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

2

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25 **Summary**

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

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42 **Keywords: Human Evolution, Palaeoanthropology, Climatic change, Extinction**

43

44 **Introduction**

45 The genus *Homo* has existed for at least 2.8 million years¹. Reports dealing with the
46 extinction of past *Homo* species mostly focus on the disappearance of a single taxon, *H.*
47 *neanderthalensis*, and almost all existing works point to either climate change or to the contact with
48 the technologically advanced *H. sapiens* as the potential causal explanations²⁻⁴. This is appropriate
49 since competition and climatic changes are thought to be the most important factors explaining
50 species extinction⁵⁻⁷. However, this kind of investigation is extremely rare for earlier *Homo* species,
51 even though the Earth's climate swung repeatedly between warm interglacial and cold glacial
52 conditions during the history of our genus. Elucidating the mechanisms behind the fate of our
53 ancestors is made even more important by the current, ever-increasing pressure that rapid and
54 extreme climate change will continue to put on our own species and the entire living biota.

55 Here we fill this gap in our understanding by investigating climatic niche evolution in
56 *Homo*, using a high-resolution past climate emulator^{8,9} which provides temperature and rainfall
57 yearly maxima and minima and net primary productivity with a 1000-year resolution, over the last 5
58 Ma. We considered six species, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H.*
59 *neanderthalensis* and *H. sapiens*. Given the taxonomic uncertainty surrounding the status of some
60 human remains, we also repeated the analyses testing different taxonomic attributions. Therefore,
61 for each of the six species, we identified a 'core' fossil record, restricted to reasonably certain
62 attributions of individual fossil occurrences and archaeological layers with lithic industry to a single
63 species (Figure S1). Then, we repeated the analyses under a less conservative 'extended'
64 subdivision of the fossil record, whereby individual remains and archaeological layers for which no
65 unique taxonomic attribution was possible were ascribed to more than one candidate species. We
66 divided each fossil *Homo* species record into discrete, consecutive time bins, minimizing the
67 variance of the time bin lengths and number of localities, by means of likelihood optimization. The
68 fossil record of *H. neanderthalensis* and *H. sapiens* is vastly richer than those of earlier species. For
69 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 conservatism¹⁰ 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

95 this hypothesis statistically, we randomized 10,000 times the D values of all replicates across the
 96 time bins and compared the median D per bin to the distribution of random values.
 97

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

101 Results

102 Climatic niche evolution in *Homo*

103 Our results provide a clear confirmation that niche conservatism applies generically to all
 104 *Homo* species for most of their existence. But for three species only, *H. heidelbergensis*, *H. erectus*
 105 and *H. neanderthalensis*, we found a sudden, statistically significant drop in D just before
 106 extinction, indicating that their climatic niche widths shrunk suddenly just before they vanished
 107 (Figure 1, Table S1). These patterns do not change whether the 'core' or 'extended' fossil records
 108 are used (see Table S2 and Figure S3 for the 'extended' record), do not depend on the specific

