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### **A major change in rate of climate niche envelope evolution during hominid history**

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# Journal Pre-proof



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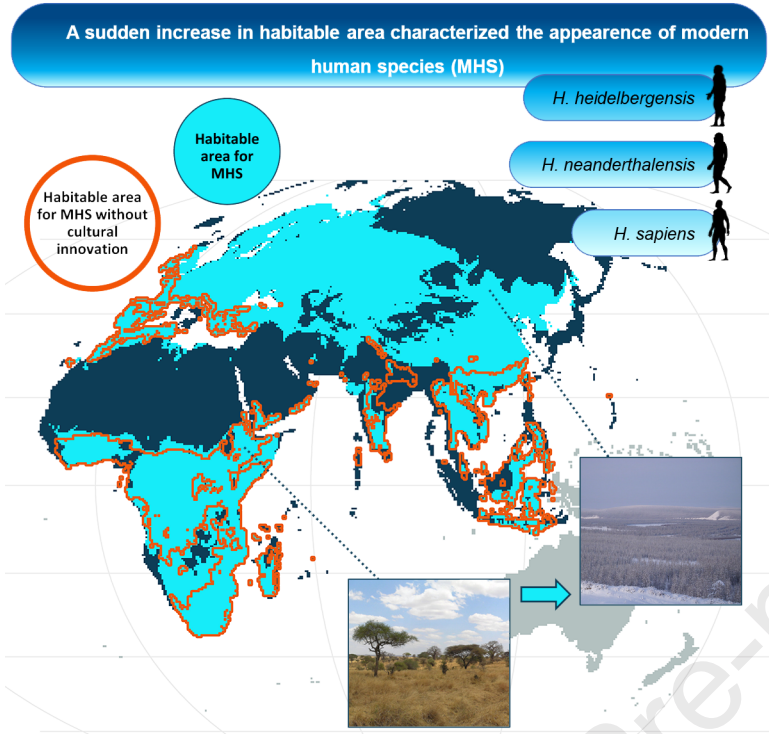
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Journal Pre-proof

1 **A major change in rate of climate niche envelope evolution during hominid**  
2 **history**

3

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27

28 **Summary**

29 *Homo sapiens* is the only species alive able to take advantage of its cognitive abilities  
30 to inhabit almost all environments on Earth. Humans are able to culturally construct, rather  
31 than biologically inherit, their occupied climatic niche to a degree unparalleled within the  
32 animal kingdom. Precisely when hominins acquired such an ability remains unknown, and  
33 scholars disagree on the extent to which our ancestors shared this same ability. Here, we  
34 settle this issue using fine-grained palaeoclimatic data, extensive archaeological data and  
35 phylogenetic comparative methods. Our results indicate that whereas early hominins were  
36 forced to live under physiologically suitable climatic conditions, with the emergence of *H.*  
37 *heidelbergensis*, the *Homo* climatic niche expanded beyond its natural limits, despite  
38 progressive harshening in global climates. This indicates that technological innovations  
39 providing effective exploitation of cold and seasonal habitats predated the emergence of  
40 *Homo sapiens*.

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## 53 **Introduction**

54           The genus *Homo* has existed for some three million years (Harmand et al., 2015;  
55 Villmoare et al., 2015). For one third of this stretch of time, human species were confined to  
56 tropical and sub-tropical Africa, which is the homeland of the genus (Carotenuto et al., 2016;  
57 Lordkipanidze et al., 2007) and is rich in the warm, savanna-like environments to which most  
58 early hominins were best adapted (Lee-Thorp et al., 2010; White et al., 2009). With the  
59 emergence of *Homo erectus* some 2 Ma ago, *Homo* began to disperse outside of Africa but  
60 remained confined to low latitudes, possibly because of physiological limits to cold tolerance  
61 (Dunbar et al., 2014) combined with the inevitable constraints of biogeographical barriers  
62 and habitat variability. However, later *Homo* species were able to expand their distribution to  
63 Northern Europe and Western Siberia, even as the contemporaneous establishment of full  
64 glacial cycles was making global temperatures colder than ever before during the history of  
65 the genus *Homo*. Findings in Happisburgh and Pakefield (UK) date the earliest occurrence of  
66 *Homo* at the southern edge of the boreal zone at some 0.7-0.9 Ma (Parfitt et al., 2010). The  
67 occupation of such northern temperate and boreal zones presents a number of notable  
68 challenges. Not only was the cold itself challenging for hominins physiologically adapted to  
69 African climates, but seasonality imposes extreme annual resource fluctuations, which imply  
70 a reliance on hunted meat for survival (Pearce et al., 2014). Adaptations facilitating survival  
71 in cold environments may have included the use of fire, shelters or clothing, weapons useful  
72 to bring down large game species (Thieme, 1997), as well as extended social networks, with  
73 vulnerable infants being particularly susceptible to mortality (Spikins et al., 2019; Martin et  
74 al. 2020).

