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

Highlights

- Climate change is a major factor in evolution, shaping the history of life on Earth
- Humans usually feel excluded by climate change-induced extinction risk
- We demonstrate that climate change drove past human species extinct

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In Brief

At least six different *Homo* species populated the World during the Pleistocene. The extinction of all but one of them is currently shrouded in mystery, despite the enormous importance of the matter. We used a novel past climate emulator and an extensive fossil database to model climatic niche evolution in *Homo*. We found statistically robust evidence that extinction in past *Homo* species has a genuine climatic drive. In the case of Neanderthals, the increased extinction risk was probably exacerbated by competition with *H. sapiens*.

Raia et al., 2020, One Earth *3*, 1–11
October 23, 2020 © 2020 Elsevier Inc.
https://doi.org/10.1016/j.oneear.2020.09.007

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

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https://doi.org/10.1016/j.oneear.2020.09.007

SCIENCE FOR SOCIETY The message of the extinction rebellion protest movement, that human-induced climate change poses a threat to our species' survival, is reawakening consciences worldwide. Climate change is known to have been a major player in the turnover of species throughout the geological record. Were our ancestors, forged through the continually oscillating Pleistocene glacial cycles, not shielded from this danger? To date, the lack of sufficiently detailed and long-timescale climate information and the scarcity of data on early humans have left this question unanswered. By combining a mammoth data collation and analysis with novel paleoclimate modeling, we discovered that, for vanished human species, extinction had a candid, unquestionable climatic drive, which in the case of Neanderthals adds to the effect of competition with ourselves. Notably, *Homo sapiens* is the only species whose climatic niche was still expanding toward the end of our analysis, when the Neanderthals went extinct.

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. Here, we use a recently implemented past climate emulator and an extensive fossil database spanning 2,754 archaeological records to model climatic niche evolution in *Homo*. We find 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 coincides with increased vulnerability to climate change. In the case of Neanderthals, the 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.

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 1,000 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 ka time bins (and we repeated the analyses using 2 ka 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 with the ECN, meaning that during the bin duration the species experienced 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 aging 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 previous expectation was that, on average, D values of individual bins were uniformly constant throughout each species' existence. This niche conservatism[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 Pleistocenic 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 with the distribution of random values.

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). These patterns do not change whether the "core" or "extended" fossil records are used (see Figure S3 for the "extended" record, and Zenodo: https://doi.org/10.5281/zenodo.4040848 for additional results), 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° (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 climates (Figures S6 and S7). 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 that climatic changes possibly had a role in extinction (Figure S8). For paleontological species, extinction coincides with their disappearance from the fossil record. Yet, while some such paleontological 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.[11] These morphological species are conventionally referred to as "transitional" forms. In our records, *H. habilis* and *H. ergaster* probably represent transitional forms.[12] In particular, we included fossil remains referred to by some as *H. rudolfensis*[12–14] within our "*H. habilis.*" Debate is mounting as to whether early *Homo* species could be grouped into a single, highly variable taxon,[15] but see Rightmire and colleagues[16] and Hublin[16,17] Our choice to collapse the records of *H. habilis* and *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 D in the last bin of *H. habilis* is artificial, as the grouping might

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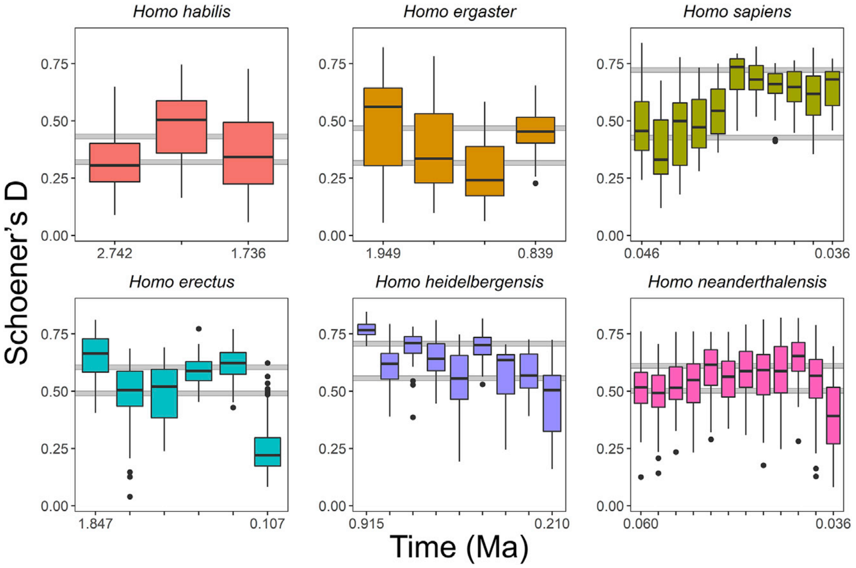

Figure 1. Degree of Niche Overlap between a Niche Occupied during a Specific Time Bin and the Species Evolutionary (Total) Niche (Measured in Terms of Schoener's *D* Values, y Axis), Using the Core Record

