

Nature, culture and human occupation of Planet Earth

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Abstract

Homo sapiens is possibly the most ecologically plastic animal species ever, capable to overcome climatic variability beyond its physiological limits by means of culture. This adaptability has a strong cultural component which required the development both new technologies and major social changes sometimes in our distant past^{1,2}. Highly contentious archaeological evidence suggests these innovations may have predated the emergence of our own species³. Here we studied climate niche width evolution in *Homo*, using fine-detailed palaeoclimatic data while controlling for phylogenetic effects. Our results point to sudden widening of the climatic niches exploited by *Homo* starting with the emergence of *H. heidelbergensis*. From the Middle Pleistocene, *Homo* ceased to be confined to physiologically suitable regions, despite progressive harshening of global climatic conditions. These results suggest cultural modernity, and its associated technological advancements, including habitual use of fire and clothing, appeared before the emergence of our own species.

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PR, AM, MM and MDF conceived the study. AM, MM, MMod, TR, AP, NE and PH produced and collected the data. AM, MM, MDF, SC and CS performed the analyses. POH, FC, LM, LR, JADF, TR, AP, NE, and PH contributed in critique of analyses and interpretation. PS contributed in discussion of cultural and social contexts. All the authors contributed to writing.

Homo sapiens is possibly the most ecologically plastic animal species ever, capable to overcome climatic variability beyond its physiological limits by means of culture. This adaptability has a strong cultural component which required the development both new technologies and major social changes sometimes in our distant past^{1,2}. Highly contentious archaeological evidence suggests these innovations may have predated the emergence of our own species³. Here we studied climate niche width evolution in *Homo*, using fine-detailed palaeoclimatic data while controlling for phylogenetic effects. Our results point to sudden widening of the climatic niches exploited by *Homo* starting with the emergence of *H. heidelbergensis*. From the Middle Pleistocene, *Homo* ceased to be confined to physiologically suitable regions, despite progressive harshening of global climatic conditions. These results suggest cultural modernity, and its associated technological advancements, including habitual use of fire and clothing, appeared before the emergence of our own species.

Main

The genus *Homo* has existed for some three million years^{4,5}. For one third of this stretch of time, human species were confined to tropical and sub-tropical Africa, which is the homeland of the genus^{6,7} and is rich in the warm, savanna-like environments to which most early hominins were best adapted^{8,9}. With the emergence of *Homo erectus* some 2 Ma, our ancestors began to disperse outside of Africa but kept away from boreal latitudes, possibly because of physiological limits to cold tolerance¹. However, later *Homo* species were able to expand their distribution to Northern Europe and Western Siberia, despite the advent of full glacial cycles which were making global temperatures colder than ever before during the history of the genus *Homo*. Findings in Happisburgh and Pakefield (UK) date the earliest presence of *Homo* at the southern edge of the boreal zone at some 0.7-0.9 Ma¹⁰. The occupation of such northern temperate and boreal zones presents a number of notable challenges. Not only does the cold itself present a challenge for hominins physiologically adapted to environments in Africa, but seasonality imposes extreme annual resource fluctuations, which imply a reliance on hunted meat for survival⁷ and limits to population densities which threaten the maintenance of mating networks. Technological adaptations facilitating survival in cold environments may have included the use of fire, shelters or clothing, with vulnerable infants being particularly susceptible to mortality. Technological advances such as the use of spears may have facilitated the hunting of typically large mammals¹¹ whilst social adaptations to care for higher injury rate may also have been important². At the same time cultural changes may have been necessary to enable knowledge transmission over large regions, and across generations, with archaeological evidence suggesting the emergence of larger networks of communication^{1,2}.

Clothing manufacturing leaves very little in the way of fossil remains¹². The first microwear evidence of hide-scraping (for manufacturing clothes) at Hoxne (UK), Biache-Saint-Vaast, Pech de l'Azé and Abri Peyrony (France) and Shöningen (Germany)¹³⁻¹⁵ are just some 50ka old at the most. Only the two most recent human species, *H. neanderthalensis* and *H. sapiens*, left incontrovertible evidence that they were able to produce complex, cold-proof clothing at that time. To make things more complex, in the particular case of *H. neanderthalensis* biological adaptation, besides material culture, was possibly involved in their ability to withstand the cold. Neanderthals possessed relatively short limbs, and a large midface and nasal cavity proposed to be specific cold adaptations, to heat and humidify inspired air, although the issue is definitely unresolved^{16,17}. In contrast to any other *Homo*, *H. sapiens* is considered the only species in the genus able to occupy cold regions through a genuinely cultural process, driven by our technology including the mastering of fire, ever-improving clothing craftsmanship and construction of shelters^{15,18-20}. This view sets *H. sapiens* apart from any other human species in terms of cognitive skills and implicitly rejects the idea that older

Homo may have had sufficiently modern material culture to overcome climatic harshness²¹. With such a poor fossil record of clothes, tools to produce them and great uncertainty about deep-past local paleoclimates and human dispersal timing and direction, the issue of when humans first became cognitively and culturally able to extend their climatic tolerance beyond their physiological limits remains very difficult to decipher.