109 predictions of the paleoclimate emulator (Figure S4) and remain almost identical when the
110 geographic resolution of the paleoclimatic data is aggregated at 5 degrees (Figure S5). The sudden
111 drop in climatic niche width pertains only to the last bin of extinct species and disappears altogether
112 when temporal trends in climatic adaptation are removed by randomizing fossil locality ages and
113 climates (Figures S6-7). Most importantly, the drop disappears when real fossil locality ages are
114 used, but global climatic trends in space and time are removed by shuffling climatic layers across
115 fossil localities, suggesting climatic changes possibly had a role in extinction (Figure S8). For
116 paleontological species, extinction coincides with their disappearance from the fossil record. Yet,
117 while some such paleontological extinctions represent the termination of a phyletic lineage (i.e. a
118 true extinction), in some other cases the species evolved instead into a morphologically distinct
119 descendant through an anagenetic process¹¹. These morphological species are conventionally
120 referred to as ‘transitional’ forms. In our records, *H. habilis* and *H. ergaster* probably represent
121 transitional forms¹². In particular, we included fossil remains referred to by some as *H.*
122 *rudolfensis*¹²⁻¹⁴ within our ‘*H. habilis*’. Debate is mounting as to whether early *Homo* species could
123 be grouped into a single, highly variable taxon¹⁵, but see refs.^{16,17}. Our choice to collapse the
124 records of *H. habilis* and *H. rudolfensis* into a single species makes it possible to consider them in
125 the analyses (their respective fossil records would be too small to be statistically meaningful
126 otherwise). Yet, this also opens the possibility that the absence of the drop in *D* in the last bin of *H.*
127 *habilis* is artificial, as the grouping might include a species that went extinct plus its anagenetic
128 descendant. The same is true of *H. ergaster*, which might represent a mere regional variant of *H.*
129 *erectus*¹², whether or not it later gave origin to *H. heidelbergensis* (which is first recognized at the
130 875 ka old site of Gombore II, Melka Kunture, Ethiopia¹⁸). To account for these taxonomic
131 uncertainties, we repeated the analyses on 1) *H. habilis* grouped with *H. ergaster*, which would
132 correspond to a single early African hominin scenario; and 2) an *H. ergaster* plus *H. erectus* group
133 which corresponds to the classic, *H. erectus sensu lato* definition. We found that a statistically
134 significant drop in the last bin *D* belongs to the latter, and not to the former (Figure S9). This

135 confirms that the strong decrease in niche overlap between the last BCN and the ECN is absent in
136 the only living *Homo* species (*H. sapiens*) and in early African transitional species, regardless of the
137 taxonomic arrangement used.

138 *H. heidelbergensis* is often recognized as the putative ancestor to both *H. sapiens* and *H.*
139 *neanderthalensis*, or of the latter at least^{19,20}. Finds in Dali and Jinniushuan (China), Narmada
140 (India) and Steinheim (Germany) are all younger than the earliest appearance in the fossil record of
141 both *H. sapiens* (at Jebel Irhoud, Morocco, recently dated back to 315 ka²¹) and *H. neanderthalensis*
142 (at Sima del Los Huesos, Spain, dated at 434 ka²²). This indicates that *H. heidelbergensis*
143 underwent at least one speciation event without being replaced by its descendant (i.e. a case of
144 budding speciation²³) rather than transforming into any offspring. Hence, its disappearance
145 represents a true extinction.

146 *H. erectus* last survived in Java, Indonesia, at Ngandong and Sambungmacan. The dating of
147 this material is highly contentious but has been now confidently placed at 117 to 107 ka²⁴. This
148 indicates *H. erectus* would be contemporary but geographically separated from both *H. sapiens* and
149 *H. neanderthalensis*²⁵⁻²⁷. Regardless, *H. erectus* could not have been the anagenetic ancestor to
150 either of them. Therefore, its extinction represents the true termination of a phyletic lineage. We
151 also repeated the niche overlap analyses for *H. erectus* removing Ngandong and Sambungmacan
152 from the record and found again that its last bin BCN is statistically less overlapped with ECN than
153 any other bin (Figure S10).

154 *H. neanderthalensis* had a long story of contact, and interbreeding, with *H. sapiens*. The
155 species went extinct in Europe some 41 to 39 ka²⁸. There is no concern about the recognition of *H.*
156 *neanderthalensis* as a true species which left no descendants. *H. neanderthalensis* last stand was
157 contentiously placed at 24 ka at Gorham's cave in Gibraltar²⁹. This dating has been met with fierce
158 skepticism³⁰ so we prudently decided to keep Gorham's cave out of the analyses. However, the
159 presence of *H. neanderthalensis* in Southern Europe after 50 ka is well accepted in the scientific
160 literature³¹ and in our results. The drop in the last bin Schoener's D in *H. neanderthalensis* does not

161 depend on the temporal resolution of the bin, as is confirmed by using 1 kyr long bins (Figure S11).

