LETTER

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1 # The timing and spatiotemporal patterning of Neanderthal disappearance

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**The timing of Neanderthal disappearance and the extent to which they overlapped with the earliest incoming anatomically modern humans (AMHs) in Eurasia are key questions in palaeoanthropology[1,2]. Determining the spatiotemporal relationship between the two populations is crucial if we are to understand the processes, timing and reasons leading to the disappearance of Neanderthals and the likelihood of cultural and genetic exchange. Serious technical challenges, however, have hindered reliable dating of the period, as the radiocarbon method reaches its limit at ~50,000 years ago[3]. Here we apply improved accelerator mass spectrometry $^{14}$C techniques to construct robust chronologies from 40 key Mousterian and Neanderthal archaeological sites, ranging from Russia to Spain. Bayesian age modelling was used to generate probability distribution functions to determine the latest appearance date. We show that the Mousterian ended by 41,030–39,260 calibrated years BP (at 95.4% probability) across Europe. We also demonstrate that succeeding 'transitional' archaeological industries, one of which has been linked with Neanderthals (Châtelperronian)[4], end at a similar time. Our data indicate that the disappearance of Neanderthals occurred at different times in different regions. Comparing the data with results obtained from the earliest dated AMH sites in Europe, associated with the Uluzzian technocomplex[5], allows us to quantify the temporal overlap between the two human groups. The results reveal a significant overlap of 2,600–5,400 years (at 95.4% probability). This has important implications for models seeking to explain the cultural, technological and biological elements involved in the replacement of Neanderthals by AMHs. A mosaic of populations in Europe during the Middle to Upper Palaeolithic transition suggests that there was ample time for the transmission of cultural and symbolic behaviours, as well as possible genetic exchanges, between the two groups.**

European Palaeolithic sites contain the best evidence for the replacement of one human group (Neanderthals) by another (AMHs)[1]. The nature and process of the replacement, both in cultural and genetic terms, has been the focus of extensive research[1,6,7]. Recent studies of complete Neanderthal and modern human genomic sequences suggest that Neanderthals and AMHs interbred outside Africa[7]. This resulted in an introgression of 1.5–2.1% of Neanderthal-derived DNA[8], or perhaps more[9], in all modern non-African human populations. The analysis of three Neanderthal mitochondrial DNA (mtDNA) genomes from Denisova (Russian Altai), Vindija (Croatia) and Mezmaiskaya (Russian North Caucasus) indicates that the greatest amount of gene flow into non-African AMHs occurred after these Neanderthal populations had separated from each other[8]. At present it is not clear whether interbreeding occurred once or several times outside Africa[10], or where it happened. After the interbreeding episode(s), Neanderthals and their distinctive material culture disappeared and were replaced across Eurasia by AMHs, but the precise timing of this has remained difficult to identify in the absence of a reliable chronological framework[3].

Recent research has shown that radiocarbon ages have usually underestimated the true age of Palaeolithic remains, sometimes by several millennia[3]. This is due largely to problems in removing modern carbon contamination from old organic samples at the limit of the $^{14}$C method.

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The application of more rigorous chemical protocols[11–13] has recently resulted in improved reliability and accuracy. Several determinations that had previously supported late Neanderthal survival have been shown to be marked underestimates (for example, Vindija[14], Zafarraya[15] and Mezmaiskaya[16]) and should be set to one side.

We performed extensive accelerator mass spectrometry (AMS) dating of critical late or final Mousterian archaeological horizons from 40 sites across Europe and the Mediterranean rim to explore the timing of Neanderthal extinction (Fig. 1a and Supplementary Methods). We also dated succeeding 'transitional' contexts, containing stone tool industries associated either with AMHs or with Neanderthals. These include Uluzzian (distributed across peninsular Italy and southern Greece and attributed to AMHs on the basis of associated AMH deciduous teeth excavated in Cavallo Cave[5]) and Châtelperronian (France and Cantabrian Spain) layers, currently linked with Neanderthals on the basis of skeletal and technological evidence, although the association is debated[17,18]. Other transitional industries, such as the Szeletian and Bohunician of central and eastern Europe have not been dated as part of this study, nor have sites outside Europe, such as in the far northern Arctic fringes of Eurasia, where late Mousterian industries have been reported[19].

