provide additional evidence that cultural diffusion played a role in changes in technology and behavior in the period 400 to 250 ka. Furthermore, the complexity of Levallois stone knapping, demonstrated in extensive experimental knapping and refitting studies [reviewed by Schlanger (112)], means that it can in all probability only be learned through close and prolonged observation combined with active instruction (113, 114), supporting our earlier argument for intensified intergroup interactions around 400 ka.

Interestingly, Hérisson and Soriano (110) make an argument that is similar to the one that we are making here about fire use. These authors observe "...a possible pseudosynchrony of technological changes at a continental scale for the LP/MP [Lower Paleolithic/Middle Paleolithic] time period [...] The *simultaneity of the timing of changes across Europe, Asia and Africa* is perceived when we examine global data with an error margin of more or less 10 ka, a third of the duration of the Upper Palaeolithic" (italics added). That these fast technological changes occur in a wide range of environments, over major parts of the Old World, in their view negates "... *the impact of biological human species and environmental factors*" (110) (italics added). Additionally, the authors emphasize that against the canvas of these swift and large-scale changes, each region shows specific technological traits and trajectories strongly linked to regional cultural patterns, suggesting that Levallois was introduced relatively quickly and integrated with local technological traditions, a conclusion supported by a study of early Levallois assemblages from central Italy, dated between 295 and 290 ka (104).

Given the narrow timeframe, large area, and multiple populations involved, we agree with these authors that demic diffusion (e.g., refs. 109 and 115) is unlikely to explain the large-scale pattern, despite evidence suggestive of occasional expansions of the ranges of Middle Pleistocene early *H. sapiens* (e.g., ref. 116). Note also that, given the more complicated nature of transmission of Levallois technology compared with fire use, and probable role of active teaching (113, 114), questions are raised about the developmental and social context involved. The long juvenile period of Neandertals and early modern humans has been linked to the need to learn extensive, complex physical and social skills (117, 118). A longer life span allows more time spent on learning and more chances to observe others, including those in other groups (13). A modern human pattern of life history may have emerged by the middle part of the Middle Pleistocene (86, 119), creating opportunities for learning complex technical skills and for the diffusion of such skills. In addition, Kuhn and Stiner (120) have highlighted changes in spatial organization in this period, in particular the persistent reuse of places to which hominins were attracted by the availability of imported resources and other hominins, providing a new "evolutionary arena for social interaction"; this could have involved teaching. A further change in the archaeological record for stone tools, the appearance of identifiable regional traditions in the MSA in Africa, may be linked to the learned traditions of long-lived subpopulations, among other factors (121). This provides additional support for the emergence of characteristic forms of cultural behavior, present in *H. sapiens* now, in this period.

Discussion

A thorough review of the spatiotemporal patterns of early fire use and Levallois was beyond the remit of our paper; instead, we focused on pattern interpretation and generating a hypothesis that in our view can push archaeological studies of the Middle Pleistocene in a new direction, if only by stimulating new work explicitly aimed at proving our hypothesis wrong, and by doing so, advance the field's knowledge about the timeline of past behavioral developments.

The Levallois and fire records can be contrasted with that for Acheulean handaxe technology (the main, other widely distributed, distinctive, and chronologically somewhat constrained example of skill transfer occurring early in the Paleolithic). A striking and important difference with Levallois and with regular fire use is that it took hundreds of thousands of years from the first appearance of handaxes in the African record (1.75 Ma) (122) or in the Levant (1.4 to 1.2 Ma) (123) before handaxe technology first showed up in the technological repertoire of the early occupants of Europe, at 0.6 to 0.7 Ma (124–127). Hence, the Acheulean record seems more consistent with a demic scenario (128–130). Indeed, the appearance of Acheulean handaxe technology outside of Africa (its identifiable source area) is widely seen as the result of hominin dispersals (125, 130), a hypothesis supported by phylogeographic analysis of the Acheulean record (131) and, in Europe, by fine-grained patterns of its presence and absence (128, 130, 132). According to some, the Acheulean record even suggests a genetic transmission scenario. Corbey et al. (133) have emphasized the "noncultural" character of the Acheulean "type fossil" and interpreted the "conservative" handaxe as primarily the result of genetic rather than of cultural transmission (see also ref. 134). This interpretation has received several rebuttals highlighting the variability of the Acheulean record (e.g., refs. 135–137), which is considerable, certainly in its later phases (e.g., ref. 125). While we are not negating the possibility of earlier cultural diffusion, the contrast with the Acheulean record, which seems to be best described by demic explanations, supports our argument that fire use and Levallois represent the first clear-cut examples of widespread cultural diffusion of technology during human evolution.