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 gray 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 aging uncertainty of individual fossil localities.

include a species that went extinct plus its anagenetic descendant. The same is true of *H. ergaster*, which might represent a mere regional variant of *H. erectus*,[12] whether or not it later gave origin to *H. heidelbergensis* (which is first recognized at the 875 ka old site of Gombore II, Melka Kunture, Ethiopia[18]). To account for these taxonomic uncertainties, we repeated the analyses on (1) *H. habilis* grouped with *H. ergaster*, which would correspond to a single early African hominin scenario; and (2) an *H. ergaster* plus *H. erectus* group which corresponds to the classic, *H. erectus sensu lato* definition. We found that a statistically significant drop in the last bin *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.[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[21]) and *H. neanderthalensis* (at Sima del Los Huesos, Spain, dated at 434 ka[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[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 117–107 ka.[24] This indicates that *H. erectus* would be contemporary but geographically separated from both *H. sapiens* and *H. neanderthalensis*.[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 41–39 ka.[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.[29] This dating has been met with fierce skepticism,[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[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 ka 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 randomizing the natural history of climatic adaptation and variation erases the pattern (Figures S6–S8), 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 barycenter of the ECN and the barycenter of each BCN. The results of this analysis indicate that two extinct species, *H. heidelbergensis* and *H. erectus*, faced highly unusual climatic conditions before 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

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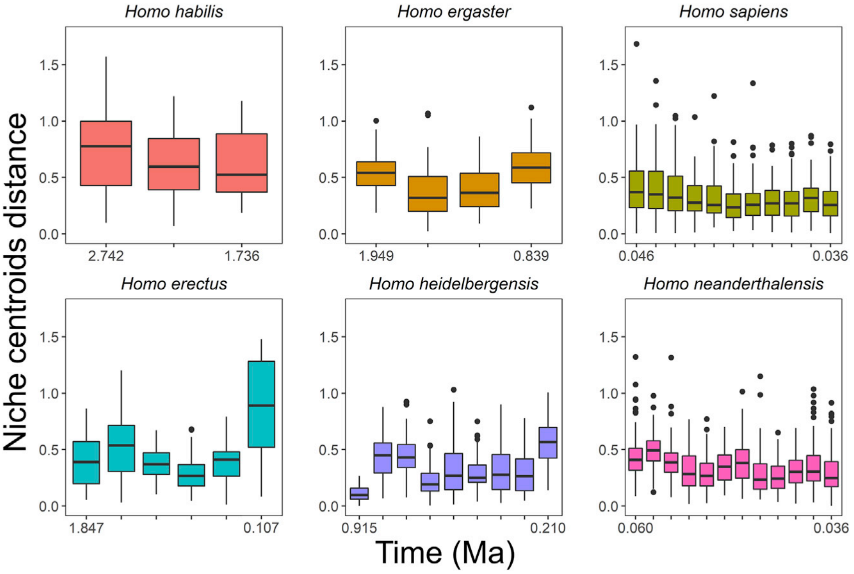

Figure 2. The Multivariate Distance between the Barycenters of the Climatic Niche Occupied by the Species in Individual Time Bins as Compared with the Species Evolutionary (Total) Niche

The temporal range for each species is reported at the extremes of the x axis, and on the y axis the Euclidean distance values.

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.

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. Because 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 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). Using Spearman's rho, we found that, except for *H. erectus*, the two metrics are significantly correlated less than 5% of the time using the extended record (Zenodo: https://doi.org/10.5281/zenodo.4040848). 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 *H. 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 45 ka[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*. Because *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 Zenodo:https://doi.org/10.5281/zenodo.4040848). 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).

CNFA results confirm that climate change *per se* played an important role for extinction in past *Homo* species, consistent 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

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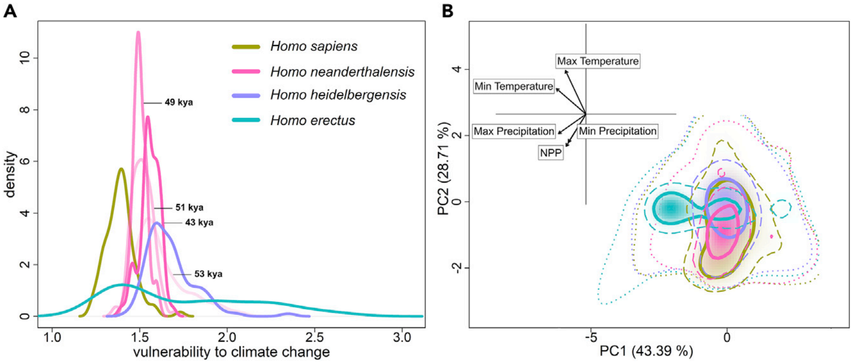

Figure 3. Density Plots of Climate-Induced Vulnerability to Extinction (A) and PCA Plots of Species Niches (B)

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.

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.[4,36,37] While previous modeling approaches found that climate change, rather than the contact with *H. sapiens* was the main cause of extinction in Neanderthals,[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.

