Past Extinctions of Homo Species Coincided with Increased Vulnerability to Climatic Change

Authors: Pasquale Raia1,8*, Alessandro Mondanaro1,2, Marina Melchionna1, Mirko Di Febbraro3, José A.F. Diniz-Filho4, Thiago F. Rangel4, Philip B. Holden5, F. Carotenuto1, Neil R. Edwards5, Matheus S. Lima-Ribeiro4, Antonio Profico6, Luigi Maiorano7, Silvia Castiglione1, Carmela Serio1, Lorenzo Rook2

Affiliations:
1 Dipartimento di Scienze della Terra, dell’Ambiente e delle Risorse. Università di Napoli Federico II, 80126, Napoli, Italy
2 Dipartimento di Scienze della Terra. Università degli studi di Firenze, 50121 Firenze, Italy
3 Dipartimento di Bioscienze eTerritorio. Università del Molise, C. da Fonte Lappone, 15, 86090 Pesche, Isernia, Italy
4 Departamento de Ecologia, ICB, Universidade Federal de Goiás. Goiânia, GO, Brasil.
5 School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, UK.
6 Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Rome, Italy
7 Department of Biology and Biotechnologies “Charles Darwin”, University of Rome “La Sapienza”, viale dell’Università 32, 00185 Roma.
8 Lead Contact

*Correspondence: pasquale.raia@unina.it.
Summary

At least six different *Homo* species populated the World during the latest Pliocene to the Pleistocene. The extinction of all but one of them is currently shrouded in mystery, and no consistent explanation has yet been advanced, despite the enormous importance of the matter. We used a recently implemented past climate emulator and an extensive fossil database spanning 2752 archaeological records to model climatic niche evolution in *Homo*. We found strong, statistically robust evidence that the three *Homo* species representing terminating, independent lineages, *H. erectus*, *H. heidelbergensis*, and *H. neanderthalensis* lost a significant portion of their climatic niche space just before extinction, with no corresponding reduction in physical range. This reduction in species niche space coincides with increased vulnerability to climate change. In the case of Neanderthals, the climate-driven increased extinction risk was probably exacerbated by competition with *H. sapiens*. This study suggests that climate change was the primary factor in the extinction of *Homo* species, despite their great ecological plasticity and cognitive abilities.

Keywords: Human Evolution, Palaeoanthropology, Climatic change, Extinction
Introduction

The genus *Homo* has existed for at least 2.8 million years\(^1\). Reports dealing with the extinction of past *Homo* species mostly focus on the disappearance of a single taxon, *H. neanderthalensis*, and almost all existing works point to either climate change or to the contact with the technologically advanced *H. sapiens* as the potential causal explanations\(^2-4\). This is appropriate since competition and climatic changes are thought to be the most important factors explaining species extinction\(^5-7\). However, this kind of investigation is extremely rare for earlier *Homo* species, even though the Earth’s climate swung repeatedly between warm interglacial and cold glacial conditions during the history of our genus. Elucidating the mechanisms behind the fate of our ancestors is made even more important by the current, ever-increasing pressure that rapid and extreme climate change will continue to put on our own species and the entire living biota.

Here we fill this gap in our understanding by investigating climatic niche evolution in *Homo*, using a high-resolution past climate emulator\(^8,9\) which provides temperature and rainfall yearly maxima and minima and net primary productivity with a 1000-year resolution, over the last 5 Ma. We considered six species, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. Given the taxonomic uncertainty surrounding the status of some human remains, we also repeated the analyses testing different taxonomic attributions. Therefore, for each of the six species, we identified a ‘core’ fossil record, restricted to reasonably certain attributions of individual fossil occurrences and archaeological layers with lithic industry to a single species (Figure S1). Then, we repeated the analyses under a less conservative ‘extended’ subdivision of the fossil record, whereby individual remains and archaeological layers for which no unique taxonomic attribution was possible were ascribed to more than one candidate species. We divided each fossil *Homo* species record into discrete, consecutive time bins, minimizing the variance of the time bin lengths and number of localities, by means of likelihood optimization. The fossil record of *H. neanderthalensis* and *H. sapiens* is vastly richer than those of earlier species. For these two, we therefore divided the record in 1 kyr time bins (and we repeated the analyses by using
2 kyr long time bins). Over such consecutive time bins, collated from the oldest to the youngest, we
compared the climatic niche realized by the species within the bin (bin climatic niche, BCN) to the
niche the species realized throughout its entire existence (evolutionary climatic niche, ECN). Our
metric for comparison was Schoener’s $D$, which measures the degree of niche overlap between
BCN and ECN, from low ($D = 0$) to perfect ($D = 1$), taking into account both the climatic
conditions where the species was present and the background climatic variability during the
temporal interval covered by the bin. Since the BCN is necessarily included within the ECN, low
values of Schoener’s $D$ indicate that BCN is small as compared to the ECN, meaning that the
species experienced during the bin duration a limited portion of the total climatic variation
represented by its ECN (Figure S2). Conversely, at Schoener’s $D = 1$ the species experienced,
during the bin, as much climatic variation as throughout its existence. For each species and bin, we
calculated Schoener’s $D$ values 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, the replicates account for both ageing
uncertainty of individual archaeological layers and, correspondingly, for climatic uncertainty
around the actual paleoclimate of the fossil locality.