162 In summary, we find that all species representing a lineage leaving no offspring had become

163 restricted to unfavourable or otherwise narrowly defined climatic conditions just before their

164 extinction. Although artificially randomising the natural history of climatic adaptation and variation

165 erases the pattern (Figures S6-8), suggesting a climatic driver for extinction, the drop in niche

166 overlap does not indicate whether the species experienced extreme or somewhat unusual climates

167 just before their extinction, nor does it prove that climate forcing was the cause for the reduction in

168 climatic variability experienced during the last bin. To understand how unusual the climate settings

169 were for the species during their last bins, we located the BCN position within the ECN volume

170 through time, calculating the multivariate Euclidean distance between the barycentre of the ECN

171 and the barycentre of each BCN. The results of this analysis indicate that two extinct species, *H.*

172 *heidelbergensis* and *H. erectus* faced highly unusual climatic conditions prior to extinction (i.e.

173 during their respective last bins), whereas *H. neanderthalensis* and all other species do not show

174 any salient pattern (Figure 2, see Figure S12 for the ‘extended’ record). This confirms niche

175 conservatism for all non-extinct species. Among the extinct lineages, *H. heidelbergensis* and *H.*

176 *erectus* were experiencing unusual climates before extinction, with relatively restricted climatic

177 range, whereas the realized climatic niche in *H. neanderthalensis* last bin was narrow, but not

178 unusual for the species. A strong reduction in species range size before extinction (for instance in

179 the wake of the expansion of a superior competitor) provides a potential mechanism that would

180 cause Schoener’s D to drop during the last bin regardless of climatic forcing, because a small-

181 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

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 (CNFA³²). 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 45ka³³ 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.

224 We performed CNFA on the three extinct species and *H. sapiens*. Since *H. sapiens* survived all the
 225 changes in climate it experienced during its existence its vulnerability should appear lower than in
 226 the extinct species to prove climate change mattered to them.

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

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

238

239 CNFA results confirm that climate change *per se* played an important role for extinction in past
 240 *Homo* species, consistently with the observation that most species cannot cope with rapid climatic
 241 changes^{34,35}. In CNFA, the climatic change from the penultimate bin to the last is used to predict
 242 species vulnerability as it survives to the last bin. Since the last bin occurrence data are not part of
 243 the analyses, any effect of competition with fellow human species during the last bin is ruled out in

244 this analysis. Therefore, CNFA indicated there is clear evidence that all extinct species were made
 245 vulnerable to extinction by climate change, whether or not they suffered from competition with
 246 other *Homo* species. Strong arguments for human-mediated extinction, with robust archaeological
 247 evidence of geographic overlap, have been advanced so far only for Neanderthals^{4,36-37}. While
 248 previous modelling approaches found that climate change, rather than the contact with *H. sapiens*
 249 was the main cause of extinction in Neanderthals³⁸ this study indicates that climate change is the
 250 most likely candidate for the extinction of two past human species and played an important role in
 251 the demise of Neanderthals.
 252

253
 254 **Figure 4. Sensitivity of Schoener's *D* value (y-axis) to the archaeological locality ages ('core'**
 255 **record).**

256
 257 *A single, climate change-induced extinction trajectory for all Homo?*

258 The timing and pace of climate-related increase in extinction risk among extinct *Homo* species
259 might appear very different. In our modelling approach, *H. neanderthalensis* drop in Schoener's *D*
260 occurs over the last 1-2 kyr of its existence, while the drop in *H. heidelbergensis* and *H. erectus*
261 occurs over two orders of magnitude longer bins (i.e. in the 100 kyr range). We were able to
262 demonstrate this apparent difference mostly depends on the resolution of the fossil record.
263 We analysed the course of *D* within the last bin for all six species (in the case of Neanderthals and
264 *H. sapiens* we recalculated a single 'last bin' for both, using the ages bracketing the end of
265 Mousterian period, from 43 to 36 ka²⁸). We calculated Schoener's *D* per species over the 100
266 replications. At each replicate, one fossil locality was taken out of the iteration. If *D* decreases
267 towards the recent within the last bin, then removing young localities would have the effect of
268 increasing *D* values towards the recent, so that the regression of 1 minus *D* (1-*D*) against locality
269 age of the omitted record would reveal a significant negative relationship. Such an expectation was
270 statistically confirmed for *H. neanderthalensis*, *H. heidelbergensis* and for *H. erectus* only (Figure
271 4). The regression is never significant for any other species, and in one case only (*H. sapiens*) the
272 regression is significant but positive in slope, indicating *H. sapiens* was still widening its climatic
273 niche as the Neanderthals vanished. Importantly, the negative relationship which applies to Late
274 Pleistocene extinct *Homo* indicates the pace of niche narrowing during the last bin was much more
275 similar among species than the last bin lengths would suggest (Figure 4) providing evidence in
276 favour of a single, shared climate-induced extinction trajectory.