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 modeling approach, *H. neanderthalensis* drop in Schoener's D occurs over the last 1–2 ka 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 ka range). We were able to demonstrate that this apparent difference mostly depends on the resolution of the fossil record.

We analyzed 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 the Mousterian period, from 43 to 36 ka[28]). 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 toward the recent within the last bin, then removing young localities would have the effect of increasing D values toward 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. heildelbergensis*, and *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 that *H. sapiens* was still widening its climatic niche as the Neanderthals vanished. Importantly, the negative relationship that applies to Late Pleistocene extinct *Homo* indicates that 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 favor 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 with BCN by means of principal-component analysis (PCA) 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 (Figures 2 and 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 that *H. erectus* was adapted to warm climates.[39] The extinction of *H. erectus* took place during the last glacial, which 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 barycenter was the most distant from the species ECN barycenter among all bins (Figures 2 and 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 barycenter of Neanderthals was close to the ECN barycenter (Figures 2 and S12). During its last bin the species experienced a slight shift toward 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[38] just before 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

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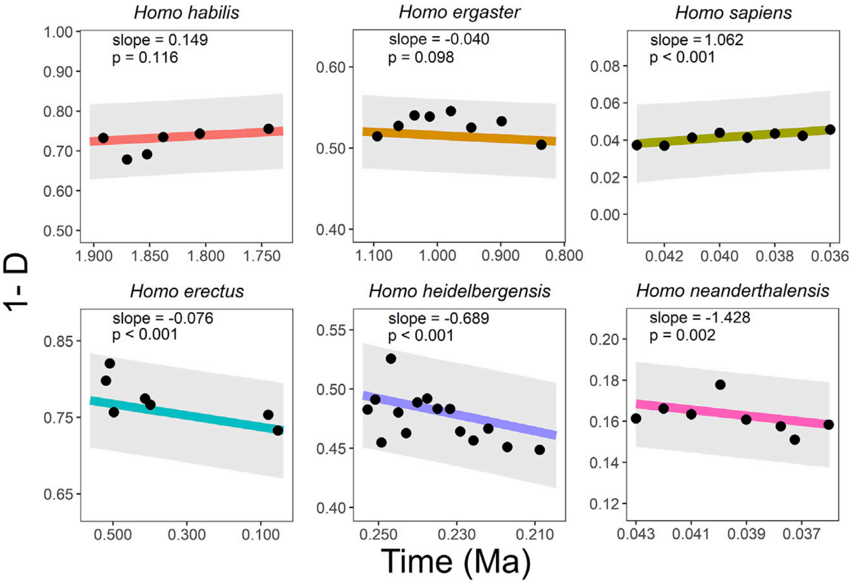

Figure 4. Sensitivity of Schoener's *D* Value (y Axis) to the Archaeological Locality Ages ("Core" Record)

The data refer to the last bin of each species (the last 10 ka 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).

demonstrated by its early disappearance at high latitudes,[40] consistent with its historical preference for warmer conditions.[41]

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.[42] 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.[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 *H. erectus* occurrences at the Solo river sites (Java), date at some 112 ka, whereas *H. sapiens* only arrived in the region much later, at some 60 ka.[25–27] On the continent, the youngest possible *H. erectus* occurrences in Asia at Zhoukoudian (154 ka in age[44]) and Dingcun (185 ka in age[45]) predate Denisovans and postdate the latest occurrence of *H. heidelbergensis* in the region,[46] which means that *H. erectus* did not live along with other hominins. In the case of *H. heidelbergensis*, the youngest localities are scattered worldwide, from Spain (Trinchera Galeria[47]) to China (Jinniushan[48]). All these localities are at least some 50 ka older than the first occurrence of *H. sapiens* outside the African continent at Mislyia.[49] This means that *H. neanderthalensis* is the only candidate species left as a potential competitor to *H. heidelbergensis*. Yet, *H. 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[50]) and Ust'-Izhul' (105 ka[51]), and are much younger than the latest occurrences of *H. heidelbergensis*. This implies that *H. neanderthalensis* is the only species for which direct competition with *H. sapiens* is possible and may have in fact contributed to its extinction.[36,37] The archaeological evidence means that the BCN contraction we observed in the last bin of extinct *Homo* species cannot be explained by competition with fellow humans, perhaps with the exception of *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[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 conditions buffer extinction risk.[55] 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[56] and, by extension, ourselves, is possibly even more powerful than is generally appreciated.

EXPERIMENTAL PROCEDURES

Resource Availability

The Supplemental Information includes the full explanation for the treatment of human fossil record and Figures S1–S16.

Lead Contact

Further information will be fulfilled by the Lead Contact, Pasquale Raia (pasquale.raia@unina.it).

Materials Availability

The fossil occurrences per species are available as "Document S1" at https://doi.org/10.5281/zenodo.4038436.

Supplemental Data Tables S1–S4 are available at https://doi.org/10.5281/zenodo.4040848.