Here, we address the more restricted issue of when during the history of *Homo* the limits of climatic tolerance expanded, and which species were involved. We do not specifically address the cultural and social adaptations that might underlie such tolerance, but rather consider the implications of our findings for the timing of such adaptations. We model climatic tolerance limits by associating palaeoclimatic values with the archaeological record to resolve the detail of the tempo and mode of past occupation of cold climates. Specifically, we test the hypothesis that *H. sapiens* developed greater climatic tolerance relative to *H. heidelbergensis* and *H. neanderthalensis* against the alternative that the exploration of climates outside natural physiological limits had already happened since the earliest of these species.

To test this, we estimated the rate of change of climatic tolerance limits across the human phylogenetic tree and searched for possible shifts in the rate, applying a method which allowed the rates to be estimated at each branch in the tree. In the present context, shifts in the rate of evolution of climatic tolerance that accrue to the clade including the Happisburgh/Pakefield hominins, *H. heidelbergensis*, plus *H. neanderthalensis* and *H. sapiens*, would indicate these hominins first acquired the capacity to develop cold-facing technological skills and cultural adaptations. Conversely, if either no rate-shift occurs, or the rate shift coincides with different clades (e.g. at the root of *Homo*) the colonization of Northern habitats would be not indicative of any sudden increase in the ability to face environmental harshness.

The human fossil record dataset we used includes 2,597 hominin occurrences associated with 727 archaeological sites. The time range of our record spans from the first occurrence of australopiths in East Africa dated to some 4.2 Ma, to the definitive advent of *H. sapiens* in Eurasia almost coincident with the demise of *H. neanderthalensis* dated some to 0.040 Ma (see Supplementary Data). Such a wide range of hominin taxa provides a thorough phylogenetic context for the analyses.

Deriving spatio-temporally detailed climate data for the past requires dynamic climate modelling, but the timescales for human evolution exceed the possibilities of direct model simulation by several orders of magnitude. To circumvent this limitation, we combine direct simulation using a computationally efficient, intermediate complexity Earth system model, PLASM-GENIE, with statistical modelling, to create a PALEO-PGEM paleoclimate emulator, capable of performing multi-million year simulations forced by observationally derived proxy timeseries for ice-sheet state, CO₂ concentration and orbital forcing²². To model climatic niche evolution, we applied phylogenetic ridge regression (*RRphylo*)²³. *RRphylo* allows us to compute evolutionary rates for each branch of the phylogeny and to estimate the ancestral phenotypes. Here the ‘phenotype’ comprises climatic tolerance limits.

By using past seasonal maxima and minima for temperature, precipitation and annual net primary productivity from PALEO-PGEM, we reconstructed and projected onto the geographical space the climatic niche limits corresponding to the ancestral species distributions (the nodes in the tree) in our fossil database. Using *RRphylo*, we were then able to infer climatic niche tolerance limits for each node in the tree and to assess whether the rate of climatic niche evolution shows any shift (i.e. acceleration or deceleration) consistent with our starting hypothesis, while accounting for phylogenetic effects. We further accounted for phylogenetic uncertainty changing the tree node ages and the tree topology randomly one hundred times. By incorporating sources of uncertainty, we defined an overall ‘habitat quality’ metric, representing the number of iterations (out of 100) a geographic cell was found habitable (i.e. fell within climatic tolerance limits) for a given species (or ancestor in the tree).