75           Unfortunately, clothing manufacturing leaves very little in the way of fossil remains  
76 (Hosfield, 2016). The first microwear evidence of hide-scraping (for manufacturing clothes)  
77 at Hoxne (UK), Biâche-Saint-Vaast, Pech de l'Azé and Abri Peyrony (France) and

78 Shöningen (Germany) (d'Errico and Henshilwood, 2007; Gilligan, 2010; Henshilwood et al.,  
79 2002) are just some 50 ka old at the most (Kittler et al., 2003; Gilligan, 2007). Only the two  
80 most recent human species, *H. neanderthalensis* and *H. sapiens*, left incontrovertible  
81 evidence that they were able to produce complex, cold-proof clothing at that time. To make  
82 things more complex, in the particular case of *H. neanderthalensis* biological adaptation,  
83 besides material culture, was possibly involved in their ability to withstand the cold. *H.*  
84 *neanderthalensis* possessed relatively short limbs, and a large midface and nasal cavity  
85 proposed to be specific cold adaptations, to heat and humidify inspired air, although the issue  
86 is far from resolved and there is evidence for the contrary (Rae et al., 2011; Benito et al.,  
87 2017; Wroe et al., 2018). In contrast to any other *Homo*, *H. sapiens* is considered the only  
88 species in the genus able to occupy cold regions through a genuinely cultural process, driven  
89 by our technology, including the mastering of fire, ever-improving clothing craftsmanship  
90 and construction of shelters (Boivin et al., 2016; Gilligan, 2010; Hiscock, 2013; Laland et al.,  
91 2001). The archaeological record of *Homo sapiens* shows our own species was able to  
92 construct its own niche, using technologies transmitted over large regions and across  
93 generations via cultural interactions. *Homo sapiens* could thus exploit climatic variability  
94 over time and space, rather than being physiologically limited by it (Banks et al., 2006, 2008,  
95 2011, 2013; Dunbar et al., 2014; Spikins et al., 2019, Nicholson et al., 2019; Xu et al., 2020).

96 This view sets *H. sapiens* apart from any other human species in terms of cognitive  
97 skills and implicitly rejects the idea that older *Homo* may have had sufficiently modern  
98 material culture to overcome climatic harshness (Roberts and Stewart, 2018). With such a  
99 poor fossil record of clothes and tools to produce them, and because of great uncertainty  
100 about deep-past local paleoclimates and human dispersal timing and direction, the issue of  
101 when humans first became cognitively and culturally able to extend their climatic tolerance  
102 beyond their physiological limits remains very difficult to decipher.

103           Here, we address the more restricted issue of when during the history of *Homo* the  
104 limits of climatic tolerance expanded, and which species were involved. We do not  
105 specifically address the cultural and social adaptations that might underlie such tolerance, but  
106 rather consider the implications of our findings for the timing of such adaptations. We model  
107 the evolution of climatic tolerance (i.e. niche) limits in the *Homo* genus by associating  
108 palaeoclimatic values with fossil occurrences in the archaeological record. Specifically, we  
109 test the hypothesis that *H. sapiens* developed greater climatic tolerance relative to *H.*  
110 *heidelbergensis* and *H. neanderthalensis* against the alternative that the exploration of  
111 climates outside natural physiological limits had already begun with the earliest of these  
112 species.

113           To test this hypothesis, we estimated the rate of change of climatic tolerance limits  
114 across the human phylogenetic tree and searched for possible shifts in the rate. We apply a  
115 method which allows us to compute the rate of evolution of climatic niche limits at each  
116 branch in the tree. In the present context, shifts in the rate of evolution of climatic tolerance  
117 that accrue to the clade including the Happisburgh/Pakefield hominins, *H. heidelbergensis*,  
118 plus *H. neanderthalensis* and *H. sapiens* (modern *Homo* species, MHS, hereafter), would  
119 indicate these hominins were the first to acquire the capacity to develop cold climate-related  
120 technological skills and cultural adaptations. Conversely, if either no rate-shift occurs, or the  
121 rate shift coincides with different clades (e.g. early *Homo* species, EHS, hereafter) the  
122 colonization of Northern habitats would not be indicative of any sudden increase in the  
123 ability to face environmental harshness.

