Climate and Human Evolution: Insights from Marine Records

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Thibaut Caley[1], Antoine Souron[2], Kevin Uno[3] and Gabriele A. Macho[4]

[1]Univ. Bordeaux, CNRS, Bordeaux INP, EPOC, UMR 5805, F-33600 Pessac, France; email: thibaut.caley@u-bordeaux.fr

[2]Univ. Bordeaux, CNRS, Ministère de la Culture, PACEA, UMR 5199, F-33600 Pessac, France; email: antoine.souron@u-bordeaux.fr

[3]Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA; email: kevinuno@g.harvard.edu

[4]Earth and Planetary Science, Birkbeck, University of London, London WC1E 7HX, England; email: Gabriele.A.Macho@gmail.com; G.Macho@bbk.ac.uk

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Abstract:

The relationship between climate and human evolution is complex and the causal mechanisms remain unknown. Here, we review and synthesize what is currently known about climate forcings on African landscapes, focusing mainly on the last 4Myr. We use information derived from marine sediment archives and data-numerical climate model comparisons and integration. There exists a heterogeneity in pan-African hydroclimate changes, forced by a 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_2 and temperature. We caution against reliance on temporal correlations between global or regional climate, environmental changes and human evolution and briefly proffer some ideas how pan-African climate trends could help create novel conceptual frameworks to determine the causal mechanisms between climate/habitat change and hominin evolution.

Introduction

The notion that climate influenced the course of human evolution has deep roots (Darwin 1871) and has been entertained in earnest since the 1920s after the discovery of the first australopiths in southern Africa; occasional wooded belts and a relative scarcity of water were suggested to have shaped human evolution (Dart 1925).

Over the last few decades evolutionary hypotheses have become more formalised. For example, Vrba (1985 and subsequent publications, see 1995 for review) proposed the *turnover-pulse hypothesis*, which postulates pulses of speciation/extinctions across clades as a consequence of prolonged climatic changes, primarily at the transitions of major astronomical cycles from 19-23kyr to 41kyr, 100kyr and 400kyr respectively. Although originally conceived to explain the turnover of bovids, for which the fossil record is relatively extensive, 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 clades and/or across Africa (e.g., Behrensmeyer 2006). Indeed, all species are habitat-specific and although large-scale changes in habitat structure may affect a number of clades 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, warm-adapted and cold-adapted clades will display different rates and timings of species-turnover. Ecological studies have since explored the eco-evolutionary processes underlying species diversity in greater detail and have shown that, in addition to thermoregulatory constraints, a taxon's dispersal potential, dietary adaptation, body mass, life history strategy, 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. 2017). Hence, the association between climate change, speciation, extinction, dispersal and 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. 2000), including sampling biases (Maxwell et al. 2018, Faith et al. 2021), discerning the mechanism underlying evolutionary processes in an extinct taxon is thus challenging, if not impossible. Consequently, whilst mapping hominin diversification and innovations onto global climate trends is appealing (e.g., deMenocal 2004, Figure 1) and may highlight specific time periods of interest, the explanatory power of such correlations is limited. Interpreting the effects of climate on later stages of hominin evolution is even more problematic.

Specifically, Potts (1995, 1996, 1998) formulated the *variability selection hypothesis*. This hypothesis is grounded in Sewall Wright's (1932, 1968) *shifting balance theory*, which mathematically explores changes in allele frequencies and genotypes in response to drift, 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 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 emphasized 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 habitat instability would not only have led to changes to allele frequencies, but to polymorphisms, thus making species/populations well-equipped to deal with novel situations without the need for further genetic modifications. Phrased differently, species/population would have become increasingly buffered against environmental stochasticity; increased

behavioural flexibility and innovations in material culture (Potts et al. 2018, 2020) would have added further advantages to the survival of hominin populations/species.

Evidently thus, whilst there is little doubt that hominin evolution was driven, or at least influenced, by climate change, the identification of causal mechanisms has remained elusive. In order to advance our understanding of the possible causal relationships, we need to primarily improve on two lines of enquiry: (a) obtain better (i.e. high-resolution) climate and habitat reconstructions through time and (b) develop theoretical frameworks for an interpretation of the climatic and ecological drivers for evolutionary change in a large-bodied, 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 landscapes, using information derived from marine sediment archives (restricted to the period from the Neogene to present day with a primary focus on the last 4Myr), data-numerical climate model comparisons and integration. The reconstruction of local environments from 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 proffer some ideas as to how these African climate trends could help create novel conceptual frameworks for an interpretation of hominin evolutionary processes.

1. Climate forcings on African landscapes

1.1 Natural forcings/causes of climate changes

Climate varies at different time scales, from years to billions of years (Figure 2). Climate variability depends on interactions between the different components of the climate system (atmosphere, ocean, cryosphere, biosphere and lithosphere) and on external forcings that affect the earth's radiative balance. External forcings are mainly related to astronomical 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.

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, 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 Zone (ITCZ) variability, monsoons and Walker Circulation control the hydrological cycle.

1.2 The ITCZ, Monsoons and Walker Circulation

The ITCZ is a tropical belt of maximum precipitation that results from deep convection migrating seasonally towards the warming hemisphere (Nicholson et al. 2013, Schneider et al. 2014). ITCZ zonal-mean position is associated with the rising branch of the global Hadley cell (Figure 3). Because of the complexity of African climate, the Congo Air Boundary (CAB), a convergence zone that marks the confluence of Indian Ocean air with unstable air from the Congo Basin, indicates the location of the southern edge of the African rain belt and

plays a fundamental role in controlling hydroclimate in the African tropics, especially in Africa's interior (Tierney et al. 2011, Howard & Washington 2019).

Monsoons are the dominant seasonal mode of climate variability in the tropics (Mohtadi et al. 2016). They can be viewed as localized seasonal migrations of the tropical convergence zone: the band of converging air and rainfall in the tropics embedded within the tropical atmospheric overturning circulation. This allows to distinguish the dynamics of low-latitude (~0–10° poleward) ITCZ from that of monsoons (~10–25° poleward) (Geen et al. 2020) (Figure 3).

In addition to tropical convergence zone migrations, a thermally direct, equatorial, zonal overturning circulation exists that converts available potential energy to kinetic energy of atmospheric motion: the Walker Circulation. The Walker Circulation is intrinsically connected to the El Niño–Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD), 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 convection and associated precipitation over the western or eastern tropical Pacific and Indian Oceans.

1.3 Relationships between precipitation and vegetation changes

Today, the distribution of vegetation and animals in Africa is related to the amount, intensity and seasonal distribution of precipitation (e.g., White 1983, Guan et al. 2014). This 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 heterogeneity in vegetation response is noteworthy and cautions against generalizations when 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 human evolution.

