

The timing and spatiotemporal patterning of Neanderthal disappearance

Tom Higham¹, Katerina Douka¹, Rachel Wood^{1,2}, Christopher Bronk Ramsey¹, Fiona Brock¹, Laura Basell³, Marta Camps⁴, Alvaro Arrizabalaga⁵, Javier Baena⁶, Cecillio Barroso-Ruiz⁷, Christopher Bergman⁸, Coralie Boitard⁹, Paolo Boscato¹⁰, Miguel Caparrós¹¹, Nicholas J. Conard^{12,13}, Christelle Draily¹⁴, Alain Froment¹⁵, Bertila Galván¹⁶, Paolo Gambassini¹⁰, Alejandro García-Moreno^{17,37}, Stefano Grimaldi¹⁸, Paul Haesaerts¹⁹, Brigitte Holt²⁰, Maria-Jose Iriarte-Chiapusso⁵, Arthur Jelinek²¹, Jesús F. Jordá Pardo²², José-Manuel Maíllo-Fernández²², Anat Marom^{1,23}, Julià Maroto²⁴, Mario Menéndez²², Laure Metz²⁵, Eugène Morin²⁶, Adriana Moroni¹⁰, Fabio Negrino²⁷, Eleni Panagopoulou²⁸, Marco Peresani²⁹, Stéphane Pirson³⁰, Marco de la Rasilla³¹, Julien Riel-Salvatore³², Annamaria Ronchitelli¹⁰, David Santamaria³¹, Patrick Semal³³, Ludovic Slimak²⁵, Joaquim Soler²⁴, Narcís Soler²⁴, Aritza Villaluenga¹⁷, Ron Pinhasi³⁴ & Roger Jacobi^{35,36,‡}

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 ago³. Here we apply improved accelerator mass spectrometry ¹⁴C 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 technocomplex⁵, 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 Africa⁷. This resulted in an introgression of 1.5–2.1% of Neanderthal-derived DNA⁸, or perhaps more⁹, 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 other⁸. At present it is not clear whether interbreeding occurred once or several times outside Africa¹⁰, 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 framework³.

Recent research has shown that radiocarbon ages have usually underestimated the true age of Palaeolithic remains, sometimes by several millennia³. This is due largely to problems in removing young carbon contamination from old organic samples at the limit of the ¹⁴C method. The application of more rigorous chemical protocols^{11–13} has recently resulted in improved reliability and accuracy. Several determinations

