

# Climate and Human Evolution: Insights from Marine Records

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- 12 Keywords: paleoclimate, human evolution, marine records, Africa, numerical modeling,
- 13 causal mechanisms
- 14

#### 15 Abstract:

- 16 The relationship between climate and human evolution is complex and the causal mechanisms
- 17 remain unknown. Here, we review and synthesize what is currently known about climate
- 18 forcings on African landscapes, focusing mainly on the last 4Myr. We use information
- 19 derived from marine sediment archives and data-numerical climate model comparisons and
- 20 integration. There exists a heterogeneity in pan-African hydroclimate changes, forced by a
- 21 combination of orbitally-paced low-latitude fluctuations in insolation, polar ice volume
- changes, tropical Sea Surface Temperature (SST) gradients, the Walker circulation and maybe
- greenhouse gases (GHGs). Pan-African vegetation changes do not follow the same pattern,
   suggestive of additional influences, such as CO<sub>2</sub> and temperature. We caution against reliance
- 25 on temporal correlations between global or regional climate, environmental changes and
- 26 human evolution and briefly proffer some ideas how pan-African climate trends could help
- 27 create novel conceptual frameworks to determine the causal mechanisms between
- 28 climate/habitat change and hominin evolution.
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#### 39 Introduction

40 The notion that climate influenced the course of human evolution has deep roots (Darwin

- 41 1871) and has been entertained in earnest since the 1920s after the discovery of the first
- 42 australopiths in southern Africa; occasional wooded belts and a relative scarcity of water were
- 43 suggested to have shaped human evolution (Dart 1925).

44 Over the last few decades evolutionary hypotheses have become more formalised. For example, Vrba (1985 and subsequent publications, see 1995 for review) proposed the 45 turnover-pulse hypothesis, which postulates pulses of speciation/extinctions across clades as a 46 consequence of prolonged climatic changes, primarily at the transitions of major astronomical 47 cycles from 19-23kyr to 41kyr, 100kyr and 400kyr respectively. Although originally 48 conceived to explain the turnover of bovids, for which the fossil record is relatively extensive, 49 50 the hypothesis was soon extended to explain major transitions in hominin evolution (deMenocal 2004). However, doubts were raised whether the hypothesis is applicable to other 51 clades and/or across Africa (e.g., Behrensmeyer 2006). Indeed, all species are habitat-specific 52 53 and although large-scale changes in habitat structure may affect a number of clades 54 simultaneously, they will do so in different ways; this concept is encapsulated in Vrba's 'habitat theory'. She argued that, exposed to the same environmental and climatic changes, 55 56 warm-adapted and cold-adapted clades will display different rates and timings of species-57 turnover. Ecological studies have since explored the eco-evolutionary processes underlying 58 species diversity in greater detail and have shown that, in addition to thermoregulatory 59 constraints, a taxon's dispersal potential, dietary adaptation, body mass, life history strategy, 60 as well as competition among species, will profoundly influence a species' response to climate change and its susceptibility to speciation/extinction (Price et al. 2012, Pires et al. 61 62 2017). Hence, the association between climate change, speciation, extinction, dispersal and 63 morphological adaptation is not straightforward and would require a multi-pronged approach for its resolution (Hagen 2023). Given the limitations of the fossil record (Behrensmeyer et al. 64 2000), including sampling biases (Maxwell et al. 2018, Faith et al. 2021), discerning the 65 66 mechanism underlying evolutionary processes in an extinct taxon is thus challenging, if not impossible. Consequently, whilst mapping hominin diversification and innovations onto 67 global climate trends is appealing (e.g., deMenocal 2004, Figure 1) and may highlight specific 68 time periods of interest, the explanatory power of such correlations is limited. Interpreting the 69 effects of climate on later stages of hominin evolution is even more problematic. 70 Specifically, Potts (1995, 1996, 1998) formulated the variability selection hypothesis. This 71 hypothesis is grounded in Sewall Wright's (1932, 1968) shifting balance theory, which 72 73 mathematically explores changes in allele frequencies and genotypes in response to drift,

- 74 natural selection, mutation and migration. Owing to random drift and local selection pressures
- some populations/species are predicted to go extinct, whilst others will traverse valleys of
- 76 lower fitness to ascend to a new adaptive peak; successful species/populations are postulated
- to accrue certain alleles and gene configurations. Contrary to Wright however, who
- random shifts in gene frequencies, Potts drew attention to the role of increased
- climatic variability during the Pleistocene as a driver for genetic change. He suggested that
- 80 habitat instability would not only have led to changes to allele frequencies, but to
- 81 polymorphisms, thus making species/populations well-equipped to deal with novel situations
- 82 without the need for further genetic modifications. Phrased differently, species/population
- 83 would have become increasingly buffered against environmental stochasticity; increased

84 behavioural flexibility and innovations in material culture (Potts et al. 2018, 2020) would

- 85 have added further advantages to the survival of hominin populations/species.
- 86 Evidently thus, whilst there is little doubt that hominin evolution was driven, or at least
- 87 influenced, by climate change, the identification of causal mechanisms has remained elusive.
- 88 In order to advance our understanding of the possible causal relationships, we need to
- 89 primarily improve on two lines of enquiry: (a) obtain better (i.e. high-resolution) climate and
- 90 habitat reconstructions through time and (b) develop theoretical frameworks for an
- 91 interpretation of the climatic and ecological drivers for evolutionary change in a large-bodied,
  92 eurybiomic and polymorphic taxon, that has no living analog. To contribute to these aims here
- we will review and synthesize what is currently known about climate forcings on African
- 94 landscapes, using information derived from marine sediment archives (restricted to the period
- 95 from the Neogene to present day with a primary focus on the last 4Myr), data-numerical
- 96 climate model comparisons and integration. The reconstruction of local environments from
- 97 the terrestrial (e.g. faunal records) (e.g., Andrews & Hixson 2014) and lacustrine sedimentary
- archives (e.g., Campisano et al. 2017), does not form part of this review. We will then briefly
- 99 proffer some ideas as to how these African climate trends could help create novel conceptual
- 100 frameworks for an interpretation of hominin evolutionary processes.
- 101

#### 102 **1. Climate forcings on African landscapes**

- 103 1.1 Natural forcings/causes of climate changes
- 104 Climate varies at different time scales, from years to billions of years (Figure 2). Climate
- 105 variability depends on interactions between the different components of the climate system
- 106 (atmosphere, ocean, cryosphere, biosphere and lithosphere) and on external forcings that
- 107 affect the earth's radiative balance. External forcings are mainly related to astronomical
- 108 forcings or are associated to internal Earth dynamic (Figure 2), which affect the radiative
- balance of the Earth and processes such as atmospheric and oceanic circulation that re-
- equilibrate the system by transporting excess energy from the equatorial to polar regions.Processes internal of the climate system imply different retroactions inside the system.
- 111 Trocesses merina of the enhale system mpry anterent renouedons inside the system.
- 112 Over the last 4Myr the effects of tectonics on climate systems reduced and the main natural
- forcings of climate change have been related to the earth's orbital variations (eccentricity,
- 114 obliquity and precession with periodicities of 100 and 400kyr, 41kyr and 21kyr, respectively)
- and atmosphere-ocean-cryosphere dynamics (Figure 2). Africa is centered on the equator and therefore most of its landmass is located at low latitudes where Intertropical Convergence
- therefore most of its landmass is located at low latitudes where Intertropical Convergence
  Tops (ITCZ) variability management and Welker Circulation control the hydrological evaluation
- 117 Zone (ITCZ) variability, monsoons and Walker Circulation control the hydrological cycle.
- 118 1.2 The ITCZ, Monsoons and Walker Circulation
- 119 The ITCZ is a tropical belt of maximum precipitation that results from deep convection
- 120 migrating seasonally towards the warming hemisphere (Nicholson et al. 2013, Schneider et al.
- 121 2014). ITCZ zonal-mean position is associated with the rising branch of the global Hadley
- 122 cell (Figure 3). Because of the complexity of African climate, the Congo Air Boundary
- 123 (CAB), a convergence zone that marks the confluence of Indian Ocean air with unstable air
- 124 from the Congo Basin, indicates the location of the southern edge of the African rain belt and