277

278 Discussion

279 Niche overlap analyses allowed us to look in detail at the realized climatic niche in *Homo*
280 species throughout their existence. We mapped the most appropriate climates derived from the BCN
281 of the last bin onto the geographical space and compared ECN to BCN by means of principal
282 component analysis to see which climatic variable has the most influence on the differences
283 between the last bin niche and the evolutionary niche (Figure 5).

284 In the case of *H. erectus*, the last BCN is the most distant from ECN among all bins (Figure
285 2, Figure S12). During this last bin *H. erectus* settled under the warmest and most humid climates
286 then available within its biogeographical region (Figure 5a). These climates were, unsurprisingly,
287 typical for South East Asia, which agrees with the fossil record and with physical evidence
288 suggesting *H. erectus* was adapted to warm climates³⁹. The extinction of *H. erectus* took place
289 during the last glacial, that is the coldest period the species had ever experienced.

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

294 We found that the last BCN barycentre of Neanderthals was close to the ECN barycentre
295 (Figure 2, Figure S12). During its last bin the species experienced a slight shift towards more arid
296 and warmer climates, which is typical of the Mediterranean area (Figure 5c). Still, although
297 statistically more vulnerable than *H. sapiens* to climate change, *H. neanderthalensis* was
298 comparatively less vulnerable than both *H. heidelbergensis* and *H. erectus* to the change in climate
299 during the last bin of its existence (Figure 3). Thus, the drop in *D* during the last bin and the
300 fragmentation of Neanderthals range³⁸ just prior to extinction might have increased exposure to
301 climate-driven extinction risk (Figure 3a) in combination with *H. sapiens* incidence. The
302 importance of climate change in Neanderthals demise is further demonstrated by its early
303 disappearance at high latitudes⁴⁰ consistent with its historical preference for warmer conditions⁴¹.

304 One potential confounding factor in explaining our results is the importance of
305 interbreeding. Significant interbreeding was found between Neanderthals and *H. sapiens* and
306 between both these species and Denisovans. Furthermore, there exists the possibility that two
307 further species (or at least two genetic strains) from ancient hominins living in Eastern Asia
308 contribute to our genome⁴². However, it has been noted that the frequency of introgression between

309 past human species and modern-day humans is probably below 2%, so that significant reproductive
310 isolation, rather than extensive inbreeding, may have occurred between these species⁴³.

