FLORE
Repository istituzionale dell'Università degli Studi di Firenze

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

(Article begins on next page)

28 April 2024

Journal Pre-proof

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

Mondanaro Alessandro, Melchionna Marina, Di Febbraro Mirko, Castiglione Silvia, B. Holden Philip, R. Edwards Neil, Carotenuto Francesco, Maiorano Luigi, Modafferi Maria, Serio Carmela, Diniz-Filho Josè A.F., Rangel Thiago, Rook Lorenzo, O'Higgins Paul, Spikins Penny, Profico Antonio, Raia Pasquale

Please cite this article as: Alessandro, M., Marina, M., Mirko, D.F., Silvia, C., Holden Philip, B., Edwards Neil, R., Francesco, C., Luigi, M., Maria, M., Carmela, S., Josè A.F., D.-F., Thiago, R., Lorenzo, R., Paul, O'H., Penny, S., Antonio, P., Pasquale, R., A major change in rate of climate niche envelope evolution during hominid history, *ISCIENCE* (2020), doi: https://doi.org/10.1016/j.isci.2020.101693.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

A sudden increase in habitable area characterized the appearence of modern human species (MHS)

Habitable area for MHS

Habitable area for MHS without cultural innovation

H. heidelbergensis

H. neanderthalensis

H. sapiens
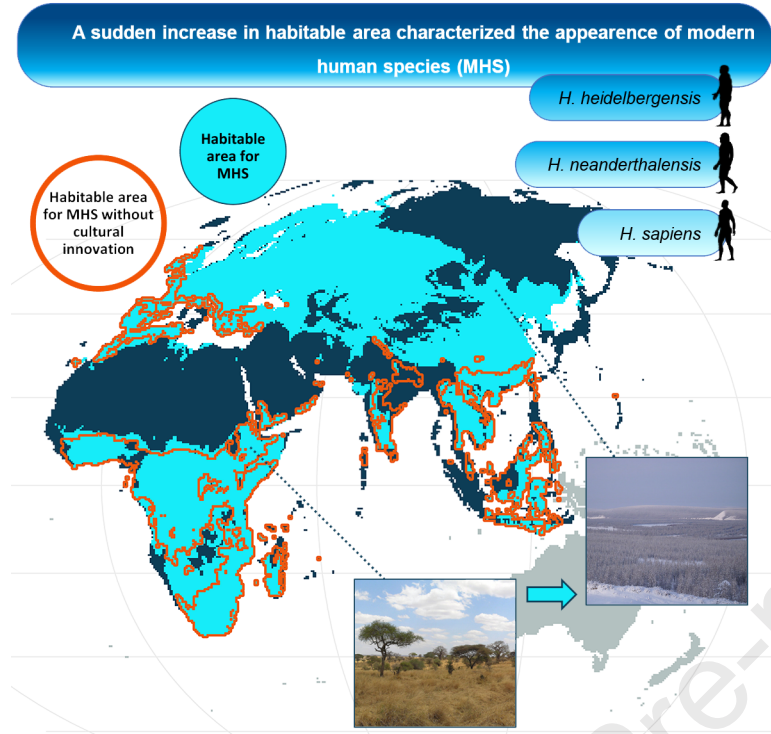
1 **A major change in rate of climate niche envelope evolution during hominid**

2 **history**

3

4 Mondanaro Alessandro[1,2], Melchionna Marina[1], Di Febbraro Mirko[3], Castiglione Silvia[1],

5 Holden Philip B.[4], Edwards Neil R.[4], Carotenuto Francesco[1], Maiorano Luigi[5], Modafferi

6 Maria[1], Serio Carmela[6], Diniz-Filho Josè A.F.[7], Rangel Thiago[7], Rook Lorenzo[2], O'Higgins

7 Paul[8], Spikins Penny[8], Profico Antonio[8], Raia Pasquale[1,9]*

8

9 [1] Department of Earth, Environmental and Resources Sciences. University of Naples "Federico II", Naples,

10 80126, Italy.

11 [2]Department of Earth Science. University of Florence, Florence, 50121, Italy.

12 [3]Department of Bioscience and Territory. University of Molise, Pesche, Isernia, 86090, Italy.

13 [4]School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, England, MK7

14 6BJ, United Kingdom.

