

Open Research Online

The Open University's repository of research publications and other research outputs

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

Journal Item

How to cite:

Mondanaro, Alessandro; Melchiona, Marina; Di Febraro, Mirko; Castiglione, Silvia; Holden, Philip B.; Edwards, Neil R.; Carotenuto, Francesco; Maiorano, Luigi; Modafferi, Maria; Serio, Carmela; Diniz-Filho, José A.F.; Rangel, Thiago; Rook, Lorenzo; O'Higgins, Paul; Spikins, Penny; Profico, Antonia and Raia, Pasquale (2020). A major change in rate of climate niche envelope evolution during hominid history. *iScience* (Early Access).

For guidance on citations see [FAQs](#).

© 2020 The Authors

Version: Accepted Manuscript

Link(s) to article on publisher's website:
<http://dx.doi.org/doi:10.1016/j.isci.2020.101693>

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

oro.open.ac.uk

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 José A.F., Rangel Thiago, Rook Lorenzo, O'Higgins Paul, Spikins Penny, Profico Antonio, Raia Pasquale

PII: S2589-0042(20)30885-3

DOI: <https://doi.org/10.1016/j.isci.2020.101693>

Reference: ISCI 101693

To appear in: *ISCIENCE*

Received Date: 3 August 2020

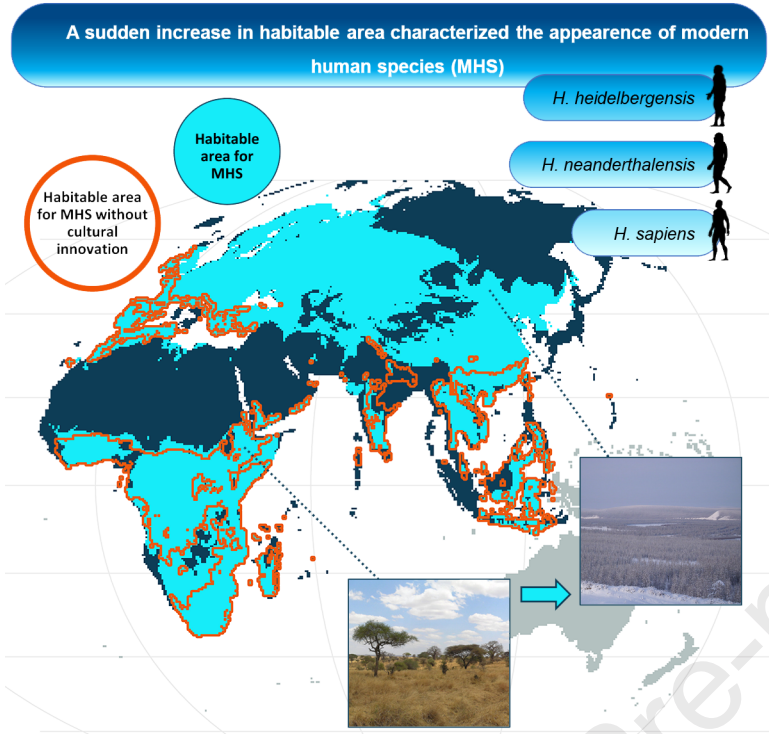
Revised Date: 3 September 2020

Accepted Date: 13 October 2020

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., José 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.

© 2020 The Author(s).



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

3

4 Mondanaro Alessandro^{1,2}, Melchionna Marina¹, Di Febbraro Mirko³, Castiglione Silvia¹,5 Holden Philip B.⁴, Edwards Neil R.⁴, Carotenuto Francesco¹, Maiorano Luigi⁵, Modafferi6 Maria¹, Serio Carmela⁶, Diniz-Filho José A.F.⁷, Rangel Thiago⁷, Rook Lorenzo², O'Higgins7 Paul⁸, Spikins Penny⁸, Profico Antonio⁸, Raia Pasquale^{1,9*}

8

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

10 80126, Italy.

11 ²Department of Earth Science. University of Florence, Florence, 50121, Italy.12 ³Department of Bioscience and Territory. University of Molise, Pesche, Isernia, 86090, Italy.13 ⁴School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, England, MK7

14 6BJ, United Kingdom.

15 ⁵Department 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 ⁷Department of Ecology, ICB, Universidade Federal de Goiás. Goiânia, 74968-755, Brasil.20 ⁸Department of Archaeology and Hull York Medical School, University of York, York, YO10 5DD, United

21 Kingdom.

22

23

24 ⁹Lead Contact25 *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

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, CO₂ 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 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 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)

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

307 Acknowledgments

308 We are grateful to Fabio di Vincenzo and Giorgio Manzi for critical discussion about the
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

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., Wohlfarth, 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 Igm 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., Nițu, E.-C., and Ștefănescu, R. (2012). New evidence of
358 adhesive as hafting material on Middle and Upper Palaeolithic artefacts from Gura Cheii-
359 Râșnov 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