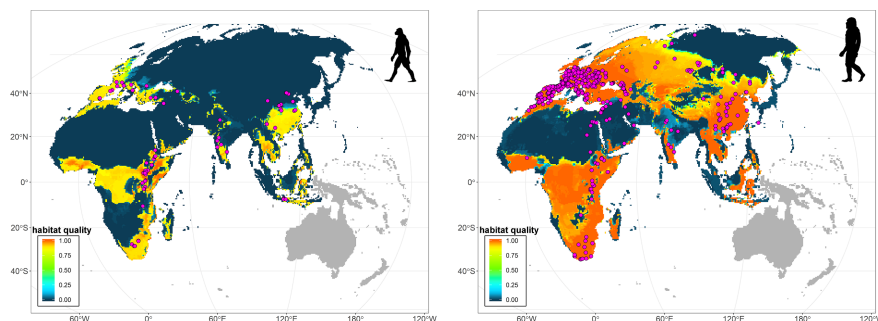


Fig. 1. Habitat quality map for early *Homo* (EHS, left) and modern human species (MHS, right). The maps show the quality of the habitats potentially suitable to human occupation for the common ancestors of EHS and MHS, respectively. Quality varies from little (blue) to highly suitable (red) areas. The fossil occurrences of EHS (*H. habilis*, *H. ergaster* and *H. erectus*) and MHS (*H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*) are superimposed on each map (pink dots).

Despite the enormous geographic variation in both the preservation potential and the intensity of paleontological sampling²⁴, our data suggest the existence of a strong association between habitat quality and the presence of fossil remains, either for EHS (Area Under The Curve (AUC) = 0.80, Fig. 1 left, AUC after subsampling the most abundant species = 0.71) or MHS (AUC = 0.81, Fig. 1 right, AUC after subsampling the most abundant species = 0.82). This strong association remains true for all nodes in the hominin tree (Extended Data Figs. 1, 2 Extended Data Tables 1, 2) and suggests that climatic variation in time and space determined the geographic ranges of our ancestors. Excluding extreme climatic values in order to mitigate the effect of potential paleoclimatic errors in the paleoclimate emulator (i.e. excluding the climatic records beyond the 90th percentile of the individual variable distribution), the AUC value for EHS decreases to 0.68, whereas it increases to as much as 0.82 for MHS (Extended Data Table 3, Extended Data Fig. 3). In contrast, repeating this test by randomly sampling the same number of point occurrences per species throughout the biogeographical domain of individual species (Extended Data Table 4, Extended Data Fig. 4) leads to a much weaker association between occurrences and climatic suitability (EHS AUC = 0.56 95%, confidence interval: 0.52-0.61; MHS AUC = 0.58, confidence interval: 0.56-0.60). This test indicates that a random placement of fossil localities within the biogeographic domain of the species leads to non-significant association between fossil remains and climatic conditions, thereby strengthening the notion that the geographic position of archaeological sites is a non-random process guided by climatic variability.