We hypothesize that around 400 ka, cultural processes supported change in technology across wide areas. This indicates, at a minimum, a degree of social tolerance for individuals from different groups, and suggests the less minimal but still plausible hypothesis that more intensive cooperative interactions within larger-scale networks were already in place, occasionally crossing the boundaries between what we usually infer to have been different biological populations within the wider hominin metapopulation. We conclude that the spatial and temporal pattern of the appearance of regular Middle Pleistocene fire use documented in the archaeological record signals more than the advent of an important tool in the hominin toolbox: the presence of cultural behavior more like that of humans today than of our great ape relatives. We suggest that long before the cultural florescence associated with the late MSA/Middle Pleistocene and to a greater extent LSA/Upper Paleolithic periods, hominins were beginning to develop the capacities for complexity, variability, and widespread diffusion of technology and behavior that we tend to associate only with *H. sapiens.*

Data Availability. All study data are included in the main text.

Acknowledgments

We thank Margherita Mussi (Sapienza University of Rome), John Speth (University of Michigan), and Raymond Corbey (Leiden University) for fruitful discussions about aspects of this study; four anonymous PNAS-reviewers for their constructive comments; and the Editor for very helpful suggestions. This study was partly financed through Leiden University's "Liveable Planet" initiative and by the "NWO Spinoza prize" awarded (to W.R.) by the Netherlands Organization for Scientific Research (NWO).

1 M. Chazan, Toward a long prehistory of fire. *Curr. Anthropol.* **58**, S351–S359 (2017).
2 R. Wrangham, *Catching Fire: How Cooking Made Us Human* (Basic Books, 2009).
3 P. P. A. Mazza *et al.*, A new Palaeolithic discovery: Tar-hafted stone tools in a European Mid-Pleistocene bone-bearing bed. *J. Archaeol. Sci.* **33**, 1310–1318 (2006).
4 P. W. Wiessner, Embers of society: Firelight talk among the Ju/'hoansi Bushmen. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 14027–14035 (2014).
5 R. Bliege Bird *et al.*, Fire mosaics and habitat choice in nomadic foragers. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 12904–12914 (2020).
6 F. Scherjon, C. Bakels, K. MacDonald, W. Roebroeks, Burning the land: An ethnographic study of off-site fire use by current and historically documented foragers and implications for the interpretation of past fire practices in the landscape. *Curr. Anthropol.* **56**, 299–326 (2015).
7 A. G. Henry, Neanderthal cooking and the costs of fire. *Curr. Anthropol.* **58**, S329–S336 (2017).
8 A. G. Henry, T. Büdel, P. L. Bazin, Towards an understanding of the costs of fire. *Quat. Int.* **493**, 96–105 (2018).
9 B. McCauley, M. Collard, D. Sandgathe, A cross-cultural survey of on-site fire use by recent hunter-gatherers: Implications for research on Palaeolithic pyrotechnology. *J. Paleolit. Archaeol.* **3**, 566–584 (2020).
10 T. M. Twomey, How domesticating fire facilitated the evolution of human cooperation. *Biol. Philos.* **29**, 89–99 (2014).
11 P. Richerson *et al.*, Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence. *Behav. Brain Sci.* **39**, e30 (2016).