- 125 plays a fundamental role in controlling hydroclimate in the African tropics, especially in
- 126 Africa's interior (Tierney et al. 2011, Howard & Washington 2019).
- 127 Monsoons are the dominant seasonal mode of climate variability in the tropics (Mohtadi et al.
- 128 2016). They can be viewed as localized seasonal migrations of the tropical convergence zone:
- 129 the band of converging air and rainfall in the tropics embedded within the tropical
- 130 atmospheric overturning circulation. This allows to distinguish the dynamics of low-latitude
- 131 ( $\sim 0-10^{\circ}$  poleward) ITCZ from that of monsoons ( $\sim 10-25^{\circ}$  poleward) (Geen et al. 2020)
- 132 (Figure 3).
- 133 In addition to tropical convergence zone migrations, a thermally direct, equatorial, zonal
- 134 overturning circulation exists that converts available potential energy to kinetic energy of
- atmospheric motion: the Walker Circulation. The Walker Circulation is intrinsically
- 136 connected to the El Niño–Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD),
- 137 which are forms of interannual climate variability in the tropical Pacific and Indian Ocean,
- respectively (Abram et al. 2020) (Figure 3). The results are increased/decreased atmospheric
- 139 convection and associated precipitation over the western or eastern tropical Pacific and Indian
- 140 Oceans.
- 141 1.3 Relationships between precipitation and vegetation changes
- 142 Today, the distribution of vegetation and animals in Africa is related to the amount, intensity
- 143 and seasonal distribution of precipitation (e.g., White 1983, Guan et al. 2014). This
- 144 connection between hydroclimate and vegetation also existed in the past and likely affected
- evolutionary processes. To illustrate, the vegetation and precipitation records show a marked
- seasonal shift across the Sahel with plant growth moving north as rain falls over the region in
- boreal summer (Figure 4). Conversely, plant growth moves south as rain falls over southern
- Africa in austral summer, although the correlation is less significant for some areas. Such
- 149 heterogeneity in vegetation response is noteworthy and cautions against generalizations when
- 150 reconstructing past environments. It is therefore crucial to reconstruct both past hydroclimate
- and vegetation changes and their potential relation in order to explore potential links with
- 152 human evolution.
- 153

# **2. Interests of marine sediment records**

155 deMenocal (1995) first linked early hominin evolution in Africa to global climate change, 156 using data from marine sediment cores. Although African terrestrial records provide crucial 157 information about land climate variability and about the specific habitats/niches occupied by extinct taxa (e.g., refugia), marine records offer a more robust chronology, a long stratigraphic 158 159 continuity and higher temporal resolution (Cohen et al., 2022). A wide range of proxies can 160 be used in marine sediment cores for terrestrial climate and environmental reconstructions (Table 1) with the advantage of direct ocean-continental comparison. For example, proxies 161 associated with marine biogenic sedimentation can be directly compared to proxies derived 162 from continental source that are transported, mainly by wind or rivers, to the oceans (Figure 163 164 5).

Because marine sediments integrate the signal of entire catchments areas, reconstructing a
 larger picture of oceanic and atmospheric dynamics is possible. Using volcanic sediments in

167 marine sediment cores, it also becomes possible to assess more precisely the synchronicity

168 and potential causal links between climate/environmental changes and human evolution (see

169 Appendices: Tectonic, volcanism and tephrochronology).

170 With these benefits in mind, an important caveat of marine core archives is that there is a

spatiotemporal scale mismatch between broad, regional marine core records and the highly
localized terrestrial fossil records that inform about primate evolution (Faith et al. 2021). For

localized terrestrial fossil records that inform about primate evolution (Faith et al. 2021). For
 example, recent biomarker isotope records from terrestrial sediments (Peppe et al. 2023, Uno

et al. 2016b) and lacustrine sediments (e.g., Lupien et al. 2022, Mitsunaga et al. 2023)

175 indicate higher ecosystem and hydroclimate variability at smaller spatial scales. In one case,

176 carbon isotope biomarker records suggest  $C_4$  vegetation at local scales that is absent in

regional records (Peppe et al. 2023). Careful consideration of how marine, lacustrine, and

178 terrestrial archives integrate vegetation and hydroclimate signals is necessary for relating

179 proxy vegetation and climate records to hominin evolution.

180

## 181 **3.** Climate and environments of Africa

182 Given the impact of tectonics and volcanism on landscapes, building the tectonic histories of 183 each basin should be a requisite step before linking continental records of environmental 184 change to regional or global climate phenomena (see review in Levin 2015); most tectonic activity in Africa in the last 10Myr has centered on the East African Rift System (EARS; see 185 Appendices: Tectonic, volcanism and tephrochronology). Whilst we acknowledge the 186 187 importance of tectonics and volcanism for the reconstruction of local habitats, our main focus 188 here is on pan-African climate over the last 4Myr, based on marine sediment cores, as this 189 may have impacted the overall course of hominin evolution; to provide a broader context, we 190 only briefly summarize marine core records that capture important climate and environmental 191 change during the Neogene.

192 3.1 Climate and environments of the Neogene

193 The Neogene period, which includes the Miocene (23.03 to 5.33Ma) and Pliocene (5.33 to 194 2.58Ma) epochs, was characterized by major environmental change that influenced primate 195 evolution in Africa. Fossils from the early and middle Miocene demonstrate a dynamic period 196 of catarrhine evolution in Africa that includes the first Afropithecus and victoriapithecines and 197 the diversification of proconsulids (Leakey & Leakey 1986, McNulty et al. 2015, Nengo et al. 198 2017). This was followed by the origin of the hominin lineage in the late Miocene around 199 7Ma (Brunet et al. 2002). But there is a dearth of long, continuous Neogene terrestrial 200 archives. Most are temporally limited and associated with fossil localities in eastern Africa. 201 As a result, marine core records have played an important role in reconstructing regional scale 202 climate and environmental change in Africa. This includes Neogene biomarker records (Uno 203 et al. 2016a, Polissar et al. 2019; see Appendices: Water and Carbon isotopes) and plant microfossil records (Morley & Richards 1993) as well as late Miocene biomarker (Feakins et 204 al. 2013, Hoetzel et al. 2013) and pollen records (Bonnefille 2010) that span the last ~10Myr. 205 206 Carbon isotope records from *n*-alkanes at DSDP sites 235 and 241in the Somali Basin were the first to demonstrate C<sub>3</sub> vegetation was predominant at the regional scale from the early 207 208 Neogene until 10Ma, when C<sub>4</sub> grasses began to spread in eastern Africa (Uno et al. 2016a). 209 Subsequent *n*-alkane carbon isotope records from the tropical Atlantic (ODP sites 659 and