15 [5]Department of Biology and Biotechnologies Charles Darwin, University of Rome La Sapienza, Rome, 00185,

16 Italy.

17 [6] Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Environmental

18 Sciences, Liverpool John Moores University, Liverpool, England, L3 3AF, United Kingdom.

19 [7]Department of Ecology, ICB, Universidade Federal de Goiás. Goiânia, 74968-755, Brasil.

20 [8]Department of Archaeology and Hull York Medical School, University of York, York, YO10 5DD, United

21 Kingdom.

22

23

24 [9]Lead Contact

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

26

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*.

41

42

43

44

45

46

47

48

49

50

51

52

Introduction

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

Unfortunately, clothing manufacturing leaves very little in the way of fossil remains (Hosfield, 2016). The first microwear evidence of hide-scraping (for manufacturing clothes) 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_2 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 ~ 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 90th

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 occured 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   Pruetz 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-handiness, 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   30×10^6 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 50×10^6 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

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

Resource availability

Lead Contact

295   Further information and requests for resources should be directed to Pasquale Raia

296   (pasquale.raia@unina.it)

297

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

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

References

321 **References**

322 Antón, S.C., and Snodgrass, J.J. (2012). Origins and Evolution of Genus *Homo*: New

323   Perspectives. Curr. Anthr. *53*, S479–96.

324 Antón, S.C., Potts, R., and Aiello, L.C. (2014). Human Evolution. Evolution of Early *Homo*:

325   An Integrated Biological Perspective. Science *345*, 1236828.

326 Amanzougaghene, N., Fenollar, F., Raoult, D., and Mediannikov, O. (2019). Where Are We

327   With Human Lice? A Review of the Current State of Knowledge. Front. Cell. Infect.

328   Microbiol. *9*, 213.

329 Attwell, L., Kovarovic, K., and Kendal, J.R. (2015). Fire in the Plio-Pleistocene: the

330   functions of hominin fire use, and the mechanistic, developmental and evolutionary

331   consequences. J. Anthropol. Sci. *93*, 1-20.

332 Baab, K.L. (2018). Evolvability and craniofacial diversification in genus *Homo*. Evolution

333   *72*, 2781-2791.

334 Banks, W.E., d'Errico, F., Dibble, H.L., Krishtalka, L., West, D., Olszewski, D., Townsend

335   Peterson, A., Anderson D.G., Gillam, G.C., Montet-White, A., Crucifix, M., Marean,

336   C.W., Sánchez-Goñi, M.-F., Wohlfarthh, B., Vanhaeren, M. (2006). Eco-cultural niche

337   modeling: New tools for reconstructing the geography and ecology of past human

338   populations, Palaeoanthropology *4*, 68–83.

339 Banks, W.E., d'Errico, F., Peterson, A.T., Vanhaeren, M., Kageyama, M., Sepulchre, P.,

340   Ramstein, G., Jost, A., Lunt, D. (2008). Human ecological niches and ranges during the

341   lgm in Europe derived from an application of eco-cultural niche modeling, J. Archaeol.

342   Sci. *35*, 481–491.

343 Banks, W.E., Aubry, T., d'Errico, F., Zilhão, J., Lira-Noriega, A., Townsend Peterson, A.

344   (2011). Eco-cultural niches of the badegoulian: Unraveling links between cultural

345   adaptation and ecology during the last glacial maximum in France. J. Anthr. Archaeol.

346   *30*, 359–374.

347   Banks, W.E., d'Errico, F., Zilhão, J. (2013). Human–climate interaction during the early

348   upper paleolithic: Testing the hypothesis of an adaptive shift between the proto-

349   aurignacian and the early aurignacian. J. Hum. Evol. *64*, 39–55.

350   Benito, B.M., Svenning, J.-C., Kellberg-Nielsen, T., Riede, F., Gil-Romera, G., Mailund, T.,

351   Kjaergaard, P.C., Sandel, B.S. (2017). The ecological niche and distribution of

352   neanderthals during the last interglacial, J. Biogeog. *44*, 51-61.