We obtained 196 AMS radiocarbon measurements and used them to build high-precision age models using Bayesian statistics on the OxCal[20] platform. This allows us to incorporate stratigraphic and other relative age information, along with the calibrated likelihoods for each site. Probability distribution functions (PDFs) corresponding with the temporal boundaries of the latest Mousterian occupations were generated (Fig. 1b and Supplementary Methods).

The results show that the Mousterian end boundary PDFs all fall before 40,000 calibrated years (cal) BP (all probability ranges are expressed at 95.4%) (Fig. 1b). When placed into a single phase Bayesian model, the PDFs result in an overall end boundary ranging from 41,030–39,260 cal BP (Fig. 1c and Supplementary Methods). This PDF represents the age of the latest European Mousterian on the basis of our data.

The combined data suggest that the Mousterian ended at a very similar time, across sites ranging from the Black Sea and the Near East, to the Atlantic coast (Fig. 1a, b). Southern Iberia has been held to represent an exception to a wider European pattern[21], with late survival of Neanderthals previously argued at sites such as Gorham's Cave, Gibraltar[22]. We could not reproduce any of the late dates from sites in this region[15] (Supplementary Methods) and it is apparent that many previous determinations underestimate the real age. It is unclear how long Neanderthals persisted in southern Iberia[15]. More dating evidence is required before we can determine whether Neanderthal presence was later here than elsewhere in Europe.

Our data also reveal differences in the spatiotemporal distribution of the latest Mousterian sites (Fig. 1b). The PDFs obtained were statistically ordered and the results show that significant differences exist between several late Mousterian contexts in different regions of Europe (Supplementary Methods). This may be attributed to the emergence of 'transitional' industries that replace the Mousterian between ~45,000–41,000