- 210 959) show a similar pattern of regional  $C_4$  expansion in northwest Africa at 10Ma; additional
- 211 hydrogen isotope records show no clear indication of hydroclimate change associated with
- spread of C<sub>4</sub> grasslands in Africa (Polissar et al. 2019). In southern Africa, combined
- biomarker, pollen, and charcoal records from ODP sites 1081 and 1085 show that grasses
- were present regionally by ~11Ma, with the spread of  $C_4$  vegetation beginning around 7.5Ma
- 215 (Hoetzel et al. 2013, Dupont et al. 2013). The Neogene marine core records from
- northwestern, eastern, and southern Africa demonstrate that  $C_4$  grasses began to spread regionally in the northern part of the continent at 10Ma and in the southern part by 7.5M
- regionally in the northern part of the continent at 10Ma and in the southern part by 7.5Ma.
  Available biomarker data suggest that hydroclimate change played a minor or insignificant
- role and, therefore,  $CO_2$  may have instead acted as the ecological driver (Polissar et al. 2019).
- An outstanding question that cannot be addressed by carbon isotopes is the role of  $C_3$  grasses
- in early Neogene ecosystems, which were no doubt present based on plant microfossil
- evidence (Peppe et al. 2023, Morley & Richards 1993).
- 223
- 224 3.2 Climate and environments of the last 4Myr
- 225 3.2.1 New 4Myr-southeastern African (Limpopo) hydroclimate stack
- Records of hydroclimate in southeastern Africa are rare over the last 4Myr, yet this is a
- crucial region regarding hominin evolution (Figure 1). Here we combine published
- hydroclimate records over the last 2Myr (Caley et al. 2018) with those between ~4 to 2Ma
- (Koutsodendris et al. 2021, Taylor et al., 2021) in order to generate a new Limpopo catchment
- hydroclimate stack over the last 4Myr (see Figure 6). We performed a principal component
- analysis (PCA) on the  $\delta^{13}C_{wax}$  and ln(Fe/Ca) hydroclimate records of site MD96-2048 (Caley et al. 2018) (Table 1). The first principal component (PC1) accounts, on average, for 71% of
- 232 the variance. Similarly, the  $\delta D_{wax}$  and  $\ln(Ti/Ca)$  hydroclimate records (Table 1) of site IODP
- U1478 (Koutsodendris et al. 2021, Taylor et al. 2021) accounts, on average, for 53% of the
- variance observed for PC1. When both PC1 are combined in a new 4Myr-southeastern
- African (Limpopo) hydroclimate stack (Figure 6e), significant changes with alternation
- between more humid and more arid conditions are evident over the last 4Myr. This finding
- prompted us to investigate whether the trends observed for southeastern Africa can be
- 239 replicated across Africa.
- 240 3.2.2 Pan-African hydroclimate.
- 241 We compiled the existing continuous hydroclimate records to cover the last 4Myr. Data are
- 242 limited to five records that are distributed across the whole of Africa and over several Myrs
- 243 (Figure 6). Most of these records are derived from  $\delta D_{wax}$  proxy, or a combination with fluvial
- runoff proxies (Figure 6 and Table 1) (**Appendices: Water and Carbon isotopes**). One
- exception is the Dust record from site ODP659. African dust records largely reflect increased
- 246 wind strength and transport (Zabel et al. 1999) however, and are not necessarily a reliable
- 247 indicator for aridity (Skonieczny et al. 2019). Nonetheless, the correspondence between  $\delta D_{wax}$
- for specific time intervals over the last 5Myr and the dust record of ODP Site 659 apparently
- support conclusions concerning the generation of dust during arid periods (Tiedemann et al.
- 250 1994) and the use of  $\delta D_{wax}$  as a humidity proxy (Kuechler et al. 2018).
- To parametrize pan-African climate variability, PCA (see Figure 6 for details) of the selected
   datasets were performed. PC1 captures the maximum variance of the data (approximately 36

253 % across all datasets), and depicts heterogeneity across the studied sites. Hydroclimate

- records from the Oman region and from western Africa share a common pattern, whereas
- records from eastern Africa (north and more particularly south) have a different pattern.

256 To investigate the forcings that control this heterogeneity at the pan-African scale, we

- conducted spectral analyses. Because some of the records have a low resolution, we
- resampled all the datasets with a mean and regular interval of 20kyr, thereby limiting our
- analyses to long term orbital forcing (eccentricity scale). Spectral analyses with REDFIT
- 260 (Schulz & Mudelsee 2002) and wavelet analyses (Torrence & Compo 1998) display strong
  261 spectral power at around the 185, 400 and 600kyr bands on PC1 (Figure 6). This corresponds
- to eccentricity forcing at 400kyr and, potentially, to weak but real eccentricity variations at
- around 200 and 600kyr (Kashiwaya et al. 2001, Laskar et al. 2004, Hilgen et al. 2020).
- Alternatively, harmonic of the 400-kyr cycle or "double" ~100-kyr cycle that result from non-
- 265 linear responses of the climate system to the main eccentricity components can also explain
- these cycles (Hilgen et al. 2015).

The 400kyr and 600kyr band comprises 11 % of the variance of the PC1. Part of the variance 267 related to orbital forcing is missing due to sampling resolution: for example, the precession 268 forcing in south-east Africa over the last 2.15Myr accounts for 25 % of the variance in the 269 InFe/Ca record, a high-resolution proxy of fluvial runoff (Caley et al. 2018). Nevertheless, the 270 271 results indicate that part of the variance in pan-African hydroclimate records is not controlled 272 by orbital forcings. These other forcings have been highlighted in various studies and may 273 relate to ice volume changes, SST gradients and the Walker circulation (Maslin et al. 2014, Caley et al. 2018, Kaboth-Bahr et al. 2021, Trauth et al. 2021, Lupien et al. 2023, Rubbelke et 274 275 al. 2023), or perhaps greenhouse gases (GHGs). Although not yet fully explored, GHGs 276 forcing could affect the hydroclimate through vegetation changes (Dupont et al. 2019) or 277 through thermodynamic impacts, as well as consequent changes in atmospheric moisture 278 content, resulting in summer monsoon precipitation change overall.

279

280 When the dominant 400kyr and 600kyr cycles are removed from PC1, the residual trend

281 correlates with gradual Walker circulation changes, ice volume changes and, to a lesser

degree, CO<sub>2</sub> concentration changes (Figure 7), confirming that all of these internal forcings

283 (Figure 2 and 7) probably affect pan-African hydroclimate variability.

284 The reconstructed pan-African climate variability, represented by PC1, clearly depicts four

285 phases during the last 4Myr that have been constrained by change point analysis (Figure 6).

286 The first phase characterizes a pan-African climate that is rather humid between 4 and

287 2.51Ma. Only eastern African records indicate successions of arid and humid periods inside

- this first phase (see Figures 6 and 8). A second phase from 2.51 to 0.95Ma shows a gradual
- drying trend, except for eastern Africa, where a humid trend is observed. This period can be
- subdivided into two intervals (before and after 1.57Ma) where various hydroclimate trends are
- 291observed, in particular in eastern Africa. A third phase of global African aridity between 950
- ka to present day is characterized by a tendency toward slightly more humid conditions from
- around 400 ka to the present.