2. Interests of marine sediment records

deMenocal (1995) first linked early hominin evolution in Africa to global climate change, using data from marine sediment cores. Although African terrestrial records provide crucial 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 continuity and higher temporal resolution (Cohen et al., 2022). A wide range of proxies can 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 associated with marine biogenic sedimentation can be directly compared to proxies derived from continental source that are transported, mainly by wind or rivers, to the oceans (Figure 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

marine sediment cores, it also becomes possible to assess more precisely the synchronicity and potential causal links between climate/environmental changes and human evolution (see **Appendices: Tectonic, volcanism and tephrochronology**).

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 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) indicate higher ecosystem and hydroclimate variability at smaller spatial scales. In one case, 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 terrestrial archives integrate vegetation and hydroclimate signals is necessary for relating proxy vegetation and climate records to hominin evolution.

3. Climate and environments of Africa

Given the impact of tectonics and volcanism on landscapes, building the tectonic histories of each basin should be a requisite step before linking continental records of environmental 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 **Appendices: Tectonic, volcanism and tephrochronology**). Whilst we acknowledge the importance of tectonics and volcanism for the reconstruction of local habitats, our main focus here is on pan-African climate over the last 4Myr, based on marine sediment cores, as this may have impacted the overall course of hominin evolution; to provide a broader context, we only briefly summarize marine core records that capture important climate and environmental change during the Neogene.

3.1 Climate and environments of the Neogene

The Neogene period, which includes the Miocene (23.03 to 5.33Ma) and Pliocene (5.33 to 2.58Ma) epochs, was characterized by major environmental change that influenced primate evolution in Africa. Fossils from the early and middle Miocene demonstrate a dynamic period of catarrhine evolution in Africa that includes the first *Afropithecus* and victoriapithecines and the diversification of proconsulids (Leakey & Leakey 1986, McNulty et al. 2015, Nengo et al. 2017). This was followed by the origin of the hominin lineage in the late Miocene around 7Ma (Brunet et al. 2002). But there is a dearth of long, continuous Neogene terrestrial archives. Most are temporally limited and associated with fossil localities in eastern Africa. As a result, marine core records have played an important role in reconstructing regional scale climate and environmental change in Africa. This includes Neogene biomarker records (Uno 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 al. 2013, Hoetzel et al. 2013) and pollen records (Bonnefille 2010) that span the last ~10Myr. Carbon isotope records from *n*-alkanes at DSDP sites 235 and 241in the Somali Basin were the first to demonstrate C_3 vegetation was predominant at the regional scale from the early Neogene until 10Ma, when C_4 grasses began to spread in eastern Africa (Uno et al. 2016a). Subsequent *n*-alkane carbon isotope records from the tropical Atlantic (ODP sites 659 and

959) show a similar pattern of regional C_4 expansion in northwest Africa at 10Ma; additional hydrogen isotope records show no clear indication of hydroclimate change associated with spread of C_4 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 (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 7.5Ma. 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).

3.2 Climate and environments of the last 4Myr

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 the variance. Similarly, the δD_{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 replicated across Africa.

3.2.2 Pan-African hydroclimate.

We compiled the existing continuous hydroclimate records to cover the last 4Myr. Data are limited to five records that are distributed across the whole of Africa and over several Myrs (Figure 6). Most of these records are derived from δD_{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 wind strength and transport (Zabel et al. 1999) however, and are not necessarily a reliable indicator for aridity (Skonieczny et al. 2019). Nonetheless, the correspondence between δD_{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. 1994) and the use of δD_{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

% 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.

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 (Schulz & Mudelsee 2002) and wavelet analyses (Torrence & Compo 1998) display strong 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-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 related to orbital forcing is missing due to sampling resolution: for example, the precession forcing in south-east Africa over the last 2.15Myr accounts for 25 % of the variance in the lnFe/Ca record, a high-resolution proxy of fluvial runoff (Caley et al. 2018). Nevertheless, the results indicate that part of the variance in pan-African hydroclimate records is not controlled by orbital forcings. These other forcings have been highlighted in various studies and may 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 al. 2023), or perhaps greenhouse gases (GHGs). Although not yet fully explored, GHGs forcing could affect the hydroclimate through vegetation changes (Dupont et al. 2019) or through thermodynamic impacts, as well as consequent changes in atmospheric moisture content, resulting in summer monsoon precipitation change overall.

When the dominant 400kyr and 600kyr cycles are removed from PC1, the residual trend correlates with gradual Walker circulation changes, ice volume changes and, to a lesser degree, CO_2 concentration changes (Figure 7), confirming that all of these internal forcings (Figure 2 and 7) probably affect pan-African hydroclimate variability.

The reconstructed pan-African climate variability, represented by PC1, clearly depicts four phases during the last 4Myr that have been constrained by change point analysis (Figure 6). The first phase characterizes a pan-African climate that is rather humid between 4 and 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 observed, 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, Van der Lubbe et al. 2021). The long-term enhancement of the Walker circulation would have

suppressed (convective) rainfall in eastern Africa (Van der Lubbe et al. 2021) and would have extended well beyond eastern Africa. Indeed, recent synthesis of terrestrial and marine proxy records over the last 620kyr found a tight correlation between moisture availability across Africa and the manifestation of the Walker Circulation driving opposing wet–dry states in 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 correlation between northern hemisphere ice-sheets expansion, decrease in CO_2 concentration and pan-African hydroclimate change.

Changes in CO_2 levels are important, as they will mediate vegetation changes (Dupont et al. 2019). This makes the use of vegetation proxies in marine sediment cores as hydroclimate proxies more complicated. Indeed, Dupont et al. (2019) found the vegetation of the Limpopo River catchment and the coastal region of southern Mozambique not only influenced by hydroclimate but also by temperature and atmospheric CO_2. 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 ~500kyr (O'Mara et al. 2022). On longer time scales, although debated (Schefuß & Dupont 2020), Polissar et al. (2019) suggested that C_4-dominated ecosystems expanded synchronously across northwestern and eastern Africa after 10Ma without substantial changes in palaeohydrology but coincident with latitudinal temperature changes and declining atmospheric CO_2. Taken together therefore, the interactions between hydrology and CO_2 concentration in deep time are not entirely clear and require further investigation. This lack of understanding also impacts our reconstruction of past vegetation, although this can be partly overcome by analyses of marine cores.

3.2.3 Pan-African vegetation.

Our compilation of vegetation data over the last 4 Myr support a synchronous expansion of C_4-dominated ecosystems across northern, southwestern, and eastern Africa after 4 Ma, with more stable conditions at around 1Ma (Figure 9) (**Appendices: Water and Carbon 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 vegetation records over the last 4Myr in southeastern Africa are missing to conclusively establish this difference.

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 (northeastern Africa). For vegetation, we used the biomass proxy ($\delta^{13}C_{wax}$) and plant reproduction proxy (desert pollen) in comparison to δD_p, a hydroclimate proxy. Analyses reveal a statistically significant, but weak, linear correlation (R = -0.54, -0.4 or 0.27) between vegetation and hydroclimate changes, suggesting additional controls on vegetation other than hydroclimate, although some biases in proxies are also possible (Table 1).