353   Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham,

354   T., and Petraglia, M.D. (2016). Ecological consequences of human niche construction:

355   Examining long-term anthropogenic shaping of global species distributions. Proc. Natl.

356   Acad. Sci. USA *113*, 6388–6396.

357   Cârciumaru, M., Ion, R.-M., Niţu, E.-C., and Ştefănescu, R. (2012). New evidence of

358   adhesive as hafting material on Middle and Upper Palaeolithic artefacts from Gura Cheii-

359   Râşnov Cave (Romania). J. Archaeol. Sci. *39*, 1942–1950.

360   Carotenuto, F., Barbera, C., and Raia, P. (2010). Occupancy, range size, and phylogeny in

361   Eurasian Pliocene to Recent large mammals. Paleobiology 36, 399–414.

362   Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., and

363   Raia, P. (2016). Venturing out safely: The biogeography of *Homo erectus* dispersal out

364   of Africa. J. Hum. Evol. *95*, 1–12.

365   Castiglione, S., Tesone, G., Piccolo, M., Melchionna, M., Mondanaro, A., Serio, C., Di

366   Febbraro, M., and Raia, P. (2018). A new method for testing evolutionary rate variation

367   and shifts in phenotypic evolution. Methods Ecol. Evol. *9*, 974–983.

368   Churchill, S.E. (1998). Cold adaptation, heterochrony, and Neandertals. Evol. Anthropol. *7*,

369   46-60.

370   Crow, T.J. (1993). Sexual selection, Machiavellian intelligence, and the origins of psychosis.

371   The Lancet *342*, 594–598.

372   d'Errico, F. (2003). The invisible frontier. A multiple species model for the origin of

373   behavioral modernity. Evol. Anthropol. *12*, 188-202.

374   d'Errico, F., and Henshilwood, C.S. (2007). Additional evidence for bone technology in the

375   southern African Middle Stone Age. J. Hum. Evol. *52*, 142–163.

376   Dunbar, R.I.M., Gamble, C., and Gowlett, J.A.J. (2014). Lucy to Language (Oxford

377   University Press).

378   El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.-J. (2016). Neandertal versus modern

379   human dietary responses to climatic fluctuations, PLOS ONE *11*, e0153277.

380   Ellison, P.T., Valeggia, C.R., Sherry, D.S. (2005). Human birth seasonality. In Seasonality in

381   primates: Studies of living and extinct human and non-human primates, Brockman, D.K.,

382   van Schaik, C.P. eds. (Cambridge University Press, Cambridge) p. 379.

383   Frayer, D.W., Lozano, M., Bermúdez de Castro, J.M., Carbonell, E., Arsuaga, J.-L.,

384   Radovčić, J., Fiore, I., and Bondioli, L. (2012). More than 500,000 years of right-

385   handedness in Europe. Laterality *17*, 51–69.

386   Fuentes, A. (2015). Integrative Anthropology and the Human Niche: Toward a Contemporary

387   Approach to Human Evolution. Am. Anthr. *117*, 302–15.

388   Fuentes, A., Wyczalkowski, M.A., and MacKinnon, K.C. (2010). Niche Construction through

389   Cooperation: A Nonlinear Dynamics Contribution to Modeling Facets of the

390   Evolutionary History in the Genus *Homo*. Curr. Anthr. *51*, 435–44.

391   Gilligan, I. (2007). Neanderthal extinction and modern human behaviour: the role of climate

392   change and clothing. World Archaeol. *39*, 499-514.

393   Gilligan, I. (2010). The prehistoric development of clothing: archaeological implications of a

394   thermal model. J. Archaeol. Method Theory *17*, 15-80.

395   Gowlett, J.A.J. (2016). The discovery of fire by humans: a long and convoluted process.

396   Philos. Trans. R. Soc. B *371*, 20150164.

397   Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn,

398   R.L., Brenet, M., Arroyo, A., et al. (2015). 3.3-million-year-old stone tools from

399   Lomekwi 3, West Turkana, Kenya. Nature *521*, 310–315.

400   Henshilwood, C.S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier,

401   N., Sealy, J.C., Valladas, H., Watts, I., and Wintle, A.G. (2002). Emergence of Modern

402   Human Behavior: Middle Stone Age Engravings from South Africa. Science *295*, 1278–

403   1280.

404   Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high

405   resolution interpolated climate surfaces for global land areas. Int. J. Climatol. *25*, 1965–

406   1978.

407   Hiscock, P. (2013). 5 Early Old World migrations of *Homo sapiens*: archaeology (Blackwell

408   Publishing Ltd).

409   Hiscock, P. (2014). Learning in Lithic Landscapes: A Reconsideration of the Hominid

410   'toolmaking' Niche. Biol. Theory *9*, 27-41.

