



# The effects of mid-to-late Pliocene climatic fluctuations on the habitat and distribution of early hominins

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## Abstract

The climatic fluctuations of the Pliocene played a substantial role in the emergence of *Homo* and *Paranthropus*. I studied the climatic suitability and affinity of hominins in Africa to understand how the regional effects of global climatic alternations influenced their occurrence in the mid-late Pliocene epoch. The modelled climatic suitability values indicate the existence of three potential main ranges in the continent. Late Pliocene climatic changes might result in notably fluctuating habitability conditions in the North, Central East, and Southern Africa. In the Afar Region, the range of the changing suitability values was narrower than in the other regions. Therefore, it can be assumed that *Australopithecus afarensis* might be more resistant to climatic fluctuations than the others.

**Keywords** Human evolution · Environmental changes · Modelling · *Homo* · *Paranthropus* · Pliocene · North · Central East · And Southern Africa · Afar Region

## Introduction

In the Pliocene Epoch in the late Neogene, the climate of Earth became characterized by notable fluctuations in global mean temperatures, high seasonality, and ice caps of greater or lesser extent at the poles. Following the warmer Miocene Epoch, the global mean temperature in the first half of the Pliocene was higher than later periods characterized by outstanding global mean temperature cooling accompanied by large-scale glacial-interglacial cycles that only started in the second part of the Pliocene (de Menocal, 1995; Zachos et al., 2001). A long-term drying term characterized the late Cenozoic climate of Africa. This trend was superimposed on the alternation of short extreme humid, and dry episodes, which was determined by the components of the eccentricity cycle of the planet (Trauth et al., 2007). Precessional changes caused extreme variability in climatic conditions 2.7–2.5, 1.9–1.7, and 1.1–0.9 million years ago (Mya) in Africa (Trauth et al., 2007).

The long-term drying of Africa resulted in notable changes in the character and range of the biomes as part

of a global process, such as the spread of large open grass habitats. The savanna biome appeared rapidly at about 8 Mya (Christin et al., 2014), followed by a parallel expansion of C4 grasses (Beerling & Osborne, 2006) and large herbivore mammals around the world (MacFadden, 2000). The decline of woodlands started as early as the Late Miocene in the Omo-Turkana Basin (Cerling et al., 2011). The wet interglacial and drier glacial alternations would have caused significant stress for the tropical forest ecosystems in Africa in the late Miocene and the Pliocene. The extant forests of Africa require nutrition-rich soils, high annual precipitation and/or groundwater, and a long rainy season with high air moisture (Reed & Rector, 2006), such as occurred in large regions of equatorial Africa during the early Pliocene. However, climate changes since the mid-Pliocene have been unfavourable for the continent's forest ecosystems.

The late Pliocene saw the start of the modern ice age and the long-term drying of Africa with episodic extreme dry periods may have had a strong negative impact on the forested and semi-forested ecosystems and arguably on the habitats of hominin species. Although certain later hominins like *Homo erectus* (Dubois, 1893) lived in more open habitat mosaics near perennial water sources (de Ruiter 2008), the habitat preference and paleoecology of early hominins were linked to wet or moderately wet conditions requiring the presence of appropriate water drainage (Cuthbert et al.,

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2017). Areas of higher rainfall, thick, fertile, and alkaline soils with patches of sub-tropical forest and thick bush were characteristic habitats of early hominins (Rayner et al., 1993). Other authors have noted that tectonically disturbed drainage patterns may have been attractive hominin habitats (Reynolds et al., 2011). Increasing late Pliocene climatic variability might have been essential in the emergence of the present-day mammalian fauna of Africa (Bobe & Eck, 2001), including the appearance of *Homo*.

The Turkana Basin changed from a semi-evergreen rain-forest to deciduous woodland and savanna during the middle-late Pliocene (Fernández & Vrba, 2006). Bobe et al. (2002) concluded that climate changes caused significant shifts in vegetation in the Omo paleo-ecosystem and other parts of Eastern Africa, possibly occurring gradually but resulting in the transition from forest ecosystems to open woodlands between 3.4–2.8 Mya (Bobe et al., 2002). It should be noted that changes in forest cover were not synchronous across regions. For example, the mid-Pliocene peak of woody vegetation in the Omo-Turkana Basin occurred earlier than in the Awash Valley (Cerling et al., 2011). In the Turkana Basin, aridification showed a continuous trend in the last Neogene era, and biomes changed from semi-evergreen rain-forest to deciduous woodland during the middle of and savanna in the late Pliocene epoch (Fernández & Vrba, 2006), which highlights the need to examine the vegetation and faunal impacts of the Pliocene climate changes individually in different regions of Africa. It is striking that the appearance of the first known *Homo* in the fossil record in 2.8–2.75 Mya (LD 350–1 specimen from Ledi-Geraru, Afar, Ethiopia) roughly coincides with the start of the rapid climatic fluctuations of 2.7–2.5 Mya (Trauth et al., 2007) and the appearance of *Homo habilis* (Leakey et al., 1964) and *Homo rudolfensis* (Alekseyev, 1978) at the end of this period in 2.4 Mya (Villmoare et al., 2015). Therefore, it is plausible that *Homo* originated in Eastern Africa, and this evolutionary event was linked to the mentioned late Pliocene climatic event near the Plio–Pleistocene boundary, which also resulted in the spread of open and arid savannah environments (Reed & Russak, 2009; Robinson et al., 2017).

The hominin adaptation to the more arid Plio-Pleistocene conditions was traditionally considered a critical factor in human evolution (Domínguez-Rodrigo et al., 2001). It was hypothesized that the increasingly unstable climatic conditions, including more frequent extreme climatic events and increasing aridity of many areas, resulted in larger bodies according to Bergmann's Rule, the relative reduction in some body parts, which is consistent with Allen's Rule in the case of bodily extremities, and enlargement of cranial capacity (Vrba, 1996). Several authors suggested that the climate-vegetation feedback during the middle and late Pliocene strongly influenced these adaptive changes (Behrensmeyer, 2006; Conroy & Pontzer, 2012; Haywood & Valdes, 2006;

Maslin et al., 2014). There is evidence that past climatic changes may also strongly impact the rise and extinction of former hominin species and the occupation patterns of larger regions. For example, Raia et al. (2020) showed that past extinctions of *Homo* species generally coincided with increased vulnerability to climatic changes and that just before their extinction, ancestral human species lost a significant portion of their climatic niche space.

There is no doubt that hominin species prior to our genus were also sensitive to environmental changes in the late Pliocene that may have played the most critical role in the emergence of *Homo* (Robinson et al., 2017). Potts (2013) found that the appearances and extinctions of hominin lineages and the emergence of essential adaptations and capacities were related to the most prolonged intervals between periods of strong climate variability. For example, the emergence of *Australopithecus afarensis* (Johanson and White, 1978) can be linked to 5 °C cooling in the mid-Pliocene, which caused a significant biome shift in Eastern Africa (Bonnefille et al., 2004). Palynological evidence suggests that this major climatic fluctuation was also linked to the appearance of the forest or forest margin-dwelling *Australopithecus africanus* (Dart, 1925) in Southern Africa during the same climatic regime. It is questionable to what extent *Australopithecus* was able to adapt to the ecological and physical stress aridification caused. However, it seems that at least *A. afarensis* and possibly *Australopithecus anamensis* (Leakey et al., 1995) were eurytopic species (Behrensmeyer & Reed, 2013).

## Research Goal

It is widely accepted that Late Pliocene climatic fluctuations may have led to the emergence of *Homo* and *Paranthropus* in Eastern Africa (e.g., de Menocal, 2004; Reed & Russak, 2009). Studies on the middle/late Pliocene mammalian faunal alternations (Alemseged et al., 2020) and the combination of the faunal and pedogenic carbonate stable isotope changes in the time of the emergence of *Homo* (Robinson et al., 2017), as well as the niche-modelling of the earliest *Homo* species (Raia et al., 2020), concluded that the appearances of *Homo* and other hominin taxa could be linked to the global climate change that occurred in the Late Pliocene era. Although Gibert et al. (2022) produced a somewhat similar model of Pliocene hominin distribution using a late Pliocene climate, the developed environment of the authors did not have a temporal resolution that could allow insight into finer temporal and climatic processes of hominin distribution. However, the potential effect of large-amplitude climatic fluctuations between the glacial and interglacial climates was not modelled previously using environmental modelling tool with a high temporal resolution for early hominin populations. In order to study the potential effect of climate changes on hominin evolution, I aimed to model the potential climate

suitability areas of the African continent for hominins based on the reconstructed paleoclimatic data of the glacial and interglacial periods in the second half of the Pliocene.

## Materials and Methods

### Study questions

1. In which areas could early hominins occur in the mid-late Pliocene epoch?
2. How could the climatic fluctuations of the Pliocene epoch affect early hominins in different regions of Africa?
3. In which climatic conditions could early hominin genera thrive?