12 I. Colagè, F. d'Errico, Culture: The driving force of human cognition. *Top. Cogn. Sci.* **12**, 654–672 (2020).
13 K. R. Hill, B. M. Wood, J. Baggio, A. M. Hurtado, R. T. Boyd, Hunter-gatherer inter-band interaction rates: Implications for cumulative culture. *PLoS One* **9**, e102806 (2014).
14 K. Sterelny, From hominins to humans: How sapiens became behaviourally modern. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 809–822 (2011).
15 A. Whiten *et al.*, Cultures in chimpanzees. *Nature* **399**, 682–685 (1999).
16 C. P. van Schaik *et al.*, Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105 (2003).
17 C. Tennie, J. Call, M. Tomasello, Ratcheting up the ratchet: On the evolution of cumulative culture. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 2405–2415 (2009).
18 V. Amati, J. Munson, J. Scholnick, Habiba, Applying event history analysis to explain the diffusion of innovations in archaeological networks. *J. Archaeol. Sci.* **104**, 1–9 (2019).
19 S. R. James, Hominid use of fire in the Lower and Middle Pleistocene: A review of the evidence. *Curr. Anthropol.* **30**, 1–26 (1989).
20 W. Roebroeks, P. Villa, On the earliest evidence for habitual use of fire in Europe. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 5209–5214 (2011).
21 J. Sergant, P. Crombé, Y. Perdaen, The 'invisible' hearths: A contribution to the discernment of Mesolithic non-structured surface hearths. *J. Archaeol. Sci.* **33**, 999–1007 (2006).
22 J. A. J. Gowlett, J. S. Brink, A. Caris, S. Hoare, S. M. Rucina, Evidence of burning from bushfires in Southern and East Africa and its relevance to hominin evolution. *Curr. Anthropol.* **58**, S206–S216 (2017).
23 S. M. Mentzer, Microarchaeological approaches to the identification and interpretation of combustion features in prehistoric archaeological sites. *J. Archaeol. Method Theory* **21**, 616–668 (2014).
24 D. M. Sandgathe, F. Berna, Fire and the genus Homo: An introduction to supplement 16. *Curr. Anthropol.* **58**, S165–S174 (2017).
25 F. H. Reidsma, A. van Hoesel, B. J. H. van Os, L. Megens, F. Braadbaart, Charred bone: Physical and chemical changes during laboratory simulated heating under reducing conditions and its relevance for the study of fire use in archaeology. *J. Archaeol. Sci. Rep.* **10**, 282–292 (2016).
26 V. Aldeias, Experimental approaches to archaeological fire features and their behavioral relevance. *Curr. Anthropol.* **58**, S191–S205 (2017).

27 A. van Hoesel, F. H. Reidsma, B. J. H. van Os, L. Megens, F. Braadbaart, Combusted bone: Physical and chemical changes of bone during laboratory simulated heating under oxidising conditions and their relevance for the study of ancient fire use. *J. Archaeol. Sci. Rep.* **28**, 102033 (2019).
28 N. Rolland, Was the emergence of home bases and domestic fire a punctuated event? A review of the Middle Pleistocene record in Eurasia. *Asian Perspect.* **43**, 248–280 (2004).
29 M. Sanz *et al.*, Early evidence of fire in south-western Europe: The Acheulean site of Gruta da Aroeira (Torres Novas, Portugal). *Sci. Rep.* **10**, 12053 (2020).
30 J. F. Peris *et al.*, The earliest evidence of hearths in Southern Europe: The case of Bolomor Cave (Valencia, Spain). *Quat. Int.* **247**, 267–277 (2012).
31 D. Hérisson, J.-L. Locht, P. Auguste, A. Tuffreau, Néandertal et le feu au Paléolithique moyen ancien. Tour d'horizon des traces de son utilisation dans le Nord de la France. *Anthropologie* **117**, 541–578 (2013).