4. Data comparison and integration with numerical climate models

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

Owing to the limited data available relating to the environment and climate of the regions of palaeoanthropological interest, and because of the limitations of the fossil record (e.g., Maxwell et al. 2018, Faith et al. 2021), it has remained challenging to establish links between climate shifts and human evolution and alternative approaches have been sought: modeling.

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

4.2 How trustworthy are these models?

To support numerical climate transient simulations, evaluations of the ability of these models 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 hydroclimate compilation (Figure 6) allows further testing of that model. We focus on precipitation, because, of the four climatic variables used to produce a climatic envelope model by Timmermann et al. (2022), three are related to precipitation. Data-model comparisons highlight some disagreements between the reconstructed and the modeled precipitation for some regions of Africa in terms of general trends and variability (the correlations are weak, but statistically significant nonetheless, Figure 11). Better concordance is found for the last 1Myr compared to the entire 3Myr record, but these correlations remain weak. These discrepancies could be the result of inherent uncertainties associated with the proxies to reconstruct the precipitation changes (Table 1) (**Appendices: Water and Carbon isotopes**), biases in model simulation, such as inappropriate insolation forcing, constant last 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 these models for evolutionary purposes are thus rendered speculative. Higher resolution data, more simulations with various models and better constraints and downscaling approaches are therefore necessary.

In addition, to bridge paleoclimate data and models, different innovations and improvements 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, Caley et al. 2014, Collins et al. 2017).

A further improvement on existing models would be to combine proxy data and climate model simulations in a mathematical framework to improve insights derived from either resource independently. Data assimilation techniques have recently been adapted for paleoclimate applications (Hakim et al. 2013, Tierney et al. 2020a), resulting in spatially complete reconstructions of multiple climate variables. A balance between proxy information and the physics and covariance structure of the climate model can thus be achieved (Tierney et al. 2020b). As more high resolution and well-dated paleoclimatic records become available, and as computing power increases, data assimilation techniques could be realized over periods 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 human evolution from modelling approaches. Until then, we need to draw on established biological and ecological principles to discern patterns in human evolution that could perhaps be linked to global climatic and environmental changes.

5. Hominin evolutionary processes and climate

Over the past several decades researchers have expanded the hominin fossil record and have assembled more detailed late Cenozoic paleoclimatic, paleoenvironmental and 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 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 & Kiessling 2015) and/or changes in the functional composition of communities as a proxy of past climates and vegetation structures (e.g., Reed 1997, Andrews & O'Brien 2000, Hempson 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 dispersals remain elusive. In part, this may be due to the limitations of the hominin fossil record (Faith et al. 2021), taphonomic bias (e.g., Behrensmeyer et al. 2000) and differential research efforts across the continent (e.g., Maxwell et al. 2018). Perhaps the biggest obstacle of relating climate to specific processes in hominin evolution however is our unique evolutionary path towards becoming increasingly eurybiomic.

As early as 3.4-2.9Ma *Australopithecus afarensis* was apparently able to cope with substantial environmental variability, both with regard to biome structure and temperature (Bonnefille et al. 2004). In fact, an increase in the prevalence of C_4 biomass on the landscape (Figures 9 and 10) is accompanied by an increase in C_4-based food consumption across all hominin taxa, except in *A. sediba* (Figure 12). (**Appendices: Water and Carbon isotopes**). This is particularly evident in hominins from South Africa, a region that exhibited higher

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. afarensis*) may simply reflect the species' dietary flexibility through precession-led biome changes, i.e. their ability to adapt to local conditions (Hopley & Maslin 2010). Even where 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 generalists (Patterson et al. 2022, Wood & Strait 2004, but see O'Brien et al. 2023). *Paranthropus boisei* demise may thus not be directly related to climate and vegetation change, but to other factors which may, of course, be indirectly related to climate and habitat changes, e.g. increased competition and predation risk due to habitat fragmentation. Only for *A. bahrelghazali* exists a possible link between morphological constraints on masticatory capabilities and the deterioration in palaeoenvironmental conditions, which may have triggered demographic changes and, ultimately, species' extinction (Macho 2015); due to limited sample sizes this suggestion is likely to remain theoretical however. In southeastern Africa, local terrestrial ecosystems were impacted by long-term aridification and extreme 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 (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.

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 opposed to the realized) niche, unless it can be unequivocally demonstrated that there exists (or existed) a narrow constraint on the genus' physiology with regard to thermoregulation, diet, photoperiodicity (i.e. life history) etc. (Soberón & Nakamura 2009). It seems 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 that apply ecological niche modeling to the distribution of *Homo* (Timmermann et al. 2022, Ruan et al. 2023, Zeller et al. 2023). *Homo* species may have had habitat preferences, but it is unclear whether they were confined to these habitats (sampling biases aside). Regardless, 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. 2019) or from Africa to Eurasia (Ao et al. 2024) or/and (b) to document how, when and where 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 Africa (Kaboth-Bahr et al. 2021) and when local populations may have become fragmented and isolated (i.e. vicariance).

For example, model results suggest that, during the mid-to-late Pliocene (4–3Ma), southern and eastern African hominins were separated by an environmental barrier which could only be crossed during particular periods, such as northern hemisphere summer at perihelion (Gibert et al. 2022). Arguably, this would have influenced the evolutionary pathways -and/or divergence?- of hominins. On a more local scale, Maslin et al. (2014) formulated the *pulsed 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 isolation, speciation/extinctions and dispersal. A similar mechanism was invoked to explain

the high morphological variability in South African *Australopithecus africanus*: as the habitat 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 risks as they become demographically unviable (Macho 2014b); (ii.) inevitably, genetic drift will occur (chance) and selective pressures acting on these sub-populations will either 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 example (Sithaldeen et al. 2015, Sørensen et al. 2023).

In summary therefore, insights obtained from proxy, model, and combined proxy-model 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 niche over the last 4Myr. Whilst it is tempting to look for commonalities in species turnover across clades, we believe that clade-specific traits need to be considered in any such comparison (*sensu* Vrba, 1995). This is important if we wish to identify the causal mechanisms between climate/habitat change and hominin evolution. Correlation does not mean causation.

Appendices:

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 (e.g., Sepulchre et al. 2006, Munday et al. 2023).

Southern Africa was subject to some moderate uplift (Dirks & Berger 2013) that resulted in dynamic, high-relief landscapes (e.g., Moore et al. 2009, Bailey et al. 2011). The main uplift occurred during Oligocene (30Ma, Burke & Gunnell 2008), early-mid Miocene (15Ma), and Pliocene-Early Pleistocene (5–2Ma; Partridge, 1998), the latter probably reflecting the southward propagation of the EARS (Hartnady & Partridge 1995).