411   Holden, P.B., Edwards, N.R., Fraedrich, K., Kirk, E., Lunkeit, F., and Zhu, X. (2016).

412   PLASIM–GENIE v1. 0: a new intermediate complexity AOGCM. Geosci. Model Dev. *9*,

413   3347-3361.

414   Holden, P.B., Edwards, N.R., Rangel, T.F., Pereira, E.B., Tran, G.T., and Wilkinson, R.D.

415   (2019). PALEO-PGEM v1. 0: a statistical emulator of Pliocene–Pleistocene climate.

416   Geosci. Model Dev. *12*, 5137-5155.

417   Hosfield, R. (2016). Walking in a Winter Wonderland? Strategies for Early and Middle

418   Pleistocene Survival in Midlatitude Europe. Curr. Anthropol. *57*, 653–682.

419   Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z., Peter, B.M., Vinckenbosch, N., Liang, Y., Yi,

420   X., He, M., Somel, M., et al. (2014). Altitude adaptation in Tibetans caused by

421   introgression of Denisovan-like DNA. Nature *512*, 194–197.

422   Joordens, J.C.A., d'Errico, F., Wesselingh, F.P., Munro, S., de Vos, J., Wallinga, J.,

423   Ankjærgaard, C., Reimann, T., Wijbrans, J.R., Kuiper, K.F., et al. (2015). *Homo erectus*

424   at Trinil on Java used shells for tool production and engraving. Nature *518*, 228–231.

425   Kittler, R., Kayser, M., and Stoneking, M. (2003). Molecular evolution of Pediculus humanus

426   and the origin of clothing. Curr. Biol. *13*, 1414-1417.

427   Laland, K.N., Odling Smee, J, and Feldman, M.W. (2001). Cultural niche construction and

428   human evolution. J. Evol. Biol. *14*, 22-33.

429   Laland, K. N., and O'Brien., M. J. (2012). Cultural Niche Construction: An Introduction.

430   Biol. Theory *6*, 191–202.

431   Lee-Thorp, J.A., Sponheimer, M., Passey, B.H., de Ruiter, D.J., and Cerling, T.E. (2010).

432   Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the

433   Pliocene. Phil. Trans. R. Soc. B *365*, 3389–3396.

434   Lenoir, M., and Villa, P. (2006). Hunting weapons of the Middle Stone Age and the Middle

435   Palaeolithic: spear points from Sibudu, Rose Cottage and Bouheben. South. Afr.

436   Humanit. *18*, 89-122.

437   Lordkipanidze, D., Jashashvili, T., Vekua, A., de León, M.S.P., Zollikofer, C.P.E., Rightmire,

438   G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., et al. (2007). Postcranial evidence

439   from early *Homo* from Dmanisi, Georgia. Nature *449*, 305–310.

440   Low, F.M., Gluckman, P.D., and Hanson, M.A. (2019). Niche Modification, Human Cultural

441   Evolution and the Anthropocene. Trends in Ecol. & Evol. *34*, 883–85.

442   Lozano, M., Mosquera, M., de Castro, J.-M.B., Arsuaga, J.-L., and Carbonell, E. (2009).

443   Right handedness of *Homo heidelbergensis* from Sima de los Huesos (Atapuerca, Spain)

444   500,000 years ago. Evol. Hum. Behav. *30*, 369–376.

445   Martin, J.S., Ringen, E.J., Duda, P., and Jaeggi, A.V. (2020). Harsh environments promote

446   alloparental care across human societies. Proc. R. Soc. B, *287*, 20200758.

447   Melchionna, M., Mondanaro, A., Serio, C., Castiglione, S., Di Febbraro, M., Rook, L., Diniz-

448   Filho, J.A.F., Manzi, G., Profico, A., Sansalone, G., and Raia, P. (2020a).

449   Macroevolutionary trends of brain mass in Primates. Biol. J. Linn. Soc. *129*, 14-25.

450   Melchionna, M., Profico, A., Castiglione, S., Sansalone, G., Serio, C., Mondanaro, A., Di

451   Febbraro, M., Rook, L., Pandolfi, L., Di Vincenzo, F., Manzi, G. and Raia, P. (2020b)

452   From Smart Apes to Human Brain Boxes. A Uniquely Derived Brain Shape in Late

453   Hominins Clade. Front. Earth Sci. *8*, 273

454   Nicholson, C.M. (2019). Shifts along a spectrum: A longitudinal study of the western

455   eurasian realized climate niche, Environ. Archaeol., 1-16.