### Rationale

The paleoclimatic reconstruction was based on my earlier research (Trájer, 2022). No georeferenced climate models with a high temporal resolution exist, except for the mid-Pliocene warm and the M2 mid-Pliocene cold periods. Therefore, benthic foraminiferal  $^{18}\text{O}/^{16}\text{O}$  value (hence:  $\delta^{18}\text{O}$ ) measurements are widely used to reconstruct past global temperature changes (Billups & Schrag, 2003; Liu et al., 2009). It is because deep-sea benthic foraminifera are characterized by seawater temperature-dependent carbon and oxygen isotopic equilibria (Graham et al., 1981). In colder climatic intervals the  $\delta^{18}\text{O}$  is higher; in warmer intervals the  $\delta^{18}\text{O}$  values are lower. Because the  $\delta^{18}\text{O}$  value measured in benthic foraminifera is broadly proportional to the global mean temperature (Jouzel et al., 1994), it can be used to reconstruct the atmospheric paleotemperature conditions or determine the extent of former ice sheets (Billups and Schrag, 2002). However, it should be noted that a single  $\delta^{18}\text{O}$  value does not characterize a given time interval because of the time averaging of measured shell material and due to regional temperature differences. However, the utility of benthic foraminifera in reconstructing global or regional climatic conditions is limited. The diagenetic alteration, freshwater inputs or evaporitic conditions, salinity modification, and vital effects of measured foraminifera species can also modify the measurable  $\delta^{18}\text{O}$  values (Peral et al., 2018). It means that  $\delta^{18}\text{O}$  is a local-to-regional signal and, its measurements provide an estimation of local/regional temperatures and not the exact temperature of a place at a specific time. On the other hand, the changes in the global mean temperature in the past have resulted in heterogeneous regional changes in temperature and precipitation conditions. This spatial heterogeneity is also clearly visible in the case of future climatic projections (Kaufmann et al., 2017).

In this study, I modelled the climatic suitability of early hominins for different periods. According to Drake and Richards (2018), ‘environmental suitability can be defined as the conditional probability of occurrence of a species given the state of the environment at a location.’ Therefore, I use the term ‘suitability’ to mean the climatic suitability of habitats for early hominins based on the summarized occurrence of the species, i.e., the number of climatic factors (expressed as percentages) that may have corresponded to early hominins at a given location.

Based on these definitions:

1. I created the fossil hominin specimens-related paleoclimatic models for all Pliocene hominin findings based on the following:
  - (a) the age of the fossil specimens,
  - (b) the coordinates of the sites of the collection and
  - (c) the age-related  $\delta^{18}\text{O}$  values. The mid-Pliocene warm and the M2 mid-Pliocene cold periods were the reference period climate models (see above).

### Selection of the model period

As noted, the emergence of *Homo* and *Paranthropus* may be associated with significant ecological stresses caused by alternating warm and humid and cold and arid episodes during the Pliocene (Potts, 2013). The preglacial environmental changes in the Pliocene formed a step-like increase in aridity in Africa (Gasse et al., 2006). However, beyond the general climatic trends, the Eastern African geologic records of the last 5 million years also show signs of rapid environmental changes (Maslin et al., 2009). The alternations of these wet and dry episodes became especially frequent after 2.7–2.6 Mya, in the turn of the Pliocene/Pleistocene epochs, causing extreme climate variability in Eastern Africa in the Quaternary period (Potts & Faith, 2015; Trauth et al., 2007). These facts indicate that the one million-year-long period before 2.5 Mya could be a key period of human evolution.

2. Reconstructed bioclimatic values by age and location were associated with each fossil specimen. As distribution limiting extrema, the highest and lowest values were selected by bioclimatic factors considering all the fossil specimen-related values.
3. I selected the one million-year-long period of 3.5 to 2.5 Mya for modelling interval and divided it into ten 100 kiloyears (kys)-long periods (time bins). Next, I reconstructed periods with the highest and lowest  $\delta^{18}\text{O}$  values within the 100 kys-long bins resulting in 20 georeferenced paleoclimatic reconstructions. In a climatic sense, these times presumably represent the most extreme periods of a time interval.

4. I determined the distribution limiting bioclimatic extrema values based on the known occurrences of ancient latest Miocene-Pliocene hominin species in Africa so that hominin species were held as a single taxonomical unit instead of investigating the climatic requirements of different species.
5. I created the models for 20 time bins (ten each characterized by lowest and highest  $\delta^{18}\text{O}$  values) in the 3.5 to 2.5 Mya period. The time bin selection aimed to produce climatic suitability models considering the coldest and the warmest periods within the studied era. These periods represent the most extreme climatic conditions, which theoretically had a notable impact on early hominin populations.
6. I calculated the differences in the modelled suitability values of the neighbouring eras (see below).
7. I calculated the modelled suitability values for 20 time bins in the selected sites of the Pliocene hominin findings. The sites were classified into four major geographical units: Chad, Ethiopia, 'Central East Africa' and 'Southern Africa'. The time bins represent the coldest and the warmest phases of the 100 kys-long periods.
8. I compared the reconstructed specimens-related paleoclimatic values using principal component analysis.
9. Using the present climatic values of 33 African cities, I evaluated the Köppen-Geiger climatic class of the paleoanthropological sites based on the reconstructed specimens-related paleoclimatic values, using principal component analysis.

The following points relate to the number of the modelled times:

1. I used two primarily paleoclimatic reconstructions as base models, modified by ratios derived from oxygen isotope values.
2. I split the studied period into ten 100 kys-long periods, then selected the times with the highest and the lowest  $\delta^{18}\text{O}$  values. It resulted in selecting a total of 20 Pliocene times in the study.
3. I classified the hominin sites into four territories: Chad, Ethiopia, Central East Africa, and Southern Africa. However, this did not constitute additional modelling, as the suitability values for the fossil sites were grouped on a spatial basis for further analysis. Supplementary Method 1 describes the logical rationale of the study in detail.

It is crucial to note that the developed model environment was based on only the 'known' and not the formerly existing, realized, and whole range of hominins. The exact determination of the realized niche is impossible for extinct species, as the fossil record is always incomplete. It is true for terrestrial

vertebrate taxa, which generally have a sparse fossil record. The comparison of the distribution of Pliocene fossil sites of mammals such as Hippopotamidae, Cercophitecidae, Suidae, and Felidae in Africa (based on the mapped data of Fossilworks.org) indicates that available and studied Pliocene-age mammal fossil-bearing outcrops are absent in Central and West Africa. Therefore, it can influence the reliability of distribution models based on the known distribution of Pliocene hominin fossil sites (Fig. 1).

Comparing the maps in Figs. 1 and 2, the known occurrence of ancient hominins in Africa largely coincides with the known Pliocene occurrence of these four mammal groups. It may reflect that excavations were conducted chiefly for fossil hominin specimens, and the other mammal taxa data are secondary to this research. Nevertheless, it suggests some caution in evaluating model results based on the known occurrence of ancient hominins. It can be said that although the fossil record data represent points from the former realized niche, the model results approximate the former fundamental ecological niche of the collective group of ancient hominins because it cannot consider, e.g., modifications from the theoretical distribution resulting from former predation pressure or inter-species interactions.

### Outline of modelling steps:

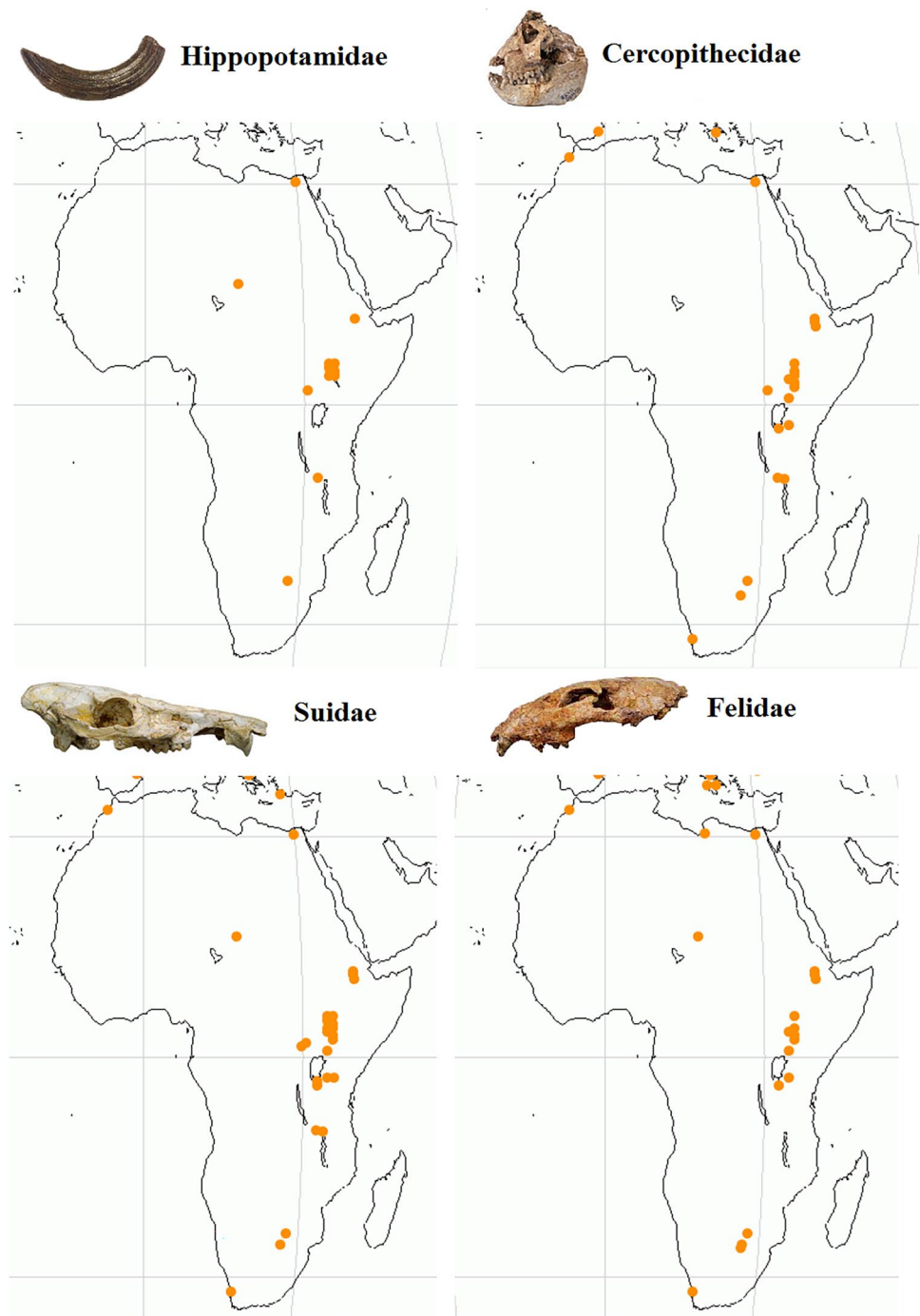
1. The coordinates of the involved fossil sites of middle-Pliocene to early Pleistocene hominins were identified.
2. The bioclimatic parameters that characterized the fossil sites during the existence of the fossil individuals were determined according to the coordinates-determined points based on the reconstructed paleoclimatic conditions.
3. The lower and upper extrema of the utilized bioclimatic variables were determined.
4. The bioclimatic values were displayed to characterize the past spatial suitability of the union of the early hominin species using the reconstructed paleoclimatic 20 times in 3.5 to 2.5 Mya BP. Figure 3 visualizes the workflow of modelling.