The major and gradual drying trend, together with the different patterns observed between

- eastern Africa and western Africa and Oman during phase 2, has been suggested to be the results
- of the synchronous development of the Indo-Pacific Walker cells at around 2.2-2Ma (Figure 7,
- 297 Van der Lubbe et al. 2021). The long-term enhancement of the Walker circulation would have

- 298 suppressed (convective) rainfall in eastern Africa (Van der Lubbe et al. 2021) and would have 299 extended well beyond eastern Africa. Indeed, recent synthesis of terrestrial and marine proxy 300 records over the last 620kyr found a tight correlation between moisture availability across 301 Africa and the manifestation of the Walker Circulation driving opposing wet-dry states in 302 eastern and western Africa with influence on early modern humans by increasing resource-rich and stable ecotonal settings (Kaboth-Bahr et al. 2021). In addition, we observe a significant 303 304 correlation between northern hemisphere ice-sheets expansion, decrease in CO<sub>2</sub> concentration 305 and pan-African hydroclimate change.
- 306 Changes in CO<sub>2</sub> levels are important, as they will mediate vegetation changes (Dupont et al.
- 307 2019). This makes the use of vegetation proxies in marine sediment cores as hydroclimate
- 308 proxies more complicated. Indeed, Dupont et al. (2019) found the vegetation of the Limpopo
- 309 River catchment and the coastal region of southern Mozambique not only influenced by
- 310 hydroclimate but also by temperature and atmospheric CO<sub>2</sub>. In northwestern Africa, increases
- in precipitation were shown to be associated with an expansion of grasslands into desert landscapes, whereas changes in  $CO_2$  predominantly drove the  $C_3/C_4$  composition of savanna
- ecosystems over the last  $\sim$ 500kyr (O'Mara et al. 2022). On longer time scales, although
- debated (Schefuß & Dupont 2020), Polissar et al. (2019) suggested that C<sub>4</sub>-dominated
- accounted (Senteria) & Dapone 2020), 1 onsola et al. (2017) baggested that et dominated
   ecosystems expanded synchronously across northwestern and eastern Africa after 10Ma
- 316 without substantial changes in palaeohydrology but coincident with latitudinal temperature
- 317 changes and declining atmospheric  $CO_2$ . Taken together therefore, the interactions between
- 318 hydrology and CO<sub>2</sub> concentration in deep time are not entirely clear and require further
- 319 investigation. This lack of understanding also impacts our reconstruction of past vegetation,
- although this can be partly overcome by analyses of marine cores.
- 321 3.2.3 Pan-African vegetation.
- 322 Our compilation of vegetation data over the last 4 Myr support a synchronous expansion of
- 323 C<sub>4</sub>-dominated ecosystems across northern, southwestern, and eastern Africa after 4 Ma, with
- 324 more stable conditions at around 1Ma (Figure 9) (Appendices: Water and Carbon
- 325 isotopes). This synchronicity of pan-African vegetation changes seems to contrast with what
- is observed in terms of pan-African hydroclimate changes (Figures 6 and 8), although
- 327 vegetation records over the last 4Myr in southeastern Africa are missing to conclusively
- 328 establish this difference.
- 329 To further test the relationship between hydroclimate and vegetation, we explored the
- correlations between these two measures at site ODP1081 (southwestern Africa) and 966-967
- 331 (northeastern Africa). For vegetation, we used the biomass proxy ( $\delta^{13}C_{wax}$ ) and plant
- reproduction proxy (desert pollen) in comparison to  $\delta D_p$ , a hydroclimate proxy. Analyses
- reveal a statistically significant, but weak, linear correlation (R = -0.54, -0.4 or 0.27) between
- 334 vegetation and hydroclimate changes, suggesting additional controls on vegetation other than
- hydroclimate, although some biases in proxies are also possible (Table 1).
- 336

#### 4. Data comparison and integration with numerical climate models

4.1 Piecing together the puzzle: extrapolating from incomplete records to a more completepicture

340 Owing to the limited data available relating to the environment and climate of the regions of

341 palaeoanthropological interest, and because of the limitations of the fossil record (e.g.,

342 Maxwell et al. 2018, Faith et al. 2021), it has remained challenging to establish links between

343 climate shifts and human evolution and alternative approaches have been sought: modeling.

344 For example, Eriksson et al. (2012) used numerical climate simulations to estimate temperature, precipitation and primary productivity over the past 120kyr to model 345 demographic changes and dispersals of human populations. Although they did not use any 346 archaeological and anthropological data to validate the model, the estimated arrival times of 347 humans on different continents predicted by the model are broadly consistent with the fossil 348 349 and archaeological record. Similarly, spatiotemporal estimates of climate and sea level 350 changes were calculated from orbital-scale global climate swings to infer human dispersals and late Pleistocene global population distributions (Timmermann & Friedrich 2016). Indeed, 351 modeling approaches have become increasingly popular over the last few years. By using 352 353 numerical climate models and their equilibrium or transient simulations, and by drawing on the paleontological/archaeological record, researchers have attempted to identify the 354 spatiotemporal habitat suitability of hominin species (d'Errico et al. 2017, Gibert et al. 2022, 355 Timmermann et al. 2022, Ruan et al. 2023, Zeller et al. 2023, Ao et al. 2024). To capture 356 important topographic barriers, which may have affected the dispersal and distribution of 357 archaic humans, topographic downscaling is realized in some studies. When determining the 358 359 spatiotemporal habitat suitability of a hominin taxon, a set of climatic variables (precipitation, temperature and net primary productivity) is simulated with numerical climate models and a 360 climatic envelope is created for specific taxa, based on the known distribution of hominin 361 362 occurrences (Timmermann et al. 2022, Gibert et al. 2022) (Figure 10); these geographic areas 363 are then assumed to represent the fundamental niche of that hominin (Soberón & Nakamura 364 2009).

365 4.2 How trustworthy are these models?

366 To support numerical climate transient simulations, evaluations of the ability of these models 367 to reproduce key paleoclimate records are required. For example, Timmermann et al. (2022) conducted a global data-model comparison and found "close agreement". Our new 368 hydroclimate compilation (Figure 6) allows further testing of that model. We focus on 369 precipitation, because, of the four climatic variables used to produce a climatic envelope 370 371 model by Timmermann et al. (2022), three are related to precipitation. Data-model 372 comparisons highlight some disagreements between the reconstructed and the modeled 373 precipitation for some regions of Africa in terms of general trends and variability (the 374 correlations are weak, but statistically significant nonetheless, Figure 11). Better concordance 375 is found for the last 1Myr compared to the entire 3Myr record, but these correlations remain 376 weak. These discrepancies could be the result of inherent uncertainties associated with the 377 proxies to reconstruct the precipitation changes (Table 1) (Appendices: Water and Carbon 378 isotopes), biases in model simulation, such as inappropriate insolation forcing, constant last 379 glacial maximum ocean bathymetry and land-sea mask (Yun et al. 2023), and/or potential biases in the applied ice-sheets and GHGs forcings. Either way, any conclusions drawn from 380 381 these models for evolutionary purposes are thus rendered speculative. Higher resolution data, 382 more simulations with various models and better constraints and downscaling approaches are

therefore necessary.

384 In addition, to bridge paleoclimate data and models, different innovations and improvements

385 should be considered. For example, chemical tracers (e.g., water or carbon isotopes,

**Appendices: Water and Carbon isotopes**), which are relevant climate proxies, should be

input directly into Earth system models. Paleoclimate information could thus be used to

- directly constrain model performance ("apples-to-apples" comparison). Furthermore,
- simulations of climate and its associated isotopic signal into models provide a "transfer
   function" between isotopic signal and the considered climate variables (Sturm et al. 2010,
- 391 Caley et al. 2014, Collins et al. 2017).