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 | / |

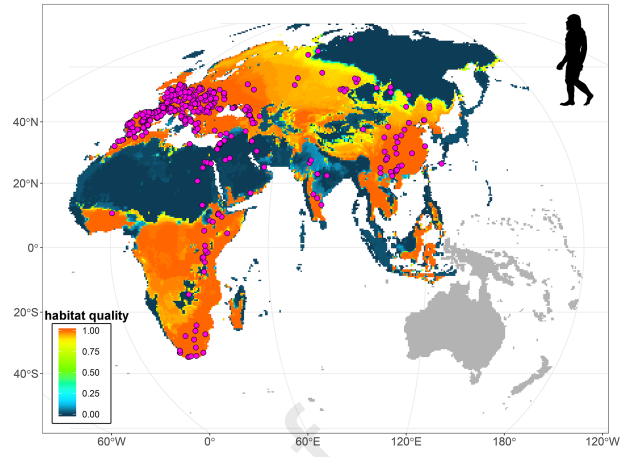
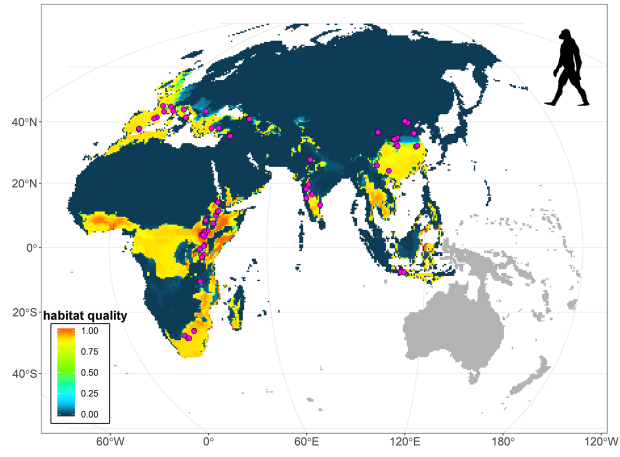
572

573

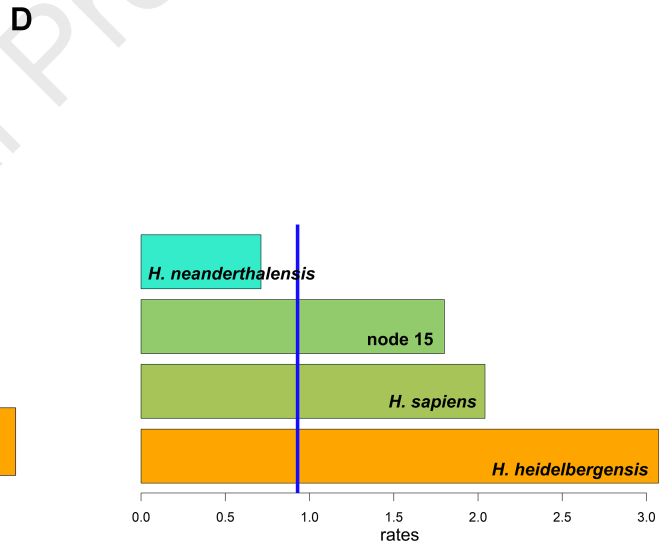
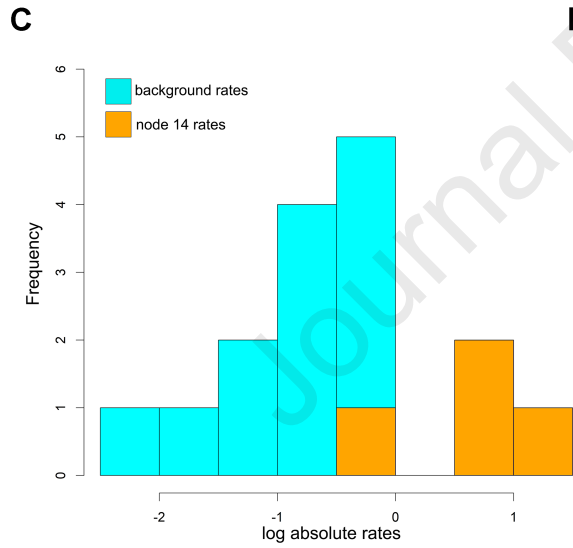
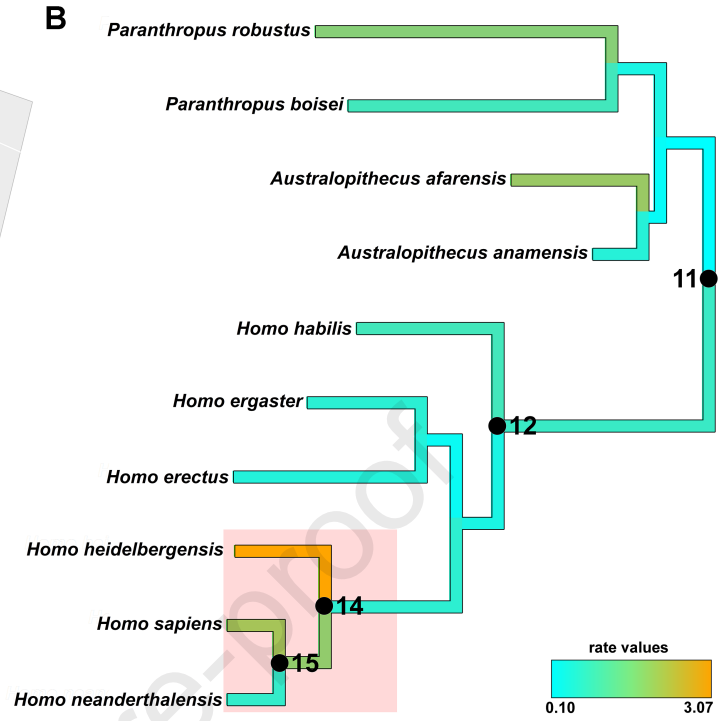
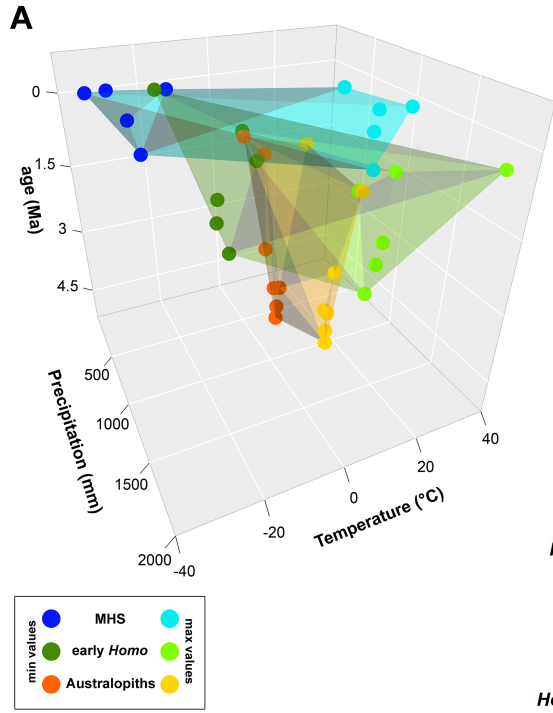
574 Supplemental Excel table title and legends