¹Oxford Radiocarbon Accelerator Unit, Research Laboratory for Archaeology & the History of Art, University of Oxford, Oxford OX1 3QY, UK. ²Research School for Earth Sciences, Australian National University, Canberra 0200, Australia. ³School of Geography, Archaeology and Palaeoecology (GAP), Queen's University Belfast, Belfast BT7 1NN, UK. ⁴School of Languages, Literatures and Cultures, College Park, 4102 Jiménez Hall, University of Maryland, Maryland 20742-4821, USA. ⁵Research Team on Prehistory (IT-622-13), IKERBASQUE, University of the Basque Country (UPV-EHU), Tomás y Valiente Street, 01006 Vitoria-Gasteiz, Spain. ⁶Departamento Prehistoria y Arqueología, Universidad Autónoma de Madrid, Campus Cantoblanco, 28049 Madrid, Spain. ⁷Fundación Instituto de Investigación de Prehistoria y Evolución Humana, Plaza del Coso 1, 14900 Lucena, Córdoba, Spain. ⁸URS, 525 Vine Street, Suite 1800, Cincinnati, Ohio 45202, USA. ⁹8 rue des Sapins, 67100 Strasbourg, France. ¹⁰Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, U.R. Preistoria e Antropologia, Università degli Studi di Siena, Via Laterina 8, 53100 Siena, Italy. ¹¹Département de Préhistoire, Muséum National d'Histoire Naturelle, 75013 Paris, France. ¹²Abt. Ältere Urgeschichte und Quartärökologie, Universität Tübingen, Schloss Hohentübingen, 72070 Tübingen, Germany. ¹³Tübingen Senckenberg Center for Human Evolution and Paleocology, Schloss Hohentübingen, 72070 Tübingen, Germany. ¹⁴Service public de Wallonie, DGO4, Service de l'Archéologie, rue des Martyrs, 22, B-6700 Arlon, Belgium. ¹⁵Laboratoire d'Éco-anthropologie et Ethnobiologie, Musée de l'Homme, 17 place du Trocadéro, 75116 Paris, France. ¹⁶Departamento de Prehistoria, Arqueología, Antropología e Historia Antigua, Universidad de La Laguna, Campus de Guajara, 38071 Tenerife, Spain. ¹⁷Monrepos Archaeological Research Centre and Museum for Human Behavioural Evolution, Schloss Monrepos, D-56567 Neuwied, Germany. ¹⁸Laboratorio di Preistoria 'B. Bagolini', Dipartimento di Lettere e Filosofia, Università degli Studi di Trento, via Tommaso Gar, 14 I-38122 Trento, Italy. ¹⁹Institut Royal des Sciences Naturelles de Belgique, rue Vautier 29, B-1000 Brussels, Belgium. ²⁰Department of Anthropology, University of Massachusetts, 103 Machmer Hall, Amherst, Massachusetts 01003, USA. ²¹School of Anthropology, Emil W. Haurly Building, University of Arizona, Tucson, Arizona 85721-0030, USA. ²²Departamento de Prehistoria y Arqueología, UNED, Paseo Senda del Rey 7, 20840, Madrid, Spain. ²³The Kimmel Center for Archaeological Science, Weizmann Institute of Science, Rehovot 76100, Israel. ²⁴Àrea de Prehistòria, Universitat de Girona, pl. Ferrater Mora 1, 17071 Girona, Spain. ²⁵CNRS, UMR 5608, TRACES, Toulouse Jean Jaurès University, Maison de la Recherche, 5 Allées Antonio Machado, 31058 Toulouse, Cedex 9, France. ²⁶Department of Anthropology, Trent University, Life and Health Sciences Building Block C, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada. ²⁷Dipartimento di Antichità, Filosofia e Storia, Università di Genova, Via Balbi 2, Genova I-16126, Italy. ²⁸Ephoreia of Paleolithic Anthropology of Southern Greece, Ardittou 34B, Athens 11636, Greece. ²⁹Università di Ferrara, Dipartimento di Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Corso Ercole I d'Este 32, I-44100 Ferrara, Italy. ³⁰Service public de Wallonie, DGO4, Direction de l'Archéologie, rue des Brigades d'Irlande, 1, B-5100 Jambes, Belgium. ³¹Departamento de Historia, Universidad de Oviedo, c/Teniente Alfonso Martínez, s/n, 33011 Oviedo, Spain. ³²Département d'Anthropologie, Université de Montréal, C. P. 6128, Succursale Centre-ville, Montréal, Québec H3T 1N8, Canada. ³³Service of Scientific Heritage, Royal Belgian Institute of Natural Sciences, 1000 Brussels, Belgium. ³⁴UCD Earth Institute and School of Archaeology, University College Dublin, Belfield, Dublin 4, Ireland. ³⁵Department of Prehistory and Europe, Franks House, The British Museum, London N1 5QJ, UK. ³⁶The Natural History Museum, Cromwell Road, London SW7 5BD, UK. ³⁷The Cantabria International Institute for Prehistoric Research (IIIPC), University of Cantabria, Avda. Los Castros, s/n. 39005 Santander, Spain.

‡Deceased.

that had previously supported late Neanderthal survival have been shown to be marked underestimates (for example, Vindija¹⁴, Zafarraya¹⁵ and Mezmaiskaya¹⁶) 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 Cave⁵) 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 reported¹⁹.

We obtained 196 AMS radiocarbon measurements and used them to build high-precision age models using Bayesian statistics on the OxCal²⁰ 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 pattern²¹, with late survival of Neanderthals previously argued at sites such as Gorham's Cave, Gibraltar²². We could not reproduce any of the late dates from sites in this region¹⁵ (Supplementary Methods) and it is apparent that many previous determinations underestimate the real age. It is unclear how long Neanderthals persisted in southern Iberia¹⁵. 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 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