Many *Homo* species were geographically widespread, and most were technologically more
advanced than any other mammal. The history of several *Homo* species is characterized by long-
distance dispersals and unique cultural innovations including clothing, implemented stone tool
technology, and fire control, that suggest they may have been able to survive under climatic
conditions exceeding the physiological tolerance of the human body. Thus, our prior expectation
was that, on average, $D$ values of individual bins were uniformly constant throughout each species’
existence. This niche conservatism\textsuperscript{10} pattern would therefore indicate that the *Homo* species were
capable of adapting either biologically or culturally to variable and fluctuating climatic conditions
despite the pervasive climate changes that occurred during their Pleistocene existences. To assess
this hypothesis statistically, we randomized 10,000 times the $D$ values of all replicates across the
time bins and compared the median $D$ per bin to the distribution of random values.

Figure 1. Degree of niche overlap between niche occupied during a specific time bin and the
species evolutionary (total) niche (measured in terms of Schoener’s $D$ values, y-axis), using the
core record.

Results

Climatic niche evolution in Homo

Our results provide a clear confirmation that niche conservatism applies generically to all
Homo species for most of their existence. But for three species only, $H$. heidelbergensis, $H$. erectus
and $H$. neanderthalensis, we found a sudden, statistically significant drop in $D$ just before
extinction, indicating that their climatic niche widths shrunk suddenly just before they vanished
(Figure 1, Table S1). These patterns do not change whether the ‘core’ or ‘extended’ fossil records
are used (see Table S2 and Figure S3 for the ‘extended’ record), do not depend on the specific
predictions of the paleoclimate emulator (Figure S4) and remain almost identical when the
geographic resolution of the paleoclimatic data is aggregated at 5 degrees (Figure S5). The sudden
drop in climatic niche width pertains only to the last bin of extinct species and disappears altogether
when temporal trends in climatic adaptation are removed by randomizing fossil locality ages and
climes (Figures S6-7). Most importantly, the drop disappears when real fossil locality ages are
used, but global climatic trends in space and time are removed by shuffling climatic layers across
fossil localities, suggesting climatic changes possibly had a role in extinction (Figure S8). For
palaeontological species, extinction coincides with their disappearance from the fossil record. Yet,
while some such palaeontological extinctions represent the termination of a phyletic lineage (i.e. a
true extinction), in some other cases the species evolved instead into a morphologically distinct
descendant through an anagenetic process\textsuperscript{11}. These morphological species are conventionally
referred to as ‘transitional’ forms. In our records, \textit{H. habilis} and \textit{H. ergaster} probably represent
transitional forms\textsuperscript{12}. In particular, we included fossil remains referred to by some as \textit{H.}
\textit{rudolfensis}\textsuperscript{12-14} within our ‘\textit{H. habilis}’. Debate is mounting as to whether early \textit{Homo} species could
be grouped into a single, highly variable taxon\textsuperscript{15}, but see refs.\textsuperscript{16,17}. Our choice to collapse the
records of \textit{H. habilis} and \textit{H. rudolfensis} into a single species makes it possible to consider them in
the analyses (their respective fossil records would be too small to be statistically meaningful
otherwise). Yet, this also opens the possibility that the absence of the drop in \textit{D} in the last bin of \textit{H.}
\textit{habilis} is artificial, as the grouping might include a species that went extinct plus its anagenetic
descendant. The same is true of \textit{H. ergaster}, which might represent a mere regional variant of \textit{H.}
\textit{erectus}\textsuperscript{12}, whether or not it later gave origin to \textit{H. heidelbergensis} (which is first recognized at the
875 ka old site of Gombore II, Melka Kunture, Ethiopia\textsuperscript{18}). To account for these taxonomic
uncertainties, we repeated the analyses on 1) \textit{H. habilis} grouped with \textit{H. ergaster}, which would
correspond to a single early African hominin scenario; and 2) an \textit{H. ergaster} plus \textit{H. erectus} group
which corresponds to the classic, \textit{H. erectus sensu lato} definition. We found that a statistically
significant drop in the last bin \textit{D} belongs to the latter, and not to the former (Figure S9). This
confirms that the strong decrease in niche overlap between the last BCN and the ECN is absent in
the only living Homo species (H. sapiens) and in early African transitional species, regardless of the
taxonomic arrangement used.

H. heidelbergensis is often recognized as the putative ancestor to both H. sapiens and H.
neanderthalensis, or of the latter at least\textsuperscript{19,20}. Finds in Dali and Jinniushuan (China), Narmada
(India) and Steinheim (Germany) are all younger than the earliest appearance in the fossil record of
both H. sapiens (at Jebel Irhoud, Morocco, recently dated back to 315 ka\textsuperscript{21}) and H. neanderthalensis
(at Sima del Los Huesos, Spain, dated at 434 ka\textsuperscript{22}). This indicates that H. heidelbergensis
underwent at least one speciation event without being replaced by its descendant (i.e. a case of
budding speciation\textsuperscript{23}) rather than transforming into any offspring. Hence, its disappearance
represents a true extinction.

H. erectus last survived in Java, Indonesia, at Ngandong and Sambungmacan. The dating of
this material is highly contentious but has been now confidently placed at 117 to 107 ka\textsuperscript{24}. This
indicates H. erectus would be contemporary but geographically separated from both H. sapiens and
H. neanderthalensis\textsuperscript{25-27}. Regardless, H. erectus could not have been the anagenetic ancestor to
either of them. Therefore, its extinction represents the true termination of a phyletic lineage. We
also repeated the niche overlap analyses for H. erectus removing Ngandong and Sambungmacan
from the record and found again that its last bin BCN is statistically less overlapped with ECN than
any other bin (Figure S10).