456   Odling-Smee, J., and K. N. Laland. (2011). Ecological Inheritance and Cultural Inheritance:

457   What Are They and How Do They Differ?. Biol. Theory *6*, 220-230.

458   Organ, C., Nunn, C.L., Machanda, Z., and Wrangham, R.W. (2011). Phylogenetic rate shifts

459   in feeding time during the evolution of *Homo*. Proc. Natl. Acad. Sci. U.S.A. *108*, 14555–

460   14559.

461   Parfitt, S.A., Ashton, N.M., Lewis, S.G., Abel, R.L., Coope, G.R., Field, M.H., Gale, R.,

462   Hoare, P.G., Larkin, N.R., Lewis, M.D. et al. (2010). Early Pleistocene human

463   occupation at the edge of the boreal zone in northwest Europe. Nature *466*, 229–233.

464   Pearce, E., Shuttleworth, A., Grove, M., and Layton, R. (2014). The costs of being a high

465   latitude hominin. In Lucy to language: The benchmark papers, Dunbar, R.I.M., Gamble,

466   C., and Gowlett, J.A.J. eds. (Oxford University Press) pp. 356-379.

467   Poza-Rey, E.M., Lozano, M., and Arsuaga, J.-L. (2017). Brain asymmetries and handedness

468   in the specimens from the Sima de los Huesos site (Atapuerca, Spain). Quat. Int. *433*,

469   32–44.

470   Profico, A., Di Vincenzo, F., Gagliardi, L., Piperno, M., and Manzi, G. (2016). Filling the

471   gap. Human cranial remains from Gombore II (Melka Kunture, Ethiopia; ca. 850 ka) and

472   the origin of *Homo heidelbergensis*. J. Anthropol. Sci. *94*, 1-24.

473   Pruetz, J.D., and Herzog, N.M. (2017). Savanna chimpanzees at Fongoli, Senegal, navigate a

474   fire landscape. Curr. Anthropol. *58*, S337-S350.

475   Quintero, I., and Wiens, J.J. (2013). What determines the climatic niche width of species?

476   The role of spatial and temporal climatic variation in three vertebrate clades. Glob. Ecol.

477   Biogeogr. *22*, 422-432.

478   Rae, T.C., Koppe, T., and Stringer, C.B. (2011). The Neanderthal face is not cold adapted. J.

479   Hum. Evol. *60*, 234–239.

480   Raia, P., Boggioni, M., Carotenuto, F., Castiglione, S., Di Febbraro, M., Di Vincenzo, F.,

481   Melchionna, M., Mondanaro, A., Papini, A., Profico, A., et al. (2018). Unexpectedly

482   rapid evolution of mandibular shape in hominins. Sci. Rep. *8*, 1-8.

483   Raia, P., Mondanaro, A., Melchionna M., Di Febbraro, M., Diniz-Filho, J.A.F., Rangel, T.F.,

484   Holden, P.B., Carotenuto, F., Edwards, N.R., Lima-Ribeiro, M.S., et al. (2020). Past

485   extinctions of *Homo* species coincided with increased vulnerability to climatic change.

486   One Earth. doi:10.1016/j.oneear.2020.09.007

487   Riede, F. (2019) Niche Construction Theory and Human Biocultural Evolution. In Handbook

488   of Evolutionary Research in Archaeology, A. Prentiss, eds. (Springer, Cham.), pp. 337-

489   358.

490 Rivals, F., Moncel, M.-H., Patou-Mathis, M. (2009). Seasonality and intra-site variation of

491   neanderthal occupations in the middle palaeolithic locality of payre (ardèche, france)

492   using dental wear analyses. J. Archaeol. Sci. *36*, 1070-1078.

493 Rizal, Y., Westaway, K.E., Zaim, Y., van den Bergh, G.D., Bettis, E.A., Morwood, M.J.,

494   Huffman, O.F., n, R.G.X., Joannes-Boyau, R., Bailey, R.M., Sidarto, et al. (2019). Last

495   appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. Nature *577*,

496   381–385.

497 Roberts, P., and Stewart, B.A. (2018). Defining the "generalist specialist" niche for

498   Pleistocene *Homo sapiens*. Nat. Hum. Behav. *2*, 542-550.

499 Roebroeks, W. (2006). The human colonisation of Europe: where are we?. J. Quat. Sci. *21*,

500   425-435.