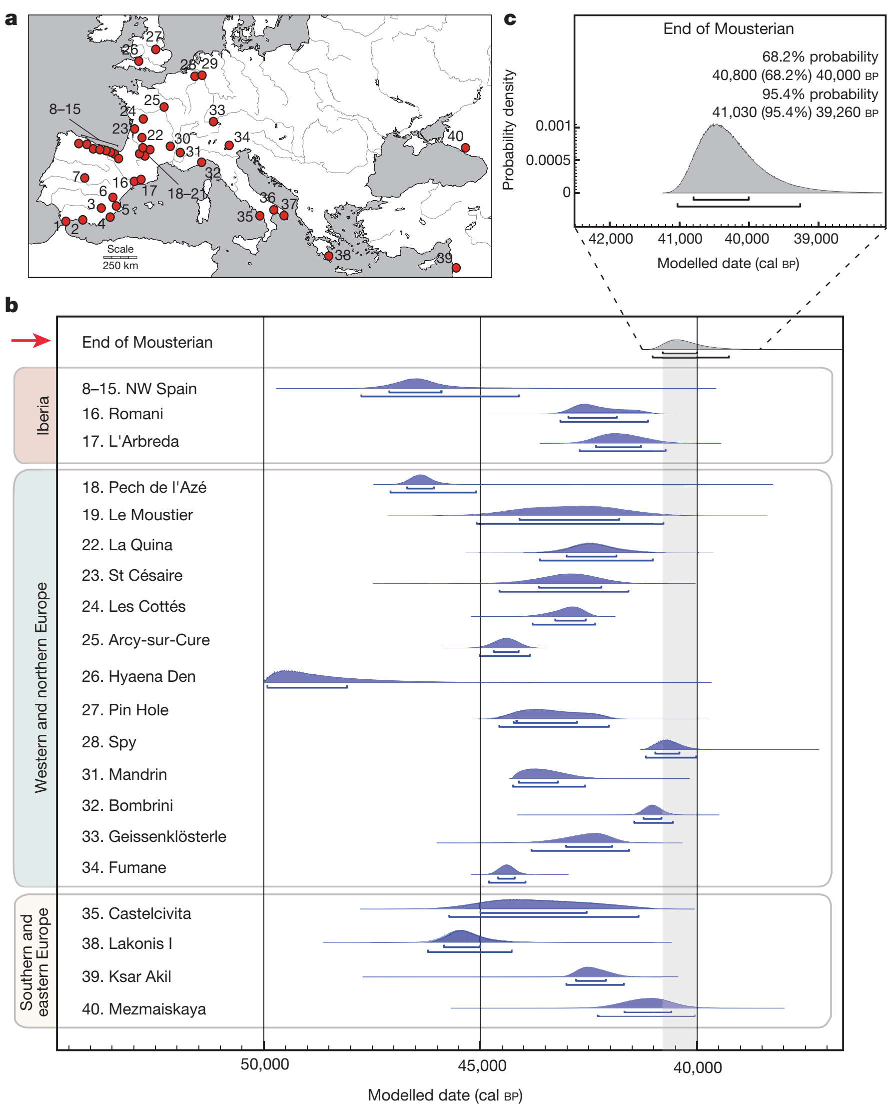


**Figure 1 | Site locations and final boundary age ranges for Mousterian and Neanderthal sites a**, Location of the 40 sites analysed and discussed in this paper. 1: Gorham's Cave; 2: Zafarraya; 3: El Niño; 4: Sima de las Palomas; 5: El Salt; 6: Quebrada; 7: Jarama VI; 8–15: La Viña, El Sidrón, La Güelga, Esquilleu, Morín, Arrillor, Labeko Koba, Lezetxiki; 16: Abric Romaní; 17: L'Arbreda; 18–21: Pech de l'Azé, Le Moustier, La Ferrassie, La Chappelle; 22: La Quina; 23: Saint-Césaire; 24: Les Cottés; 25: Arcy-sur-Cure; 26: Hyaena Den; 27: Pin Hole; 28: Spy; 29: Grotte Walou; 30: Néron; 31: Mandrin; 32: Bombrini/Mochi; 33: Geissenklösterle; 34: Fumane; 35: Castelcivita; 36: Oscurusciuto; 37: Cavallo; 38: Lakonis; 39: Ksar Akil; 40: Mezmaiskaya. **b**, Bayesian PDFs for the model boundaries of the final dated Mousterian phases by site across Europe (generated using OxCal4.2 software[20] and INTCAL13 (ref. 29)). **c**, PDF for the latest Mousterian based on the data in **b**.


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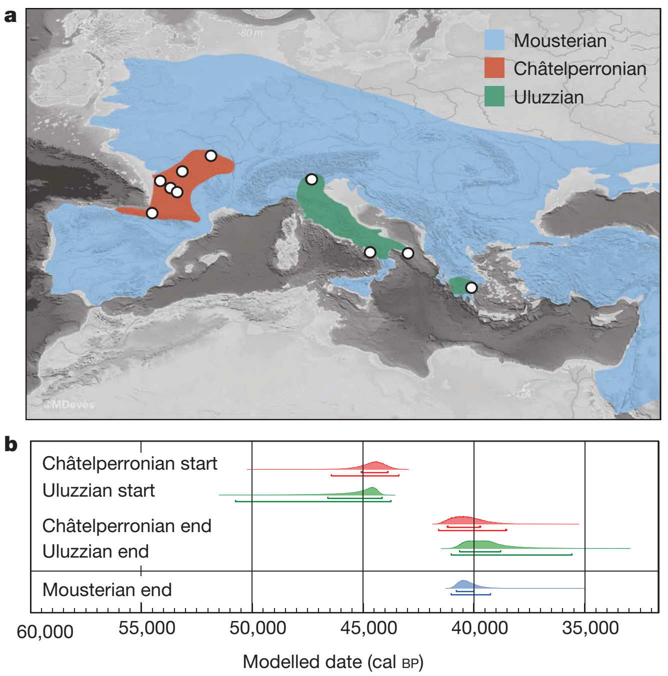


**Figure 2 | Transitional site locations and Bayesian age ranges for the start and end of the Châtelperronian and Uluzzian technocomplexes.** **a**, Geographic distribution of Châtelperronian (red), Uluzzian (green) and Mousterian (blue) technocomplexes. Map is shown with sea level at −80 m below the present day[1]. Dated 'transitional' industry site locations are shown.
8 Figure prepared by M. Devès. **b**, Bayesian modelled PDFs for the start and end boundaries of the Châtelperronian and Uluzzian in western Europe. The Mousterian end boundary (Fig. 1c) is shown for comparison. The three end boundaries overlap, despite the fact that the late Mousterian always predates the two transitional industries stratigraphically where they co-occur.

cal BP in some, but not all regions. At Fumane in Italy, for example, the Mousterian is replaced by the Uluzzian at 44,800–43,950 cal BP, while at Mochi/Bombrini on the Italy–France border the Mousterian seems to last longer—until 41,460–40,500 cal BP. In the latter region, the Aurignacian arrives after a hiatus and no transitional complexes are evident. Since both the Uluzzian and Aurignacian are linked to AMHs, this lends support to the idea of a staggered replacement of Neanderthals in Italy as they neared local extinction (Supplementary Methods). Other late Mousterian contexts in sites in northern Spain, such as Abric Romaní and L'Arbreda, are also considerably later than Fumane, suggesting that the Mousterian ended at different times in some parts of Europe.