H. neanderthalensis had a long story of contact, and interbreeding, with H. sapiens. The
species went extinct in Europe some 41 to 39 ka\textsuperscript{28}. There is no concern about the recognition of H.
neanderthalensis as a true species which left no descendants. H. neanderthalensis last stand was
contentiously placed at 24 ka at Gorham’s cave in Gibraltar\textsuperscript{29}. This dating has been met with fierce
skepticism\textsuperscript{30} so we prudently decided to keep Gorham’s cave out of the analyses. However, the
presence of H. neanderthalensis in Southern Europe after 50 ka is well accepted in the scientific
literature\textsuperscript{31} and in our results. The drop in the last bin Schoener’s D in H. neanderthalensis does not
depend on the temporal resolution of the bin, as is confirmed by using 1 kyr long bins (Figure S11).

In summary, we find that all species representing a lineage leaving no offspring had become restricted to unfavourable or otherwise narrowly defined climatic conditions just before their extinction. Although artificially randomising the natural history of climatic adaptation and variation erases the pattern (Figures S6-8), suggesting a climatic driver for extinction, the drop in niche overlap does not indicate whether the species experienced extreme or somewhat unusual climates just before their extinction, nor does it prove that climate forcing was the cause for the reduction in climatic variability experienced during the last bin. To understand how unusual the climate settings were for the species during their last bins, we located the BCN position within the ECN volume through time, calculating the multivariate Euclidean distance between the barycentre of the ECN and the barycentre of each BCN. The results of this analysis indicate that two extinct species, *H. heidelbergensis* and *H. erectus* faced highly unusual climatic conditions prior to extinction (i.e. during their respective last bins), whereas *H. neanderthalensis* and all other species do not show any salient pattern (Figure 2, see Figure S12 for the ‘extended’ record). This confirms niche conservatism for all non-extinct species. Among the extinct lineages, *H. heidelbergensis* and *H. erectus* were experiencing unusual climates before extinction, with relatively restricted climatic range, whereas the realized climatic niche in *H. neanderthalensis* last bin was narrow, but not unusual for the species. A strong reduction in species range size before extinction (for instance in the wake of the expansion of a superior competitor) provides a potential mechanism that would cause Schoener’s D to drop during the last bin regardless of climatic forcing, because a small-ranged species could only sample restricted climatic variation.
Figure 2. The multivariate distance between the barycenter of the climatic niches occupied by the species in individual time bins as compared to the species evolutionary (total) niche.

To explore this issue, we calculated the minimum convex polygon (MCP) encompassing all the localities in each bin for each extinct species. The land area covered by the MCPs represents the best-guess range size estimate of the species, and it is the most widely used metric for range size estimation in the scientific literature. Since in our analyses there are 100 replications per species to account for age uncertainty of individual fossil localities, there will be 100 different MCPs per bin. Shuffling fossil localities across bins allows us to define confidence intervals around the mean range size, making it possible to test whether the MCP of a bin is statistically different from the mean expectation. We found a statistically significant drop in range size during the last bin only in *Homo erectus*, which was nonetheless present also before the last bin (Figure S13) and is certainly exaggerated by the presence of extensive stretches of land exposed by marine low-stands during the Late Pleistocene but considered as sea surface and therefore removed by the MCP calculation in our data. For the other two extinct species, either they did not distribute over a statistically small

![Figure 2](image-url)
geographic range during their last bin or, in the case of *H. heidelbergensis*, the range was larger than ever before because of the late expansion into Eastern Asia. Using the extended record, we find the same patterns, so again there is no apparent connection between range size and Schoener’s D (Figure S13). By using Spearman’s rho, we found that the two metrics are significantly correlated less than 5% of the time, except for *H. erectus* using the extended record (Table S3). In other words, reduced land area, which ultimately defines the climatic variability the species could sample during its last bin, cannot explain the last-bin drop in Schoener’s D in *H. neanderthalensis* and *H. heidelbergensis*, while the reduction in land area for *H. erectus* occurs at a time well before the arrival of any competing homo species (see Discussion), and it is not a feature of the last bin only. The lack of association between patterns of geographic occupancy and reduction in the realized niche therefore still points to a genuine reduction in the climatic variability experienced by the extinct species during their last stands.

Species vulnerability to climate change

To assess whether there is a direct connection between climatic change and increased exposure to extinction risk in extinct species we used climatic niche factor analysis (CNFA\(^{32}\)). CNFA is used in conservation studies to calculate the expected vulnerability of species to future climate change by projecting species climatic preferences ahead in time. In the present context, we calculated climate change-induced vulnerability during the last bin of each species as inferred from their realized niche preferences during their penultimate bin and by the climatic conditions they faced during their last bin (see Experimental Procedures). In the case of *Homo neanderthalensis*, we calculated vulnerability in the last bin by using different early bins to model the realized climatic niche. It is important to do so because the arrival of *H. sapiens* in Europe at 45ka\(^{33}\) might have influenced the realized niche in Neanderthals before the beginning of the last bin, mixing climate-induced and competition effects at estimating vulnerability in the last bin.
We performed CNFA on the three extinct species and *H. sapiens*. Since *H. sapiens* survived all the changes in climate it experienced during its existence its vulnerability should appear lower than in the extinct species to prove climate change mattered to them.

Our results show striking differences in vulnerability between *H. sapiens* and the significantly more vulnerable extinct species (Figure 3, Table S4). Intriguingly, *H. neanderthalensis* was still found to be more vulnerable than *H. sapiens*, regardless of whether the bins used to calculate vulnerability in the last bin predate or postdate the arrival of *H. sapiens* in Europe (Figure 3). Eventually, holding climate constant between the penultimate and last bin generates statistically lower vulnerability for the extinct species only, indicating the direct influence of climate change on their survival (Figure S14).