32 J. Jaubert *et al.*, Early Neanderthal constructions deep in Bruniquel Cave in southwestern France. *Nature* **534**, 111–114 (2016).
33 A. G. Henry, A. S. Brooks, D. R. Piperno, Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc. Natl. Acad. Sci. U.S.A.* **108**, 486–491 (2011).
34 R. Shimelmitz *et al.*, 'Fire at will': The emergence of habitual fire use 350,000 years ago. *J. Hum. Evol.* **77**, 196–203 (2014).
35 P. Karkanas *et al.*, Evidence for habitual use of fire at the end of the Lower Paleolithic: Site-formation processes at Qesem Cave, Israel. *J. Hum. Evol.* **53**, 197–212 (2007).
36 R. Barkai, J. Rosell, R. Blasco, A. Gopher, Fire for a reason: Barbecue at Middle Pleistocene Qesem Cave, Israel. *Curr. Anthropol.* **58**, S314–S328 (2017).
37 R. Shahack-Gross *et al.*, Evidence for the repeated use of a central hearth at Middle Pleistocene (300ky ago) Qesem Cave, Israel. *J. Archaeol. Sci.* **44**, 12–21 (2014).
38 R. Dennell, *The Palaeolithic Settlement of Asia* (Cambridge University Press, 2009).
39 S. Weiner, Q. Xu, P. Goldberg, J. Liu, O. Bar-Yosef, Evidence for the use of fire at Zhoukoudian, China. *Science* **281**, 251–253 (1998).
40 X. Gao, S. Zhang, Y. Zhang, F. Chen, Evidence of hominin use and maintenance of fire at Zhoukoudian. *Curr. Anthropol.* **58**, S267–S277 (2017).
41 D. Richter *et al.*, The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle Stone Age. *Nature* **546**, 293–296 (2017).
42 S. E. Bentsen, Using pyrotechnology: Fire-related features and activities with a focus on the African Middle Stone Age. *J. Archaeol. Res.* **22**, 141–175 (2014).
43 L. R. Backwell *et al.*, New excavations at Border Cave, KwaZulu-Natal, South Africa. *J. Field Archaeol.* **43**, 417–436 (2018).
44 L. Wadley *et al.*, Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science* **369**, 863–866 (2020).
45 K. S. Brown *et al.*, Fire as an engineering tool of early modern humans. *Science* **325**, 859–862 (2009).
46 L. Wadley, L. Backwell, F. d'Errico, C. Sievers, Cooked starchy rhizomes in Africa 170 thousand years ago. *Science* **367**, 87–91 (2020).
47 M. J. Walker *et al.*, Combustion at the late Early Pleistocene site of Cueva Negra del Estrecho del Río Quípar (Murcia, Spain). *Antiquity* **90**, 571–589 (2016).
48 S. E. Rhodes *et al.*, Fire in the early Palaeolithic: Evidence from burnt small mammal bones at Cueva Negra del Estrecho del Río Quípar, Murcia, Spain. *J. Archaeol. Sci. Rep.* **9**, 427–436 (2016).
49 N. Alperson-Afil, N. Goren-Inbar, *The Acheulian Site of Gesher Benot Ya'aqov Volume II: Ancient Flames and Controlled Use of Fire* (Springer Science & Business Media, 2010).
50 N. Alperson-Afil, Spatial analysis of fire: Archaeological approach to recognizing early fire. *Curr. Anthropol.* **58**, S258–S266 (2017).
51 P. B. Beaumont, The edge: More on fire-making by about 1.7 million years ago at Wonderwerk Cave in South Africa. *Curr. Anthropol.* **52**, 585–595 (2011).
52 F. Berna *et al.*, Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. *Proc. Natl. Acad. Sci. U.S.A.* **109**, E1215–E1220 (2012).
53 C. K. Brain, "The occurrence of burnt bones at Swartkrans and their implications for the control of fire by early hominids" in *Swartkrans: A Cave Chronicle of Early Man*, C. K. Brain, Ed. (Transvaal Museum, 1993), pp. 229–242.