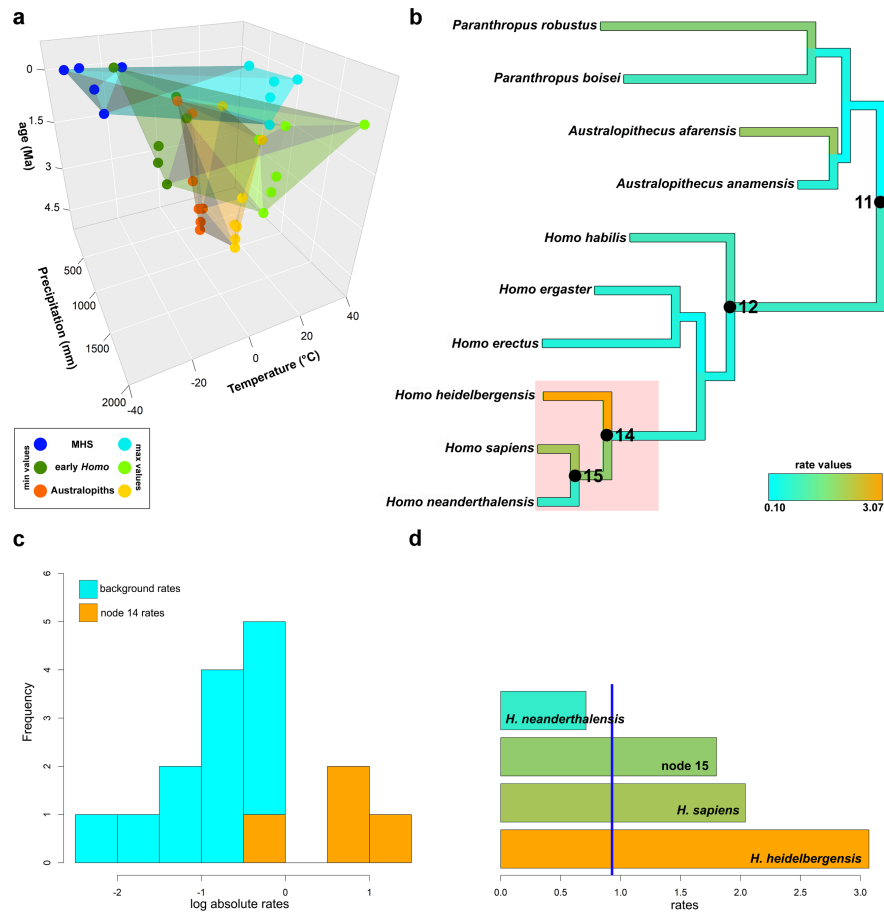


Fig. 2. Climatic niche evolution in hominins. **a**, The climatic niche volume occupied by hominin clades through time. **b**, The hominin tree used in this study. The branch colours are proportional to the multivariate rate of climatic niche evolution for each branch in the tree. At the MHS common ancestor (14) an acceleration in the rate of evolution in climatic tolerance limits occurs (shaded area). The common ancestor to all species within *Homo* is indicated by node 12. **c**, The distribution of the rates of niche evolution for the MHS clade (deep blue) compared to the rest of the branches in the tree (light blue). **d**, The individual rates of niche evolution for the tree branches forming the MHS clade. The average rate for the entire tree is indicated by the vertical blue line. MHS = modern *Homo* species, EHS = *Homo* species exclusive of MHS, Australopithecus = species in the genus *Paranthropus* and *Australopithecus*.

As expected, we found that the clade identified by *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* and their common ancestor experienced a significant rate shift towards wider climatic tolerance (Fig. 2). The rate shift does not depend on the phylogenetic hypothesis we applied, neither it depends on the selection of species we used. Shuffling the tree node ages (to account for common ancestors dating uncertainty) and species positions in the hominin tree (to account for phylogenetic uncertainty) 100 times the shift reappears for this very clade 95 times (Table 1). Subsampling the most abundant species (randomly selecting no more than 100 fossil occurrences per species) to account for sampling differences between species still leads, 91 times out of a hundred, to a significant rate shift in the MHS clade. We also repeated the phylogenetic reshuffling by randomly removing one species at once. Under this latter design, the MHS shift occurs 86 times out of 100, and 23 additional times the shift involves two, rather than three, MHS species. Individually, *H. sapiens* and *H. heidelbergensis* appears in 86 significant rate shifts, *H. neanderthalensis* in 85, and no shift appears outside the MHS clade, meaning that the rate shift pertains to these species only and is not guided

preferentially by any of the three (Table 1).

The estimates of climatic niche limits at nodes in the hominin phylogeny suggest that the rate shift in the climatic niche limits for the MHS clade was not an exclusively biological process. At the root of the hominin tree (node 11, Extended Data Table 1), the predicted range in temperatures spans from 20°C (coldest quarter of the year) to 29.9°C (warmest quarter), and in mean rainfall from 12 mm (driest quarter) to 512 mm (wettest quarter). This is entirely consistent with today's African savannah environment²⁵. At the node subtending the pair *H. ergaster* plus *H. erectus* (which is the first hominin to disperse over Asia and Europe), the corresponding figures are 0.7°C to 31.9°C for temperature range and from 4.8 mm to 1080 mm for precipitation range. These estimates are reasonable considering both the range expansion into temperate regions and the colonization of warm and humid environments (Indonesia) by *H. erectus*^{6,26,27}. Yet, at the common ancestor to the three MHS, the estimates for temperature extremes span from minus 21.1°C to plus 31.4°C and precipitation from 0.7 mm to 905 mm. Although the common ancestor to MHS was an African species which probably never experienced these extreme climates²⁸, the estimates agree perfectly with the notion that a sudden widening to climatic niche limits occur with the advent of this ancestor, whose offspring lived after the onset of fully glacial Pleistocene conditions²⁹. The massive increase in the (estimated) range of thermal conditions suitable the MHS clade taxa (marked by a 20°C decrease in minimum temperature as compared to the hominin tree root, Fig. 3) does not depend on the phylogenetic hypothesis we applied. By using 100 different tree topologies and branch lengths to account for phylogenetic uncertainty, we found a significant trend in the temperature of the coldest quarter experienced by hominins 97 times (Fig. 3), whereas no trend is found in the warmest quarter temperatures. This means that hominins, and MHS in particular, were able to expand, rather than track, their climatic envelope, by constructing their own niche culturally, starting with the appearance of the MHS. In fact, the increase in temperature range cannot be explained by physiological adaptation *per se*^{12,30}. We found that in African species and ancestors, the average temperature of the coldest quarter of the year was no less than 9.4°C, meaning that the winter chill is unlikely to have been a problem for them (Extended Data Table 5). In contrast, within the range of temperatures experienced by *H. heidelbergensis*, the coldest quarter of the year was as cold as -12.3°C, suggesting specific cultural equipment to fend off the risk of hypothermia was needed (Extended Data Table 5). Although *H. erectus* may have occasionally faced similarly extreme temperature minima, it lived under much warmer and more humid climates on average (Extended Data Table 1a, Fig. 3), and the ability to master fire (which might greatly mitigate the effects of cold weather) is not attested before 350 ka³¹, which is much later than the first appearance of *H. erectus* at nearly 2 Ma but still fully consistent with its use by any or all MHS.