Rifting on the EARS started at the end of the Oligocene (WoldeGabriel et al. 1990), with clear indications of rifting by 15–10Ma (McDougall & Brown 2009, Roberts et al. 2012). During the Quaternary, this rifting would have been facilitated by the propagation of faults 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 1.2×10^6 km^3, Rochette et al. 1998) of basalt effusions (Courtillot et al. 2003) distributed today between Yemen and Ethiopia.

Volcanism in the central sector of the Ethiopian rift also began in the Oligocene and can be grouped into six episodes (WoldeGabriel et al. 1990). In the Pliocene, voluminous ignimbrites (e.g. Butajira ignimbrite, > 250 m thick) were described and correlated with tephras from the Gulf of Aden (WoldeGabriel et al. 1992). Abebe et al. (2007) recognized two episodes of activity in the Quaternary: 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. 2016).

The fill of the Ethiopian rift is dominated by volcano-clastic and fluvio-lacustrine sediments 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 et al. 1992). Within these sedimentary formations, numerous hominin fossils and stone tools were found (e.g. White et al. 2003, Niespolo et al. 2021, Delagnes et al., 2023).

Given the presence of numerous volcanic tuffs in the region, most fossils and artifacts are 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 position and the correlations together with ages, uncertainties of the tuffs dating are a matter 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, Arabian sea), where it is then possible to apply other dating methods (e. g. Brown et al. 1992, deMenocal & Brown 1999).

By transferring the marine chronology to continental tuffs, uncertainties in dating can be reduced. Uncertainties with benthic isotope stratigraphy of the LR04 age model (Lisieski & Raymo 2005) are 30kyr from 5–4 Ma, 15kyr from 4–3Ma, 6kyr from 3–1Ma, and 4kyr from 1–0Ma; they are lower than most of the continental tuffs ages, in particular for the last 3Myr (Roberts et al. 2021, Vidal et al., 2022). The majority of tephras and cryptotephras in marine 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 discovered in the future to improve chronologies (Albaredes et al. 2023).

2. Water and Carbon isotopes

Water isotopes

Water isotopes are excellent tracers of the hydrological cycle (e.g., Craig & Gordon 1965, Gat 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 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.

Water isotopes are expressed in per mil (‰) using δ notation: δD or $\delta^{18}O = (R_{sample} - R_{standard})/R_{standard}*1000$ and represent the relative deviation of R (the isotope ratio, D/H or $^{18}O/^{16}O$) in the sample from a standard, usually Vienna Standard Mean Ocean Water (VSMOW) with δD or $\delta^{18}O = 0$ ‰.

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 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 δD_{wax} proxy has been increasingly used over the past decades in paleoclimate studies of marine sediment cores (e.g. Schefuß et al. 2005, Collins et al. 2017, Kuechler et al. 2013, Tierney et al. 2017, Caley et al. 2018) to infer indirect changes in the regional hydrological cycle across Africa. Although the δD_{wax} is commonly interpreted as a proxy for the amount of regional rainfall, interpretation can be more complex, because the δD_p value depends on other climate influences (precipitation, temperature, source effect, circulation regime) and on additional environmental and physiological processes related to the climate and the vegetation (relative humidity, vegetation changes, biosynthesis of the lipids) (Sachse et al. 2012).

In marine sediment cores, the seawater oxygen isotope composition ($\delta^{18}O_{sw}$) is preserved in carbonates from various organisms such as foraminifers. The carbonate isotopic concentration ($\delta^{18}O_c$) 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 (Urey 1947, Shackleton 1974). For benthic foraminifera, it has long been assumed that the deep temperature effect on $\delta^{18}O_c$ is negligible. Therefore, benthic $\delta^{18}O_c$ records and stack (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), for example between a marked cooling step at 2.73Ma and the first major glaciation at 2.15 Ma. Hence, $\delta^{18}O_{sw}$ is better suited as a proxy for polar ice volume changes rather than the benthic $\delta^{18}O_c$ signal (Figure 7) (Rohling et al. 2021). In addition, a vast majority of marine 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 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. 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).

Carbon isotopes

Carbon isotopes are expressed in per mil (‰) using δ notation: $\delta^{13}C = (R_{sample} - R_{standard})/ R_{standard}*1000$ and represents the relative deviation of R (the isotope ratio, $^{13}C/^{12}C$) in the sample from a standard (usually Vienna Pee Dee Belemnite (VPDB), a marine carbonate). $\delta^{13}C$ is used as a proxy for the proportion of C_3 and C_4 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 interpretations of carbon isotopes as paleodiets are not that straightforward and should also consider independent proxies (e.g., morphology, dental microwear and mesowear) that are more directly linked to mechanical properties of diet items.

Summary points:

- Although African terrestrial records provide crucial information on land climate variability, 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.

- A heterogeneity for pan-African hydroclimate changes is observed over the last 4Myr. The forcings that control this heterogeneity of variability are a combination of orbitally paced low-latitude fluctuations in insolation, polar ice volume changes, tropical SST gradients and the walker circulation and maybe GHGs changes.

- Our compilation of vegetation data over the last 4Myr show an expansion of the C_4-dominated ecosystems across northern, southwestern, and eastern Africa over the last 4Myr with more stable conditions at around 1Ma, but this is not mirrored by the observed pan-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 factors including atmospheric CO_2 concentrations and temperature.

- 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 whether these correlations reflect causal processes. We highlight a few areas where we believe that focused research effort would be warranted.

- 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 climate changes. To bridge paleoclimate data and models, the inclusion of chemical tracers (for example water and carbon isotopes, forward proxy modelling) relevant to proxies directly in Earth system models should be considered. Data assimilation techniques adapted for paleoclimate applications may further improve reconstructions of past climates.

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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
$\delta^{13}C$ plant waxes	Vegetation (biomass, C_3 vs C_4 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_{org} ; 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 (ε_{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