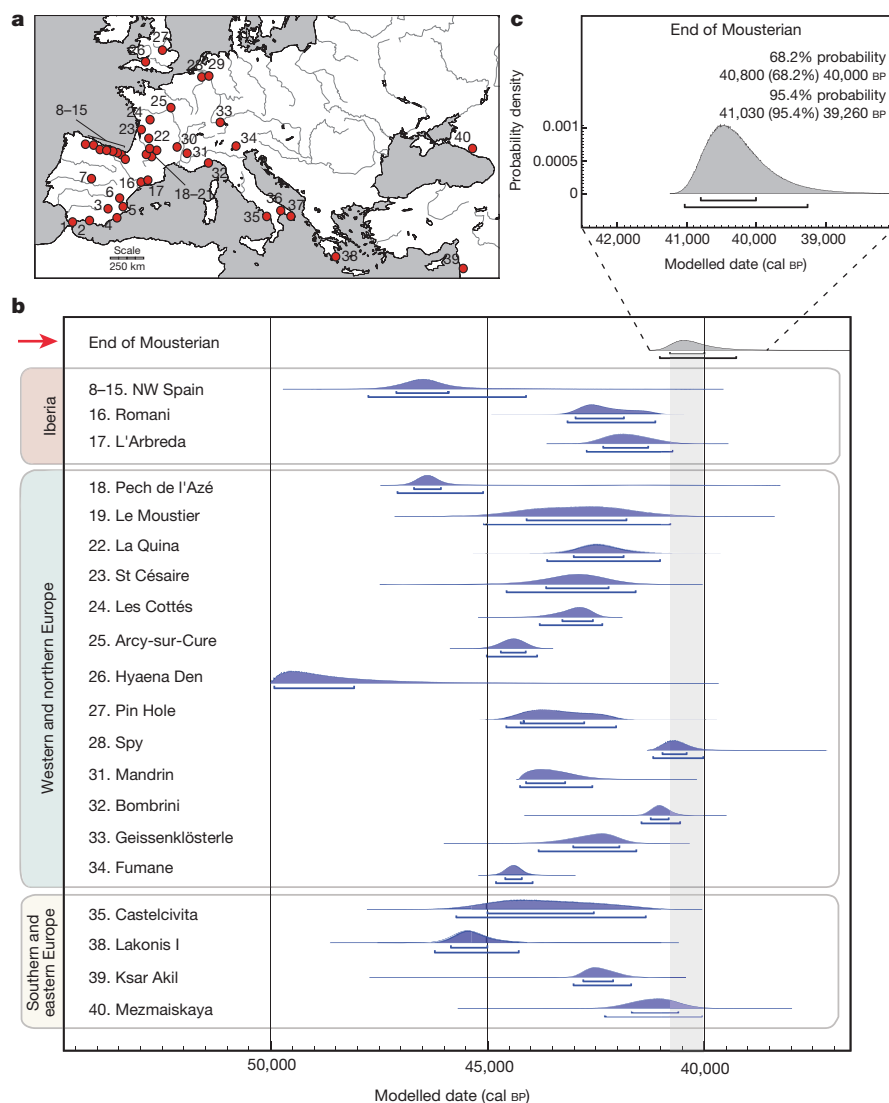


Figure 1 | Site locations and final boundary age ranges for Mousterian and Neanderthal sites

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 Romani; 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: Oscuruscuito; 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 software²⁰ and INTCAL13 (ref. 29)). **c**, PDF for the latest Mousterian based on the data in **b**.