501 Sánchez-Quinto, F., and Lalueza-Fox, C. (2015). Almost 20 years of Neanderthal

502   palaeogenetics: adaptation, admixture, diversity, demography and extinction. Phil. Trans.

503   R. Soc. B *370*, 20130374–20130374.

504 Shimelmitz, R., Kuhn, S.L., Jelinek, A.J., Ronen, A., Clark, A.E., and Weinstein-Evron, M.

505   (2014). `Fire at will': The emergence of habitual fire use 350,000 years ago. J. Hum.

506   Evol. *77*, 196–203.

507 Spikins, P., Needham, A., Wright, B., Dytham, C., Gatta, M., and Hitchens, G. (2019).

508   Living to fight another day: The ecological and evolutionary significance of Neanderthal

509   healthcare. Quat. Sci. Rev. *217*, 98–118.

510 Thieme, H. (1997). Lower Palaeolithic hunting spears from Germany. Nature 385, 807–810.

511 Ulijaszek, S.J., Strickland, S.S. (1993). Seasonality and human ecology (Cambridge

512   University Press).

513 Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J.,

514   Braun, D.R., Arrowsmith, J.R., and Reed, K.E. (2015). Paleoanthropology. Early *Homo*

515   at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science *347*, 1352–1355.

516 Wang, Y., Heintzman, P.D., Newsom, L., Bigelow, N.H., Wooller, M.J., Shapiro, B., and

517   Williams, J.W. (2017). The southern coastal Beringian land bridge: cryptic refugium or

518   pseudorefugium for woody plants during the Last Glacial Maximum?. J. Biogeogr. *44*,

519   1559-1571.

520 White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., and

521   WoldeGabriel, G. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids.

522   Science *326*, 64-86.

523 Wroe, S., Parr, W.C.H., Ledogar, J.A., Bourke, J., Evans, S.P., Fiorenza, L., Benazzi, S.,

524   Hublin, J.-J., Stringer, C., Kullmer, O., et al. (2018). Computer simulations show that

525   Neanderthal facial morphology represents adaptation to cold and high energy demands,

526   but not heavy biting. Proc. R. Soc. B *285*, 20180085.

527 Xiang, L., Crow, T., and Roberts, N. (2019). Cerebral torque is human specific and unrelated

528   to brain size. Brain Struct. Funct. *224*, 1141–1150.

529 Xu, C., Kohler, T. A., Lenton, T.M., Svenning, J. C., and Scheffer, M. (2020). Future of the

530   human climate niche. Proc. Natl. Acad. Sci. *117*, 11350-11355.

531

532

533

534

535

536

Main figure titles and legends

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

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

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

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

Main tables and legends

567

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.