Data and Code Availability

The software code used in this study is available at https://doi.org/10.5281/zenodo.4036012.

Fossil Occurrence Data

We considered six species, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*; *H. luzonensis*,

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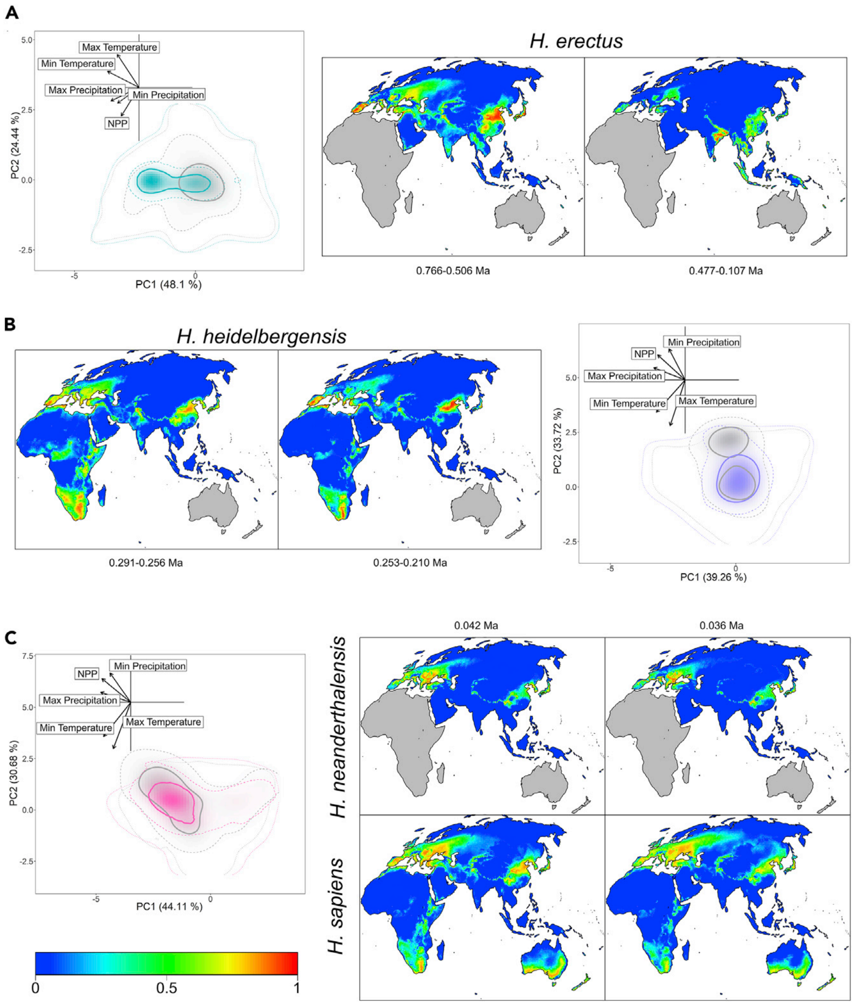

Figure 5. PCA Plots and Map Projections of the Climatic Niches of the Last Bin for Each Species as Contrasted to Its Evolutionary Niche

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 gray area, last bin BCN by the colored area. The lines represent the 50% (solid), 90% (dashed), and background climate (dotted) isopleths. Vector 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.

H. floresensis, *H. naledi*, *H. antecessor*, and Denisovan hominins were excluded because their fossil records were much too 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,[57] using the Intcal13 calibration curve for the Northern hemisphere, the shcal13 curve for the Southern hemisphere, and the marine13 curve for marine samples.[58]

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 1,435 archaeological layers (single localities may contain >1 archaeological layer) in the "core" record and 1,527 archaeological records in the "extended" record (Figure S1, Document S1, explained in full in the Supplemental Information). The total number of age estimates is 2,754. Over 40% of the dating refers 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: (1) the presence of fossil remains attributed to a given taxon, (2) the age limits of the individual species (i.e., an occurrence in Africa older than the first appearance of *H. heidelbergensis* and younger than the last appearance of *H. habilis* was attributed to *H. ergaster*), and (3) the stone tool industry present (i.e., French Mousterian stone tools were invariably assigned to *H. neanderthalensis* because no other *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, none of the three criteria above was met, meaning that the archaeological layer (or the toolmaker) cannot be ascribed to a single species. For instance, *H. erectus* earliest occurrence outside Africa at Dmanisi, Georgia, is found in association with Oldowan stone tools,[60] whereas younger *H. erectus* and *H. ergaster* samples are associated to the Acheulean stone industry. For this reason, Dmanisi could be attributed to either *H. ergaster* or *H. erectus* and therefore falls in the "extended" record of both. The same applies with earliest *H. sapiens*, which is associated to the Acheulean at Jebel Irhoud[21] when Acheulean was still implemented by *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, and Uluzzian[61,62]). For all these cases, we used the "extended" record duplicating multiple-attribution records and adding the duplicates to each possible *Homo* species.