Supplementary Table 1 shows the utilized bioclimatic variables in modelling.

### Fossil sites

Since the applied modelling method is based on the absolute extremes of the climatic values and does not respect the frequency of the climatic values with weighting, it does not require the involvement of all known fossil sites. Therefore, I selected 19 late Miocene and Pliocene-age early hominins fossil sites ranging between 6.935–2.58 Mya BP (Table 1). The selected sites represent the most

**Fig. 1** Maps of Pliocene fossil sites of Hippopotamidae, Cercopithecidae, Suidae and Felidae in Africa. Occurrence points are marked with dark orange

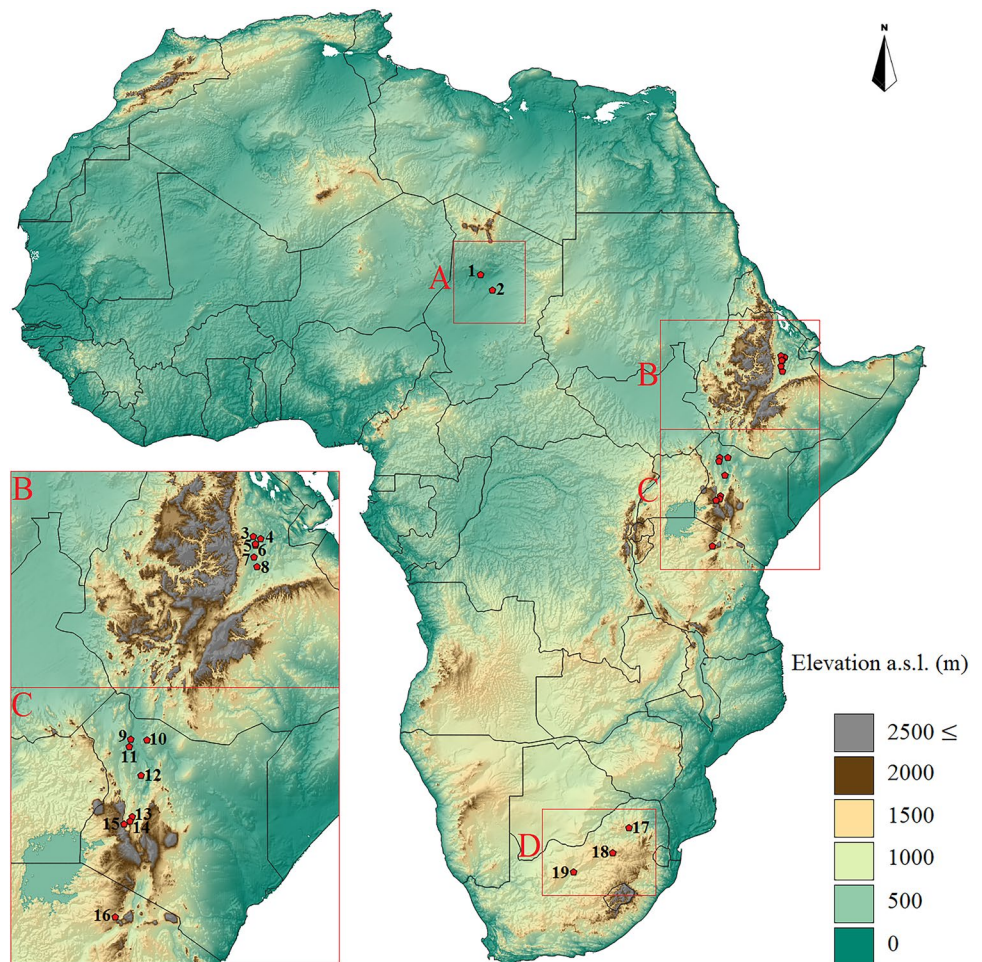


important fossils sites of early hominins for almost the entire Pliocene and Latest Miocene epochs in Northern, Eastern, and Southern Africa: Djurab Desert, Chad; Ledi-Geraru, Ethiopia; Middle Awash, Ethiopia, Aramis Ethiopia, Dikika, Ethiopia, Lomekwi, Kenya; Allia Bay, Kenya; Lothagam, Kenya; Kanapoi, Kenya; Kapsomin, Kenya; Aragai, Kenya; Tabarin, Kenya; Laetoli, Tanzania; Makapansgat, South Africa; Sterkfontein, South Africa and Taung, South Africa (see Fig. 2).

### The mid-Pliocene climate models

I accessed 2.5 arc-minutes (~5 km) spatial resolution georeferenced past climatic models from the dataset of PaleoClim.org website (Brown et al., 2018): the mid-Pliocene warm period (3.205 Mya; Hill, 2015) and the M2 mid-Pliocene cold period (ca. 3.3 Mya; Dolan et al., 2015) models. The  $\delta^{18}\text{O}$  values of benthic foraminiferal carbonate strongly relate to the mean temperature of seawater. The

**Fig. 2** The fossil sites of early hominins were involved in the study. **1:** Djurab Desert, Chad; **2:** Koro-Toro, Chad; **3:** Woranso–Mille, Ethiopia; **4:** Ledi-Geraru, Ethiopia; **5:** Hadar, Ethiopia; **6:** Dikika, Ethiopia; **7:** Aramis Ethiopia; **8:** Middle Awash, Ethiopia; **9:** Lomekwi, Kenya; **10:** Allia Bay, Kenya; **11:** Lothagam, Kenya; **12:** Kanapoi, Kenya; **13:** Kapsomin, Kenya; **14:** Aragai, Kenya; **15:** Tabarin, Kenya; **16:** Laetoli, Tanzania; **17:** Makapansgat, South Africa; **18:** Sterkfontein and South Africa; **19:** Taung, South Africa (A: ‘Chad grid’, B: Ethiopia grid’, C: ‘Central East Africa grid’ and D: ‘Southern Africa’ grid)



period between 2.5 and 3.5 Mya was considered critical in the evolution of *Homo* because the genus appeared at the turn of the second and last third of this period, 2.775 Mya (LD 350–1 mandible, Ledi-Geraru site; Villmoare et al., 2015). To study the potential effect of the fluctuation of glacial and interglacial periods on the environmental suitability of Pliocene hominins, I divided the coldest and warmest stages of the episodes of the studied one million years, determined by the  $\delta^{18}\text{O}$  (‰) values (maximum: the coldest, minimum: the warmest episode within the selected hundred thousand years period), into one hundred thousand years models (Fig. 4).