Our data therefore indicate cold climates (hence Northern latitudes and temperate latitudes during glacial periods) remained unavailable for any species other than the MHS triplet. It is important to remark that a literal interpretation of our modelled estimate of annual mean minimum temperature of - 20°C as the condition experienced by our ancestors is unlikely and not necessary to our conclusions. There is uncertainty in the paleoclimatic estimates²² and our ancestors might have used cryptic refugia offering milder conditions³². In addition, all MHS species used to dwell in cave environments that were climatically less extreme than open air, and the use of fire and clothing shields against extreme temperatures and wind chill^{12,15,30}. Instead, we are suggesting that MHS had sufficient technology to produce clothing and manage fire at will on a daily basis. The emergence of behavioural modernity, including complex social interactions, the habitual use of fire³¹ and the ability to work hide, wood and ivory^{11,14} may well place the appearance of such 'modern' cultural attributes to the Middle Stone Age at some 350 kya, and so extend to extinct human species³. Brain asymmetry and right-handedness, usually linked with advanced cognitive skills^{33,34}, is common to *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*³⁵⁻³⁷. It has been demonstrated that range expansion towards northern, sub-boreal regions similarly pertain to these three species only¹⁰, which is important since range expansion to previously unoccupied regions is itself part of behavioral modernity³.

In contrast to MHS, EHS either did not venture outside Africa or went across Eurasia longitudinally. *Homo erectus* spread across Africa and Eurasia up to Java at some 1.7 Ma, but never settled north of the Mediterranean area or southeast China⁶. Yet, from the appearance of *H. heidelbergensis* onward, the far North was

no longer completely uninhabitable, despite it was becoming more inhospitable than ever before because of the cooling trend in global climate. The jump in the rates of evolution in climatic niche width (driven by a sudden increase in tolerance to the cold, Fig. 3) is the most important result we found.

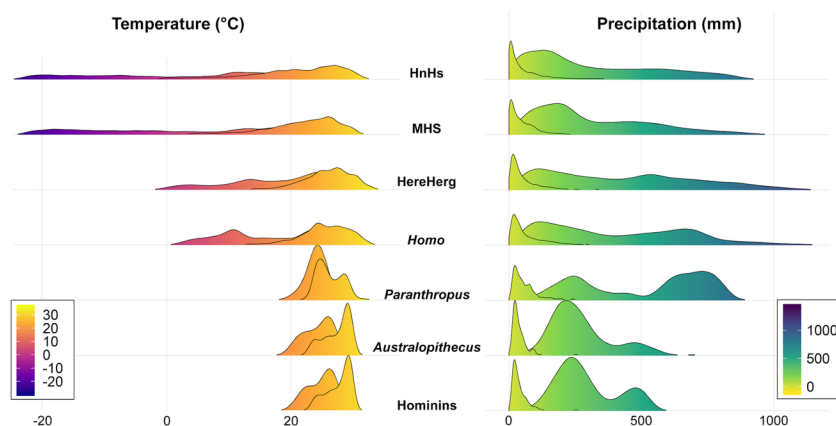


Fig. 3. Estimated temperature and precipitation ranges at several nodes in the human phylogenetic tree. The individual rows represent the density distribution of minimum and maximum temperature and precipitation, respectively, collapsed together. HnHs = common ancestor to *H. neanderthalensis* and *H. sapiens*, MHS = Common ancestor to *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*, HereHerg = common ancestor to *H. erectus* and *H. ergaster*, Homo = common ancestor to *Homo* species, *Paranthropus* = common ancestor to all *Paranthropus* species, *Australopithecus* = common ancestor to all *Australopithecus* species, Hominins = common ancestor to hominins.