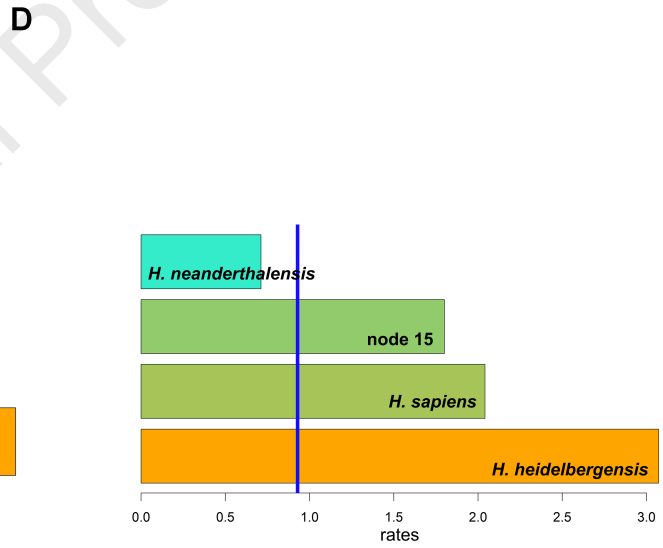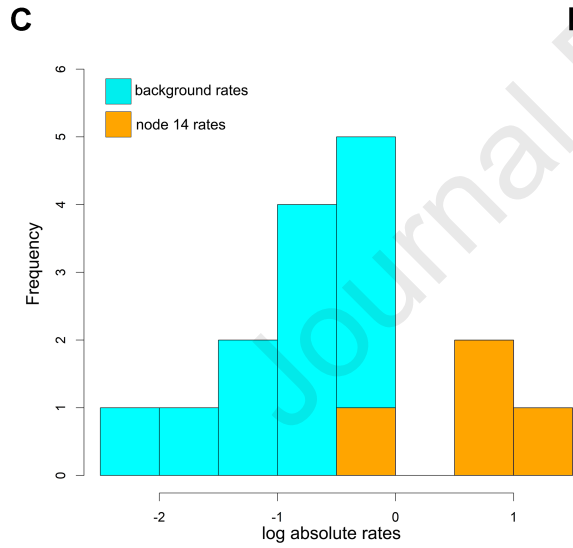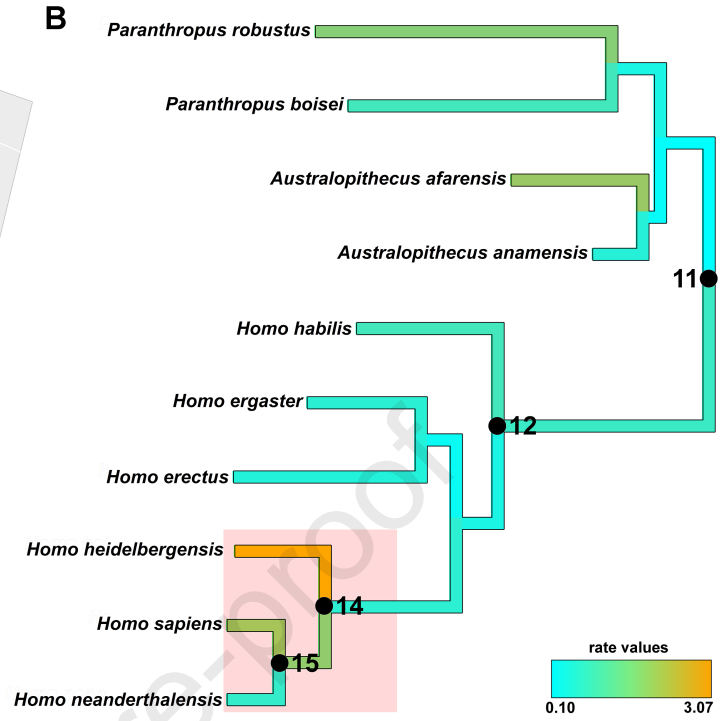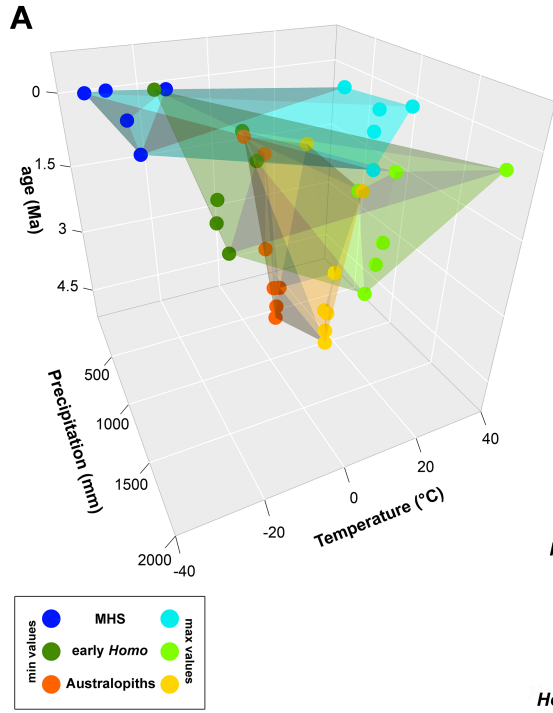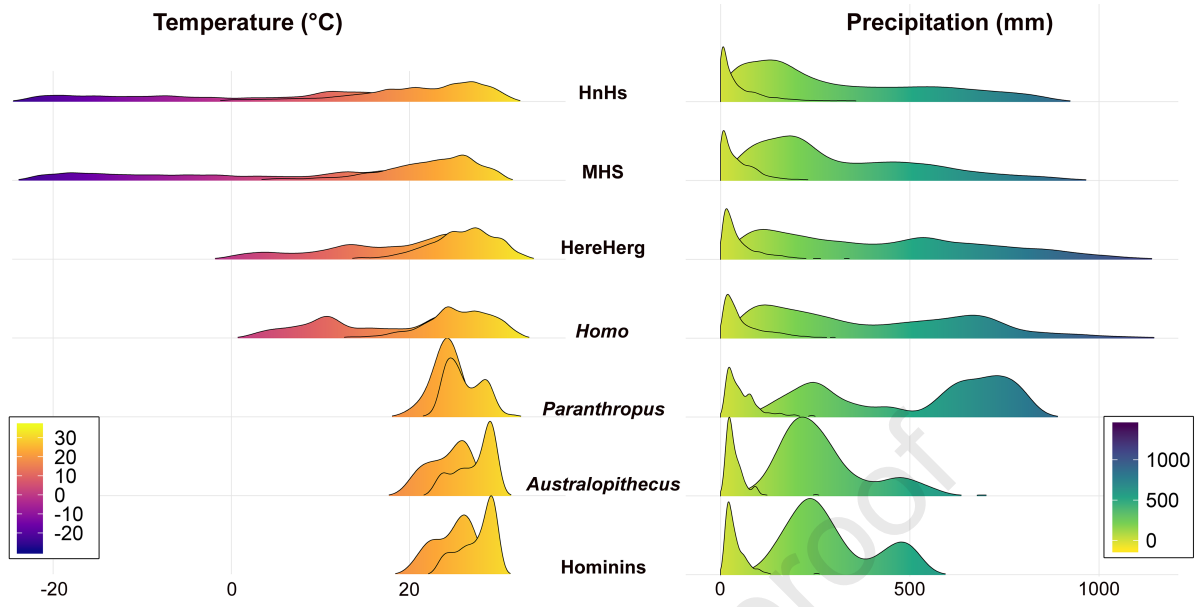| Species	Shift	Node with two species	Node with three species	*H. heidelbergensis*	*H. neanderthalensis*	*H. sapiens*
H. heidelbergensis	86	23	63	/	75	74
H. neanderthalensis	85	22	63	74	/	74
H. sapiens	86	23	63	75	74	/