Monthly maximum and minimum temperatures were unavailable in these simulations, so creating certain bioclimatic variables is impossible. However, comparing the two climatic models, in the mid-Pliocene warm period the climate of Africa was warmer than in the M2 cold period (Fig. 5; see also Supplementary Fig. 1). Supplementary Method 2. shows the reconstruction of the fossil sites’ bioclimatic variables and Supplementary Method 3. describes the steps of environmental suitability modelling. Supplementary Table 2 shows the  $\delta^{18}\text{O}$  (‰) values and the modifying factors during

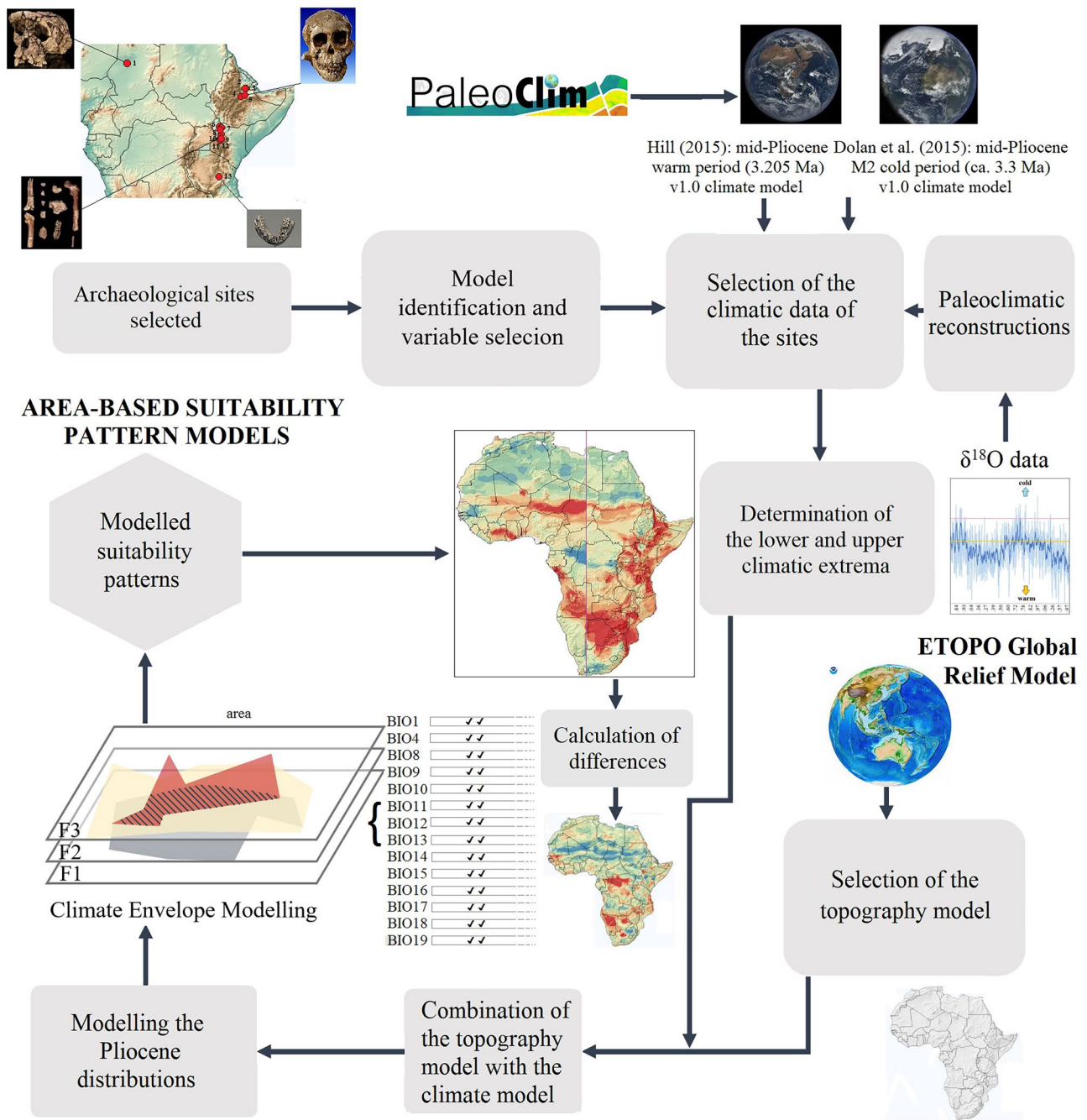
the warmest and coldest periods by 100 kys in 2.5–3.5 Ma BP.

Supplementary Method 2. shows the reconstruction of the fossil sites’ bioclimatic variables and Supplementary Method 3. describes the steps of environmental suitability modelling.

Supplementary Table 2 shows the  $\delta^{18}\text{O}$  (‰) values and the modifying factors during the warmest and coldest periods by 100 kys in 2.5–3.5 Ma BP.

### Determination of the climatic extrema

All ecological modelling techniques aim for an adequate number of points for data processing. For area-based occurrence data, the statistical filtering of the extrema is inevitable because the areal climatic data can always be considered averages. It can be problematic when an area is too big, large-scale climatic trends appear, or the topography varies. Either lowlands or mountain ranges disturb the processing of the averaged climatic values. In contrast, in the case of point-like climatic data, such as fossil record site-nature occurrence data, the extrema of the individual sites can be



**Fig. 3** The visualization of the workflow of the climatic suitability modelling

held independently. In the case of a single climatic variable, considering each site’s data, the maximum and the minimum values can be held as the distribution limiting upper and lower limits. The hominin clade’s union is a composite containing different species with different habitat preferences. In this case, the climatic distribution-limiting values can be held as the spectrum of the environmental tolerance of the early hominins. Thus, in this study, the entire hominin clade was treated as a single entity regarding its

environmental tolerance. However, it should be emphasized that this is not a dynamic speciation model but uses fixed upper/lower thermal limits of the hominin clade, and due to this niche conservation concept, does not provide a test of speciation resulting from niche differentiation in response to Pliocene climate changes. Nevertheless, the models indicate in which periods the early hominin taxa could be vulnerable to climatic changes in the Pliocene. It means 14×2 bioclimatic factors in the model in the case of each species

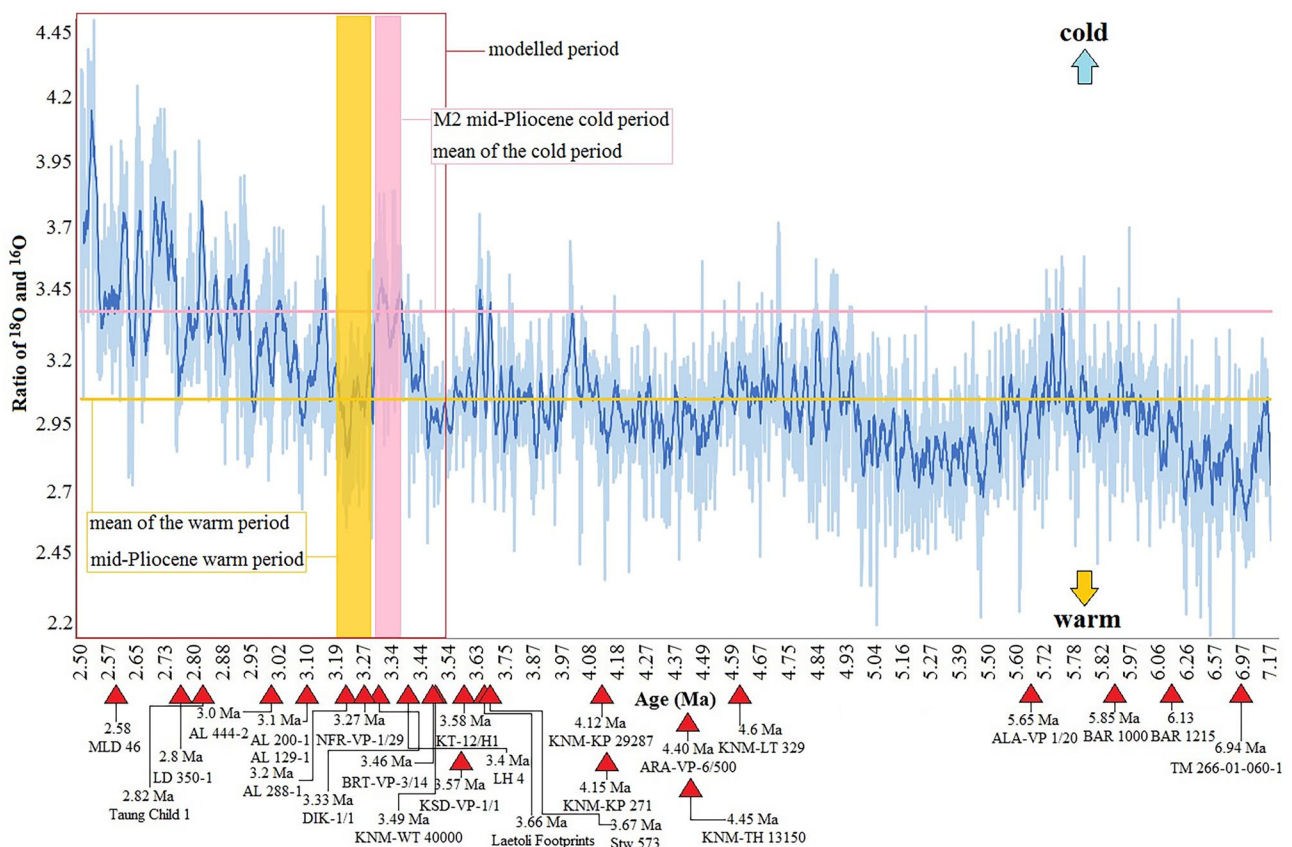
**Table 1** Some important details of the sites involved in the study by hominin specimens