124           The human fossil dataset we used includes 2,597 occurrences of hominid remains and  
125 artefacts associated with 727 archaeological sites. The time range of our record spans from  
126 the first occurrence of australopiths in East Africa dated to some 4.2 Ma, to the definitive  
127 advent of *H. sapiens* in Eurasia almost coincident with the demise of *H. neanderthalensis*

128 dated at 0.040 Ma (see Dataset S1, Raia et al., 2020). Such a wide range of hominin taxa  
129 provides a thorough phylogenetic context for the analyses.

130 Deriving spatio-temporally detailed climate data for the past requires dynamic climate  
131 modelling, but the timescales for human evolution exceed the possibilities of direct model  
132 simulation by several orders of magnitude. To circumvent this limitation, we combine direct  
133 simulation using a computationally efficient, intermediate complexity Earth system model,  
134 PLASM-GENIE, with statistical modelling, to create PALEO-PGEM, a paleoclimate  
135 emulator, capable of performing multi-million year simulations forced by observationally  
136 derived proxy timeseries for ice-sheet state, CO<sub>2</sub> concentration and orbital forcing (Holden et  
137 al., 2016; 2019). To model the realized climatic niche evolution, we applied phylogenetic  
138 ridge regression (*RRphylo*, Castiglione et al., 2018). *RRphylo* allows us to compute  
139 evolutionary rates for each branch of the phylogeny and to estimate the ancestral phenotypes  
140 (Raia et al., 2018; Melchionna et al., 2020a; Baab, 2018). Here the ‘phenotype’ comprises  
141 climatic tolerance limits.

142 By using past annual maxima and minima for temperature, precipitation and net  
143 primary productivity from PALEO-PGEM, we reconstructed and projected onto the  
144 geographical space the climatic niche limits corresponding to the ancestral species  
145 distributions (the nodes in the tree) in our fossil database. Using *RRphylo*, we were then able  
146 to infer climatic niche tolerance limits (Quintero and Wiens, 2013) for each node in the tree  
147 and to assess whether the rate of climatic niche evolution shows any shift (i.e. acceleration or  
148 deceleration) consistent with our starting hypothesis, while accounting for the effect of shared  
149 inheritance. We accounted for phylogenetic uncertainty by perturbing the tree node ages and  
150 the tree topology randomly one hundred times. By incorporating phylogenetic uncertainty in  
151 this way, we were able to define an overall ‘habitat quality’ (HQ) metric, representing the

152 number of times (out of 100 repetitions) a geographic cell was found habitable (i.e. fell  
153 within climatic tolerance limits) for a given ancestor in the tree.

154

## 155 **Results**

### 156 **The association between the distribution of fossil species and habitat quality**

157 We used the Area Under the Curve (AUC) metric to measure the association between  
158 habitat quality and the location of fossil occurrences. At  $AUC = 1$ , the association would be  
159 perfect.  $AUC = 0$  would indicate perfect inverse relation, whereas  $AUC \sim 0.5$  indicates  
160 random association. We found that despite the enormous geographic variation in both the  
161 preservation potential and the intensity of paleontological sampling (Carotenuto et al., 2010),  
162 there is a strong association between the geographic position of archaeological remains and  
163 the inferred suitability of the environmental conditions, for both EHS ( $AUC = 0.80$ , Figure 1  
164 left,  $AUC$  after subsampling the most abundant species = 0.71) and MHS ( $AUC = 0.81$ ,  
165 Figure 1 right,  $AUC$  after subsampling the most abundant species = 0.82). This strong  
166 association remains valid for all nodes in the hominin tree (Figures S1-S2, Tables S1-S2) and  
167 suggests that climatic variation in time and space strongly controlled the geographic ranges of  
168 our ancestors. Excluding extreme climatic values (i.e. climatic records beyond the 90<sup>th</sup>  
169 percentile of the individual variables distributions) in order to mitigate the effect of potential  
170 errors in the paleoclimate emulator, the  $AUC$  value for EHS decreased to 0.68, whereas it  
171 increased to as much as 0.82 for MHS (Table S3, Figure S3). We repeated this test by  
172 randomly placing species fossil occurrences throughout their biogeographical domain (Table  
173 S4, Figure S4) to simulate a scenario of no association between the archaeological record and  
174 habitat quality. Under this simulation, the  $AUC$  values drop towards 0.5, which indicate non-  
175 significant association between the two variables (EHS  $AUC = 0.56$ ; 95% confidence  
176 interval: 0.52-0.61; MHS  $AUC = 0.58$ , confidence interval: 0.56-0.60). This finding

177 reinforces the notion that the geographic position of archaeological sites is a non-random  
178 process guided by climatic variability.