**Figure 3. Density plots of climate-induced vulnerability to extinction (a) and PCA plots of species niches.** In the case of *H. neanderthalensis*, we used the climatic preferences of several bins (before and after the arrival of *H. sapiens* in Europe) to infer vulnerability in the last bin.

CNFA results confirm that climate change *per se* played an important role for extinction in past *Homo* species, consistently with the observation that most species cannot cope with rapid climatic changes\(^{34,35}\). In CNFA, the climatic change from the penultimate bin to the last is used to predict species vulnerability as it survives to the last bin. Since the last bin occurrence data are not part of the analyses, any effect of competition with fellow human species during the last bin is ruled out in
this analysis. Therefore, CNFA indicated there is clear evidence that all extinct species were made vulnerable to extinction by climate change, whether or not they suffered from competition with other *Homo* species. Strong arguments for human-mediated extinction, with robust archaeological evidence of geographic overlap, have been advanced so far only for Neanderthals\textsuperscript{4,36-37}. While previous modelling approaches found that climate change, rather than the contact with *H. sapiens* was the main cause of extinction in Neanderthals\textsuperscript{38} this study indicates that climate change is the most likely candidate for the extinction of two past human species and played an important role in the demise of Neanderthals.

**Figure 4.** Sensitivity of Schoener’s $D$ value (y-axis) to the archaeological locality ages (‘core’ record).

*A single, climate change-induced extinction trajectory for all Homo?*
The timing and pace of climate-related increase in extinction risk among extinct Homo species might appear very different. In our modelling approach, H. neanderthalensis drop in Schoener’s D occurs over the last 1-2 kyr of its existence, while the drop in H. heidelbergensis and H. erectus occurs over two orders of magnitude longer bins (i.e. in the 100 kyr range). We were able to demonstrate this apparent difference mostly depends on the resolution of the fossil record. We analysed the course of D within the last bin for all six species (in the case of Neanderthals and H. sapiens we recalculated a single ‘last bin’ for both, using the ages bracketing the end of Mousterian period, from 43 to 36 ka). We calculated Schoener’s D per species over the 100 replications. At each replicate, one fossil locality was taken out of the iteration. If D decreases towards the recent within the last bin, then removing young localities would have the effect of increasing D values towards the recent, so that the regression of 1 minus D (1-D) against locality age of the omitted record would reveal a significant negative relationship. Such an expectation was statistically confirmed for H. neanderthalensis, H. heidelbergensis and for H. erectus only (Figure 4). The regression is never significant for any other species, and in one case only (H. sapiens) the regression is significant but positive in slope, indicating H. sapiens was still widening its climatic niche as the Neanderthals vanished. Importantly, the negative relationship which applies to Late Pleistocene extinct Homo indicates the pace of niche narrowing during the last bin was much more similar among species than the last bin lengths would suggest (Figure 4) providing evidence in favour of a single, shared climate-induced extinction trajectory.

Discussion

Niche overlap analyses allowed us to look in detail at the realized climatic niche in Homo species throughout their existence. We mapped the most appropriate climates derived from the BCN of the last bin onto the geographical space and compared ECN to BCN by means of principal component analysis to see which climatic variable has the most influence on the differences between the last bin niche and the evolutionary niche (Figure 5).
In the case of *H. erectus*, the last BCN is the most distant from ECN among all bins (Figure 2, Figure S12). During this last bin *H. erectus* settled under the warmest and most humid climates then available within its biogeographical region (Figure 5a). These climates were, unsurprisingly, typical for South East Asia, which agrees with the fossil record and with physical evidence suggesting *H. erectus* was adapted to warm climates. The extinction of *H. erectus* took place during the last glacial, that is the coldest period the species had ever experienced.

Similar evidence is found for *H. heidelbergensis*. As with *H. erectus*, the BCN of this species’ last bin barycentre was the most distant from the species ECN barycentre among all bins (Figure 2, Figure S12). The occurrences of the species are unsurprisingly found in relatively warm areas, which were to be found in the Indian sub-continent and Southern Asia (Figure 5b).

We found that the last BCN barycentre of Neanderthals was close to the ECN barycentre (Figure 2, Figure S12). During its last bin the species experienced a slight shift towards more arid and warmer climates, which is typical of the Mediterranean area (Figure 5c). Still, although statistically more vulnerable than *H. sapiens* to climate change, *H. neanderthalensis* was comparatively less vulnerable than both *H. heidelbergensis* and *H. erectus* to the change in climate during the last bin of its existence (Figure 3). Thus, the drop in $D$ during the last bin and the fragmentation of Neanderthals range just prior to extinction might have increased exposure to climate-driven extinction risk (Figure 3a) in combination with *H. sapiens* incidence. The importance of climate change in Neanderthals demise is further demonstrated by its early disappearance at high latitudes consistent with its historical preference for warmer conditions.