The temporal range of the 'transitional' technocomplexes was also examined. With regard to the Châtelperronian, it is apparent on stratigraphic grounds that the Mousterian precedes it at all sites where both occur. However, our results show that the Châtelperronian at some sites (for example, Arcy-sur-Cure) starts statistically significantly before the end of the Mousterian at other sites in Europe such as Abric Romaní and Geissenklösterle (Germany). If Neanderthals were responsible for both Mousterian and Châtelperronian, the implication is that there was considerable regional variation in their behaviour and adaptation strategies during this transition period. Assuming that the Châtelperronian is associated with Neanderthals, we combined the end boundaries for both into a single-phase Bayesian model and obtained a final 'Neanderthal' end PDF of 40,890–39,220 cal BP. The result is indistinguishable from the final Mousterian PDF, showing that uncertainty over the authorship of the Châtelperronian does not affect the age estimated for the last Neanderthals; they did not survive after ~41,000–39,000 cal BP (Fig. 2b).

By comparing the final Neanderthal PDF with those obtained for the start of the Uluzzian at the Cavallo site[23], we can quantify the temporal overlap between Neanderthals and the earliest western European AMHs (Fig. 2b). The difference is significant and ranges from 2,600 to 5,400 years at 95.4% probability. Coexistence has been linked previously with the possibility of cultural transmission from AMHs to Neanderthals, termed 'acculturation'[24], as a means of accounting for late Neanderthal

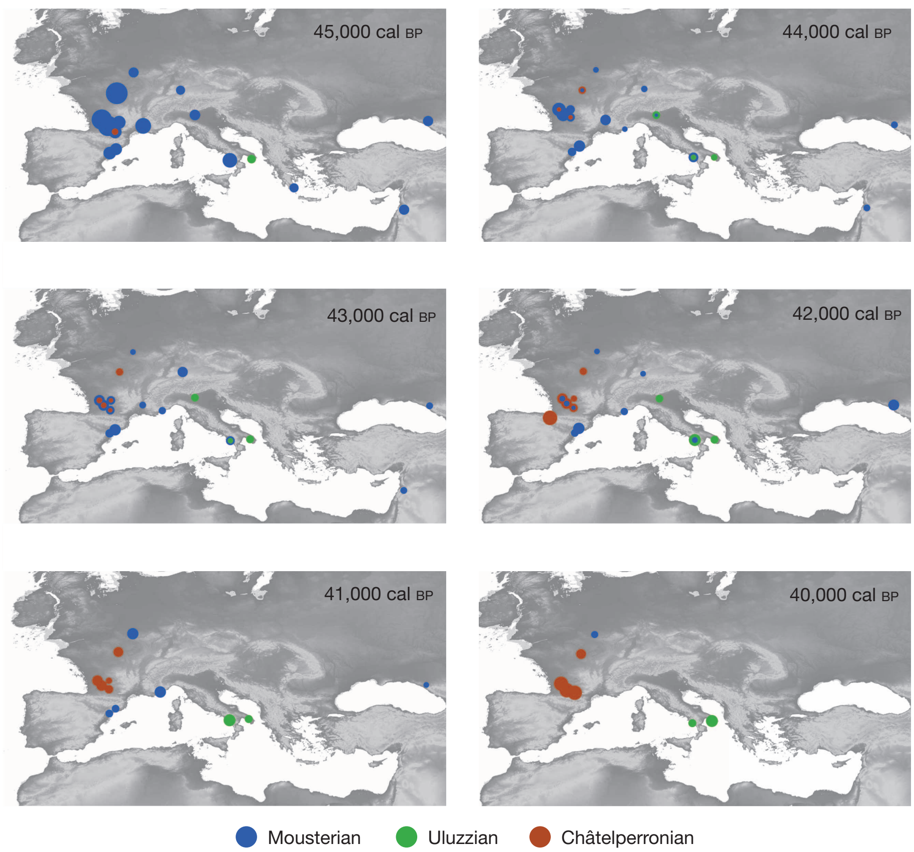


**Figure 3 | Time slices for western Europe between 45,000 and 40,000 cal BP showing the distribution of the Mousterian, Châtelperronian and Uluzzian modelled ages.** The size of the dots represents increasing and decreasing levels of the 95.4% probability ranges determined from the duration (date range) of each industry, as calculated by individual Bayesian site models (Supplementary Methods). Dots with two colours indicate the transition from one date industry range to the next.