179

### 180 **Rates of hominin climatic niche limit evolution**

181 We found that the clade identified by *H. heidelbergensis*, *H. neanderthalensis*, and *H.*  
182 *sapiens* and their common ancestor experienced a significant evolutionary rate shift towards  
183 wider climatic tolerance (Figure 2). The rate shift does not depend on the specific  
184 phylogenetic hypothesis (tree topology) assumed, neither does it depend on the selection of  
185 species we used. Randomly changing the tree node ages (to account for dating uncertainty)  
186 and species positions in the hominin tree (to account for phylogenetic uncertainty) 100 times  
187 the shift appears for this clade 95 times (Table 1). Subsampling the most abundant species  
188 (randomly selecting no more than 100 fossil occurrences per species) to account for sampling  
189 differences between species, the shift appears 91 times out of a hundred. We also repeated the  
190 phylogenetic reshuffling randomly removing one species at once. Under this latter design, the  
191 MHS shift occurs 63 times out of 100, and 23 additional times the shift involves two, rather  
192 than three, MHS species. Individually, *H. sapiens* and *H. heidelbergensis* appear in 86 rate  
193 shifts, *H. neanderthalensis* in 85, and no shift appears outside the MHS clade, demonstrating  
194 that the rate shift pertains to these species only and is not guided preferentially by any of the  
195 three (Table 1).

196

### 197 **Discussion**

198 The estimated values of realized climatic niche limits at nodes in the hominin  
199 phylogeny suggest that the rate shift in the climatic niche limits for the MHS clade was not an  
200 exclusively biological process. At the root of the hominin tree (node 11, Table S1), the  
201 predicted range in annual temperatures spans from 20°C (coldest quarter of the year) to

202 29.9°C (warmest quarter), and in mean rainfall from 12 mm (driest quarter) to 512 mm  
203 (wettest quarter). This is entirely consistent with today's African savannah environment  
204 (Hijmans et al., 2005). At the node subtending the pair *H. ergaster* plus *H. erectus* (which is  
205 the first hominin to disperse over Southern Eurasia), the corresponding figures are 0.7°C to  
206 31.9°C for temperature range and from 4.8 mm to 1080 mm for precipitation range. These  
207 estimates are reasonable considering both the range expansion into temperate regions and the  
208 colonization of warm and humid environments (Indonesia) by *H. erectus* (Carotenuto et al.,  
209 2016; Joordens et al., 2015; Rizal et al., 2019). Yet, at the common ancestor to the three  
210 MHS, the estimates for annual temperature extremes span from minus 21.1°C to plus 31.4°C  
211 and for annual precipitation from 0.7 mm to 905 mm. Although the common ancestor to  
212 MHS was an African species which probably never experienced these extreme climates  
213 (Profico et al., 2016), the values agree qualitatively with the notion that a sudden widening of  
214 climatic niche limits occurred with the advent of this ancestor, whose offspring lived after the  
215 onset of fully glacial Pleistocene conditions (Churchill, 1998). The massive increase in the  
216 estimated range of thermal conditions suitable for the MHS clade taxa (marked by a 20°C  
217 decrease in minimum temperature of the coldest season of the year as compared to the  
218 hominin tree root, Figures 3, S5) does not depend on the phylogenetic hypothesis we applied,  
219 and surpasses what is expected by a random process of increased phenotypic variance over  
220 time (namely the Brownian motion model of evolution, see Supplemental Information for full  
221 explanation). Using 100 different tree topologies and branch lengths to account for  
222 phylogenetic uncertainty, we found a significant trend in the temperature of the coldest  
223 season realized by hominins 97 times (Figure 3), whereas no trend was found in the  
224 maximum temperatures of the warmest season. We found that in African species and  
225 ancestors, the average temperature of the coldest quarter of the year was no less than 9.4°C,  
226 meaning that the winter chill is unlikely to have been a problem for them (Table S5). In

227 contrast, within the range of temperatures experienced by *H. heidelbergensis*, the coldest  
228 quarter of the year was as cold as -12.3°C, suggesting specific technological and cultural  
229 adaptations were needed to fend off the risk of hypothermia and to live in the highly-  
230 seasonal, cold northern environments (Ulijaszek and Strickland 1993; Ellison et al., 2005;  
231 Gilligan, 2007; Rivals et al., 2009; El Zaatari et al., 2016). These adaptations may have  
232 included fitted clothing (Amanzougaghene et al., 2019), thrown spears (Lenoir and Villa,  
233 2006) or adhesives (Cârciumaru et al., 2012), and enhanced healthcare practices (Spikins et  
234 al., 2019).