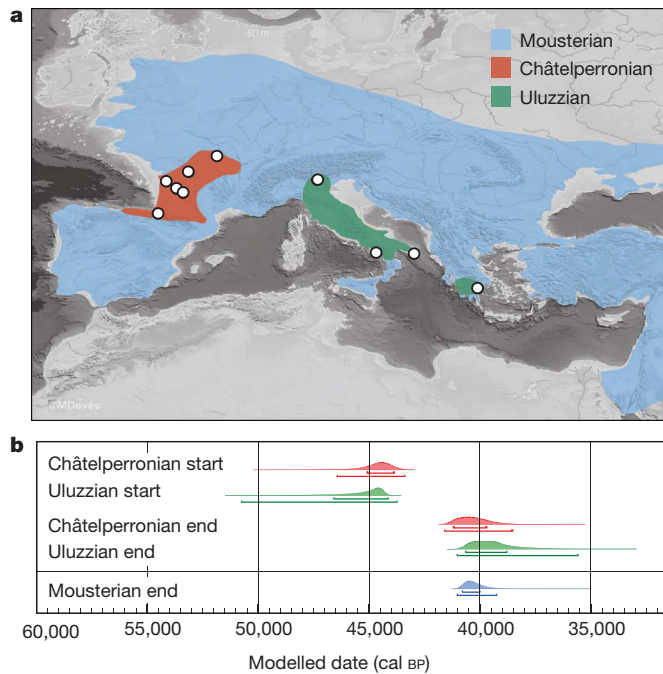


Figure 2 | Transitional site locations and Bayesian age ranges for the start and end of the Châtelperronian and Uluzzian technocomplexes. **a**, Geographic distribution of Châtelperronian (red), Uluzzian (green) and Mousterian (blue) technocomplexes. Map is shown with sea level at -80 m below the present day¹. Dated 'transitional' industry site locations are shown. Sea-level template map 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, but the late Mousterian always predates the two transitional industries stratigraphically where they co-occur.

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 Romani 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 Romani 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 $\sim 41,000$ – $39,000$ cal BP (Fig. 2b).

By comparing the final Neanderthal PDF with those obtained for the start of the Uluzzian at the Cavallo site²³, 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 technical and behavioural development. The early presence of AMHs in Mediterranean Europe by $\sim 45,000$ – $43,000$ cal BP (ref. 23) and the

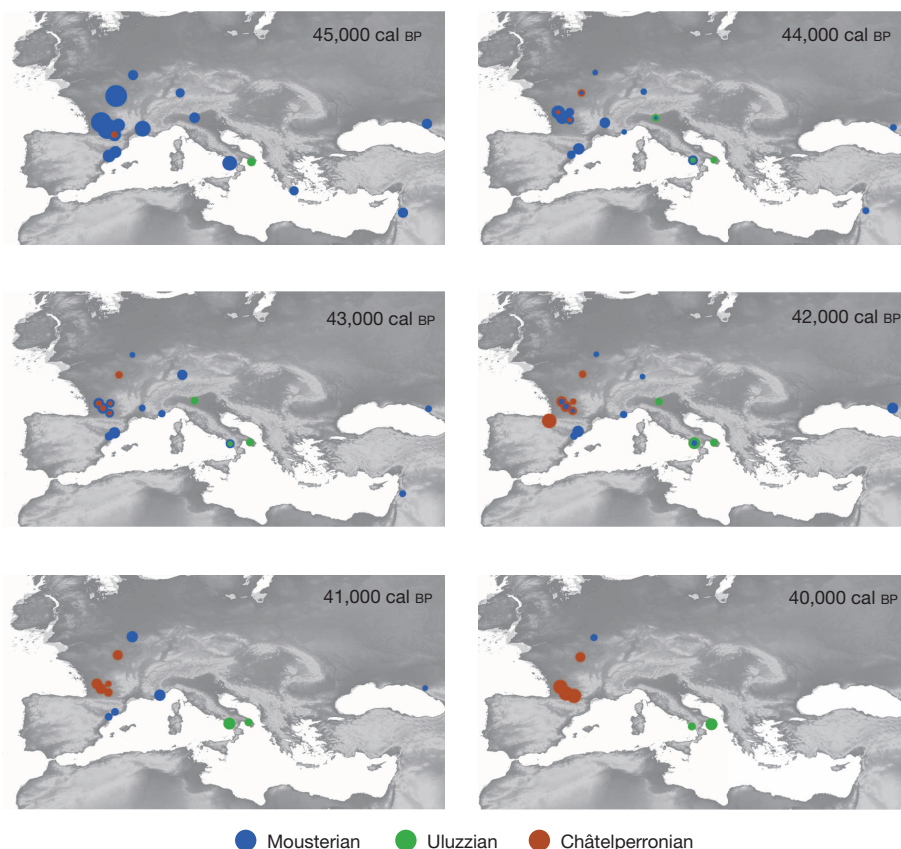


Figure 3 | Time slices for western Europe between 45,000 and 40,000 cal BP showing the distribution of the Mousterian, Châtelperronian and Uluzzian modelled ages. The size of the dots represents increasing and decreasing levels of the 95.4% probability ranges determined from the duration (date range)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

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 previously²⁶. An acid–base oxidation/stepped combustion (ABOX-SC) method was used for charcoal¹³. Radiocarbon ages are given as conventional ages BP as described previously²⁷. Corrections were made to bone collagen AMS determinations using a laboratory pre-treatment background subtraction²⁸. 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 and Marine13 (ref. 29) calibration curves 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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