392 A further improvement on existing models would be to combine proxy data and climate 393 model simulations in a mathematical framework to improve insights derived from either 394 resource independently. Data assimilation techniques have recently been adapted for 395 paleoclimate applications (Hakim et al. 2013, Tierney et al. 2020a), resulting in spatially complete reconstructions of multiple climate variables. A balance between proxy information 396 397 and the physics and covariance structure of the climate model can thus be achieved (Tierney 398 et al. 2020b). As more high resolution and well-dated paleoclimatic records become available, 399 and as computing power increases, data assimilation techniques could be realized over periods 400 spanning millions of years and the outcomes could be used to force different models. Only then will we possibly be able to demonstrate an unequivocal link between climate change and 401 402 human evolution from modelling approaches. Until then, we need to draw on established 403 biological and ecological principles to discern patterns in human evolution that could perhaps be linked to global climatic and environmental changes. 404

405 406

# 5. Hominin evolutionary processes and climate

407 Over the past several decades researchers have expanded the hominin fossil record and have 408 assembled more detailed late Cenozoic paleoclimatic, paleoenvironmental and 409 paleoecological archives, both at the global (this contribution) and the local scale (e.g., Campisano et al. 2017, Potts et al. 2018.). Moreover, much effort has been expended to 410 411 document changes in mammalian community structure through time (e.g., Bobe et al. 2002, Werdelin & Lewis 2005) with the aim to identify turnover pulses (Vrba 1995, but see Bibi & 412 Kiessling 2015) and/or changes in the functional composition of communities as a proxy of 413 past climates and vegetation structures (e.g., Reed 1997, Andrews & O'Brien 2000, Hempson 414 415 et al. 2015, Rowan et al. 2016, Robinson et al. 2017). Yet, the climatic and environmental drivers underpinning hominin diversity, extinction/speciation, morphological adaptations and 416 417 dispersals remain elusive. In part, this may be due to the limitations of the hominin fossil 418 record (Faith et al. 2021), taphonomic bias (e.g., Behrensmeyer et al. 2000) and differential 419 research efforts across the continent (e.g., Maxwell et al. 2018). Perhaps the biggest obstacle 420 of relating climate to specific processes in hominin evolution however is our unique 421 evolutionary path towards becoming increasingly eurybiomic.

422 As early as 3.4-2.9Ma Australopithecus afarensis was apparently able to cope with substantial

423 environmental variability, both with regard to biome structure and temperature (Bonnefille et

424 al. 2004). In fact, an increase in the prevalence of  $C_4$  biomass on the landscape (Figures 9 and

425 10) is accompanied by an increase in  $C_4$ -based food consumption across all hominin taxa,

- 426 except in *A. sediba* (Figure 12). (Appendices: Water and Carbon isotopes). This is
- 427 particularly evident in hominins from South Africa, a region that exhibited higher

428 hydroclimate variability over the last 4 Myr than northeastern Africa (Figures 6 and 11).

- However, the supposed 'broadened dietary niche' of South African hominins (like in *A*.
- 430 *afarensis*) may simply reflect the species' dietary flexibility through precession-led biome
- 431 changes, i.e. their ability to adapt to local conditions (Hopley & Maslin 2010). Even where
- 432 hominins are apparently specialized in their dietary adaptations, as in the case of
- *Paranthropus boisei*, detailed analyses of the nutritional components of the possible diet
   implies that they were nonetheless eclectic feeders (Macho 2014a) as well as habitat
- 435 generalists (Patterson et al. 2022, Wood & Strait 2004, but see O'Brien et al. 2023).
- 436 Paranthropus boisei demise may thus not be directly related to climate and vegetation
- 437 change, but to other factors which may, of course, be <u>indirectly</u> related to climate and habitat
- 438 changes, e.g. increased competition and predation risk due to habitat fragmentation. Only for
- 439 *A. bahrelghazali* exists a possible link between morphological constraints on masticatory
- 440 capabilities and the deterioration in palaeoenvironmental conditions, which may have
- triggered demographic changes and, ultimately, species' extinction (Macho 2015); due to
- 442 limited sample sizes this suggestion is likely to remain theoretical however. In southeastern
- 443 Africa, local terrestrial ecosystems were impacted by long-term aridification and extreme
- 444 precessional hydroclimate variability between around 1 and 0.6 Ma (Caley et al. 2018). It is
- intriguing (and perhaps no coincidence) that the new Limpopo hydroclimate stack matches
- the presence of *P. robustus* with the more humid climate trend observed over the last 4Myr
- 447 (Figures 1 and 6) and may point towards a particular niche adaptation in *P. robustus* (Caley et
- al. 2018), a suggestion which needs to be explored further in the future.
- 449 With the emergence of *Homo*, habitat tolerances increased even further, aided by material culture (Potts et al. 2018, 2020). This makes it impossible to define Homo's fundamental (as 450 opposed to the realized) niche, unless it can be unequivocally demonstrated that there exists 451 (or existed) a narrow constraint on the genus' physiology with regard to thermoregulation, 452 diet, photoperiodicity (i.e. life history) etc. (Soberón & Nakamura 2009). It seems 453 454 improbable, however, that these traits are/were narrowly defined within any of the Homo species. Hence, we remain cautious about overinterpreting the outcomes of modeling studies 455 456 that apply ecological niche modeling to the distribution of *Homo* (Timmermann et al. 2022, 457 Ruan et al. 2023, Zeller et al. 2023). Homo species may have had habitat preferences, but it is 458 unclear whether they were confined to these habitats (sampling biases aside). Regardless, 459 these models are useful for a number of purposes: (a) to identify potential dispersal corridors, e.g. from the coastal regions to the African interior during the Plio-Pleistocene (Joordens et al. 460 2019) or from Africa to Eurasia (Ao et al. 2024) or/and (b) to document how, when and where 461 462 habitats became fragmented, particularly within Africa during the Plio-Pleistocene; this will aide our understanding of hominin dispersals within Africa, e.g. between western and eastern 463 Africa (Kaboth-Bahr et al. 2021) and when local populations may have become fragmented 464
- 465 and isolated (i.e. vicariance).
- 466
- For example, model results suggest that, during the mid-to-late Pliocene (4–3Ma), southern
- 468 and eastern African hominins were separated by an environmental barrier which could only be
- 469 crossed during particular periods, such as northern hemisphere summer at perihelion (Gibert
- 470 et al. 2022). Arguably, this would have influenced the evolutionary pathways -and/or
- 471 divergence?- of hominins. On a more local scale, Maslin et al. (2014) formulated the *pulsed*
- 472 *climate variability hypothesis,* which considers inter-basin connections to be periodically
- disrupted by extreme wet–dry cycles. These disruptions, in turn, could have led to hominin
- 474 isolation, speciation/extinctions and dispersal. A similar mechanism was invoked to explain

- the high morphological variability in South African *Australopithecus africanus*: as the habitat
- 476 periodically expanded and contracted (e.g., orbital forcing), peripheral populations may have
- become isolated only to fuse again when environmental conditions permitted (Brain 1985).
  The biological implications of such dynamic changes in habitat structure (and size) are three-
- fold: (i.) small populations/species with restricted habitat sizes are faced with high extinction
- 480 risks as they become demographically unviable (Macho 2014b); (ii.) inevitably, genetic drift
- 481 will occur (chance) and selective pressures acting on these sub-populations will either
- 482 eliminate (extinction) or speed up evolutionary changes; and (iii.) the subsequent merging of
- temporarily separated populations may lead to the mixing of genes and the emergence of
- novelty (Scerri et al. 2019, van Holstein & Foley 2022), as demonstrated for baboons, for
- 485 example (Sithaldeen et al. 2015, Sørensen et al. 2023).
- 486 In summary therefore, insights obtained from proxy, model, and combined proxy-model
- 487 climate reconstructions are crucial for an understanding of hominin evolutionary processes,
- but to draw conclusions is complex. Early humans have no living analog for comparison and
- they are unique amongst primates in the way in which they have expanded their ecological
- 490 niche over the last 4Myr. Whilst it is tempting to look for commonalities in species turnover
   491 across clades, we believe that clade-specific traits need to be considered in any such
- 491 across clades, we believe that clade-specific traits need to be considered in any such 492 comparison (*sensu* Vrba, 1995). This is important if we wish to identify the causal
- 492 comparison (*sensu* viba, 1995). This is important if we wish to identify the causal493 mechanisms between climate/habitat change and hominin evolution. Correlation does not
- 494 mean causation.
- 495