311 Competition might in principle generate patterns similar to those we found and attribute to
312 climatic forcing. However, the evidence for such direct effect of interaction between species is very
313 limited except for Neanderthals. The youngest unquestionable *H. erectus* occurrences at the Solo
314 river sites (Java), date at some 112 ka, whereas *Homo sapiens* only arrived in the region much later,
315 at some 60 ka²⁵⁻²⁷. On the continent, the youngest possible *H. erectus* occurrences in Asia at
316 Zhoukoudian (154 ka in age⁴⁴), and Dingcun (185 ka in age⁴⁵) predate Denisovans and post-date the
317 latest occurrence of *Homo heidelbergensis* in the region⁴⁶ which means that *H. erectus* did not live
318 along with other hominins. In the case of *Homo heidelbergensis*, the youngest localities are
319 scattered worldwide, from Spain (Trinchera Galeria⁴⁷) to China (Jinniushan⁴⁸). All these localities
320 are at least some 50 ka older than the first occurrence of *Homo sapiens* outside the African
321 continent at Mislyia⁴⁹. This means that *Homo neanderthalensis* is the only candidate species left as
322 a potential competitor to *Homo heidelbergensis*. Yet, *Homo neanderthalensis* was confined to
323 Europe and the Middle East until very recently. The oldest occurrences of this species in Asia are at
324 Denisova (163 ka⁵⁰) and Ust'-Izhul' (105 ka⁵¹) and are much younger than latest occurrences of *H.*
325 *heidelbergensis*. This implies that *Homo neanderthalensis* is the only species for which direct
326 competition with *H. sapiens* is possible and may have in fact contributed to its extinction³⁶⁻³⁷. The
327 archaeological evidence means that the BCN contraction we observed in the last bin of extinct
328 *Homo* species cannot be explained by competition with fellow humans, perhaps with the exception
329 of *H. neanderthalensis*. This study provides the first strong evidence that climate change was a
330 common extinction factor shared by all our ancestors. By virtue of their cognitive skills, recent
331 human species were able to exploit a combination of fire control, clothing, and dispersal ability⁵²⁻⁵⁴
332 that would surely have helped to mitigate the effects of climate change on their survival by
333 effectively manipulating their own microclimates or moving rapidly to settle under better
334 conditions. Indeed, it has been recently demonstrated empirically that such protected microclimatic

335 conditions buffer extinction risk⁵⁵. Yet, not even *Homo* species, some of the most technologically
336 advanced, plastic and ecologically widespread species ever, were immune to global change. For
337 multiple reasons, not least the spectacular advances in technologies available to shield modern
338 humans from directly experiencing their own local climate, and the agricultural enhancement of
339 natural primary production, our methodology cannot meaningfully be applied directly to the future
340 of *H. sapiens*. But our own future depends critically on the health of Earth's supporting ecosystems
341 and the entire living biota, and our analysis provides a stark warning concerning the power of
342 anthropogenic future climate change to translate directly into extinction risk for other species less
343 well-equipped to adapt than sp. *Homo*. This suggests that the threat posed by the current,
344 anthropogenic climate change for global wildlife⁵⁶ and, by extension, ourselves, is possibly even
345 more powerful than is generally appreciated.

346

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

354 We considered six species, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H.*
355 *neanderthalensis* and *H. sapiens*; *H. luzonensis*, *H. floresensis*, *H. naledi*, *H. antecessor* and
356 Denisovan hominins were excluded because their fossil records were too much stratigraphically and
357 geographically restricted to study climatic niche evolution. We extensively reviewed the literature
358 collecting *Homo* fossil occurrence data. Each occurrence includes information about the latitude
359 and the longitude of the site, the archaeological layer and the absolute age of the dated sample. Only
360 absolute dating estimates (i.e. radiocarbon, ESR, palaeomagnetism) were used. When available, we
361 also included information about which sample was used for the dating and its lab code. Radiocarbon
362 dates were calibrated by using the “Bchron” R package⁵⁷, using Intcal13 calibration curve for the
363 Northern hemisphere, shcal13 curve for the Southern hemisphere and marine13 curve for marine
364 samples⁵⁸.

365 We evaluated and confirmed the reliability of every single age according to the latest
366 published literature (Supplemental Experimental Procedures). Age estimates come with dating
367 uncertainty. Time averaging of the archaeological layers adds to this uncertainty. To account for
368 this, for each archaeological site (or layer) age estimate we retrieved from the collected estimates a
369 minimum age and a maximum age (calculated according to individual estimates and their respective
370 confidence intervals).

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

376

377 *Core and extended records*

378 Each individual occurrence in the record was attributed to a given species depending on: i)
379 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 *H. heidelbergensis* and younger than the last appearance of *H. habilis* was attributed to *H. ergaster*) and iii) 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, 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, *H. erectus* earliest occurrence outside Africa at Dmanisi, Georgia, is found in association with Oldowan stone tools⁶⁰ 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 Irhoud²¹ 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, Uluzzian⁶¹⁻⁶²). For all these cases, we used the ‘extended’ record duplicating multiple-attribution records and adding the duplicates to each possible *Homo* species.