235 For some, the process of cultural niche construction (Laland et al., 2001; Laland and  
236 O'Brien 2012) through which human cultural traits have changed the human adaptive niche,  
237 and in turn selective pressures and ecological inheritance (Odling-Smee and Laland,  
238 2011) traces back to the very emergence of the genus *Homo* at some 2.5 million years  
239 ago (Antón and Josh Snodgrass 2012; Antón et al., 2014). At that time, increasing  
240 dependence on stone artefact production and social learning (Hiscock 2014) and on  
241 collaboration (Fuentes et al., 2010; Fuentes 2015) may have been particularly influential in  
242 allowing hominins to not only escape their biological constraints, but also to actively change  
243 the environmental and ecological niches of other species (Low et al., 2019). The occasional  
244 use of fire has similarly deep roots in human history (Gowlett, 2016; Organ et al., 2011;  
245 Pruett and Herzdog, 2017). Yet, the habitual use of fire (Shimelmitz et al., 2014) and the  
246 ability to work hide, wood and ivory (d'Errico and Henshilwood, 2007; Thieme, 1997) is  
247 attested at a much later date, during the Middle Stone Age (d'Errico, 2003) and attached to  
248 MHS only. Brain asymmetry and right-handedness, usually linked with advanced cognitive  
249 skills (Crow, 1993; Xiang et al., 2019; Melchionna et al., 2020b), similarly characterize MHS  
250 (Frayer et al., 2012; Lozano et al., 2009; Poza-Rey et al., 2017). In contrast to MHS, EHS  
251 either did not venture outside Africa or went across Eurasia longitudinally. *Homo erectus*

252 spread across Africa and Eurasia up to Java at some 1.7 Ma, but never settled north of the  
253 Mediterranean area or southeast China (Carotenuto et al., 2016). From the appearance of *H.*  
254 *heidelbergensis* onward, Northern, presumably colder habitats were no longer completely  
255 uninhabitable.

256         The jump in the rates of evolution in climatic niche width (driven by a sudden  
257 increase in tolerance to the cold, Figure 3) had enormous consequence in terms of geographic  
258 range. By modelling climatic niche limits according to a random walk with constant variance  
259 process (i.e. the Brownian motion model of evolution, BM), and assuming as habitable all  
260 geographic cells with habitat quality  $> 0.25$ , the rate shift accounts for a twofold increase in  
261 viable geographic range at the ancestor of MHS (node 14 in the tree), for a net gain of some  
262  $30 \times 10^6 \text{ km}^2$  (roughly the land surface of the African continent). At node 15, the ancestor of  
263 *H. sapiens* and *H. neanderthalensis*, the habitable area becomes nearly three times larger than  
264 expected under BM, corresponding to a geographic extension of some  $50 \times 10^6 \text{ km}^2$ . This  
265 massive increase in habitable area mostly represents expansion into northern latitudes,  
266 testifying to the importance of the rate shift in the colonization of Eurasia (Figure S5).

267         Although there is consistent evidence that *Homo* species may have exchanged genes  
268 with positive fitness consequences in cold environments by means of genetic introgression,  
269 this evidence is limited to the last 40 kya and invariably pertains to local *Homo sapiens*  
270 populations (Huerta-Sánchez et al., 2014; Sánchez-Quinto and Lalueza-Fox, 2015), meaning  
271 it occurs much later than the rate shift, and after the actual colonization of northern territories.

272         Although the real consequences of any individual cultural or technological adaptation  
273 introduced by MHS will almost certainly be a matter for debate for some time, our results  
274 indicate that these hominins were able to overcome the challenges imposed by life in  
275 northern habitats by a non-biological process, suggesting that behavioral modernity,

276 interpreted as the capacity to use technology and culture to overcome the constraints imposed  
277 by natural climate variability on the geographic distribution, is not limited to *H. sapiens*.

278

## 279 **Limitations of the Study**

280         The very concept of niche construction in *Homo* implies cultural advancements (fitted  
281 clothing manufacture, intentional fire, the production of tools made of perishable material  
282 such as bone, hide and wood) and improved social connections and skills that leave little to  
283 no archaeological evidence (Riede, 2019). Rather than focusing on such scarce evidence, we  
284 therefore focused on one of the major consequences of these cultural advances, that is the  
285 occupation of areas and climates outside the physiological niche limits of humans. A  
286 limitation of our findings is that the precise connection between the expansion of the climatic  
287 niche limits and advancements in material culture cannot easily be determined. Still, it relies  
288 on paleoclimate modelling that necessarily comes with uncertainty around the estimates.  
289 Nevertheless, our study confidently demonstrates the importance of cultural niche  
290 construction in the evolution of *Homo*, and how the sudden evolution of such niche-  
291 construction abilities shaped the geography of our own lineage in the deep past.