Although there is consistent evidence that *Homo* species may have exchanged genes with positive fitness consequences in cold environments by means of introgression, this evidence is limited to the last 40 kya and invariably pertains to local *Homo sapiens* populations^{38,39}. Studies on living humans indicate the range of climatic extremes, particularly winter temperatures, experienced by MHS invoke technological and cultural rather than biological adaptation to life in the highly seasonal, cold northern environments. Fire is the most obvious innovation⁴⁰, and whereas occasional use of fire has deep roots in human history^{41,42}, its habitual use is much more recent, tracing back to no more than the Middle Stone age³¹. Other less obvious adaptations may have been equally, if not more, important such as fitted clothing⁴³, thrown spears⁴⁴ or adhesives⁴⁵. Cultural transmission across regions and generations may also have been significant to occupying more northerly latitudes⁷, as well as social changes such as healthcare practices². Whether any of these adaptations played the primary role in enabling expansion remains unclear. Furthermore, the relative significance of biological, technological, social or cultural adaptations will almost certainly be a matter for debate for some period. However overcoming the challenges imposed in the consistent occupation of northern latitudes since the appearance of *H. heidelbergensis* suggest behavioral modernity is not limited to *H. sapiens*, and that our own genus became able to master inhospitable habitats well before the appearance of our species, possibly as far back in time as one million years ago.

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Table 1. Percentage of significant rate shifts in niche width calculated through phylogenetic reshuffling . The table lists the percentage of significant shifts that occurred at nodes with two or three species, as well as the occurrence of each of the three *Homo* species in each significant shift.

Species	Shift	Node with two species	Node with three species	H. heidelbergensis	H. neanderthalensis
H. heidelbergensis	86	23	63	/	75
H. neanderthalensis	85	22	63	74	/
H. sapiens	86	23	63	75	74

Methods

Fossil occurrence and phylogenetic data

The human fossil database is available as Supplementary Data. This dataset was further implemented by adding the occurrence of four hominin species from scientific literature. Specifically, we added the fossil occurrences belonging to *Australopithecus anamensis*, *A. afarensis*, *Paranthropus boisei*, and *P. robustus* . We excluded other hominin species because their stratigraphically or geographically restricted fossil record prevent performing realistic inference about their climatic niche limits.

For each fossil occurrence included in the dataset, we recorded latitude and longitude, the archaeological layer yielding the remains, and the absolute age of the dated sample. Where available, we also included information about which sample was used for dating the relative lab code. Radiocarbon dates were calibrated using Intcal13 calibration curve for the Northern hemisphere, shcal13 curve for the Southern hemisphere, and marine13 curve for marine samples. Age estimates come with uncertainty. Time averaging of the archaeological layers adds to this uncertainty. To account for this, for each archaeological site (or layer) age estimate we retrieved from the collected estimates the minimum age and the maximum age (calculated according to individual estimates and their respective confidence intervals).

Environmental predictors

Environmental predictors were generated using a paleoclimate emulator²². The method applies Gaussian process emulation of the singular value decomposition of ensembles of runs from the intermediate complexity atmosphere-ocean GCM PLASIM-GENIE with varied boundary-condition forcing (CO₂, orbit and ice-volume). Spatial fields of i) minimum seasonal temperature (hereafter, “MinTemp”) , ii) maximum seasonal temperature (hereafter, “MaxTemp”), iii) minimum seasonal precipitation (hereafter, “MinPrec”), iv) maximum seasonal precipitation (hereafter, “MaxPrec”), and v) net primary productivity (hereafter, “NPP”) are then emulated at 1,000 year intervals, driven by time-series of scalar boundary-condition forcing, and assuming the climate is in quasi-equilibrium. The emulator uses CO₂ from Antarctic ice cores for the last 800,000 years⁴⁶. Prior to 800 ka, and for the entire sea-level record, it uses the CO₂ and sea-level reconstructions in ref. 47. Contemporary values of the four bioclimatic variables were derived from WorldClim²⁵, while NPP observations were derived from MOD17A3H (MODIS; <https://lpdaac.usgs.gov/products/mod17a3hv006/>). Current bioclimatic variables and the NPP were interpolated onto the same 0.5° grid and combined with emulated anomalies. Temperature anomalies were additively combined with current temperatures, while precipitation and NPP anomalies were combined with current precipitations using a hybrid additive/multiplicative approach²².