396

397 *Environmental predictors*

398 Environmental predictors were generated using a paleoclimate emulator⁹. The approach
399 applies Gaussian process emulation of the singular value decomposition of ensembles of runs from
400 the intermediate complexity atmosphere-ocean GCM PLASIM-GENIE with varied boundary-
401 condition forcing (CO₂, orbit and ice-volume). Spatial fields of i) minimum seasonal temperature,
402 ii) maximum seasonal temperature, iii) minimum seasonal precipitation, iv) maximum seasonal
403 precipitation, and v) net primary productivity are then emulated at 1,000 year intervals, driven by
404 time-series of scalar boundary-condition forcing, and assuming the climate is in quasi-equilibrium.
405 For the orbital parameter inputs, we applied the 5 million-year calculation of Berger and Loutre⁶³.

406 We used CO₂ from Antarctic ice cores for the last 800,000 years⁶⁴. Prior to 800 ka, and for the
407 entire sea-level record, we used the CO₂ and sea-level reconstructions in ref. 65. Contemporary
408 observations of the four bioclimatic variables were derived from WorldClim⁶⁶, while NPP
409 observations were derived from MOD17A3H⁶⁷. The observations were interpolated onto the same
410 0.5° grid and combined with emulated anomalies. Temperature anomalies were additively
411 combined with observations, while precipitation and NPP anomalies were combined with
412 observations using a hybrid additive/multiplicative approach⁹.

413 The native-resolution (5°) emulations were extensively validated against model inter-
414 comparisons of the mid-Holocene, the Last Glacial Maximum, the Last Interglacial and the mid-
415 Pliocene warm period (see ref. 9). Glacial-interglacial variability was validated against the
416 observationally based global temperature reconstructions⁶⁸.

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

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

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

429

430

431 *Climatic niche evolution*

432 Once the species records (both ‘core’ and ‘extended’) were prepared, we removed
 433 duplicated records falling in the same cell and 1 kyr-long temporal layer of the environmental grid
 434 used in the subsequent analyses. After this procedure, we obtained the following numbers of species
 435 occurrences: 26 (30 ‘extended’) for *H. habilis*, 45 (60 ‘extended’) for *H. ergaster*, 61 (104
 436 ‘extended’) for *H. erectus*, 261 (358 ‘extended’) for *H. heidelbergensis*, 1361 (1447 ‘extended’) for
 437 *H. neanderthalensis* and 849 (904 ‘extended’) for *H. sapiens*. We decided to use the last occurrence
 438 of *H. neanderthalensis* core record as lower age limit also for the *H. sapiens* record. To account for
 439 the effect of dating uncertainty, we produced, around each age estimate, a uniform distribution
 440 spanning from the minimum to the maximum estimate. Then, we randomly sampled a single date
 441 within this range, and performed niche similarity tests (see below). This procedure was repeated
 442 100 times, and niche similarity results of the 100 replicates were eventually pooled together. For
 443 each species and replicated date, we randomly generated a set of 10,000 background points, which
 444 were used as pseudo-absences together with observed presences to perform the niche similarity
 445 tests. The 10,000 pseudo-absences were subdivided across the time periods where each species
 446 occurred, proportionally to the number of fossil occurrences falling within each time bin. As
 447 sampling areas for background points, we chose well-known biogeographic boundaries for each
 448 species. Specifically, we sampled Africa for *H. habilis* and *H. ergaster*, Eurasia for *H. erectus* and
 449 *H. neanderthalensis*, and a combination of both areas for *H. heidelbergensis* and *H. sapiens*. To
 450 reduce the risk of sampling non-accessible areas according to species dispersal abilities, we
 451 generated background points for each species within a specific area drawn as a 1,000 km buffer
 452 around the convex hull surrounding all known species occurrences.

453

454

455 *Niche overlap analysis*

456 Since the framework to perform niche overlap tests requires at least five occurrences per bin
 457 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 archaeological 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 together⁶⁹. This approach reduces the effect of environmental truncation⁷⁰ (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.