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 (CO_2, orbit, and ice volume). Spatial fields of (1) minimum seasonal temperature, (2) maximum seasonal temperature, (3) minimum seasonal precipitation, (4) maximum seasonal precipitation, and (5) 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] Before 800 ka, and for the entire sea-level record, we used the same CO_2 and sea-level reconstructions as Stap and colleagues.[65] Contemporary observations of the four bioclimatic variables were derived from WorldClim,[66] while

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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 Holden and colleagues[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 2,754 (0.62%) are above 55° 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, *H. 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 ka 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 the 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 pseudoabsences together with observed presences to perform the niche similarity tests. The 10,000 pseudoabsences 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 ka. In particular, we set the bin length 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 toward the end of their existence. The same does not apply to *H. neanderthalensis* and *H. sapiens*, whose fossil record is highly skewed in favor 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) 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 with 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.[69] This approach reduces the effect of environmental truncation[70] (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 and colleagues[71] and adopted in several studies dealing with fossil species.[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 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 with 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.[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,[73,74] a metric that ranges from 0 (no niche overlap) to 1 (complete niche overlap). We performed niche similarity tests *sensu* Warren and colleagues,[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. In 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 most influence 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 (Figure S5), by randomizing fossil locality ages (and their relative climatic variables) across bins (Figures S6 and S7), and by erasing the effect of climatic change altogether shuffling climatic data across fossil localities (Figure S8).

Assessing Vulnerability to Climatic Change

CNFA assesses the vulnerability to climatic change.[32] This is an adaptation of ecological niche factor analysis 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

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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 demonstrated for three species only (*H. heidelbergensis*, *H. erectus*, and *H. neanderthalensis*) we assessed CNFA for these species and compared their vulnerabilities with each other and to those of their only contemporary congenerics, *H. sapiens*. In the case of *H. sapiens* and *H. neanderthalensis*, bin length is as small as 1 ka (we similarly tested bin length = 2 ka). However, it has been demonstrated that the pace of climatic change occurs at almost the same temporal resolution of these bins.[59] Therefore, for these species only we chose to compare non-contiguous bins. *Homo neanderthalensis* extinction is statistically placed during the interval 41–39 ka.[28] The end of Neanderthal's specific stone tool technology, the Mousterian, is similarly placed in the 43–36 ka interval.[28] Therefore, we decided to use the BCN of *H. neanderthalensis* and *H. sapiens* calculated during the 43–42 ka time interval as their second to last bin BCN and the climatic predictions during the 37–36 ka time interval as their "last" bin climatic settings. However, competition effect with *H. sapiens* could already be in place at the 43–42 ka time interval. This would result in a narrow realized niche at 43–42 ka and would mix competition and climate change-induced effects in calculating vulnerability. Therefore, we also performed CNFA using 48–49 ka, 50–51 ka, and 52–53 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 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 analyze 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 toward 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. habilis*, *H. ergaster*, and *H. sapiens*. For *H. neanderthalensis* and *H. 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. sapiens*. We pooled all the occurrences of the two species from the extinction age of *H. neanderthalensis* to the beginning of end-Mousterian period (that is 43–36 ka) and repeated the leave-one-out procedure on this 8 ka long last bin. The starting hypothesis was that a significant and positive relationship would only apply for *H. neanderthalensis*.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.oneear.2020.09.007.

ACKNOWLEDGMENTS

Work by J.A.F.D.-F. and T.F.R. has been continuously supported by CNPq productivity grants. Our research program on macroecology and climate change is developed in the context of the National Institute of Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation supported by MCTIC/CNPq/FAPEG (grants 465610/2014-5 and 201810267000023). We are grateful to Philip Sexton and Nigel Harris for insightful comments on an earlier version of this manuscript.

AUTHOR CONTRIBUTIONS

P.R., J.A.F.D.-F., M.D.F., F.C., L.M., and T.F.R. conceived the paper. A.M., M.M., A.P., L.R., and P.R. prepared the human fossil record database. N.R.E., P.B.H., M.S.L.-R., and T.F.R. provided the bioclimatic variables. F.C., M.D.F., and A.M. adapted the variables to the geographic scale used in the article. M.D.F., A.M., P.R., M.M., S.C., and C.S. wrote the computer codes. P.R. led the writing. All authors have contributed to write the manuscript.

DECLARATION OF INTEREST

The authors declare no conflict of interest.