One potential confounding factor in explaining our results is the importance of interbreeding. Significant interbreeding was found between Neanderthals and *H. sapiens* and between both these species and Denisovans. Furthermore, there exists the possibility that two further species (or at least two genetic strains) from ancient hominins living in Eastern Asia contribute to our genome. However, it has been noted that the frequency of introgression between
past human species and modern-day humans is probably below 2%, so that significant reproductive
isolation, rather than extensive inbreeding, may have occurred between these species.\textsuperscript{43}

Competition might in principle generate patterns similar to those we found and attribute to
climatic forcing. However, the evidence for such direct effect of interaction between species is very
limited except for Neanderthals. The youngest unquestionable \textit{H. erectus} occurrences at the Solo
river sites (Java), date at some 112 ka, whereas \textit{Homo sapiens} only arrived in the region much later,
with \textit{H. erectus} at some 60 ka\textsuperscript{25-27}. On the continent, the youngest possible \textit{H. erectus} occurrences in Asia at
Zhoukoudian (154 ka in age\textsuperscript{44}), and Dingcun (185 ka in age\textsuperscript{45}) predate Denisovans and post-date the
latest occurrence of \textit{Homo heidelbergensis} in the region\textsuperscript{46} which means that \textit{H. erectus} did not live
along with other hominins. In the case of \textit{Homo heidelbergensis}, the youngest localities are
scattered worldwide, from Spain (Trinchera Galeria\textsuperscript{47}) to China (Jinniushan\textsuperscript{48}). All these localities
are at least some 50 ka older than the first occurrence of \textit{Homo sapiens} outside the African
continent at Mislyia\textsuperscript{49}. This means that \textit{Homo neanderthalensis} is the only candidate species left as
a potential competitor to \textit{Homo heidelbergensis}. Yet, \textit{Homo neanderthalensis} was confined to
Europe and the Middle East until very recently. The oldest occurrences of this species in Asia are at
Denisova (163 ka\textsuperscript{50}) and Ust’-Izhul’ (105 ka\textsuperscript{51}) and are much younger than latest occurrences of \textit{H.
heidelbergensis}. This implies that \textit{Homo neanderthalensis} is the only species for which direct
competition with \textit{H. sapiens} is possible and may have in fact contributed to its extinction\textsuperscript{36-37}. The
archaeological evidence means that the BCN contraction we observed in the last bin of extinct
\textit{Homo} species cannot be explained by competition with fellow humans, perhaps with the exception
of \textit{H. neanderthalensis}. This study provides the first strong evidence that climate change was a
common extinction factor shared by all our ancestors. By virtue of their cognitive skills, recent
human species were able to exploit a combination of fire control, clothing, and dispersal ability\textsuperscript{52-54}
that would surely have helped to mitigate the effects of climate change on their survival by
effectively manipulating their own microclimates or moving rapidly to settle under better
conditions. Indeed, it has been recently demonstrated empirically that such protected microclimatic

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conditions buffer extinction risk. Yet, not even *Homo* species, some of the most technologically
advanced, plastic and ecologically widespread species ever, were immune to global change. For
multiple reasons, not least the spectacular advances in technologies available to shield modern
humans from directly experiencing their own local climate, and the agricultural enhancement of
natural primary production, our methodology cannot meaningfully be applied directly to the future
of *H. sapiens*. But our own future depends critically on the health of Earth's supporting ecosystems
and the entire living biota, and our analysis provides a stark warning concerning the power of
anthropogenic future climate change to translate directly into extinction risk for other species less
well-equipped to adapt than sp. *Homo*. This suggests that the threat posed by the current,
anthropogenic climate change for global wildlife and, by extension, ourselves, is possibly even
more powerful than is generally appreciated.
Figure 5. PCA plots and map projections of the climatic niches of the last bin for each species as contrasted to its evolutionary niche.

Experimental Procedures

Fossil occurrence data
We considered six species, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*; *H. luzonensis*, *H. floresensis*, *H. naledi*, *H. antecessor* and *H. luzonensis*. Denison hominins were excluded because their fossil records were too much stratigraphically and geographically restricted to study climatic niche evolution. We extensively reviewed the literature collecting *Homo* fossil occurrence data. Each occurrence includes information about the latitude and the longitude of the site, the archaeological layer and the absolute age of the dated sample. Only absolute dating estimates (i.e. radiocarbon, ESR, palaeomagnetism) were used. When available, we also included information about which sample was used for the dating and its lab code. Radiocarbon dates were calibrated by using the “Bchron” R package, using Intcal13 calibration curve for the Northern hemisphere, shcal13 curve for the Southern hemisphere and marine13 curve for marine samples.

We evaluated and confirmed the reliability of every single age according to the latest published literature (Supplemental Experimental Procedures). Age estimates come with dating 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 a minimum age and a maximum age (calculated according to individual estimates and their respective confidence intervals).

The fossil record includes 759 fossil localities, amounting to 1435 archaeological layers (single localities may contain > 1 archaeological layer) in the ‘core’ record and 1527 archaeological records in the ‘extended’ record (Figure S1, Data S1). The total number of age estimates is 2752. Over 40% of the dating refer to the 14C method (92.3% of which refer to AMS dating). Additional common dating methods are ESR (14.3%), Thermoluminescence (12.7%) and OSL (11.7%).

**Core and extended records**

Each individual occurrence in the record was attributed to a given species depending on: i) the presence of fossil remains attributed to a given taxon, ii) the age limits of the individual species
(i.e. an occurrence in Africa older than the first appearance of \textit{H. heidelbergensis} and younger than
the last appearance of \textit{H. habilis} was attributed to \textit{H. ergaster}) and iii) the stone tool industry
present (i.e. French Mousterian stone tools were invariably assigned to \textit{H. neanderthalensis} because
no other \textit{Homo} species implemented this Mousterian tradition$^{28,59}$). By applying these criteria, we
produced a ‘core’ record for each species. In some one third of the cases, neither of the three criteria
above was met, meaning that the archaeological layer (or the toolmaker) cannot be ascribed to a
single species. For instance, \textit{H. erectus} earliest occurrence outside Africa at Dmanisi, Georgia, is
found in association with Oldowan stone tools$^{60}$ whereas younger \textit{H. erectus} and \textit{H. ergaster}
samples are associated to the Acheulean stone industry. For this reason, Dmanisi could be attributed
to either \textit{H. ergaster} or \textit{H. erectus} and therefore falls in the ‘extended’ record of both. The same
applies with earliest \textit{H. sapiens}, which is associated to the Acheulean at Jebel Irhoud$^{21}$ when
Acheulean was still implemented by \textit{H. heidelbergensis}, meaning that Acheulean samples younger
than Jebel Irhoud cannot be attributed with certainty to either of the two species. The problem
becomes even more important for transitional industries (e.g. Szeletian, Bohunician, Uluzzian$^{61-62}$).
For all these cases, we used the ‘extended’ record duplicating multiple-attribution records and
adding the duplicates to each possible \textit{Homo} species.