Number	Referred specimen	Species	Age	Mean age	site	Reference
1	TM 266–01-060–1	<i>Sahelanthropus tchadensis</i> Brunet et al., 2002	7.04 ± 0.18 Ma to 6.83 ± 0.45 Ma <sup>1</sup>	6.935	Djurab Desert, Chad	Lebatard et al. (2008), Brunet et al. (2002)
2	KT-12/H1	<i>Australopithecus bahrelghazali</i> Brunet et al., 1995	3.58 ± 0.27 Ma	3.58	Koro Toro, Chad	Lebatard et al. (2008), Brunet et al. (1995)
3a	KSD-VP-1/1	<i>Australopithecus afarensis</i> Johanson et al., 1978	3,570 ± 0,014 Ma	3.57	Woranso-Mille, Ethiopia	Saylor et al. (2016)
3b	BRT-VP-3/14	<i>Australopithecus deyiremeda</i> Haile-Selassie et al., 2015	3.596–3.330 Ma	3.463	Woranso–Mille, Ethiopia	Haile-Selassie et al. (2015)
3c	NFR-VP-1/29	<i>Australopithecus afarensis</i> Johanson et al., 1978	3.330–3.207 Ma	3.2685	Woranso-Mille, Ethiopia	Haile-Selassie et al. (2016)
4	LD 350–1	<i>Homo sp.</i>	2.80 to 2.75 Ma	2.775	Ledi-Geraru, Ethiopia	Villmoare et al. (2015)
5a	AL 200–1	<i>Australopithecus afarensis</i> Johanson et al., 1978	3.10 ± 0.10 Ma	3.1	Hadar, Ethiopia	Johanson and Taieb (1976)
5b	AL 129–1	<i>Australopithecus afarensis</i> Johanson et al., 1978	3.10 ± 0.10 Ma	3.1	Hadar, Ethiopia	Johanson and Taieb (1976)
5c	AL 444–2	<i>Australopithecus afarensis</i> Johanson et al., 1978	3.0 ± 0.02 Ma	3	Hadar, Ethiopia	Kimbel and Johanson (2004)
6	DIK-1/1	<i>Australopithecus afarensis</i> (Johanson et al., 1978)	3.31 to 3.35 Ma	3.33	Dikika, Ethiopia	Alemseged et al., (2006)
7	ARA-VP-6/500	<i>Ardipithecus ramidus</i> White et al., 1994	4.425–4.375 Ma	4.4	Aramis, Ethiopia	White et al. (1994)
8a	AL 288–1	<i>Australopithecus afarensis</i> Johanson et al., 1978	3.22–3.18 Ma	3.2	Middle Awash, Ethiopia	Walter (1994)
8b	ALA-VP 1/20	<i>Ardipithecus kadabba</i> Haile-Selassie, 2001	5.65 ± 0.150 Ma	5.65	Middle Awash, Ethiopia	Haile-Selassie (2001)
9	KNM-WT 40000	<i>Homo (Kenyanthropus) platyops</i> * (Leakey et al., 2001)	3.4–3.57 Ma	3.485	Lomekwi, Kenya	Leakey et al. (2001)
10	KNM-KP 29287	<i>Australopithecus anamensis</i>	4.17 ± 0.03 to 4.07 ± 0.02 Ma	4.12	Allia Bay, Kenya	Leakey et al. (1998)
11	KNM-LT 329	<i>Australopithecus anamensis</i> Leakey et al., 1995	4.60 ± 0.40 Ma	4.6	Lothagam, Kenya	McDougall et al. (2003)
12	KNM-KP 271	<i>Australopithecus anamensis</i> Leakey et al., 1995	4.102 ± 0.020 to 4.196 ± 0.020 Ma	4.149	Kanapoi, Kenya	Leakey et al. (1995)
13	BAR 1000	<i>Orrorin tugenensis</i> Senut et al. 2001	5.8–5.9 Ma	5.85	Kapsomin, Kenya	Sawada et al. (2002)
14	BAR 1215	<i>Orrorin tugenensis</i> Senut et al. 2001	6.17 ± 0.15 Ma to 6.09 ± 0.14 Ma	6.13	Aragai, Kenya	Sawada et al. (2002), Senut et al. (2001)



**Table 1** (continued)

Number	Referred specimen	Species	Age	Mean age	site	Reference
15	KNM-TH 13150	<i>Australopithecus ana-</i> <i>mensis</i>	4.48–4.41 Ma	4.445	Tabarin, Kenya	Deino et al. (2002)
		Leakey et al., 1995				
16a	LH 4	<i>Australopithecus</i> <i>afarensis</i>	3.40±0.50 Ma	3.4	Laetoli, Tanzania	Leakey et al. (1976)
		Johanson et al., 1978				
16b	Laetoli Footprints	bipedial hominin	3.66 Ma	3.66	Laetoli, Tanzania	Leakey and Hay (1979), Masao et al. (2016)
			<sup>19</sup> Masao et al. (2016)			
17	MLD 46	<i>Australopithecus afri-</i> <i>canus</i>	2.58 Ma	2.58	Makapansgat, South Africa	Herries et al. (2013)
		Dart, 1925				
18	Stw 573	<i>Australopithecus sp.</i>	3.67±0.16 Ma	3.67	Sterkfontein, South Africa	Granger et al. (2015)
19	Taung Child 1	<i>Australopithecus afri-</i> <i>canus</i> Dart, 1925	3.03–2.61 Ma	2.82	Taung, South Africa	Herries et al. (2013)

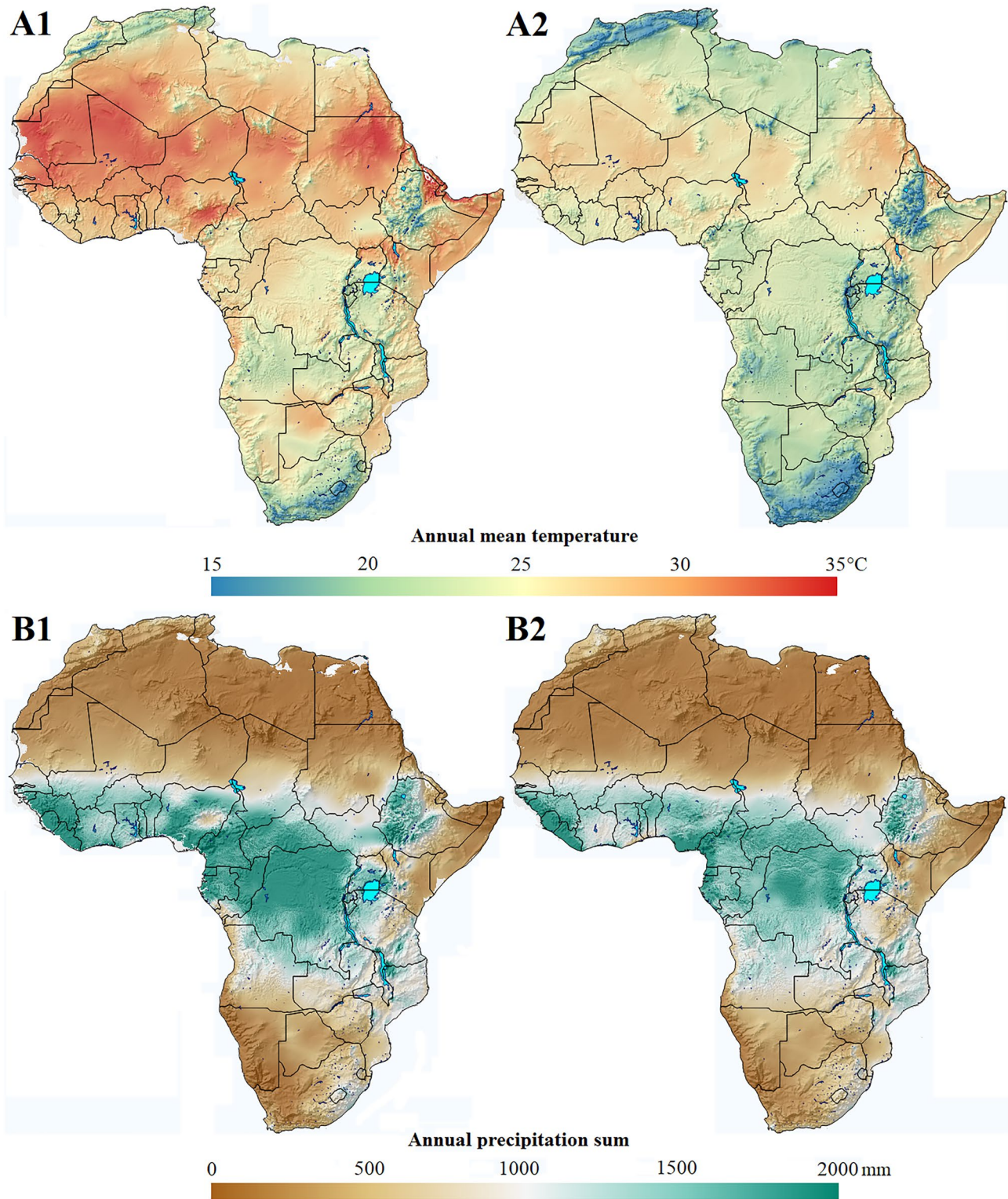


**Fig. 4** The ratio of the  $\delta^{18}\text{O}$  values of benthic foraminiferal carbonate 2.58–6.98 Mya, based on globally distributed records, according to Lisiecki and Raymo (2005), including the mid-Pliocene warm period

and the mid-Pliocene glacial stage (blue line: 10th-grade moving average) and the temporal position of the studied early hominine finds in the timescale

is an adequate number for distribution modelling purposes which were performed in Quantum GIS (2019). Supplementary Method 3 shows the reconstructed mid-Pliocene

warm period-based bioclimatic values by fossil specimens and the derived lower and upper limits used in the modelling. Supplementary Table 3 exhibits the fossil Pliocene



**Fig. 5** The mapped annual mean temperature and precipitation conditions of the used mid-Pliocene interglacial (A1, B1) and glacial (A2, B2) models were used in this study with modern seashores and country borders

hominins-related  $d^{18}\text{O}$  (‰) values and the modifying factors. Supplementary Table 4 presents the reconstructed mid-Pliocene warm period-based bioclimatic values by fossil specimens and the derived lower and upper limits used in the modelling.