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

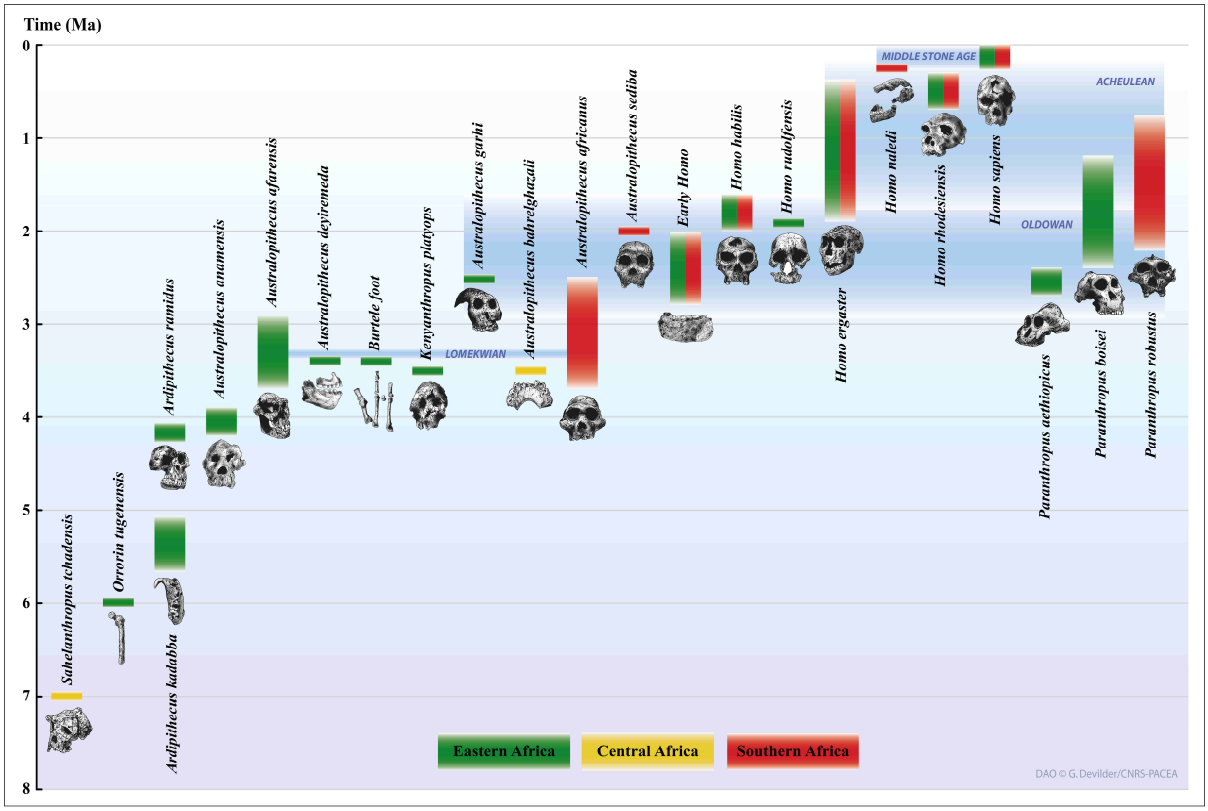

Figure 1: Stratigraphic ranges of African hominin taxa and associated lithic industries. Modified after Sahle et al. (2013), Beyene et al. (2013), Wood & Boyle (2016), Plummer et al. (2023) and references herein. Hominin taxinomy is debated and actual paleobiodiversity may be partly overestimated by taxinomic practices or underestimated due to taphonomic issues, making it extremely difficult to have a clear understanding of the real paleobiodiversity.

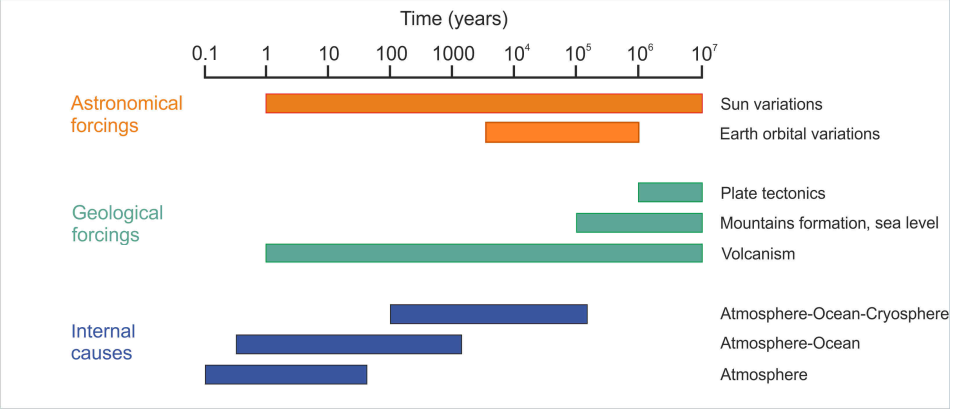

Figure 2: Schematic of main natural forcings/causes of climate changes (adapted from Bard 2002).

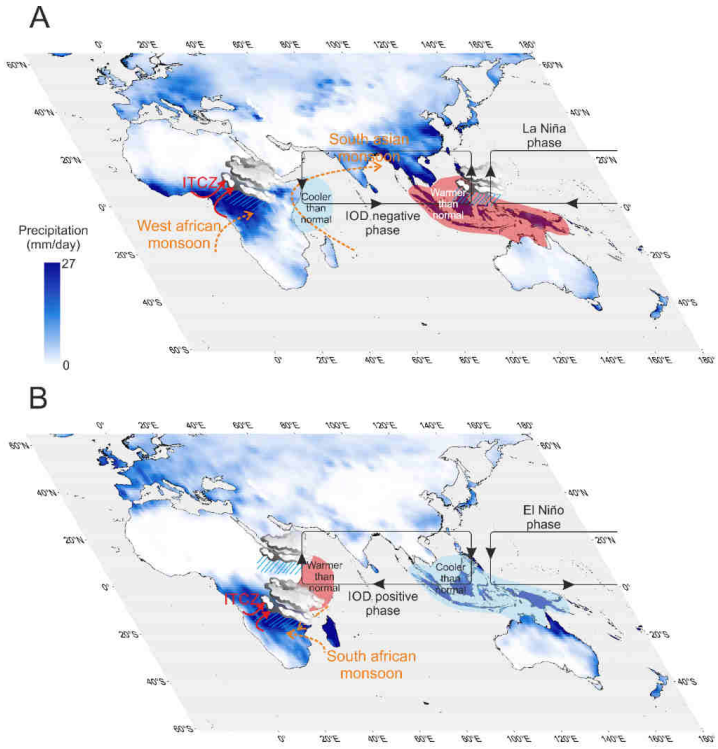

Figure 3: Main modern hydroclimate processes and changes at low latitudes and their impact on Africa. A. Averaged precipitation rates for August and B. January (Chen et al. 2002). Tropical inter-annual climate variabilities (ENSO: El Niño Southern Oscillation and IOD: Indian Ocean Dipole) are illustrated as examples of configuration but not necessary entirely dependent and are not necessarily linked with latitudinal variability (ITCZ: InterTropical Convergence Zone migration, size and strength and regional monsoon systems).