Received: October 15, 2019
Revised: June 1, 2020
Accepted: September 23, 2020
Published: October 15, 2020

REFERENCES

1. Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., Di Maggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., and Reed, K.E. (2015). Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science *348*, 1326.
2. Gilpin, W., Feldman, M.W., and Aoki, K. (2016). An ecocultural model predicts Neanderthal extinction through competition with modern humans. Proc. Natl. Acad. Sci. U S A *113*, 2134–2139.
3. Foley, R.A. (1994). Speciation, extinction, and climatic change in hominid evolution. J. Hum. Evol. *26*, 277–289.
4. Sørensen, B.S. (2011). Demography and the extinction of European Neanderthals. J. Anthropol. Archaeol. *30*, 17–29.
5. Silvestro, D., Castiglione, S., Mondanaro, A., Serio, C., Melchionna, M., Piras, P., Di Febbraro, M., Carotenuto, F., Rook, L., and Raia, P. (2020). A 450 million years long latitudinal gradient in age-dependent extinction. Ecol. Lett. *23*, 439–446.
6. Moritz, C., and Agudo, R. (2013). The future of species under climate change: resilience or decline? Science *341*, 504–508.
7. Mayhew, P.J., Jenkins, G.B., and Benton, T.G. (2008). A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. Proc. R. Soc. Lond. B *275*, 47–53.
8. Rangel, T.F., Edwards, N.R., Holden, P.B., Diniz-Filho, J.A.F., Gosling, W.D., Coelho, M.T.P., Cassemiro, F.A.S., Rahbek, C., and Colwell, R.K. (2018). Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums, and graves. Science *361*, eaar5452.
9. Holden, P.B., Edwards, N.R., Rangel, T.F., Pereira, E.B., Tran, G.T., and Wilkinson, R.D. (2019). PALEO-PGEM v1.0: a statistical emulator of Pliocene-Pleistocene climate. Geosci. Model. Dev. *12*, 5137–5155.
10. Wiens, J.J., and Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. *36*, 519–539.
11. Parins-Fukuchi, C., Greiner, E., MacLatchy, L.M., and Fisher, D.C. (2019). Phylogeny, ancestors, and anagenesis in the hominin fossil record. Paleobiology *45*, 378–393.
12. Wood, B., and Leakey, M. (2011). The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa. Evol. Anthropol. *20*, 264–292.