292

## 293 **Resource availability**

### 294 **Lead Contact**

295 Further information and requests for resources should be directed to Pasquale Raia  
296 ([pasquale.raia@unina.it](mailto:pasquale.raia@unina.it))

297

### 298 **Materials Availability**

299 This study did not generate any new material.

300

**301 Data and Code Availability**

302 The human fossil record and phylogenetic tree of hominins are available as supplemental data  
303 files. The functions used in this study are freely available as parts of the package RRphylo.  
304 Environmental niche limits (climatic variables) for each hominin species, to generate  
305 estimates at the tree nodes (ancestors) are available in Table S1.

306

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309 main findings presented here.

310

**311 Author Contributions**

312 P.R., A.M., M.M. and M.D.F. conceived the study. A.M., M.M., M.Mod., T.R., A.P., N.E.  
313 and P.H. produced and collected the data. A.M., M.M., M.D.F., S.C. and C.S. performed the  
314 analyses. P.O.H., F.C., L.M., L.R., J.A.D.F., T.R., A.P., N.E., and P.H. contributed in critique  
315 of analyses and interpretation. P.S. contributed in discussion of cultural and social contexts.  
316 All the authors contributed to writing.

317

**318 Declaration of Interests**

319 The authors declare no conflict of interests.

320

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**537 Main figure titles and legends**

538 **Figure 1. Habitat quality map for early *Homo* (EHS, left) and modern human species**  
539 **(MHS, right).** The maps show the quality of the habitats potentially suitable for occupation  
540 by the common ancestors of EHS and MHS, respectively. Quality varies from little (blue) to  
541 highly suitable (red) areas. The fossil occurrences of EHS (*H. habilis*, *H. ergaster* and *H.*  
542 *erectus*) and MHS (*H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*) are  
543 superimposed on each map (pink dots). See also Figure S1 and Table S1.

544  
545 **Figure 2. Climatic niche evolution in hominins.** (A) Three-dimensional plot of the climatic  
546 niche space occupied by the hominin clades through time. (B) The hominin tree used in this  
547 study. The branch colors are proportional to the multivariate rate of climatic niche evolution  
548 for each branch in the tree. At the MHS common ancestor (14) an acceleration in the rate of  
549 evolution in climatic tolerance limits occurs (shaded area). The common ancestor to all  
550 species within *Homo* is indicated by node 12. (C) The distribution of the rates of niche  
551 evolution for the MHS clade (deep blue) compared to the rest of the branches in the tree  
552 (light blue). (D) The individual rates of niche evolution for the tree branches forming the  
553 MHS clade. The average rate for the entire tree is indicated by the vertical blue line. MHS =  
554 modern *Homo* species, EHS = *Homo* species exclusive of MHS, Australopiths = species in  
555 the genus *Paranthropus* and *Australopithecus*.

556  
557 **Figure 3. Estimated temperature and precipitation ranges at several nodes in the**  
558 **human phylogenetic tree.** The individual rows represent the density distribution of  
559 minimum and maximum temperature and precipitation, respectively, collapsed together.  
560 HnHs = common ancestor to *H. neanderthalensis* and *H. sapiens*, MHS = Common ancestor  
561 to *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* HereHerg = common ancestor to

562 *H. erectus* and *H. ergaster*, *Homo* = common ancestor to *Homo* species, *Paranthropus* =  
 563 common ancestor to all *Paranthropus* species, *Australopithecus* = common ancestor to all  
 564 *Australopithecus* species, Hominins = common ancestor to hominins.