484 We calculated BCN to ECN niche overlap by using the analytical framework proposed by
485 Broennimann et al.⁷¹ and adopted in several studies dealing with fossil species^{38,72}. Under this
486 approach, the environmental space defined for each species (i.e. all the environmental conditions
487 intersected by the species fossil localities and by the pseudoabsences within the background area) is
488 decomposed by means of principal components analysis (PCA). Environmental conditions of
489 individual BCNs and ECN were in turn projected into the PCA space, separately for each species.
490 The BCNs can then be compared to their respective ECN in PCA space. The density of the
491 background environments and species occurrences across the first two PCs were calculated by a
492 kernel density smoother and, respectively, divided by the maximum number of occurrences in any
493 one cell of the environmental space and by the number of sites with the most common
494 environment⁵². The resulting density grids of $r \times r$ cells in the environmental space were used to
495 compute niche overlaps between each temporal bin and the total niche in terms of Schoener's D ⁷³⁻⁷⁴,
496 a metric that ranges from 0 (no niche overlap) to 1 (complete niche overlap). We performed niche
497 similarity tests *sensu* Warren et al.⁷⁴, a procedure that evaluates if the two niches being compared
498 (i.e. BCN and ECN) are more similar/different than expected by chance. The test proceeds by
499 comparing the niche overlap values (Schoener's D) between each temporal bin and the evolutionary
500 niche to a null distribution of 100 overlap values, yielding a significant outcome if the observed
501 Schoener's D value is higher ("niche conservatism" hypothesis) or lower ("niche divergence"
502 hypothesis) than the 95th percentile of the null distribution ($P < 0.05$).

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

508 All climatic niche evolution analyses were performed using both the 'core' and 'extended'
509 records. We tested the effect of paleoclimate emulator predictions on the temporal patterns of niche

510 overlap per species repeating the analyses by always using the current climatic variables
511 irrespective of fossil locality ages (Figure S4), by using the climatic data aggregated at 5° spatial
512 resolution (Figures S5), by randomizing fossil locality ages (and their relative climatic variables)
513 across bins (Figures S6-7), and by erasing the effect of climatic change altogether shuffling climatic
514 data across fossil localities (Figures S8).

515

516 *Assessing vulnerability to climatic change*

517 Climate niche factor analysis (CNFA) assesses the vulnerability to climatic change³². This is
518 an adaptation of ecological niche factor analysis (ENFA) that assesses the vulnerability of a species
519 to climatic change accounting for the contribution of niche specialization (the narrowness of species
520 climatic tolerance) and exposure (the differences between current and future climatic conditions
521 inside present-day habitat). To implement CNFA, for each species we used its penultimate bin BCN
522 and the climatic data for the last BCN. We developed CNFA over 100 replicates for each species.
523 Vulnerability values were then compared among species by means of ANOVA and post-hoc Tukey
524 HSD tests. Since extinction (as opposed to possible instances of anagenetic transformation)
525 associated to climate change was evidenced for three species only (*H. heidelbergensis*, *H. erectus*
526 and *H. neanderthalensis*) we assessed CNFA for these species and compared their vulnerabilities to
527 each other and to those of their only contemporary congeners, *H. sapiens*. In the case of *H.*
528 *sapiens* and *H. neanderthalensis*, bin length is as small as 1 kyr (we similarly tested bin length = 2
529 kyr). However, it has been demonstrated that the pace of climatic change occurs at almost the same
530 temporal resolution of these bins⁵⁹. Therefore, for these species only we chose to compare non-
531 contiguous bins. *Homo neanderthalensis* extinction is statistically placed during the interval 41-39
532 ka²⁸. The end of Neanderthals specific stone tool technology, the Mousterian, is similarly placed in
533 the 43 to 36 ka interval²⁸. Therefore, we decided to use the BCN of *H. neanderthalensis* and *H.*
534 *sapiens* calculated during the 43 to 42 ka time interval as their second to last bin BCN and the
535 climatic predictions during the 37 to 36 ka time interval as their ‘last’ bin climatic settings.