\textbf{Environmental predictors}

Environmental predictors were generated using a paleoclimate emulator$^9$. The approach
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 (\textit{CO}_2, orbit and ice-volume). Spatial fields of i) minimum seasonal temperature,
ii) maximum seasonal temperature, iii) minimum seasonal precipitation, iv) maximum seasonal
precipitation, and v) net primary productivity 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.
For the orbital parameter inputs, we applied the 5 million-year calculation of Berger and Loutre$^{63}$. 
We used CO$_2$ from Antarctic ice cores for the last 800,000 years$^{64}$. Prior to 800 ka, and for the entire sea-level record, we used the CO$_2$ and sea-level reconstructions in ref. 65. Contemporary observations of the four bioclimatic variables were derived from WorldClim$^{66}$, while NPP observations were derived from MOD17A3H$^{67}$. The observations were interpolated onto the same 0.5° grid and combined with emulated anomalies. Temperature anomalies were additively combined with observations, while precipitation and NPP anomalies were combined with observations using a hybrid additive/multiplicative approach$^9$.

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 (see ref. 9). Glacial-interglacial variability was validated against the observationally based global temperature reconstructions$^{68}$.

The emulator assumption of an invariant relationship between sea level and ice-sheet state neglects the asymmetry of ice sheets under glaciation and deglaciation and furthermore assumes that ice sheets were located similarly in all previous Pliocene-Pleistocene glaciations. In the present context this is of minor importance, since $Homo$ occurrences are mostly located far away from the frost line. For instance, only 17 occurrences out of 2752 (0.62%) are above 55 degrees in latitude and above 52°N the percentage is only 3%, of which 98% of occurrences (85 out of 87) are for the single, non-extinct species, $Homo sapiens$.

Paleoclimate anomalies at climate model resolution (5°) are downscaled onto the observed modern climatology at 0.5° spatial resolution using bilinear interpolation.

We generated predictors spanning from the oldest $Homo$ occurrence at Ledi Geraru, Ethiopia, to 36 ka, which is the youngest available occurrence for $H. neanderthalensis$, the last human species to go extinct.

Climatic niche evolution
Once the species records (both ‘core’ and ‘extended’) were prepared, we removed duplicated records falling in the same cell and 1 kyr-long temporal layer of the environmental grid used in the subsequent analyses. After this procedure, we obtained the following numbers of species occurrences: 26 (30 ‘extended’) for *H. habilis*, 45 (60 ‘extended’) for *H. ergaster*, 61 (104 ‘extended’) for *H. erectus*, 261 (358 ‘extended’) for *H. heidelbergensis*, 1361 (1447 ‘extended’) for *H. neanderthalensis* and 849 (904 ‘extended’) for *H. sapiens*. We decided to use the last occurrence of *H. neanderthalensis* core record as lower age limit also for the *H. sapiens* record. To account for the effect of dating uncertainty, we produced, around each age estimate, a uniform distribution spanning from the minimum to the maximum estimate. Then, we randomly sampled a single date within this range, and performed niche similarity tests (see below). This procedure was repeated 100 times, and niche similarity results of the 100 replicates were eventually pooled together. For each species and replicated date, we randomly generated a set of 10,000 background points, which were used as pseudo-absences together with observed presences to perform the niche similarity tests. The 10,000 pseudo-absences were subdivided across the time periods where each species occurred, proportionally to the number of fossil occurrences falling within each time bin. As sampling areas for background points, we chose well-known biogeographic boundaries for each species. Specifically, we sampled Africa for *H. habilis* and *H. ergaster*, Eurasia for *H. erectus* and *H. neanderthalensis*, and a combination of both areas for *H. heidelbergensis* and *H. sapiens*. To reduce the risk of sampling non-accessible areas according to species dispersal abilities, we generated background points for each species within a specific area drawn as a 1,000 km buffer around the convex hull surrounding all known species occurrences.

**Niche overlap analysis**

Since the framework to perform niche overlap tests requires at least five occurrences per bin to run, we aggregated the records of *H. habilis*, *H. ergaster*, *H. erectus* and *H. heidelbergensis* in
temporal bins longer than 1 kyr. In particular, we set the bin length so as to minimize the number of occurrences per bin and the bin length. A maximum likelihood optimization function was written specifically to achieve this goal. Although poor, the record of each species follows a Gaussian distribution, being rare both at the beginning and towards the end of their existence. The same does not apply to *H. neanderthalensis* and *H. sapiens*, whose fossil record is highly skewed in favour of recent archaeological localities. For these species, we calculated the skewness of the distribution of age estimates and removed the localities in the right (i.e. old age) of the age estimate distribution until skew became < 1, therefore making the distribution less skewed. By applying this procedure, the record of *H. neanderthalensis* was cut to 60 ka. The record of *H. sapiens* was cut to 45 ka. The cut records of both species still represent > 90% of the total number of occurrences. Even by cutting the record to reduce the skewness of the age distribution of archaeological layers, the number of archaeological localities per bin in *H. neanderthalensis* and *H. sapiens* still greatly varies across time bins. This introduces a potential bias since locality-rich bins might represent a larger portion of the ECN by chance. Therefore, for *H. neanderthalensis* and *H. sapiens*, we randomly excluded from each bin in each replicate sufficient archaeologic localities (i.e. fossil occurrences) as to reduce the maximum number of localities per bin below the 33rd percentile of the number of localities per bin distribution.