13. Leakey, M.G., Spoor, F., Dean, M.C., Feibel, C.S., Antón, S.C., Kiarie, C., and Leakey, L.N. (2012). New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. Nature *488*, 201–204.
14. Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scoot, N., Kwekason, A., and Dean, M.C. (2015). Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*. Nature *519*, 83–86.
15. Lordkipanidze, D., Ponce de Leon, M.S., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., and Zollikofer, C.P.E. (2013). A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. Science *342*, 326–331.
16. Rightmire, G.P., Margvelashvili, A., and Lordkipanidze, D. (2019). Variation among the Dmanisi hominins: multiple taxa or one species? Am. J. Phys. Anthropol. *168*, 481–495.
17. Hublin, J.J. (2014). Paleoanthropology: *Homo erectus* and the limits of a paleontological species. Curr. Biol. *24*, R82–R84.
18. Profico, A., Di Vincenzo, F., Gagliardi, L., Piperno, M., and Manzi, G. (2016). Filling the gap. Human cranial remains from Gombore II (Melka Kunture, Ethiopia; ca. 850 ka) and the origin of *Homo heidelbergensis*. J. Anthropol. Sci. *94*, 41–63.
19. Stringer, C. (2012). The status of *Homo heidelbergensis* (Schoetensack 1908). Evol. Anthropol. *21*, 101–107.
20. Meyer, M., Arsuaga, J.L., de Filippo, C., Nagel, S., Aximu-Peter, A., Nickel, B., Martìnez, I., Gracia, A., de Castro, J.M.B., Carbonell, E., et al. (2016). Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature *531*, 504–507.
21. Richter, D., Grün, R., Joannes-Boyau, R., Steele, T.E., Amani, F., Rué, M., Fernandes, P., Raynal, J.P., Geraards, D., Ben-Ncer, A., et al. (2017). The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle stone age. Nature *546*, 293–296.
22. Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Tèllez, G., Sharp, W.D., Quam, R.M., Falguères, C., Panthoja-Perez, A., Bischoff, J., et al. (2014). Neandertal roots: cranial and chronological evidence from Sima de los Huesos. Science *344*, 1358–1363.
23. Silvestro, D., Warnock, R.C.M., Gavryushkina, A., and Stadler, T. (2018). Closing the gap between palaeontological and neontological speciation and extinction rate estimates. Nat. Commun. *9*, 5237.
24. Rizal, Y., Westaway, K.E., Zaim, Y., van den Bergh, G.D., Bettis, E.A., Morwood, M.J., and Westaway, M.C. (2020). Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. Nature *577*, 381–385.
25. Aubert, M., Setiawan, P., Oktaviana, A.A., Brumm, A., Sulistyarto, P.H., Saptomo, E.W., and Zhao, J.X. (2018). Palaeolithic cave art in Borneo. Nature *564*, 254.
26. Westaway, K.E., Louys, J., Awe, R.D., Morwood, M.J., Price, G.J., Zhao, J.X., and Compton, T. (2017). An early modern human presence in Sumatra 73,000–63,000 years ago. Nature *548*, 322–325.
27. O'Connell, J.F., Allen, J., Williams, M.A.J., Williams, A.N., Turney, C.S.M., Spooner, N.A., Kammiga, J., Brown, G., and Cooper, A. (2018). When did *Homo sapiens* first reach Southeast Asia and Sahul? Proc. Natl. Acad. Sci. U S A *115*, 8482–8490.
28. Higham, T., Douka, K., Wood, R., Ramsey, C.R., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruìz, C., et al. (2014). The timing and spatiotemporal patterning of Neanderthal disappearance. Nature *512*, 306–309.
29. Finlayson, C., Giles-Pacheco, F., Rodríguez-Vidal, J., Fa, D.A., Lòpez, J.M.G., Pèrez, A.S., Finlayson, G., Allue, E., Preysler, J.B., Càceres, I., et al. (2006). Late survival of Neanderthals at the southernmost extreme of Europe. Nature *443*, 850–853.
30. Zilhão, J., and Pettitt, P. (2006). On the new dates for Gorham's Cave and the late survival of Iberian Neanderthals. Before Farming 2006/3 *2006*, 1–9.
31. Carrión, J.S., Ochando, J., Fernández, S., Blasco, R., Rosell, J., Munuera, M., Amorós, G., Martín-Lerma, I., Finlayson, S., Giles, F., et al. (2018). Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard cave. Rev. Palaeobot. Palynol. *259*, 63–80.
32. Rinnan, D.S., and Lawler, J. (2019). Climate-niche factor analysis: a spatial approach to quantifying species vulnerability to climate change. Ecography *42*, 1494–1503.
33. Hublin, J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, M., et al. (2020). Initial Upper Palaeolithic *Homo sapiens* from Bacho Kiro cave, Bulgaria. Nature *581*, 299–302.
34. Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., et al. (2011). Has the Earth's sixth mass extinction already arrived? Nature *471*, 51–57.
35. Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., et al. (2013). How does climate change cause extinction? Proc. R. Soc. Lond. B *280*, 20121890.
36. Banks, W.E., D'errico, F., Peterson, A.T., Kageyama, M., Sima, A., and Sànchez-Goñi, M.F. (2008). Neanderthal extinction by competitive exclusion. PLoS One *3*, e3972–e3978.
37. Timmermann, A. (2020). Quantifying the potential causes of Neanderthal extinction: abrupt climate change versus competition and interbreeding. Quat. Sci. Rev. *238*, 106331.
38. Melchionna, M., Di Febbraro, M., Carotenuto, F., Rook, L., Mondanaro, A., Castiglione, S., Serio, C., Vero, A.V., Tesone, G., Piccolo, M., et al. (2018). Fragmentation of Neanderthals' pre-extinction distribution by climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. *496*, 146–154.
39. Collard, M., and Cross, A. (2017). Thermoregulation in *Homo erectus* and the Neanderthals: a reassessment using a segmented model. In Human Paleontology and Prehistory, A. Marom and E. Hovers, eds. (Springer International Publishing), pp. 161–174.
40. Nielsen, T.K., and Riede, F. (2018). On research history and neanderthal occupation at its northern margins. Europ. J. Archaeol. *21*, 506–527.
41. Benito, B.M., Svenning, J.-C., Kellberg-Nielsen, T., Riede, F., Gil-Romera, G., Mailund, T., Kjaergaard, P.C., and Sandel, B.S. (2017). The ecological niche and distribution of Neanderthals during the Last Interglacial. J. Biogeog. *44*, 51–61.
42. Teixeira, J.C., and Cooper, A. (2019). Using hominin introgression to trace modern human dispersals. Proc. Natl. Acad. Sci. U S A *116*, 15327–15332.
43. Currat, M., and Excoffier, L. (2011). Strong reproductive isolation between humans and Neanderthals inferred from observed patterns of introgression. Proc. Natl. Acad. Sci. U S A *108*, 15129–15134.
44. Shen, G.J., Gao, X., Zhao, J.X., and Collerson, K.D. (2004). U-Series dating of Locality 15 at Zhoukoudian, China, and implications for hominid evolution. Quat. Res. *62*, 208–213.
45. Yang, S.X., Huang, W.W., Hou, Y.M., and Yuan, B.Y. (2014). Is the Dingcun lithic assembly a "chopper-chopping tool industry", or "Late Acheulian"? Quat. Int. *321*, 3–11.
46. Kaifu, Y. (2017). Archaic hominin populations in Asia before the arrival of modern humans: their phylogeny and implications for the "Southern Denisovans". Curr. Anthropol. *58*, S418–S433.
47. Arnold, L.J., Demuro, M., Parés, J.M., Pérez-González, A., Arsuaga, J.L., de Castro, J.M.B., and Carbonell, E. (2015). Evaluating the suitability of extended-range luminescence dating techniques over early and Middle Pleistocene timescales: published datasets and case studies from Atapuerca. Spain. Quat. Int. *389*, 167–190.
48. Bahain, J.J., Falguères, C., Shao, Q., Tombret, O., Duval, M., and Dolo, J.M. (2015). La datation ESR/U-Th de restes paléontologiques, un outil pour estimer le possible remaniementdes niveaux archéologiques? Quaternaire *26*, 213–223.
49. Hershkovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., and Arsuaga, J.L. (2018). The earliest modern humans outside Africa. Science *359*, 456–459.
50. Derevianko, A.P., Postnov, A.V., Rybin, E.P., Kuzmin, Y.V., and Keates, S.G. (2005). The Pleistocene peopling of Siberia: a review of environmental and behavioral aspects. Indo-pacific Prehist. Assoc. Bull. *3*, 57–68.