### Classification of former climatic conditions

As noted above, ancient hominins could have notable climatic distribution limiting extrema. First, however, it would be important to establish which environments were preferred and avoided by ancient hominins. Because the former bioclimatic variables were reconstructed using all specimens-related climatic values, comparing them to the values of presently existing sites was possible. Since paleoclimates are not always fully comparable with existing climate conditions, it seems better to use Principal Component Analysis (PCA) to compare the current climatic characteristics of African sites. To classify the former climate conditions, I used the updated version (Kottek et al., 2006) of the Köppen–Geiger climate classification system (Geiger, 1954; Köppen, 1918). This system contains five main climate categories (tropical, dry, temperate, continental, polar) and several sub-groups based on seasonal precipitation and temperature patterns. Using PAST paleontological statistics software (Hammer et al., 2001), I employed the same bioclimatic variables of the 33 African cities as the basis for comparison with the reconstructed former climatic conditions. Supplementary Table 5 exhibits the bioclimatic values of the selected African cities.

## Results

### The main distribution areas of early hominins

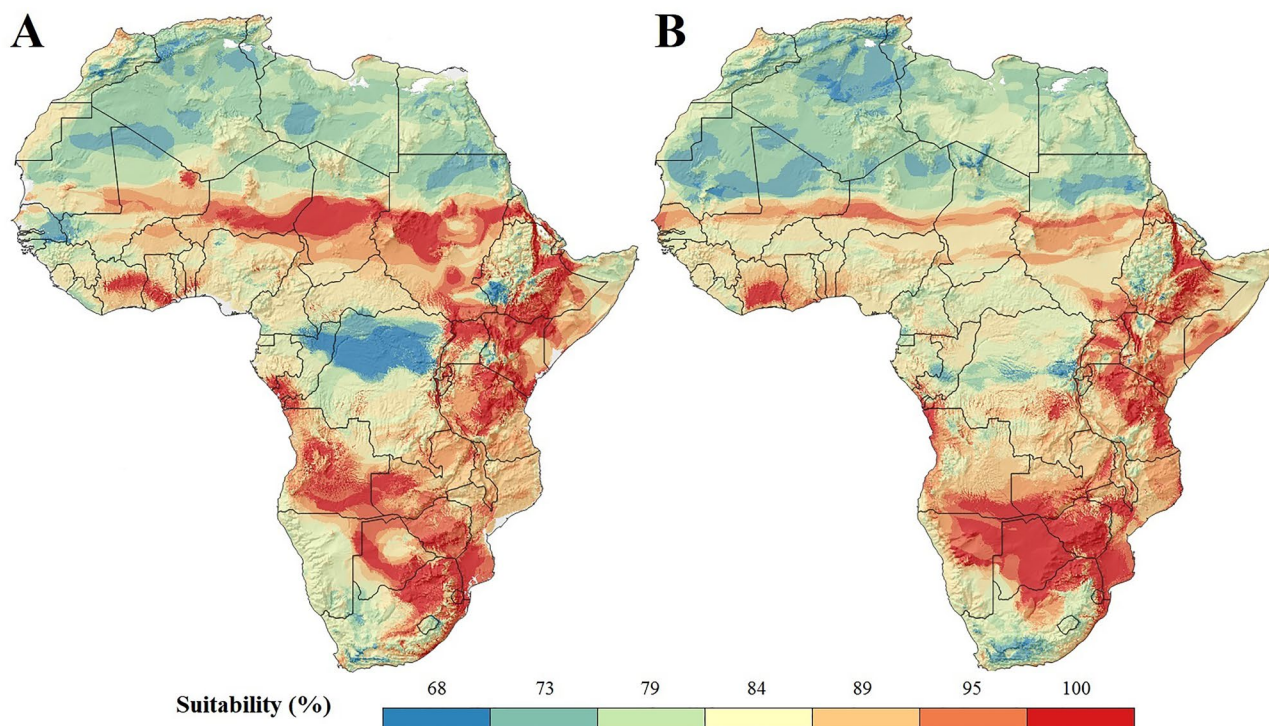
Based on the glacial and interglacial mean suitability patterns of the 3.5–2.5 Mya period, three slightly interconnected distribution ranges of hominins existed in Africa: one in the southern transition zone of Northern Africa, approximately in the present-day Sahel zone; a second in Eastern Africa along the Great Rift Valley; and the third in Southern Africa. Some smaller potential occurrences can also be seen in Western Africa. The Sahel region was not climatically suitable for early hominins during the glacial phases. A common element of the glacial and interglacial models is that the central and northern regions of present-day Sahara, Central Africa, and the southernmost regions of Southern Africa were less suitable for hominin species. The mean Pliocene hominin suitability values of the interglacial (Fig. 6A) and glacial (Fig. 6B) periods show substantially different patterns.

### Modelled alternations of suitability values

The models show a notable, albeit variable, level of contraction of early hominin habitats during the colder phases of the period 3.5–2.5 Mya BP in the Sahel zone of Northern Africa. In this region, the aridification caused by cold periods may have resulted in the fragmentation and almost total disappearance of the early hominin-suitable areas. This region's most serious habitat contractions occur in 2.933, 2.816, 2.713, 2.651, and 2.532 Mya BP when the modelled mean suitability values dropped below 73% in notable parts of the present-day Northern Sahel region. In 3.339, 3.296, 3.141, 3.001, 2.933, 2.816, 2.713, 2.651, and 2.532 Mya BP, almost the entire Sahara appears uninhabitable for Pliocene hominins. While the western part of Southern Africa was hostile to hominins in warm climatic phases, the model results suggest that hominins retreated from this region in the glacial periods. In Eastern Africa, the potential range of the early hominins is generally wider in the greenhouse climate model than in the glacial climate model (Fig. 7). While in the interglacial periods, the south Sahel belt of Northern Africa and the northern part of Eastern Africa may have been hostile for hominin species, in the glacial periods, the habitable areas could disappear from this region. In general, the wetter parts of the Sahara could only be suitable for hominins in the interglacial eras. These changes were not accompanied by the north-to-south direction shift of habitable areas for hominins, which indicates serious ecological crises during the glacial periods in Northern Africa. In Southern Africa, the climatic fluctuations resulted in the redistribution of the climatically suitable areas, although in the warmest periods, large regions of South Africa became suitable for hominin species.

### Inter-period suitability changes

There are notable suitability differences between the adjacent interglacial and glacial periods except for the period pairs of 3.339–3.296, 3.289–3.189, and 2.713–2.651 Mya BP. Based on the model results, the most notable parallel habitat expansions occurred in Northern and Eastern Africa between the periods of 3.436–3.398, 3.296–3.289, 3.141–3.074, 3.001–2.987, 2.933–2.883, 2.816–2.751, 2.651–2.637, and 2.532–2.505 Mya BP. The most serious parallel habitats lost in Northern and Eastern Africa could have occurred in the periods of 3.398–3.339, 3.189–3.141, 3.074–3.001, 2.987–2.933, 2.883–2.816, 2.751–2.713, and 2.637–2.532 Mya BP. The modelled values show that habitat instability may have increased in Northern and Eastern Africa over time in the 3.5–2.5 Mya period because the most notable habitat gains and losses plausibly occurred in the second part of the period. In South Africa, notable habitat gains can be seen in the period pairs of 3.459–3.436,



**Fig. 6** The average suitability of the climate of Africa for early hominins in the mid-Pliocene greenhouse (A) and glacial periods (B) in 2.506–3.459 Mya BP (with modern seashores and country borders).

3.398–3.339, 3.189–3.141, 3.074–3.001, and 2.532–2.505 Mya BP; notable habitat losses occurred in 3.436–3.398, 3.296–3.289, 3.141–3.074 and 3.001–2.987 Mya BP. Almost continent-wide habitat gains occurred in 2.933–2.883, 2.816–2.751, 2.651–2.637 Mya BP, and a continent-wide habitat expansion can be seen in 2.532–2.506 Mya BP. The most devastating continent-wide habitat declines could have occurred in 2.883–2.816, 2.751–2.713, and 2.532–2.506 Mya BP (Fig. 8).