For each *Homo* species, we compared each BCN to the ECN. The former was built by pooling the paleoclimatic variables estimates at the individual archaeological layers falling within the same bin together. Similarly, the ECN was computed by taking together the paleoclimatic variables of all the fossil records and background points (i.e. unsampled localities) of the focal species together. This approach reduces the effect of environmental truncation (i.e. the failure to capture the full environmental range experienced by the species) on niche estimation by including the highest possible amount of information on niche features. Moreover, we can track realized niche oscillations through time within the full set of niche characteristics exhibited by a species through its existence.
We calculated BCN to ECN niche overlap by using the analytical framework proposed by Broennimann et al.\textsuperscript{71} and adopted in several studies dealing with fossil species\textsuperscript{38,72}. Under this approach, the environmental space defined for each species (i.e. all the environmental conditions intersected by the species fossil localities and by the pseudoabsences within the background area) is decomposed by means of principal components analysis (PCA). Environmental conditions of individual BCNs and ECN were in turn projected into the PCA space, separately for each species. The BCNs can then be compared to their respective ECN in PCA space. The density of the background environments and species occurrences across the first two PCs were calculated by a kernel density smoother and, respectively, divided by the maximum number of occurrences in any one cell of the environmental space and by the number of sites with the most common environment\textsuperscript{52}. The resulting density grids of $r \times r$ cells in the environmental space were used to compute niche overlaps between each temporal bin and the total niche in terms of Schoener’s $D$\textsuperscript{73-74}, a metric that ranges from 0 (no niche overlap) to 1 (complete niche overlap). We performed niche similarity tests \textit{sensu} Warren et al.\textsuperscript{74}, a procedure that evaluates if the two niches being compared (i.e. BCN and ECN) are more similar/different than expected by chance. The test proceeds by comparing the niche overlap values (Schoener’s $D$) between each temporal bin and the evolutionary niche to a null distribution of 100 overlap values, yielding a significant outcome if the observed Schoener’s $D$ value is higher (“niche conservatism” hypothesis) or lower (“niche divergence” hypothesis) than the 95th percentile of the null distribution (P < 0.05).

Given the importance of the change in overlap for the last bin BCN in most species, we back-projected the density of occurrences of the last bin calculated in the PCA environmental space onto the geographical space. This way we could map geographically the areas where the climatic conditions were appropriate for the species during the last bin. The PCA plots can be inspected to see which climatic variables influence the most the differences between ECN and the last bin BCN.

All climatic niche evolution analyses were performed using both the ‘core’ and ‘extended’ records. We tested the effect of paleoclimate emulator predictions on the temporal patterns of niche
overlap per species repeating the analyses by always using the current climatic variables irrespective of fossil locality ages (Figure S4), by using the climatic data aggregated at 5° spatial resolution (Figures S5), by randomizing fossil locality ages (and their relative climatic variables) across bins (Figures S6-7), and by erasing the effect of climatic change altogether shuffling climatic data across fossil localities (Figures S8).

Assessing vulnerability to climatic change

Climate niche factor analysis (CNFA) assesses the vulnerability to climatic change\textsuperscript{32}. This is an adaptation of ecological niche factor analysis (ENFA) that assesses the vulnerability of a species to climatic change accounting for the contribution of niche specialization (the narrowness of species climatic tolerance) and exposure (the differences between current and future climatic conditions inside present-day habitat). To implement CNFA, for each species we used its penultimate bin BCN and the climatic data for the last BCN. We developed CNFA over 100 replicates for each species. Vulnerability values were then compared among species by means of ANOVA and post-hoc Tukey HSD tests. Since extinction (as opposed to possible instances of anagenetic transformation) associated to climate change was evidenced for three species only (\textit{H. heidelbergensis}, \textit{H. erectus} and \textit{H. neanderthalensis}) we assessed CNFA for these species and compared their vulnerabilities to each other and to those of their only contemporary congenerics, \textit{H. sapiens}. In the case of \textit{H. sapiens} and \textit{H. neanderthalensis}, bin length is as small as 1 kyr (we similarly tested bin length = 2 kyr). However, it has been demonstrated that the pace of climatic change occurs at almost the same temporal resolution of these bins\textsuperscript{59}. Therefore, for these species only we chose to compare non-contiguous bins. \textit{Homo neanderthalensis} extinction is statistically placed during the interval 41-39 ka\textsuperscript{28}. The end of Neanderthals specific stone tool technology, the Mousterian, is similarly placed in the 43 to 36 ka interval\textsuperscript{28}. Therefore, we decided to use the BCN of \textit{H. neanderthalensis} and \textit{H. sapiens} calculated during the 43 to 42 ka time interval as their second to last bin BCN and the climatic predictions during the 37 to 36 ka time interval as their ‘last’ bin climatic settings.
However, competition effect with *Homo sapiens* could already be in place at the 43 to 42 ka time interval. This would result in a narrow realized niche at the 43 to 42 ka and would mix competition and climate change-induced effects in calculating vulnerability. Therefore, we also performed CNFA using 48 to 49 ka, 50 to 51 ka and 52 to 53 ka bins to calculate vulnerability in the last bin. Finally, we used CNFA to test the hypothesis that ignoring climate change extinct species would not become vulnerable during their last bin. To this aim, we held the climate constant between the penultimate and last bin for each of the six species under scrutiny and repeated CNFA. For Neanderthals only, we also repeated CNFA using different time intervals as to represent the penultimate bin, as explained above. We expected that by holding climate constant between the last two bins per species, vulnerability would drop for the extinct species only if climate really mattered to their extinction. After vulnerabilities were estimated, for each species we compared the two distributions (i.e. ignoring or including climate change) by means of Student’s T test (Figure S14).