The native-resolution (5°) emulations were extensively validated against model inter-comparisons of the

mid-Holocene, the Last Glacial Maximum, the Last Interglacial and the mid-Pliocene warm period. Glacial-interglacial variability was validated against the observationally based global temperature reconstructions⁴⁸. Paleoclimate anomalies at climate model resolution (5°) were downscaled onto the observed modern climatology at 0.5° spatial resolution using bilinear interpolation. We used the entire bioclimatic predictors in order to consider the last 5 million years of human evolution.

Definition of the Climatic Niche limits for *Homo* species

For each hominin species, we built a climatic envelope. We pooled together all bioclimatic values associated to their fossil occurrences. Then, we selected the recorded minimum values for MinTemp, MinPrec, and NPP, and the maximum values for MaxTemp, MaxPrec, and NPP. We repeated this procedure over 100 replicates. At each replication, the age of each individual archaeological locality was sampled at random from the uniform distribution spanning from the estimated minimum to the maximum locality age. Thus, replication accounts for both ageing uncertainty of individual archaeological layers and, correspondingly, for climatic uncertainty around the paleoclimatic estimates concerning the fossil localities. Finally, for each bioclimatic variable, we took the mean value from each resulting distribution of temperature, precipitation and NPP minima and maxima. Taken together, these mean values of bioclimatic extremes represent a conservative estimate of the climatic range realized for each hominin species during its history, avoiding putting too much faith on extreme values attached to individual replicates and locality.

Definition of the Climatic Niche limits for common ancestors in the hominin tree

The hominin phylogenetic tree was obtained by combining the Primate (and human) phylogenetic information published in recent papers⁴⁹⁻⁵¹. We started by using the six climatic variables, representing the limits (minima and maxima) in temperature, precipitation and NPP. Since these variables are highly correlated to each other, we reduced covariation among variables by performing a Principal Component Analysis (PCA) on climatic variables associated with each hominin species occurrence in the fossil record. Then, we extracted the PC scores and used them as a multivariate dataset for the phylogenetic ridge regression.

We used the PC scores estimated by *RRphylo* at each node and back transformed the scores in climatic variables (MinTemp, MinPrec, min NPP, MaxTemp, MaxPrec, max NPP). For each node in the hominin tree, we mapped geographically the areas associated with its corresponding climatic estimates (i.e. the limits of the climatic envelope). The resulting map thus represents the geographic areas estimated to be climatically suitable for occupation by each ancestor in the tree. To account for uncertainty around the ages of individual nodes in the hominin phylogeny, we repeated the entire procedure at each node over 100 replicates by using the 100 alternative phylogenies generated from *swapONE* function embedded in the *RRphylo* package. This function randomly changes the tree topology and branch lengths although it is possible to keep specific clades monophyletic. However, we accounted for a few, well-supported, monophyletic clades which are present in the hominin tree. In particular, in swapping the tree tips, we kept *H. ergaster* and *H. erectus* as sister species. We similarly kept monophyletic the clade subtending to the four australopithecines in the tree, the clade representing the genus *Homo*, and the clade including *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. Eventually, we recorded the number of times a given geographical cell counts as climatically suitable out of the 100 replicates. For each cell, estimated habitat quality thus ranges between 0 (never suitable irrespective of the phylogenetic tree used for climatic reconstructions at the tree nodes) to 1 (100 times suitable). Since the inclusion of particular taxa in the data may alter significantly the result of PCA ordination⁵² we repeated the swap procedure leaving one species at random out of the tree for each replicate.

To measure the association between climatic suitability and the presence of human species, we calculated the Area Under receiver-operator Curve (AUC) averaging over the 100 replicates. AUC theoretically ranges from 0 to 1. However, since random sampling points, (pseudoabsences) are not real absences, AUC cannot reach 1⁵³, as the maximum AUC value depends on the actual (unknown) area of distribution of the species. To obtain a null distribution of AUC values and assess significance for the real AUC, for each node in the tree we sampled 100 times as many point occurrences as with the real data (i.e. the fossil occurrences of the species descending from that node) within the biogeographic domain of the species, and calculated the

random AUC. Climatic tolerance values at the tree node represent the estimated tolerance limits for hominin ancestors. Since these values are estimated, rather than observed, to assess the association between fossil localities and habitat quality for each ancestral species estimates we selected the fossil occurrences of its descendants, provided they are not included in a descending node which was itself tested. For instance, the EHS ancestor was tested by selecting the fossil occurrence of *H. habilis*, *H. erectus* and *H. ergaster*, but not *H. sapiens*, *H. neanderthalensis* and *H. sapiens* which were considered only descendant to the MHS ancestor. To account for sampling differences between the hominin species we analysed, we repeated the AUC computation after sampling randomly no more than 100 occurrences per species at each replicate.