The modelled suitability values showed varying degrees of fluctuation depending on the area and modelled time. In the case of Chad, the suitability values varied between 64–100%, with a mean value of 84% and a standard deviation (SD) of 12.02%. The suitability values of Ethiopia ( $n=6$ ) varied between 82–100% (mean: 93%, SD: 4.90%). For Central Eastern Africa (Kenya, Tanzania,  $n=8$ ), suitability values varied between 61–100% (mean: 84%, SD: 10.58%). In Southern Africa (South Africa,  $n=3$ ), these values were 71–100% (mean: 89%, SD: 8.97%) (Fig. 9).

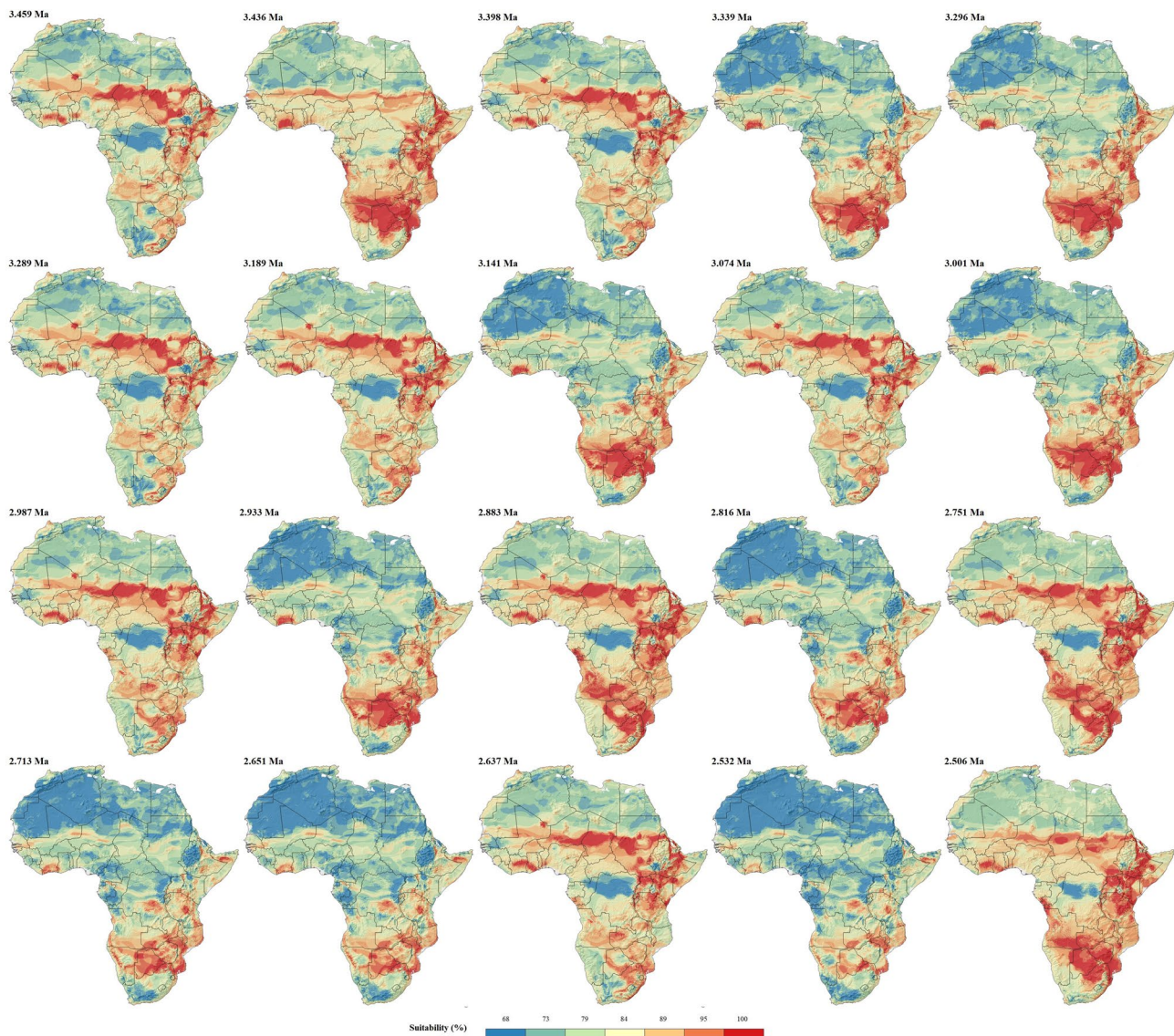
### Climatic affinity of early hominins

The PCA of the reconstructed paleoclimatic conditions of the Pliocene hominin sites showed that the fossil specimens related to them could be classified into six main groups:  $\alpha$

It should be noted that both tropical deserts and tropical rainforest areas show low suitability values

group – BAR 1000 (11), BAR 1215 (12), and KNM-TH 13150 (13) specimens of *A. anamensis* and *Orrorin tugenensis*;  $\beta$  group – LH4 (14) and Laetoli Footprints (15): *A. afarensis* and unspecified bipedal hominin traces (the Laetoli Footprints were perhaps made by *A. afarensis* (Sellers et al., 2005));  $\chi$  group – KNM-WT 40000 (7), KNM-KP 29287 (8), KNM-LT 329 (9) and KNM-KP 271 (10): *A. anamensis* and *Homo (Kenyanthropus\*) platyops* (\* belongs to *Homo* according to Cela-Conde & Ayala, 2003);  $\delta$  group – TM 266-01-060-1 (1), LD 350-1 (2), AL 288-1 (3), ALA-VP 1/20 (4), ARA-VP-6/500 (5), DIK-1/1 (6), KT-12/H1 (19), KSD-VP-1/1 (20), BRT-VP-3/14 (21), NFR-VP-1/29, (22), AL 200-1 (23), AL 129-1 (24), AL 444-2 (25): *A. afarensis*, *A. bahrelghazali*, *A. deyiremeda*, *Ar. kadabba*, *Ar. ramidus*, early *Homo*, and *S. tchadensis*;  $\epsilon$  group – Stw 573 (17) undetermined *Australopithecus sp.*, and MLD 46 (16) *Australopithecus africanus*;  $\phi$  group – Taung Child 1 (18): *A. africanus* (Fig. 10A).

The paleoclimate of the sites can be compared with the climate of the selected 33 contemporary African cities. The paleoclimate of the sites related to the BAR 1000 (11) and BAR 1215 (12) *O. tugenensis*, and the KNM-TH 13150 (13) *A. anamensis* specimens can be characterized as the intersection of the relatively humid, tropical savanna (*Aw*) and subtropical highland oceanic (*Cwb*) climates. The specimens