Please cite this article in press as: Raia et al., Past Extinctions of *Homo* Species Coincided with Increased Vulnerability to Climatic Change, One Earth (2020), https://doi.org/10.1016/j.oneear.2020.09.007

51. Chlachula, J., Drozdov, N.I., and Ovodov, N.D. (2003). Last interglacial peopling of Siberia: the Middle Palaeolithic site Ust'-Izhul', the upper Yenisei area. Boreas *32*, 506–520.
52. Attwell, L., Kovarovic, K., and Kendal, J.R. (2015). Fire in the Plio-Pleistocene: the functions of hominin fire use, and the mechanistic, developmental and evolutionary consequences. J. Anthr. Sci. *93*, 1–20.
53. Gilligan, I. (2010). The prehistoric development of clothing: archaeological implications of a thermal model. J. Archaeol. Method Theor. *17*, 15–80.
54. Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., and Raia, P. (2016). Venturing out safely: the biogeography of *Homo erectus* dispersal out of Africa. J. Hum. Evol. *93*, 1–12.
55. Suggitt, A.J., Wilson, R.J., Isaac, N.J.B., Beale, C.M., Auffret, A.G., August, T., Bennie, J.J., Crick, H.Q.P., Duffield, S., Fox, R., et al. (2018). Extinction risk from climate change is reduced by microclimatic buffering. Nat. Clim. Change *8*, 713–717.
56. Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., et al. (2008). Attributing physical and biological impacts to anthropogenic climate change. Nature *453*, 353–357.
57. Parnell, A. (2016). Bchron: Radiocarbon dating, age-depth modelling, relative sea level rate estimation, and non-parametric phase modelling, R package version 4.1.1 https://rdrr.io/cran/Bchron/.
58. Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friederich, M., et al. (2016). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon *55*, 1869–1887.
59. Mellars, P.A. (2015). The Neanderthal Legacy: An Archaeological Perspective from Western Europe (Princeton University Press).
60. Rightmire, G.P., Lordkipanidze, D., and Vekua, A. (2006). Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. J. Hum. Evol. *50*, 115–141.
61. Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta, D., Vicino, G., Starnini, E., et al. (2015). The makers of the Protoaurignacian and implications for Neandertal extinction. Science *348*, 793–796.
62. Hublin, J.-J. (2014). The modern human colonization of western Eurasia: when and where? Quat. Sci. Rev. *118*, 194–210.
63. Berger, A., and Loutre, M.-F. (1999). Parameters of the Earth's orbit for the last 5 Million years in 1 kyr resolution. PANGAEA. https://doi.org/10.1594/PANGAEA.56040.
64. Luethi, D., Le Floch, M., Bereiter, B., Bluner, T., Barnola, J.-M., Siegenthaler, U., Raynaud, D., Jouzel, J., Fischer, H., Kawamura, K., and Stocker, T.F. (2008). High-resolution carbon dioxide concentration record 650,000–800,000 years before present. Nature *453*, 379–382.
65. Stap, L.B., Van De Wal, R.S.W., De Boer, B., Bintanja, R., and Lourens, L.J. (2017). The influence of ice sheets on temperature during the past 38 million years inferred from a one-dimensional ice sheet-climate model. Clim. Past *13*, 1243–1257.
66. Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. *25*, 1965–1978.
67. Running, S., Mu, Q., and Zhao, M. (2015). MOD17A3H. https://doi.org/10.5067/MODIS/MOD17A3H.006.
68. Koehler, P., Bintanja, R., Fischer, H., Joos, F., Knutti, R., Lohmann, G., and Masson-Delmotte, V. (2010). What caused Earth's temperature variations during the last 800,000 years? Data-based evidence on radiative forcing and constraints on climate sensitivity. Quat. Sci. Rev. *29*, 129–145.
69. Maiorano, L., Cheddadi, R., Zimmermann, N.E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B.I., Pearman, P.B., Psomas, A., et al. (2013). Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Glob. Ecol. Biogeogr. *22*, 302–317.
70. Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., and Kueffer, C. (2014). Unifying niche shift studies: insights from biological invasions. Trends Ecol. Evol. *29*, 260–269.
71. Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., et al. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. *21*, 481–497.
72. Di Febbraro, M., Carotenuto, F., Castiglione, S., Russo, D., Loy, A., Maiorano, L., and Raia, P. (2017). Does the jack of all trades fare best? Survival and niche width in Late Pleistocene megafauna. J. Biogeogr. *44*, 2828–2838.
73. Schoener, T.W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology *51*, 408.
74. Warren, D.L., Glor, R.E., and Turelli, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution *62*, 2868–2883.