536 However, competition effect with *Homo sapiens* could already be in place at the 43 to 42 ka time
537 interval. This would result in a narrow realized niche at the 43 to 42 ka and would mix competition
538 and climate change-induced effects in calculating vulnerability. Therefore, we also performed
539 CNFA using 48 to 49 ka, 50 to 51 ka and 52 to 53 ka bins to calculate vulnerability in the last bin.

540 Finally, we used CNFA to test the hypothesis that ignoring climate change extinct species
541 would not become vulnerable during their last bin. To this aim, we held the climate constant
542 between the penultimate and last bin for each of the six species under scrutiny and repeated CNFA.
543 For Neanderthals only, we also repeated CNFA using different time intervals as to represent the
544 penultimate bin, as explained above. We expected that by holding climate constant between the last
545 two bins per species, vulnerability would drop for the extinct species only if climate really mattered
546 to their extinction. After vulnerabilities were estimated, for each species we compared the two
547 distributions (i.e. ignoring or including climate change) by means of Student's T test (Figure S14).

548

549

550

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

552 The resolution of the fossil record in *H. neanderthalensis* and *H. sapiens* is significantly denser than
553 in older, early *Homo* species. Therefore, the last bin drop in Schoener's D in *H. erectus* and *H.*
554 *heidelbergensis* can only appear at a much coarser temporal scale than in *H. neanderthalensis*. To
555 verify the hypothesis that these scales are actually not that different, we devised a strategy to
556 analyse niche overlap within the last bin in all species. Ideally, if the decrease in niche overlap in *H.*
557 *erectus* and *H. heidelbergensis* occurs within the last bin the regression of D values against the ages
558 of the archaeological layers would appear significant and positive (i.e. lower D values towards the
559 present). However, D is a property of bins, rather than of individual fossil localities. Therefore, to
560 perform the regression we devised a leave-one-out procedure. Under this procedure, we took each
561 replicate of the niche overlap test, removed one locality at a time from the bin, and recalculated D

562 after each removal. The same process was repeated for all replicates. Then, we fitted a linear mixed
563 effect regression of D values against the age of the localities, using the replicates as the random
564 effect. A positive relationship between D and age would indicate that the last bin D increases when
565 that particular locality is removed. The positive sign of the slope would therefore indicate that
566 younger localities within the last bin contribute more than older localities within the bin. A positive
567 relationship is therefore not expected to occur in non-extinct species lineages, that is *H. habilis*, *H.*
568 *ergaster* and *H. sapiens*. For *H. neanderthalensis* and *H. sapiens*, we coarsened the record to verify
569 the hypothesis that the temporal resolution of the last bin drop in D is similar across extinct species,
570 and that no such evidence would appear for *H. sapiens*. We pooled all the occurrences of the two
571 species from the extinction age of *H. neanderthalensis* to the beginning of end-Mousterian period
572 (that is 43 to 36 ka) and repeated the leave-one-out procedure on this 8 kyr long last bin. The
573 starting hypothesis was that a significant and positive relationship would only apply for *H.*
574 *neanderthalensis*.

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593

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Figure legends

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

808

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

813

814 **Figure 3. Density plots of climate-induced vulnerability to extinction (a) and PCA plots of**
815 **species niches. In the case of *H. neanderthalensis*, we used the climatic preferences of several**
816 **bins (before and after the arrival of *H. sapiens* in Europe) in infer vulnerability in the last bin.**
817 The principal components plots of species climatic niches, indicating the position of each species'
818 niche during their respective last bins. The solid line includes 50% of the species climatic niche
819 space, the dashed line includes 90% of the species climatic niches. The dotted lines include 95% of
820 the background climates (i.e. regardless of where the species presences were recorded). The
821 correlation between individual variables and the PC eigenvectors is illustrated by the direction and

822 magnitude of the vectors, so that the contribution of individual variables to the direction of change
823 in the climatic niche from ECN to the last BCN is represented. The percentage of climatic variance
824 represented by each PC vector is indicated on the axes.

825

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

831

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

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