54 A. I. R. Herries, D. Curnoe, J. W. Adams, A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quat. Int.* **202**, 14–28 (2009).
55 J. A. J. Gowlett, R. W. Wrangham, Earliest fire in Africa: Towards the convergence of archaeological evidence and the cooking hypothesis. *Azania* **48**, 5–30 (2013).
56 S. Hlubik, F. Berna, C. Feibel, D. Braun, J. W. K. Harris, Researching the nature of fire at 1.5 Mya on the site of FxJj20 AB, Koobi Fora, Kenya, using high-resolution spatial analysis and FTIR spectrometry. *Curr. Anthropol.* **58**, S243–S257 (2017).
57 S. Hlubik *et al.*, Hominin fire use in the Okote member at Koobi Fora, Kenya: New evidence for the old debate. *J. Hum. Evol.* **133**, 214–229 (2019).
58 R. Wrangham, R. Carmody, Human adaptation to the control of fire. *Evol. Anthropol.* **19**, 187–199 (2010).
59 G. Isaac, Early hominids and fire at Chesowanja, Kenya. *Nature* **296**, 870 (1982).
60 P. Goldberg, F. Berna, M. Chazan, Deposition and diagenesis in the Earlier Stone Age of Wonderwerk Cave, Excavation 1, South Africa. *Afr. Archaeol. Rev.* **32**, 613–643 (2015).
61 M. C. Stahlschmidt *et al.*, On the evidence for human use and control of fire at Schöningen. *J. Hum. Evol.* **89**, 181–201 (2015).
62 W. Roebroeks, K. MacDonald, F. Scherjon, "Establishing patterns of early fire use in human evolution" in *The Beef behind All Possible Pasts. The Tandem Festschrift in Honour of Elaine Turner and Martin Street*, S. Gaudzinski-Windheuser, O. Jöris, Eds. (Verlag des Römisch-Germanischen Zentralmuseums, 2021), pp. 7–16.
63 J. A. J. Gowlett, J. W. K. Harris, D. Walton, B. A. A. Wood, Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. *Nature* **294**, 125–129 (1981).
64 J. D. Clark, J. W. K. Harris, Fire and its roles in early hominid lifeways. *Afr. Archaeol. Rev.* **3**, 3–27 (1985).
65 M. Mussi, F. Altamura, R. Bonnefille, D. De Rita, R. T. Melis, The environment of the Ethiopian highlands at the Mid Pleistocene Transition: Fauna, flora and hominins in the 850-700 ka sequence of Gombore II (Melka Kunture). *Quat. Sci. Rev.* **149**, 259–268 (2016).
66 J. Chavaillon, A. Berthelet, "The archaeological sites of Melka Kunture" in *Studies on the Early Paleolithic Site of Melka Kunture, Ethiopia*, J. Chavaillon, M. Piperno, Eds. (Istituto Italiano di Preistoria e Protostoria, 2004), pp. 25–80.
67 D. M. Sandgathe, Identifying and describing pattern and process in the evolution of hominin use of fire. *Curr. Anthropol.* **58**, S360–S370 (2017).
68 S. Pääbo, The diverse origins of the human gene pool. *Nat. Rev. Genet.* **16**, 313–314 (2015).
69 M. J. Hubisz, A. L. Williams, A. Siepel, Mapping gene flow between ancient hominins through demography-aware inference of the ancestral recombination graph. *bioRxiv* [Preprint] (2019). https://www.biorxiv.org/content/10.1101/687368v1 (Accessed 30 March 2020).
70 M. Meyer *et al.*, Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature* **531**, 504–507 (2016).
71 C. Posth *et al.*, Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. *Nat. Commun.* **8**, 16046 (2017).
72 P. U. Clark *et al.*, The middle Pleistocene transition: Characteristics, mechanisms, and implications for long-term changes in atmospheric pCO2. *Quat. Sci. Rev.* **25**, 3150–3184 (2006).