# 496 Appendices:

- 497 1. Tectonic, volcanism and tephrochronology:
- The African plate is fragmenting in its eastern part, along an axis that forms the East African rift (East African Rift System: EARS). Most tectonic activity in Africa in the last 10Myr has centered on the EARS. Paleo-modeling studies have shown that uplift of the African plateau led to a drastic reorganization of atmospheric circulation, engendering strong aridification and paleoenvironmental changes, in part reflecting the setting of present-day vegetation patch work in Africa (a.g., Sapulahra et al. 2006, Mundau et al. 2022)
- 503 work in Africa (e.g., Sepulchre et al. 2006, Munday et al. 2023).
- 504 Southern Africa was subject to some moderate uplift (Dirks & Berger 2013) that resulted in
- 505 dynamic, high-relief landscapes (e.g., Moore et al. 2009, Bailey et al. 2011). The main uplift
- 506 occurred during Oligocene (30Ma, Burke & Gunnell 2008), early-mid Miocene (15Ma), and
- 507 Pliocene-Early Pleistocene (5–2Ma; Partridge, 1998), the latter probably reflecting the
- southward propagation of the EARS (Hartnady & Partridge 1995).
- 509 Rifting on the EARS started at the end of the Oligocene (WoldeGabriel et al. 1990), with
- 510 clear indications of rifting by 15–10Ma (McDougall & Brown 2009, Roberts et al. 2012).
- 511 During the Quaternary, this rifting would have been facilitated by the propagation of faults
- 512 linked to the presence of large felsic volcanic centers (Abebe et al. 2007). This coincides with
- the surface manifestation of a hot spot, responsible for the emission of Ethiopian trapps
- around 30Ma, a considerable volume (at least  $1.2 \times 10^6 \text{ km}^3$ , Rochette et al. 1998) of basalt
- 515 effusions (Courtillot et al. 2003) distributed today between Yemen and Ethiopia.

- 516 Volcanism in the central sector of the Ethiopian rift also began in the Oligocene and can be
- 517 grouped into six episodes (WoldeGabriel et al. 1990). In the Pliocene, voluminous ignimbrites
- 518 (e.g. Butajira ignimbrite, > 250 m thick) were described and correlated with tephras from the
- 519 Gulf of Aden (WoldeGabriel et al. 1992). Abebe et al. (2007) recognized two episodes of 520 activity in the Ouaternary: between 2 and 1 Ma and since 650 ka. This last volcanic episode is
- associated with large calderas (e.g. Corbetti: 20 x 15 km; Shala: 20 x 18 km; Hutchison et al.
- 522 2016).
- 523 The fill of the Ethiopian rift is dominated by volcano-clastic and fluvio-lacustrine sediments
- 524 drained by the Awash and Omo rivers. These are mostly fluvio-deltaic deposits, within which
- numerous volcanic tuffs are interspersed (at least 130 recorded around Lake Turkana, Brown
- tet al. 1992). Within these sedimentary formations, numerous hominin fossils and stone tools
- 527 were found (e.g. White et al. 2003, Niespolo et al. 2021, Delagnes et al., 2023).
- 528 Given the presence of numerous volcanic tuffs in the region, most fossils and artifacts are
- 529 dated based on their stratigraphic position relative to these tuffs. The latter can be dated if
- they contain sanidine crystals using potassium-argon (K-Ar) method or argon-argon (Ar-Ar)
   methods. However, some tuffs are impossible to date. For most of the others, the stratigraphic
- 531 methods. However, some turns are impossible to date. For most of the others, the stratigraphic 532 position and the correlations together with ages, uncertainties of the tuffs dating are a matter
- 532 of debate (Brown et al. 2012, Sahle et al. 2019, Vidal et al., 2022). These led some authors to
- look for volcanic layers, tephras or cryptoptephras in the oceanic domain (Gulf of Aden,
- 535 Arabian sea), where it is then possible to apply other dating methods (e. g. Brown et al. 1992,
- 536 deMenocal & Brown 1999).
- 537

538 By transferring the marine chronology to continental tuffs, uncertainties in dating can be 539 reduced. Uncertainties with benthic isotope stratigraphy of the LR04 age model (Lisieski & 540 Raymo 2005) are 30kyr from 5–4 Ma, 15kyr from 4–3Ma, 6kyr from 3–1Ma, and 4kyr from 541 1-0Ma; they are lower than most of the continental tuffs ages, in particular for the last 3Myr 542 (Roberts et al. 2021, Vidal et al., 2022). The majority of tephras and cryptotephras in marine 543 sediment cores have been found between ca. 4Ma and 0.75Ma (Sarna-Wojcicki et al. 1985, Brown et al. 1992, deMenocal & Brown 1999, Feakins et al. 2007) but more could be 544 discovered in the future to improve chronologies (Albaredes et al. 2023). 545

- 546
- 547 2. Water and Carbon isotopes
- 548 Water isotopes
- 549 Water isotopes are excellent tracers of the hydrological cycle (e.g., Craig & Gordon 1965, Gat
- 550 1996). Because of small chemical and physical differences between the main isotopic forms
- of the water molecule ( $H_2^{16}O$ , HDO,  $H_2^{18}O$ ), an isotopic fractionation occurs, principally
- 552 during phase transitions of water (evaporation and condensation processes). Stable water
- isotopes have therefore been measured in a large variety of archives to reconstruct regional
- climate variations.
- 555 Water isotopes are expressed in per mil (‰) using  $\delta$  notation:  $\delta D$  or  $\delta^{18}O = (R_{sample} R_{standard})/$
- 556  $R_{standard}$ \*1000 and represent the relative deviation of R (the isotope ratio, D/H or <sup>18</sup>O/<sup>16</sup>O) in
- the sample from a standard, usually Vienna Standard Mean Ocean Water (VSMOW) with  $\delta D$ or  $\delta^{18}O = 0$  ‰.