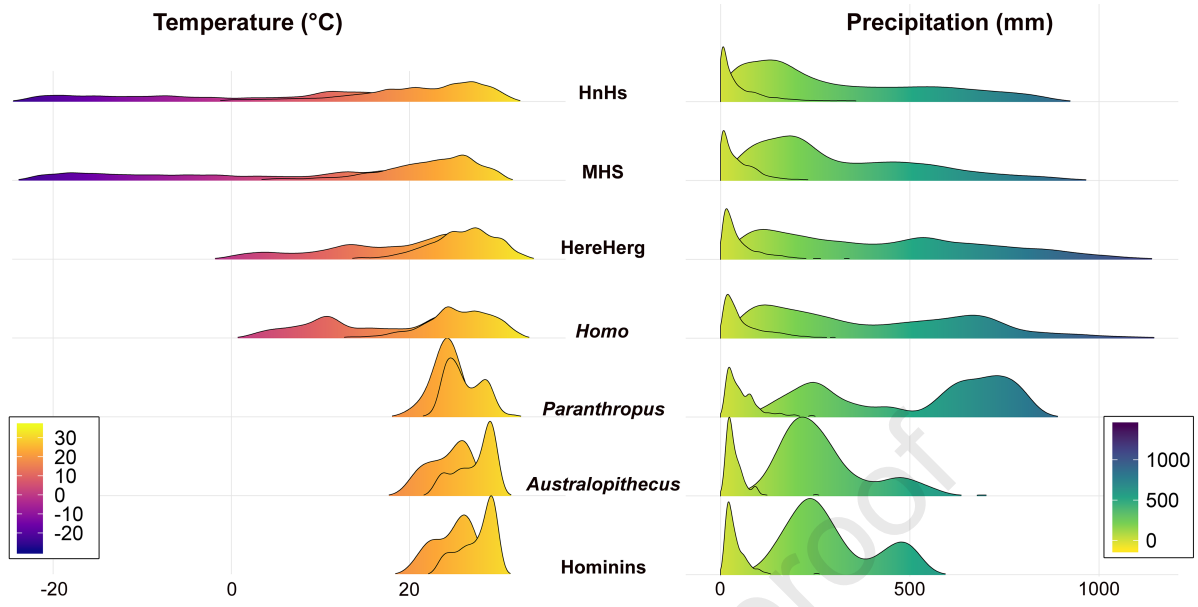
575 **Dataset S1. The Archaeological record of homininds. Related to Figures 1 – 3.**

576



Journal Pre-proof





- *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