73 A. C. Sorensen, On the relationship between climate and Neandertal fire use during the Last Glacial in south-west France. *Quat. Int.* **436**, 114–128 (2017).
74 P. J. Richerson, R. Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution* (University of Chicago Press, 2005).
75 S. J. Lycett, M. Collard, W. C. McGrew, Are behavioral differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. *Am. J. Phys. Anthropol.* **142**, 461–467 (2010).
76 J. Fort, Synthesis between demic and cultural diffusion in the Neolithic transition in Europe. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 18669–18673 (2012).
77 C. Perreault, The pace of cultural evolution. *PLoS One* **7**, e45150 (2012).
78 A. Jerardino, J. Fort, N. Isern, B. Rondelli, Cultural diffusion was the main driving mechanism of the Neolithic transition in southern Africa. *PLoS One* **9**, e113672 (2014).

79 L. Hazelwood, J. Steele, "Colonising new landscapes: Detectability of the first phase" in *The Colonization of Unfamiliar Landscapes: The Archaeology of Adaptation*, M. Rockman, J. Steele, Eds. (Routledge, 2003), pp. 203–221.
80 J. J. Hublin, Out of Africa: Modern human origins special feature: The origin of Neandertals. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 16022–16027 (2009).
81 A. Gómez-Robles, Dental evolutionary rates and its implications for the Neanderthal-modern human divergence. *Sci. Adv.* **5**, eaaw1268 (2019).
82 S. E. Churchill, *Thin on the Ground: Neandertal Biology, Archeology and Ecology* (John Wiley & Sons, Ltd, 2014).
83 F. Mafessoni *et al.*, A high-coverage Neandertal genome from Chagyrskaya Cave. *bioRxiv* [Preprint] (2020). https://www.biorxiv.org/content/10.1101/2020.03.12.988956v1 (Accessed 25 June 2020).
84 A. C. Pisor, M. Surbeck, The evolution of intergroup tolerance in nonhuman primates and humans. *Evol. Anthropol.* **28**, 210–223 (2019).
85 B. Fruth, G. Hohmann, Food sharing across borders: First observation of intercommunity meat sharing by Bonobos at LuiKotale, DRC. *Hum. Nat.* **29**, 91–103 (2018).
86 S. L. Robson, B. Wood, Hominin life history: Reconstruction and evolution. *J. Anat.* **212**, 394–425 (2008).
87 D. W. Bird, R. B. Bird, B. F. Codding, D. W. Zeanah, Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. *J. Hum. Evol.* **131**, 96–108 (2019).
88 L. C. Aiello, R. I. M. Dunbar, Neocortex size, group size, and the evolution of language. *Curr. Anthropol.* **34**, 184–193 (1993).
89 R. I. M. Dunbar, Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22**, 469–493 (1992).
90 R. I. M. Dunbar, "Why only humans have language" in *The Prehistory of Language*, R. Botha, C. Knight, Eds. (Oxford University Press, 2009), pp. 12–35.
91 J. Gowlett, C. Gamble, R. Dunbar, Human evolution and the archaeology of the social brain. *Curr. Anthropol.* **53**, 693–722 (2012).
92 A. B. Migliano *et al.*, Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. *Sci. Adv.* **6**, eaax5913 (2020).
93 A. S. Brooks *et al.*, Long-distance stone transport and pigment use in the earliest Middle Stone Age. *Science* **360**, 90–94 (2018).
94 J. Féblot-Augustins, "Raw material transport patterns and settlement systems in the European Lower and Middle Palaeolithic: Continuity, change and variability" in *The Middle Palaeolithic Occupation of Europe*, W. Roebroeks, C. Gamble, Eds. (University of Leiden, 1999), pp. 193–214.
95 A. Turq, W. Roebroeks, L. Bourguignon, J.-P. Faivre, The fragmented character of Middle Palaeolithic stone tool technology. *J. Hum. Evol.* **65**, 641–655 (2013).