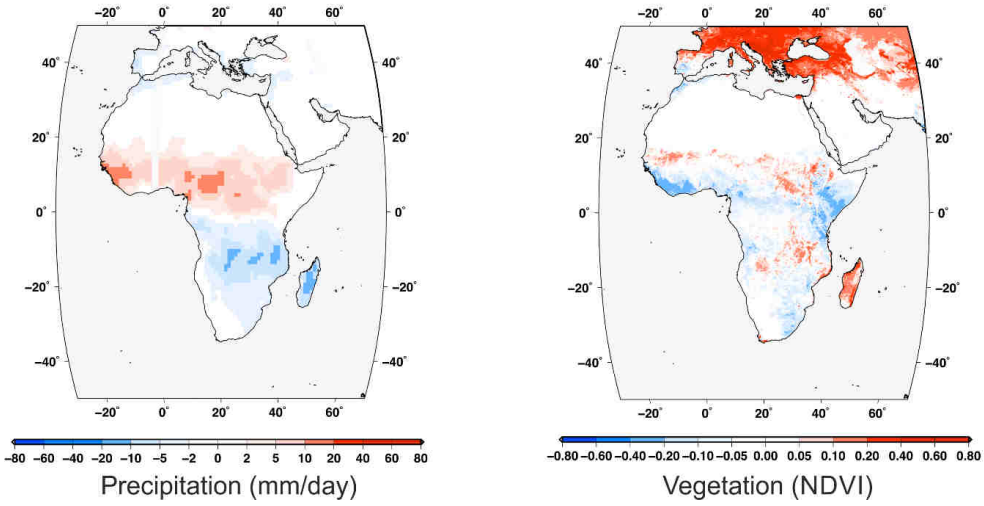

Figure 4: Anomaly (August-January) for precipitation (Chen et al. 2002) and vegetation (NDVI: Normalized Difference Vegetation Index) in Africa (Vermote et al. 2014). NDVI quantifies vegetation by measuring the difference between near-infrared (which vegetation strongly reflects) and red light (which vegetation absorbs).

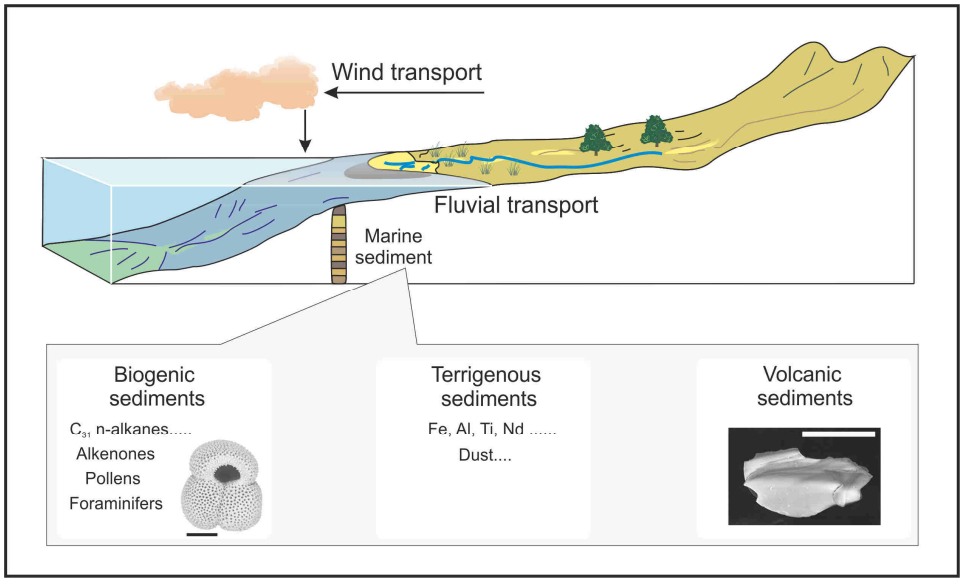

Figure 5: Scheme of sediment transport from the continent (source) to the ocean (sink) and main sediments in marine environment. SEM images from marine sediments (left to right) of the planktonic foraminifera *G. ruber*, and volcanic glass shard from the East African Rift System (indicated scale is 100µm).

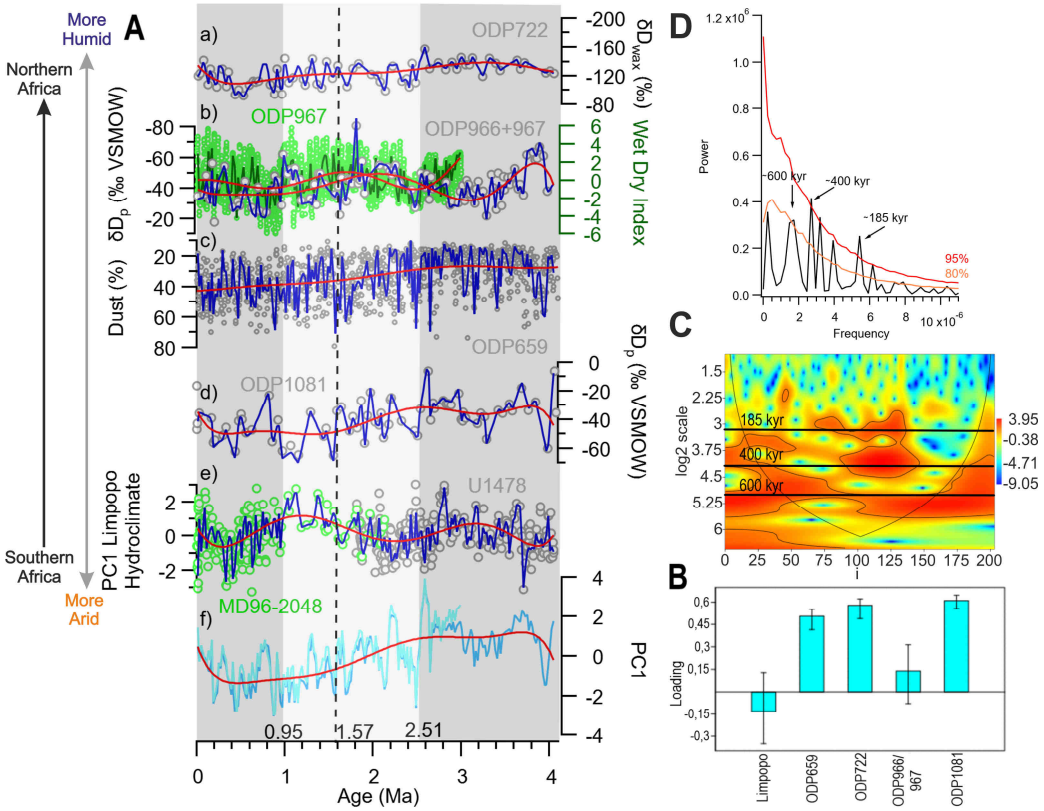

Figure 6: Pan-African hydroclimate variability over the last 4 Myr based on marine sediment cores. A. a) δD of the n-C_{31} alkane of plant waxes at site ODP722 (Huang et al. 2007). b)Blue line shows δD of precipitation (δD_p) at ODP966& 967 (Lupien et al. 2023). Standard error means was 4.3 ‰ for δD_p. Green line shows the Wet-Dry index from ODP967 (Grant et al. 2017). c) Dust percentage at ODP659 (Tiedemann 1994). d) δD of precipitation derived from the vegetation correction of δD_{wax} at site ODP1081 (Rubbelke et al. 2023). The average standard deviation was 1.81 ‰ for δD_{wax} and mean error for δD of precipitation was 3.7 ‰. e) PC1 of hydroclimate records from the Limpopo region, sites MD96-2048 and IODP U1478 (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 and fluctuations. Grey shading and dash line depict the four phases that have been constrained 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. Wavelet transform on the PC1 based on Torrence & Compo (1998). The significance level 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-alarm level at the 95 % and 80 % confidence interval).