- 559 The cuticular wax layers of higher terrestrial plant leaves contain large amounts of long-chain
- n-alkanes, n-alcohols, n-alkanoic acids, which are well preserved in the sedimentary record
- over geological timescales (Sachse et al. 2012). As water is the primary hydrogen source of
- 562 photosynthesizing organisms and their biosynthetic products organic hydrogen preserved in
- sediments may record the isotopic composition of water used during photosynthesis and could
- be used as a paleohydrological proxy (Sternberg 1988). The  $\delta D_{wax}$  proxy has been increasingly used over the past decades in paleoclimate studies of marine sediment cores (e.g.
- 566 Schefuß et al. 2005, Collins et al. 2017, Kuechler et al. 2013, Tierney et al. 2017, Caley et al.
- 567 2018) to infer indirect changes in the regional hydrological cycle across Africa. Although the
- $\delta D_{\text{wax}}$  is commonly interpreted as a proxy for the amount of regional rainfall, interpretation
- 569 can be more complex, because the  $\delta D_p$  value depends on other climate influences
- 570 (precipitation, temperature, source effect, circulation regime) and on additional environmental
- and physiological processes related to the climate and the vegetation (relative humidity,
- 572 vegetation changes, biosynthesis of the lipids) (Sachse et al. 2012).
- 573 In marine sediment cores, the seawater oxygen isotope composition ( $\delta^{18}O_{sw}$ ) is preserved in
- 574 carbonates from various organisms such as foraminifers. The carbonate isotopic concentration
- 575  $(\delta^{18}O_c)$  is mainly controlled by the temperature dependence of the equilibrium fractionation of
- calcite precipitation and by the isotopic composition of seawater in which the shell grew
- 577 (Urey 1947, Shackleton 1974). For benthic foraminifera, it has long been assumed that the
- 578 deep temperature effect on  $\delta^{18}O_c$  is negligible. Therefore, benthic  $\delta^{18}O_c$  records and stack 579 (LR04, Lisieski & Raymo 2005) have been used to document polar ice volume changes and
- associated glacial/interglacial periods given that the waning and waxing of ice-sheets control
- the global  $\delta^{18}O_{sw}$  changes. Recent studies indicate that significant changes in deep ocean
- temperature exist (Elderfield et al. 2012, Sosdian & Rosenthal 2009) and that this can create
- large temporal offset during the onset of the Plio-Pleistocene ice ages (Rohling et al. 2014),
- 584 for example between a marked cooling step at 2.73Ma and the first major glaciation at 2.15
- 585 Ma. Hence,  $\delta^{18}O_{sw}$  is better suited as a proxy for polar ice volume changes rather than the 586 benthic  $\delta^{18}O_c$  signal (Figure 7) (Rohling et al. 2021). In addition, a vast majority of marine
- 586 benthic  $\delta^{18}O_c$  signal (Figure 7) (Rohling et al. 2021). In addition, a vast majority of marine 587 sediment cores have age models based on stratigraphic alignment of the  $\delta^{18}O_c$  of benthic
- foraminifera, which measures changes in ice volume and deep ocean temperature. The use of
- 589 a single global alignment target (LR04  $\delta^{18}O_c$  global stack) neglects regional differences of
- several thousand years in the timing of benthic  $\delta^{18}$ O change during glacial terminations.
- 591 Regional  $\delta^{18}O_c$  stacks have therefore been proposed and offer better stratigraphic alignment
- targets although they are currently limited to the last 150kyr (Lisieski & Stern 2016).
- 593 Carbon isotopes
- 594 Carbon isotopes are expressed in per mil (‰) using  $\delta$  notation:  $\delta^{13}C = (R_{sample} R_{standard})/$
- 595  $R_{standard}$ \*1000 and represents the relative deviation of R (the isotope ratio, <sup>13</sup>C/<sup>12</sup>C) in the
- sample from a standard (usually Vienna Pee Dee Belemnite (VPDB), a marine carbonate).
- 597  $\delta^{13}$ C is used as a proxy for the proportion of C<sub>3</sub> and C<sub>4</sub> vegetation preserved in soil
- carbonates, fossil teeth, and leaf waxes. For reviews of how carbon stable isotopes are used to
- reconstruct hominin paleoenvironments see Cerling (2014) and Levin (2015). Some recent
- studies (e.g., Blondel et al. 2018, Souron 2018 and references herein) point out that
- 601 interpretations of carbon isotopes as paleodiets are not that straightforward and should also
- 602 consider independent proxies (e.g., morphology, dental microwear and mesowear) that are
- 603 more directly linked to mechanical properties of diet items.

#### 604 Summary points:

- 605 Although African terrestrial records provide crucial information on land climate variability,
- 606 marine records offer the possibility of more robust chronology, a stratigraphic continuity with
- a high temporal resolution and the advantage of direct ocean-continental comparison. By
- transferring the marine chronology to continental tuffs, a global coherent framework with
- hominin fossils, artefacts, climate and environmental changes can be established.
- 610 A heterogeneity for pan-African hydroclimate changes is observed over the last 4Myr. The
- 611 forcings that control this heterogeneity of variability are a combination of orbitally paced low-
- 612 latitude fluctuations in insolation, polar ice volume changes, tropical SST gradients and the
- 613 walker circulation and maybe GHGs changes.
- 614 Our compilation of vegetation data over the last 4Myr show an expansion of the C<sub>4</sub>-
- dominated ecosystems across northern, southwestern, and eastern Africa over the last 4Myr
- 616 with more stable conditions at around 1Ma, but this is not mirrored by the observed pan-
- 617 African hydroclimate changes. This may indicate that the feed-back loops between climate
- and vegetation are more complex, whereby vegetation changes likely reflect a combination of
- 619 factors including atmospheric CO<sub>2</sub> concentrations and temperature.
- 620 Although temporal correlations between global or regional climate, environmental changes
- and human evolution can be observed over the last 4Myr, we raise some concerns as to
- 622 whether these correlations reflect causal processes. We highlight a few areas where we
- 623 believe that focused research effort would be warranted.
- 624 We advocate that more numerical transient simulations with various climate models and
- better constraints and downscaling approaches should be conducted in order to assess the
- range of model responses and the robustness of the mechanisms leading to the simulated
- 627 climate changes. To bridge paleoclimate data and models, the inclusion of chemical tracers
- 628 (for example water and carbon isotopes, forward proxy modelling) relevant to proxies directly
- 629 in Earth system models should be considered. Data assimilation techniques adapted for
- 630 paleoclimate applications may further improve reconstructions of past climates.
- 631

#### 632 **DISCLOSURE STATEMENT**

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#### **OPTIONAL ELEMENTS**

- **Reference Annotations:**
- Vrba (1995): the turnover-pulse hypothesis: pulses of speciation/extinctions, and dispersals across clades due to prolonged climatic changes.
- de Menocal (1995): Pioneering work based on marine cores that linked human evolution to global climate change.
- Potts (1998): variability selection hypothesis: increased climatic variability as a driver for genetic change (human's unique adaptability).
- Cerling (2014): summary of the use of stable isotopes to reconstruct hominin environments.
- Uno et al. (2016a): first Neogene biomarker records in marine cores.
- Faith et al. (2021): sampling biases affect our interpretation of the hominin fossil record, i.e., gaps in spatiotemporal sampling.
- Timmermann et al. (2022): first long transient climate simulation to identify the spatiotemporal habitat suitability of hominin species.
- Ao et al. (2024): an example of data-model integrative approach that identify potential dispersal corridors from Africa to Asia.

Proxies	Climate/environmental variables	Potential biases/complexity
δD plant waxes	Hydrological cycle (precipitation amount, circulation regime)	Source effect, seasonality, temperature effect, relative humidity, vegetation changes
δ <sup>13</sup> C plant waxes	Vegetation (biomass, C <sub>3</sub> vs C <sub>4</sub> plants)	Source effect, plant physiological versus climatic parameters, seasonal timing of leaf wax formation, effect of vegetation
Pollen	Vegetation	Actualism, Plant physiological versus climatic parameters, seasonal timing of pollen formation, transport effect and mode of transport (river vs wind)
XRF ratio	Wet-dry index; wet: high terrestrial input via river; dry: low terrestrial input via river	Source in the catchment and vegetation role on sediment load, sea level effect
Terrestrial organic carbon (C <sub>org</sub> ; BIT)	Wet: increased terrigenous organic matter supply by river; dry: decreased terrigenous organic matter supply by river	Diagenesis, source in the catchment
Dust	Wet: less dust input into the Ocean; dry: more dust input into the Ocean	Source effect, wind strength and transport effect, calculation of fluxes
Radiogenic isotope signatures of detrital material ( $\epsilon_{nd}$ )	Provenance, dispersal, and climate-driven supply of sediments	Source. Grain size effects.
Ba/Ca and $\delta^{18}O_{sea water}$ in planktonic foraminifera	Riverine freshwater input	Source effect, changes in atmospheric circulation, advection, sea level effect

1247 Table 1: Main proxies for terrestrial climate and environmental reconstructions in marine
1248 sediment cores.





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1261 Figure 1: Stratigraphic ranges of African hominin taxa and associated lithic industries.