technical and behavioural development. The early presence of AMHs in Mediterranean Europe by ~45,000–43,000 cal BP (ref. 23) and the potential overlapping time may have acted as a stimulus for putative Neanderthal innovative and symbolic behaviour in the millennia before their disappearance. When we compare the start and end boundary PDFs for both Uluzzian and Châtelperronian sites we observe that they are very similar (Fig. 2b). This may provide further support for an acculturation model. Alternatively, this similarity in the start dates of the two industries might be seen as reflecting an AMH authorship for both. If this were the case, then the distribution of early modern humans would be wider than expected. Since the physical evidence linking these industries to different human groups is scarce, these interpretations are potentially prone to change with new excavation data.

High-precision chronometric data and Bayesian modelling allows us to map the spatiotemporal relationship between the three technocomplexes during the period ~45,000–41,000 cal BP as a series of time slices (Fig. 3 and Supplementary Methods). Since there is little to no robust evidence for interstratification of the transitional industries within Mousterian archaeological layers, we conclude that the chronological overlap observed must have also involved a degree of spatial separation between the two populations, regardless of whether Neanderthals were responsible for the Châtelperronian or not. In turn, this suggests that the dispersal of early AMHs was initially geographically circumscribed, proceeding step-wise, with the Uluzzian first and the Aurignacian following a few millennia later. The transitional industries, including those not analysed here, may be broadly contemporaneous technocomplexes that remained spatially distinct from one another. Rather than a rapid model of replacement of autochthonous European Neanderthals by incoming AMHs, our results support a more complex picture, one characterized by a biological and cultural mosaic that lasted for several thousand years.

## METHODS SUMMARY

AMS radiocarbon dating was undertaken at the Oxford Radiocarbon Accelerator Unit, University of Oxford. Collagen was extracted using the methods outlined previously[11,25]. Shell samples were dated according to the protocol outlined previously[26] An acid–base oxidation/stepped combustion (ABOx-SC) method was used for charcoal[13]. Radiocarbon ages are given as conventional ages BP as described previously[27]. Corrections were made to bone collagen AMS determinations using a laboratory pre-treatment background subtraction[28]. Bones analysed range from very well preserved (a maximum of 14.9wt% collagen) to poorly preserved (a minimum of ~1.0wt% collagen). C:N atomic ratios and other analytical parameters were measured to determine the quality of the extracted collagen. The INTCAL13 (ref. 29) calibration curve and the OxCal4.2 (ref. 20) program were used in the calibration and Bayesian age modelling. Supplementary Methods contains details of the archaeological sites investigated, the samples used, all determinations and the full Bayesian analysis.

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**Supplementary Information** is available in the online version of the paper.

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**Author Contributions** T.H. and R.J. conceived the project. T.H. obtained funding and directed the project. T.H., R.W., K.D., F.B., C.B.R. and A.Ma. performed pre-treatment chemistry, AMS dating and Bayesian analysis using OxCal. T.H., R.W., K.D., L.B. and R.J. sampled materials for AMS dating. T.H. and K.D. wrote the paper and all co-authors contributed to the draft. K.D. and T.H. produced the figures and illustrations. R.J., L.B., M.C., A.A., J.B., C.B.-R., C.Be., C.Bo., P.B., M.C., N.J.C., C.D., A.F., B.G., P.G., A.G.-M., S.G., P.H., B.H., M.-J.I.-C., A.J., J.F.J.P., J.-M.M.-F., J.M., M.M., L.M., E.M., A.Mo., F.N., E.P., M.P., S.P., M.d.I.R., J.R.-S., A.R., D.S., P.S., L.S., J.S., N.S., A.V. and R.P. provided permits and archaeological samples, expertise on site sequences and prior data for the modelling.

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| | | AOP | ☐ | Author corrx | ☐ |
| | | Extended Data | ☐ | Web summary | ☐ |
| | | | | Accession codes link | ☐ |