96 N. Goren-Inbar, A. Belfer-Cohen, Reappraisal of hominin group size in the Lower Paleolithic: An introduction to the special issue. *J. Hum. Evol.* **144**, 102821 (2020).
97 C. D. Huff, J. Xing, A. R. Rogers, D. Witherspoon, L. B. Jorde, Mobile elements reveal small population size in the ancient ancestors of Homo sapiens. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2147–2152 (2010).
98 L. S. Premo, J.-J. Hublin, Culture, population structure, and low genetic diversity in Pleistocene hominins. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 33–37 (2009).
99 M. Kuhlwilm *et al.*, Ancient gene flow from early modern humans into Eastern Neanderthals. *Nature* **530**, 429–433 (2016).
100 R. Pennington, "Hunter-gatherer demography" in *Hunter-Gatherers: An Interdisciplinary Perspective*, C. Panter-Brick, R. H. Layton, P. Rowley-Conwy, Eds. (Cambridge University Press, Cambridge, UK, 2001), pp. 170–204.
101 M. Grove, E. Pearce, R. I. M. Dunbar, Fission-fusion and the evolution of hominin social systems. *J. Hum. Evol.* **62**, 191–200 (2012).
102 M. White, N. Ashton, Lower Palaeolithic core technology and the origins of the Levallois method in North-Western Europe. *Curr. Anthropol.* **44**, 598–608 (2003).
103 A. Malinsky-Buller, The muddle in the Middle Pleistocene: The Lower–Middle Paleolithic transition from the Levantine perspective. *J. World Prehist.* **29**, 1–78 (2016).
104 S. Soriano, P. Villa, Early Levallois and the beginning of the Middle Paleolithic in central Italy. *PLoS One* **12**, e0186082 (2017).
105 M.-H. Moncel *et al.*, Early Levallois core technology between Marine Isotope Stage 12 and 9 in Western Europe. *J. Hum. Evol.* **139**, 102735 (2020).
106 C. A. Tryon, J. T. Faith, Variability in the Middle Stone Age of Eastern Africa. *Curr. Anthropol.* **54**, S234–S254 (2013).
107 S. Wurz, Technological trends in the Middle Stone Age of South Africa between MIS 7 and MIS 3. *Curr. Anthropol.* **54**, S305–S319 (2013).
108 D. S. Adler *et al.*, Early Levallois technology and the Lower to Middle Paleolithic transition in the Southern Caucasus. *Science* **345**, 1609–1613 (2014).
109 Y. Zaidner, M. Weinstein-Evron, The emergence of the Levallois technology in the Levant: A view from the Early Middle Paleolithic site of Misliya Cave, Israel. *J. Hum. Evol.* **144**, 102785 (2020).
110 D. Hérisson, S. Soriano, A view of the Lower to Middle Paleolithic boundary from Northern France, far from the Near East? *J. Hum. Evol.* **145**, 102814 (2020).
111 Y. Hu *et al.*, Late Middle Pleistocene Levallois stone-tool technology in southwest China. *Nature* **565**, 82–85 (2019).
112 N. Schlanger, Understanding Levallois: Lithic technology and cognitive archaeology. *Camb. Archaeol. J.* **6**, 231–254 (1996).
113 S. J. Lycett, N. von Cramon-Taubadel, M. I. Eren, Levallois: Potential implications for learning and cultural transmission capacities. *Lithic Technol.* **41**, 19–38 (2016).
114 T. Wynn, F. L. Coolidge, Beyond symbolism and language: An introduction to Supplement 1, working memory. *Curr. Anthropol.* **51**, S5–S16 (2010).
115 R. Foley, M. M. Lahr, Mode 3 technologies and the evolution of modern humans. *Camb. Archaeol. J.* **7**, 3–36 (1997).
116 I. Hershkovitz *et al.*, The earliest modern humans outside Africa. *Science* **359**, 456–459 (2018).
117 C. P. van Schaik, G. R. Pradhan, C. Tennie, Teaching and curiosity: Sequential drivers of cumulative cultural evolution in the hominin lineage. *Behav. Ecol. Sociobiol.* **73**, 2 (2019).