572

573

Supplemental Excel table title and legends

574

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

576
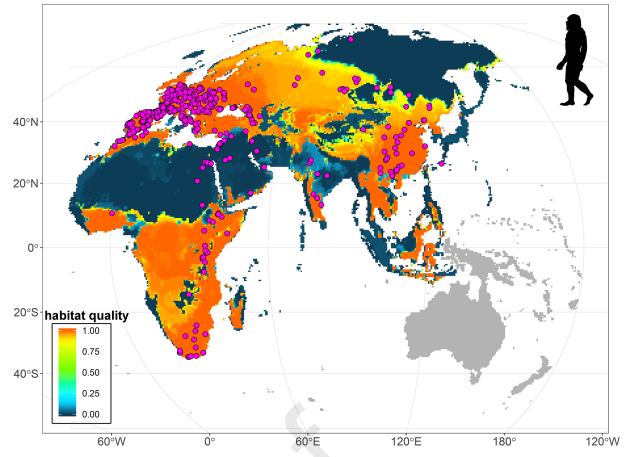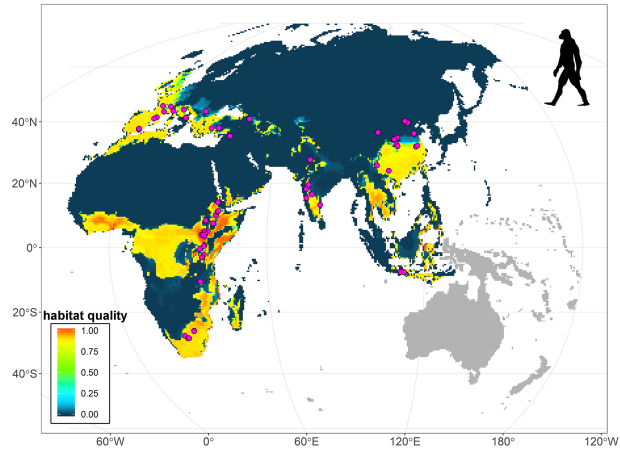
- *Homo sapiens* ecological niche oversteps our physiological tolerance limits by means of culture
- The origin of technological advancement endowing *Homo* with niche-construction ability are unknown
- We demonstrated earlier *Homo* species preceded *H. sapiens* in the ability to overcome natural variability