565

566

## 567 Main tables and legends

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

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

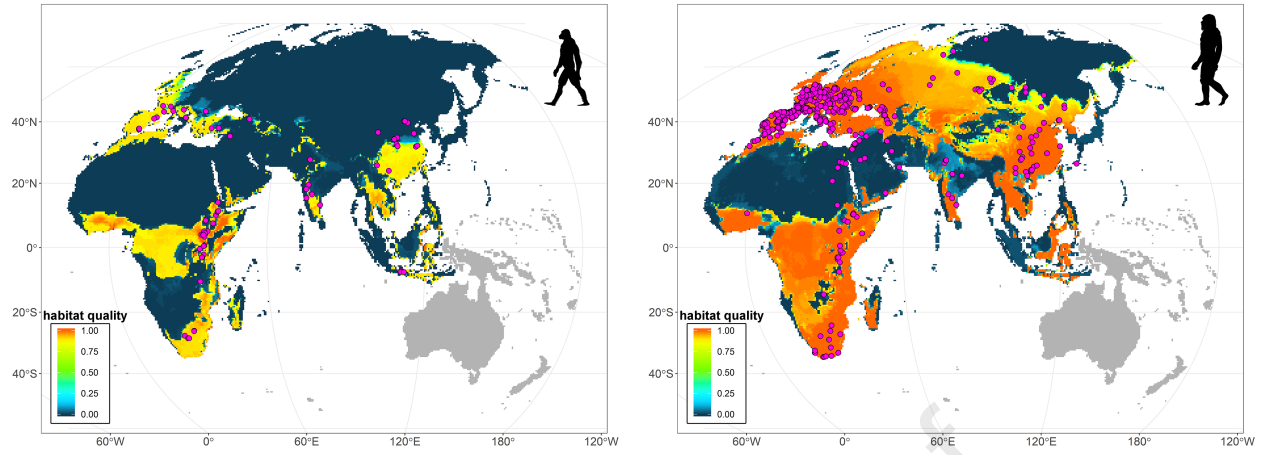
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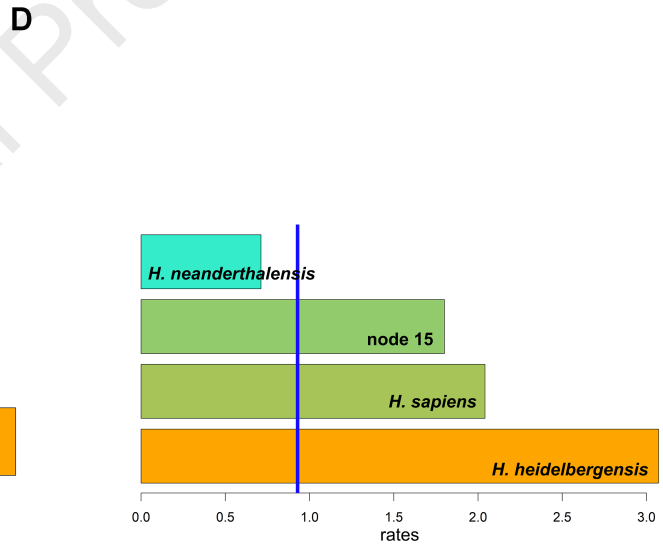
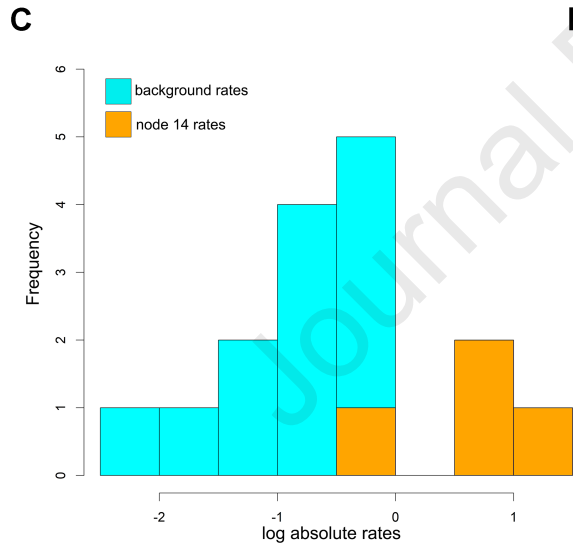
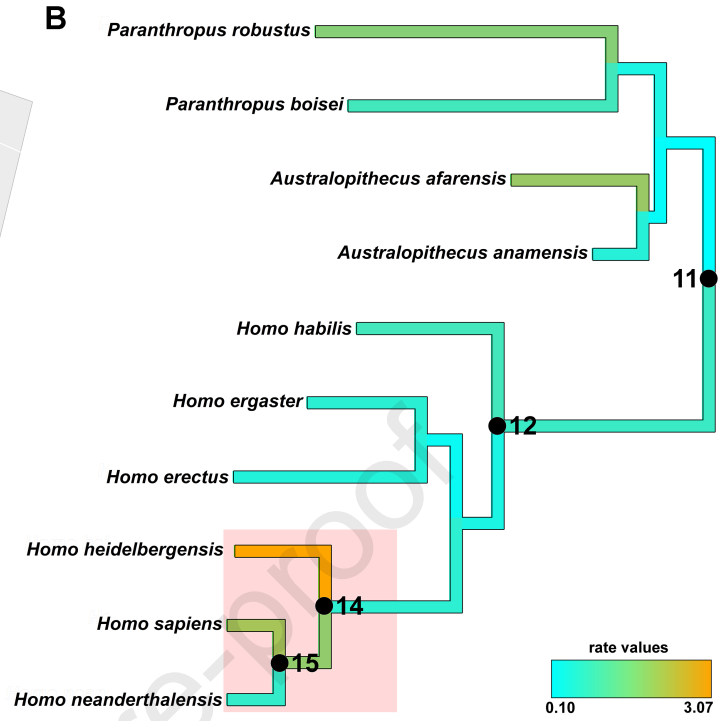
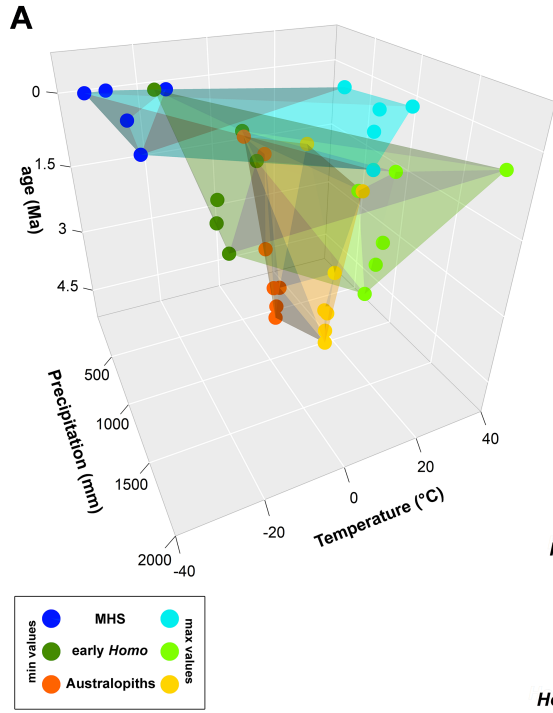
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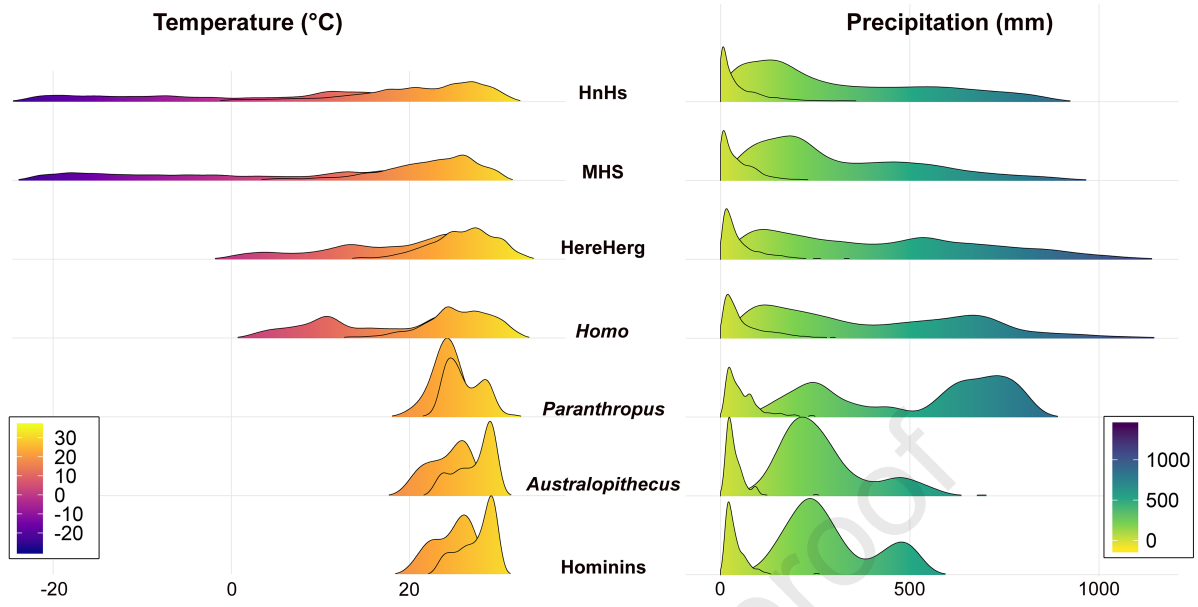
## 574 Supplemental Excel table title and legends

575 **Dataset S1. The Archaeological record of homininds. Related to Figures 1 – 3.**

576







- *Homo sapiens* ecological niche oversteps our physiological tolerance limits by means of culture
- The origin of technological advancement endowing *Homo* with niche-construction ability are unknown
- We demonstrated earlier *Homo* species preceded *H. sapiens* in the ability to overcome natural variability

Journal Pre-proof