1262 Modified after Sahle et al. (2013), Beyene et al. (2013), Wood & Boyle (2016), Plummer et

al. (2023) and references herein. Hominin taxinomy is debated and actual paleobiodiversity

1264 may be partly overestimated by taxinomic practices or underestimated due to taphonomic

issues, making it extremely difficult to have a clear understanding of the realpaleobiodiversity.

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1328 Tropical inter-annual climate variabilities (ENSO: El Niño Southern Oscillation and IOD:

1329 Indian Ocean Dipole) are illustrated as examples of configuration but not necessary entirely

1330 dependent and are not necessarily linked with latitudinal variability (ITCZ: InterTropical

- 1331 Convergence Zone migration, size and strength and regional monsoon systems).





Figure 5: Scheme of sediment transport from the continent (source) to the ocean (sink) and
main sediments in marine environment. SEM images from marine sediments (left to right) of
the planktonic foraminifera *G. ruber*, and volcanic glass shard from the East African Rift
System (indicated scale is 100μm).





1418 Figure 6: Pan-African hydroclimate variability over the last 4 Myr based on marine sediment cores. A. a)  $\delta D$  of the n-C<sub>31</sub> alkane of plant waxes at site ODP722 (Huang et al. 2007). b)Blue 1419 1420 line shows  $\delta D$  of precipitation ( $\delta D_p$ ) at ODP966& 967 (Lupien et al. 2023). Standard error 1421 means was 4.3 % for  $\delta D_p$ . Green line shows the Wet-Dry index from ODP967 (Grant et al. 1422 2017). c) Dust percentage at ODP659 (Tiedemann 1994). d)  $\delta D$  of precipitation derived from the vegetation correction of  $\delta D_{wax}$  at site ODP1081 (Rubbelke et al. 2023). The average 1423 standard deviation was 1.81 % for  $\delta D_{wax}$  and mean error for  $\delta D$  of precipitation was 3.7 %. e) 1424 1425 PC1 of hydroclimate records from the Limpopo region, sites MD96-2048 and IODP U1478 1426 (Caley et al. 2018, Koutsodendris et al. 2021, Taylor et al. 2021). f) PC1 of pan-African hydroclimate. Polynomial fit (8th degree) documented in red to demonstrate long-term trends 1427 and fluctuations. Grey shading and dash line depict the four phases that have been constrained 1428 1429 by change point analysis based on records in a) to e). B. Average PC1 loadings derived from the PCA with bootstrapped confidence intervals (Past software, Hammer et al. 2001). C. 1430 Wavelet transform on the PC1 based on Torrence & Compo (1998). The significance level 1431 1432 corresponding to p = 0.05 is plotted as a contour (chi-squared test). D. Spectral analyses on the PC1 with REDFIT (Schulz & Mudelsee 2002, the red and orange lines show the false-1433 1434 alarm level at the 95 % and 80 % confidence interval). 1435

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![](_page_36_Figure_0.jpeg)

Figure 7: Forcings on pan-African hydroclimate. a) Eccentricity variations that modulate precession (Laskar et al. 2004). b) PC1 of pan-African hydroclimate original (dash line) and residue (solid line) after removal of orbital forcings variance. c) Pacific sea surface temperature (SST) gradients (sites ODP 806 and 847 (Wara et al. 2005), site ODP 846 (Lawrence et al. 2006)). d) Component of sea-level-based ocean  $\delta^{18}$ Ow variations (Rohling et al. 2014). e) Deep-sea  $\delta^{18}O_c$  LR04 stack (Lisiecki & Raymo 2005) (see Appendices Water and Carbon isotopes). f) Atmospheric CO2 reconstructions (The CenCO2PIP Consortium 2023). The correlation coefficient (R) and corresponding significance (P) between residual PC1 pan-African hydroclimate and SST gradients (c), ice volume changes (d and e) and atmospheric CO<sub>2</sub> changes (f) are shown.

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![](_page_37_Figure_0.jpeg)

Figure 8: Major phases of pan-African hydroclimate variability. Main fluvial catchments that transport material to marine sediment cores are indicated together with the main source of material transported by winds to marine sites (see also Figure 11). Core locations with red/blue colors indicate more arid/humid hydroclimate. Core locations of vegetation records of Figure 9 are also indicated.

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![](_page_38_Figure_0.jpeg)

Figure 9: Pan-African vegetation variability over the last 4Myr based mainly on ocean cores. a)  $\delta^{13}C_{\text{leaf wax}}$  from sites ODP722 (Huang et al. 2007), DSDP231 (Feakins et al. 2013, Liddy et al. 2016) and ODP966-967 (Rose et al. 2016, Lupien et al. 2023). b) Desert pollen at site DSDP231 (Bonnefille 2010). c)  $\delta^{13}C_{\text{leaf wax}}$  at sites ODP659 and MD03-2705 (Kuechler et al. 2013, 2018, O'Mara et al. 2022).  $\delta^{13}C_{\text{soil carbonate}}$  from continental eastern Africa (Levin 2015) and references therein). e)  $\delta^{13}C_{\text{leaf wax}}$  at site ODP1081 (Rubbelke et al. 2023). f) Desert pollen at site ODP1081 and 1082 (Dupont et al. 2005, Hoetzel et al. 2015). Locations of marine sediment cores are visible on Figure 8. 

![](_page_39_Figure_0.jpeg)

Figure 10: African hominin species habitat suitability (results based on Timmermann et al.
2022). Species distribution calculated from a Mahalanobis distance model with coloured
circles represent the locations of fossils and/or archaeological artefacts associated with the
hominin groups. The time-averaged habitat suitability covering the period of respective

- hominin presence can be interpreted in terms of probability, with values ranging from 0
- 1579 (habitat unsuitable) to 1 (habitat extremely suitable) (Timmermann et al. 2022).

![](_page_40_Figure_0.jpeg)

Figure 11: Data-model comparison for African hydroclimate over the last 3Myr. A. Data in a) to e) are similar to Figure 6 a) to e), except the ln(Fe/Ca) hydroclimate record in e) (Caley et al. 2018). CESM1.2 annual simulated precipitation in a) to e) extracted from regions indicated by black frames in B. Polynomial fit (8th degree) documented in orange and red to demonstrate long-term trends and fluctuations in data and model respectively. The correlation coefficient (R) and corresponding significance (p) between data and model for specific time periods and resolution are shown. B. Wind speed at 10m and vectors of zonal and meridional surface wind stress averaged over the last 3Myr in the CESM1.2 simulation (Timmermann et al. 2022, Yun et al. 2023) for August (top) and January (down). Black frames denote the regions used for model results extraction and comparison in A.a) to e). These regions were defined as source regions of sedimentary materials transported to the studied marine cores by winds and river on the basis of present day river catchments and simulated mean wind speed and patterns over the last 3Myr in B.

![](_page_41_Figure_0.jpeg)

1635 Figure 12: Enamel  $\delta^{13}$ C (representative of diets) of early hominin taxa from southern Africa 1636 (blue), central Africa (green) and eastern Africa (orange) arranged from oldest to youngest

1637 temporal periods/fossils for each regional group of African hominins (data from Sponheimer et

al. 2013). Violin plots with the median values (red dots) are indicated.

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