We used the evolutionary rates provided by *RRphylo* to apply the function *search.shift*²³ which tests whether individual clades evolved at significantly different rates as compared to the rest of the tree. The function compares the rates attached to each branch descending from a particular node to the rates for the branches of the rest of the tree. The significance for the rate difference is assessed by means of randomization. In the case of multivariate data, as with this particular study, the multivariate rate is computed as the 2-Norm (Euclidean) vector of the rates of individual variables.

To look for possible evolutionary trends in climatic tolerances over time we used the function *search.trend*⁵⁴ in the *RRphylo* R package²³. In *search.trend*, evolutionary rates and phenotypes (including the phenotypic estimates at the nodes) are regressed against their age and the resulting slopes compared to slopes randomly generated under the Brownian motion model of evolution.

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Competing interests:

The authors declare no conflict of interest.

Supplementary Information is available for this paper.

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Extended Data Table 1. a, Paleoclimatic estimates for the hominin species in the tree and b, reconstructed climatic values at the tree nodes. Nodes refer to the node number in the tree. Mean age refers to the mean value obtained by altering the tree topology and branch lengths 100 times to account for phylogenetic uncertainty.

Extended Data Table 2. a, Paleoclimatic estimates for the hominin species in the tree and b, reconstructed climatic values at the tree nodes after subsampling the most abundant species. Mean age refers to the mean value obtained by altering the tree topology and branch lengths 100 times to account for phylogenetic uncertainty.

Extended Data Table 3. a, Paleoclimatic estimates for the hominin species in the tree and b, reconstructed climatic values at the tree nodes after removing the first decile of the climatic variable values. Nodes refer to the node number in the tree. Nodes refer to the node number in the tree. Mean age refers to the mean value obtained by altering the tree topology and branch lengths 100 times to account for phylogenetic uncertainty.

Extended Data Table 4. a, Paleoclimatic estimates for the hominin species in the tree and b, reconstructed climatic values at the tree nodes after randomly shuffling the fossil occurrence data within the biogeographical domain of individual species. Nodes refer to the node number in the tree. Mean age refers to the mean value obtained by altering the tree topology and branch lengths 100 times to account for phylogenetic uncertainty.

Extended Data Fig. 1. Maps of fossil locality distribution and habitat quality at specific nodes in the hominin tree. The association between the position of fossil localities and habitat quality is measured by means of AUC. Habitat quality is counted as the number of replicates (out of 100) a specific location (0.5 degrees geographic cells) resulted suitable according to paleoclimatic estimates. The replicates differ from each other in terms of the topology and branch lengths of the phylogeny used to produce the estimates.

Extended Data Fig. 2. Maps of fossil locality distribution and habitat quality at specific nodes in the hominin tree, after setting the maximum number of fossil localities per species at 100 for the ancestor to all *Homo* species (node 12, left), early *Homo* (node 16, middle) and MHS (node 14, right). The association between the position of fossil localities and habitat quality is measured by means of AUC. Habitat quality is counted as the number of replicates (out of 100) a specific location (0.5 degrees geographic cells) resulted suitable according to paleoclimatic estimates. The replicates differ from each other in terms of the topology and branch lengths of the phylogeny used to produce the estimates.

Extended Data Fig. 3. Maps of fossil locality distribution and habitat quality at specific nodes in the hominin tree, after excluding the first decile of the distribution of paleoclimatic estimates. The node numbers correspond to the tree in Extended Data Fig. 1. The association between the position of fossil localities and habitat quality is measured by means of AUC. Habitat quality is counted as the number of replicates (out of 100) a specific location (0.5 degrees geographic cells) resulted suitable according to paleoclimatic estimates. The replicates differ from each other in terms of the topology and branch lengths of the phylogeny used to produce the estimates.

Extended Data Fig. 4. Maps showing randomly placed fossil localities and habitat quality at specific nodes in the hominin tree. The association between the position of random fossil localities (a single random draw is depicted) and habitat quality is measured by means of AUC. Habitat quality is counted as the number of replicates (out of 100) a specific location (0.5 degrees geographic cells) resulted

suitable according to paleoclimatic estimates. The replicates differ from each other in terms of the topology and branch lengths of the phylogeny used to produce the estimates. The biogeographic domains used to place fossil localities is indicated by the pink line.