**Assessing niche overlap within the last bin of the species**

The resolution of the fossil record in *H. neanderthalensis* and *H. sapiens* is significantly denser than in older, early *Homo* species. Therefore, the last bin drop in Schoener’s $D$ in *H. erectus* and *H. heidelbergensis* can only appear at a much coarser temporal scale than in *H. neanderthalensis*. To verify the hypothesis that these scales are actually not that different, we devised a strategy to analyse niche overlap within the last bin in all species. Ideally, if the decrease in niche overlap in *H. erectus* and *H. heidelbergensis* occurs within the last bin the regression of $D$ values against the ages of the archaeological layers would appear significant and positive (i.e. lower $D$ values towards the present). However, $D$ is a property of bins, rather than of individual fossil localities. Therefore, to perform the regression we devised a leave-one-out procedure. Under this procedure, we took each replicate of the niche overlap test, removed one locality at a time from the bin, and recalculated $D$
after each removal. The same process was repeated for all replicates. Then, we fitted a linear mixed
effect regression of $D$ values against the age of the localities, using the replicates as the random
effect. A positive relationship between $D$ and age would indicate that the last bin $D$ increases when
that particular locality is removed. The positive sign of the slope would therefore indicate that
younger localities within the last bin contribute more than older localities within the bin. A positive
relationship is therefore not expected to occur in non-extinct species lineages, that is $H. \text{habilis}$, $H. \text{ergaster}$ and $H. \text{sapiens}$. For $H. \text{neanderthalensis}$ and $H. \text{sapiens}$, we coarsened the record to verify
the hypothesis that the temporal resolution of the last bin drop in $D$ is similar across extinct species,
and that no such evidence would appear for $H. \text{sapiens}$. We pooled all the occurrences of the two
species from the extinction age of $H. \text{neanderthalensis}$ to the beginning of end-Mousterian period
(that is 43 to 36 ka) and repeated the leave-one-out procedure on this 8 kyr long last bin. The
starting hypothesis was that a significant and positive relationship would only apply for $H. \text{neanderthalensis}$.

Supplemental Information: Supplemental Information will be uploaded online upon acceptance.

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Figure legends

**Figure 1.** Degree of Niche Overlap between niche occupied during a specific time bin and the species evolutionary (total) niche (measured in terms of Schoener’s $D$ values, y-axis), using the core record. Upper row, transitional, non-extinct species do not exhibit any significant change in $D$ over time. Lower row, extinct species. The 99% confidence intervals of the random distribution of Schoener’s $D$ (degree of niche overlap) across time bins are reported as horizontal dashed lines. The temporal range of the archaeological ‘core’ record for each species is reported at the extremes of the x-axis. Box and whiskers represent the interquartile distances and extreme observations obtained repeating the analyses 100 times for each species to account for ageing uncertainty of individual fossil localities.

**Figure 2.** The multivariate distance between the barycenters of the climatic niche occupied by the species in individual time bins as compared to the species evolutionary (total) niche. The temporal range for each species is reported at the extremes of the x-axis. On the y-axis the Euclidean distance values.

**Figure 3.** Density plots of climate-induced vulnerability to extinction (a) and PCA plots of species niches. In the case of *H. neanderthalensis*, we used the climatic preferences of several bins (before and after the arrival of *H. sapiens* in Europe) to infer vulnerability in the last bin. The principal components plots of species climatic niches, indicating the position of each species’ niche during their respective last bins. The solid line includes 50% of the species climatic niche space, the dashed line includes 90% of the species climatic niches. The dotted lines include 95% of the background climates (i.e. regardless of where the species presences were recorded). The correlation between individual variables and the PC eigenvectors is illustrated by the direction and
magnitude of the vectors, so that the contribution of individual variables to the direction of change in the climatic niche from ECN to the last BCN is represented. The percentage of climatic variance represented by each PC vector is indicated on the axes.

**Figure 4. Sensitivity of Schoener’s D value (y-axis) to the archaeological locality ages (‘core’ record).** The data refer to the last bin of each species (the last 10 kyr for the records of *H. neanderthalensis* and *H. sapiens*). The p-value represents the probability that the slope of D against the (omitted) locality age differs from zero. Time is indicated as million years before present. Schoener’s D is presented as its complement to 1 (i.e. 1-D).

**Figure 5. PCA plots and map projections of the climatic niches of the last bin for each species as contrasted to its evolutionary niche.** The density values derived from the PCA space are projected in the geographic space to locate the areas with the most appropriate climates for the focal species during its last bin. In the PC plots, ECN is represented by the grey area, last-bin BCN by the coloured area. The lines represent the 50% (solid), 90% (dashed) and background climate (dotted) isopleths. Vectors’ length and orientation indicate the importance of individual variables in the PCA space. Therefore, they indicate which climatic variable makes the last bin BCN different from ECN.