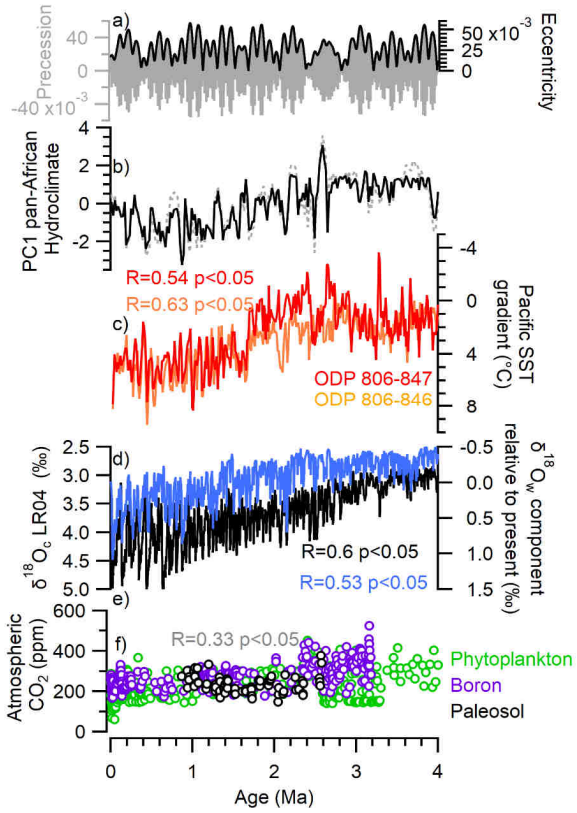

Figure 7: Forcings on pan-African hydroclimate. a) Eccentricity variations that modulate precession (Laskar et al. 2004). b) PC1 of pan-African hydroclimate original (dash line) and residue (solid line) after removal of orbital forcings variance. c) Pacific sea surface temperature (SST) gradients (sites ODP 806 and 847 (Wara et al. 2005), site ODP 846 (Lawrence et al. 2006)). d) Component of sea-level-based ocean δ^{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 CO_2 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_2 changes (f) are shown.

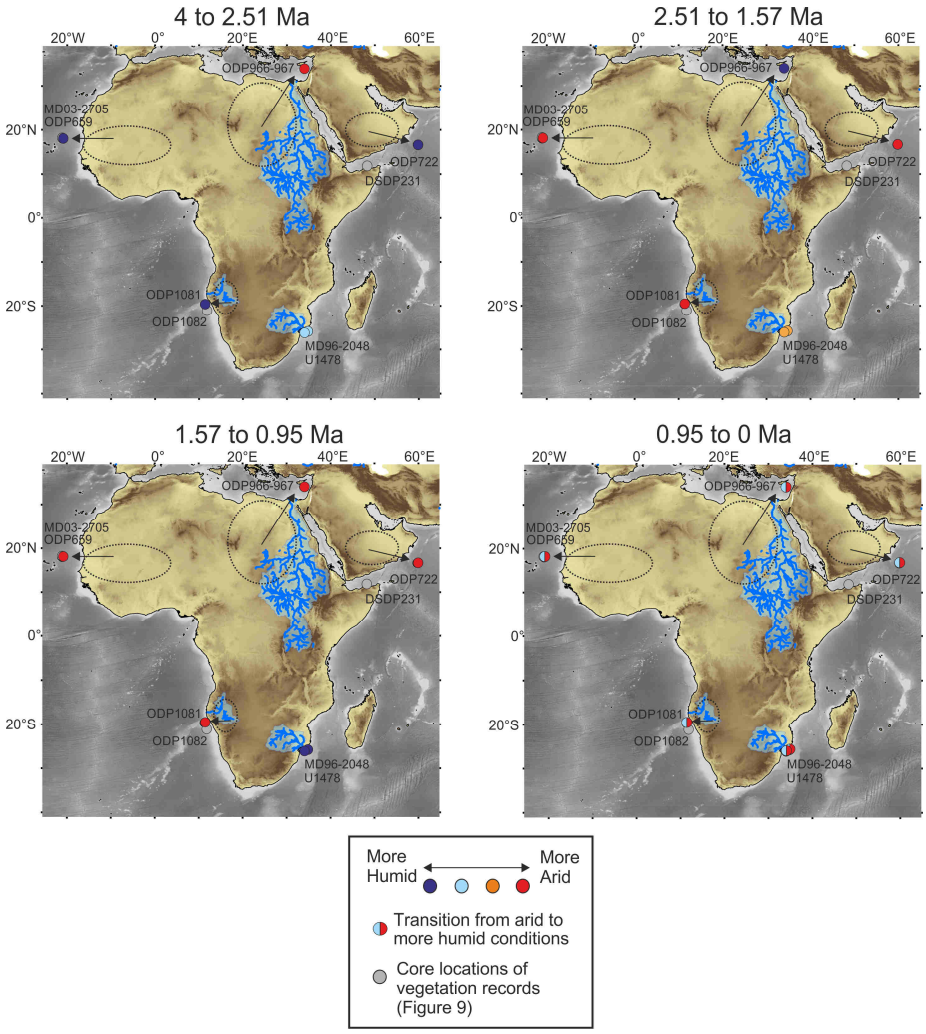

Figure 8: Major phases of pan-African hydroclimate variability. Main fluvial catchments that transport material to marine sediment cores are indicated together with the main source of material transported by winds to marine sites (see also Figure 11). Core locations with red/blue colors indicate more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