118 M. D. Gurven, R. J. Davison, T. S. Kraft, The optimal timing of teaching and learning across the life course. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **375**, 20190500 (2020).
119 T. M. Smith, Teeth and human life-history evolution. *Annu. Rev. Anthropol.* **42**, 191–208 (2013).
120 S. L. Kuhn, M. C. Stiner, Hearth and home in the Middle Pleistocene. *J. Anthropol. Res.* **75**, 305–327 (2019).
121 E. M. L. Scerri *et al.*, Did our species evolve in subdivided populations across Africa, and why does it matter? *Trends Ecol. Evol.* **33**, 582–594 (2018).
122 C. J. Lepre *et al.*, An earlier origin for the Acheulian. *Nature* **477**, 82–85 (2011).
123 O. Bar-Yosef, M. Belmaker, "Ubeidiya" in *Quaternary of the Levant: Environments, Climate Change, and Humans*, Y. Enzel, O. Bar-Yosef, Eds. (Cambridge University Press, 2017) Part III, pp. 179–185.
124 P. Antoine *et al.*, The earliest evidence of Acheulian occupation in Northwest Europe and the rediscovery of the Moulin Quignon site, Somme valley, France. *Sci. Rep.* **9**, 13091 (2019).
125 N. Ashton, R. Davis, Cultural mosaics, social structure, and identity: The Acheulean threshold in Europe. *J. Hum. Evol.* **156**, 103011 (2021).
126 M.-H. Moncel *et al.*, The origin of early Acheulean expansion in Europe 700 ka ago: New findings at Notarchirico (Italy). *Sci. Rep.* **10**, 13802 (2020).
127 P. Voinchet *et al.*, New chronological data (ESR and ESR/U-series) for the earliest Acheulian sites of north-western Europe. *J. Quat. Sci.* **30**, 610–622 (2015).
128 C. Shipton, M. White, Handaxe types, colonization waves, and social norms in the British Acheulean. *J. Archaeol. Sci. Rep.* **31**, 102352 (2020).
129 M.-H. Moncel *et al.*, Early evidence of Acheulean settlement in northwestern Europe—La Noira site, a 700,000 year-old occupation in the center of France. *PLoS One* **8**, e75529 (2013).
130 M.-H. Moncel, J. Despriée, G. Courcimaut, P. Voinchet, J.-J. Bahain, La Noira Site (Centre, France) and the technological behaviours and skills of the earliest Acheulean in western Europe between 700 and 600 ka. *J. Paleolit. Archaeol.* **3**, 255–301 (2020).
131 S. J. Lycett, Understanding ancient hominin dispersals using artefactual data: A phylogeographic analysis of Acheulean handaxes. *PLoS One* **4**, e7404 (2009).
132 N. Rolland, The Early Pleistocene human dispersals in the Circum-Mediterranean Basin and initial peopling of Europe: Single or multiple pathways? *Quat. Int.* **316**, 59–72 (2013).
133 R. Corbey, A. Jagich, K. Vaesen, M. Collard, The Acheulean handaxe: More like a bird's song than a Beatles' tune? *Evol. Anthropol.* **25**, 6–19 (2016).
134 R. Corbey, Baldwin effects in early stone tools. *Evol. Anthropol.* **29**, 237–244 (2020).
135 R. Hosfield, J. Cole, J. McNabb, Less of a bird's song than a hard rock ensemble. *Evol. Anthropol.* **27**, 9–20 (2018).
136 J. McNabb, Journeys in space and time. Assessing the link between Acheulean handaxes and genetic explanations. *J. Archaeol. Sci. Rep.* **13**, 403–414 (2017).
137 J. McNabb, Further thoughts on the genetic argument for handaxes. *Evol. Anthropol.* **29**, 220–236 (2020).