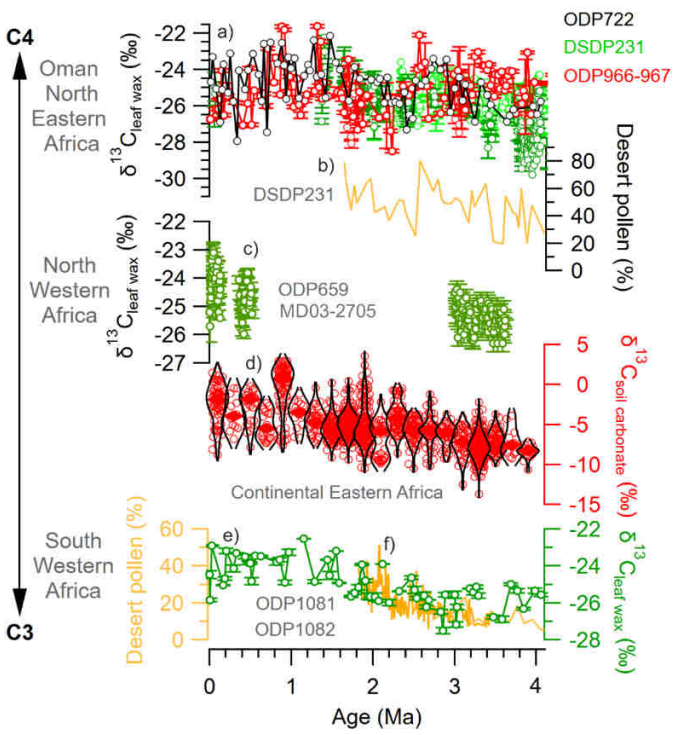

Figure 9: Pan-African vegetation variability over the last 4Myr based mainly on ocean cores. a) $\delta^{13}C_{leaf\ wax}$ from sites ODP722 (Huang et al. 2007), DSDP231 (Feakins et al. 2013, Liddy et al. 2016) and ODP966-967 (Rose et al. 2016, Lupien et al. 2023). b) Desert pollen at site DSDP231 (Bonnefille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

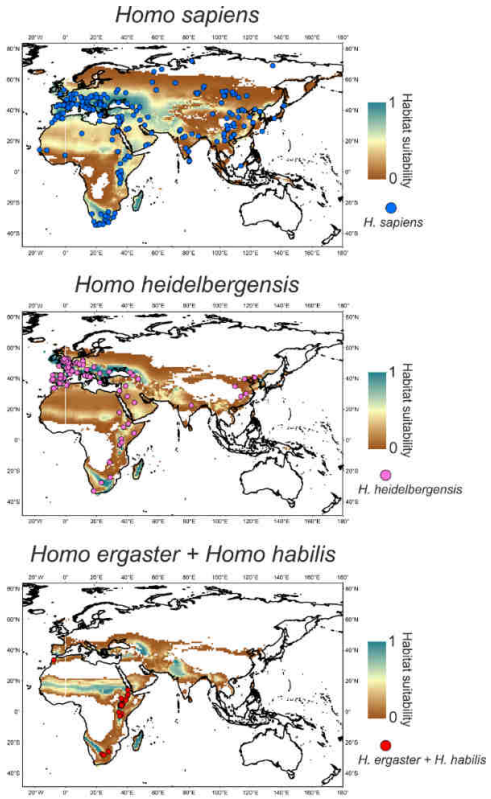

Figure 10: African hominin species habitat suitability (results based on Timmermann et al. 2022). Species distribution calculated from a Mahalanobis distance model with coloured circles represent the locations of fossils and/or archaeological artefacts associated with the hominin groups. The time-averaged habitat suitability covering the period of respective hominin presence can be interpreted in terms of probability, with values ranging from 0 (habitat unsuitable) to 1 (habitat extremely suitable) (Timmermann et al. 2022).

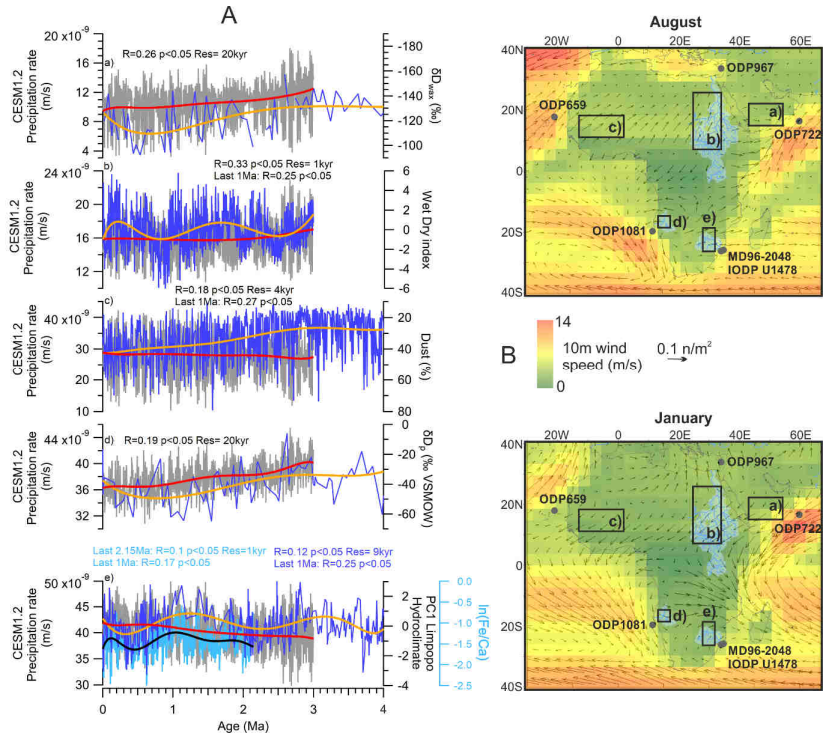

Figure 11: Data-model comparison for African hydroclimate over the last 3Myr. A. Data in a) to e) are similar to Figure 6 a) to e), except the ln(Fe/Ca) hydroclimate record in e) (Caley et al. 2018). CESM1.2 annual simulated precipitation in a) to e) extracted from regions indicated by black frames in 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.

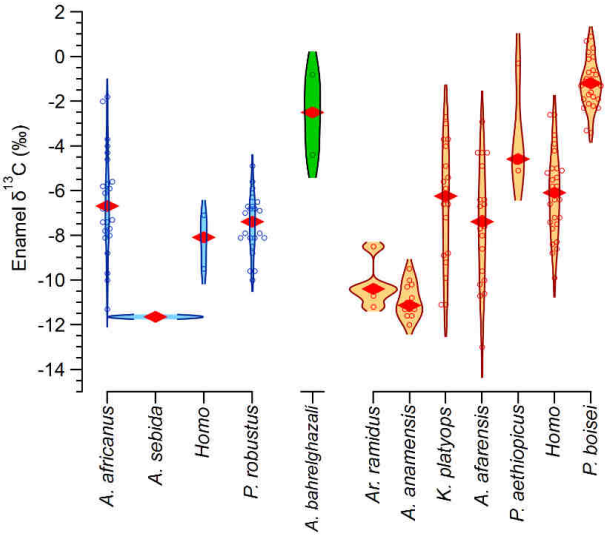

Figure 12: Enamel $\delta^{13}C$ (representative of diets) of early hominin taxa from southern Africa (blue), central Africa (green) and eastern Africa (orange) arranged from oldest to youngest temporal periods/fossils for each regional group of African hominins (data from Sponheimer et al. 2013). Violin plots with the median values (red dots) are indicated.