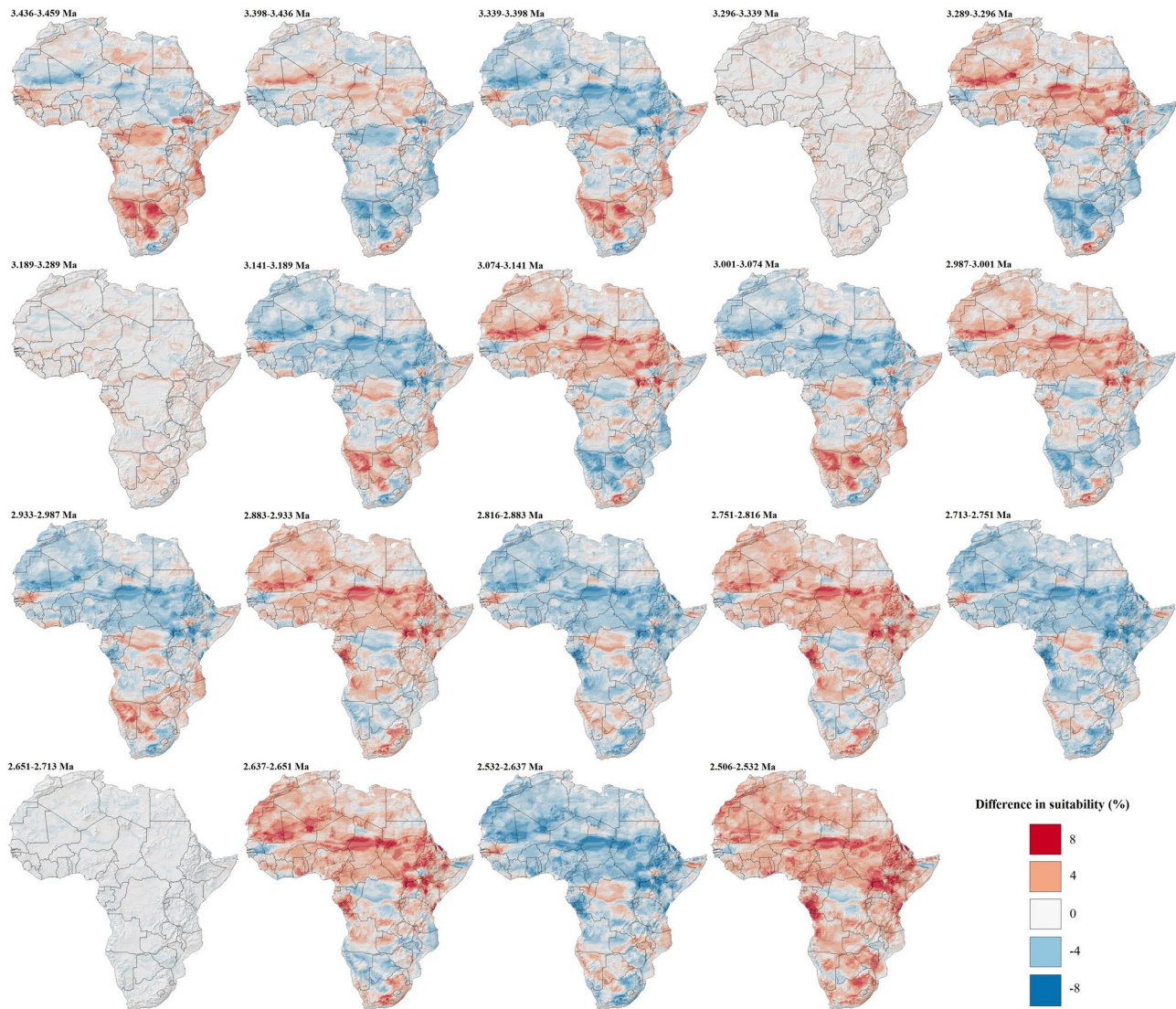


**Fig. 7** The suitability of the climate of Africa for hominins in the mid-Pliocene interglacial (A) and glacial periods (B) in 2.506–3.459 Mya BP (with modern seashores and country borders). It should be noted that both dry and wet areas exhibit low suitability values

related to the LH4 finding (14) *A. afarensis* and Laetoli Footprints bipedal hominins (15) plausibly lived under such climate, which can be characterized by the intersection of tropical savanna (*Aw*) and semi-arid (*Bsh*) climates. It is plausible that the ancient hominins related to specimens KNM-WT 40000 (7) *H. platyops* and the KNM-KP 29287 (8), KNM-LT 329 (9) and KNM-KP 271 (10) *A. anamensis* lived under hot semi-arid (*Bsh*) climatic conditions. The hominins of TM 266–01–060–1 (1) *S. tchadensis*, LD 350–1 (2) *Homo sp.*, ALA-VP 1/20 (4) *A. kadabba*, ARA-VP-6/500 (5) *A. ramidus*, and DIK-1/1 (6) and KSD-VP-1/1 (20) and NFR-VP-1/29 (22) and AL 200–1 (23) and AL 129–1 (24) and AL 444–2 (25) *A. afarensis*, BRT-VP-3/14 (21) *A. deyremeda*, MLD 46 (16) *A. africanus*, as well as the KT-12/

H1 (19) and KT-12/H1 *A. bahrelghazali* lived in a semi-arid (*Bsh*) climate. AL 288–1 (3) lived under a drier subtropical highland *Cwb* climate with notable *BSh* climatic influence. The individual of the Stw 573 *Australopithecus sp.* lived in a *Cfb* (oceanic)-like climate. It is plausible that the Taung Child 1 *A. africanus* lived under Mediterranean-like (*Csa*) climatic conditions. Thus, most of the identified fossil hominins lived in relatively dry, semi-arid (*BSh*) or tropical savanna (*Aw*) climates or in wetter but not tropical wet (e.g., tropical rainforest) conditions. Generally, Pliocene hominins did not inhabit the very dry (arid = tropical desert, *BWh*) and wet (e.g., tropical monsoon climate, *Am*) regions (Fig. 10B).

The characteristic differences among the bioclimatic extrema of *A. afarensis*, *A. africanus*, *A. anamensis*, *O.*

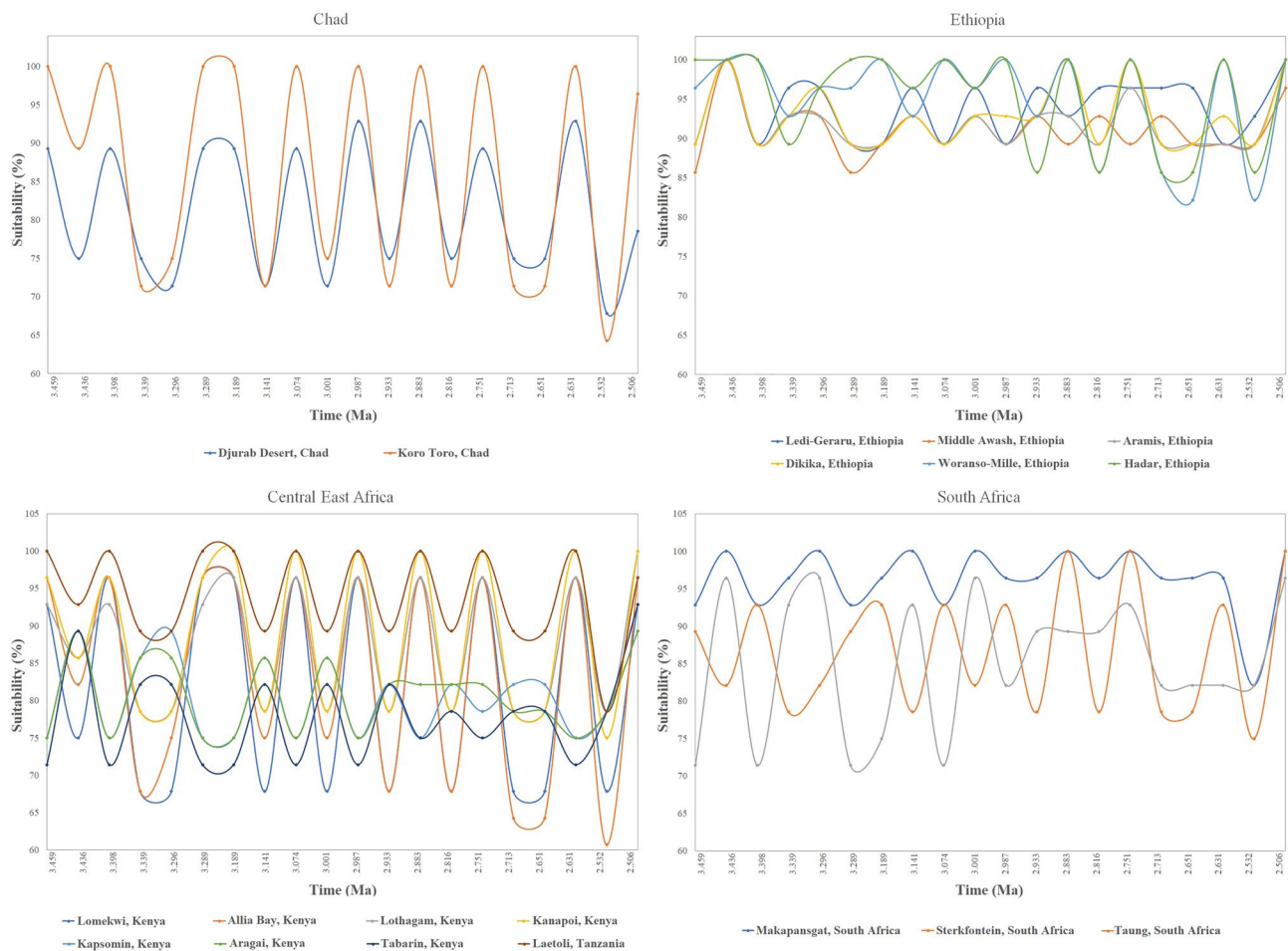


**Fig. 8** The differences in the modelled suitability values of the climate of Africa for early hominins between the mid-Pliocene greenhouse and glacial period in 2.506–3.459 Mya BP (with modern seashores and country borders)

*tugenensis* (in the case of these four species more than one specimen was involved in the study) in these four early hominins-inhabited regions can be identified. *Australopithecus afarensis* tolerated the climate of regions where the precipitation seasonality was the highest, the precipitation sums of the driest month (the same value as in the case of *A. africanus*), as well as the precipitation of the warmest quarter, were the lowest among the occurrence sites of the four species.

In the case of *A. afarensis*, the precipitation of the driest quarter could be almost as low as in the case of *A. africanus*, which exhibits the lowest corresponding value. *Australopithecus africanus* inhabited those regions where the annual mean temperature, the mean temperature of the driest and coldest quarters, as well as the precipitation sums of the

driest (the same value as in the case of *A. afarensis*) and wettest months, furthermore, the driest quarter and the precipitation of the coldest quarter were the lowest. In addition, the former climate of the archaeological sites related to this species had the highest temperature seasonality values when *A. africanus* inhabited them. The archaeological sites of *A. anamensis* occurred in regions where the annual mean temperature, the mean temperature of the warmest, coldest, driest, and wettest quarters, and the precipitation of the wettest quarter were the highest, and the temperature seasonality and the annual precipitation sum values were the lowest. *Orrorin tugenensis* occurred in a region with the lowest mean temperature in the wettest and warmest quarters, received the highest annual and quaternary rainfall sums, and the annual rainfall seasonality was the lowest (Fig. 11).



**Fig. 9** The fluctuations of the suitability values related to Pliocene hominin species in different African regions in 2.506–3.459 Mya BP

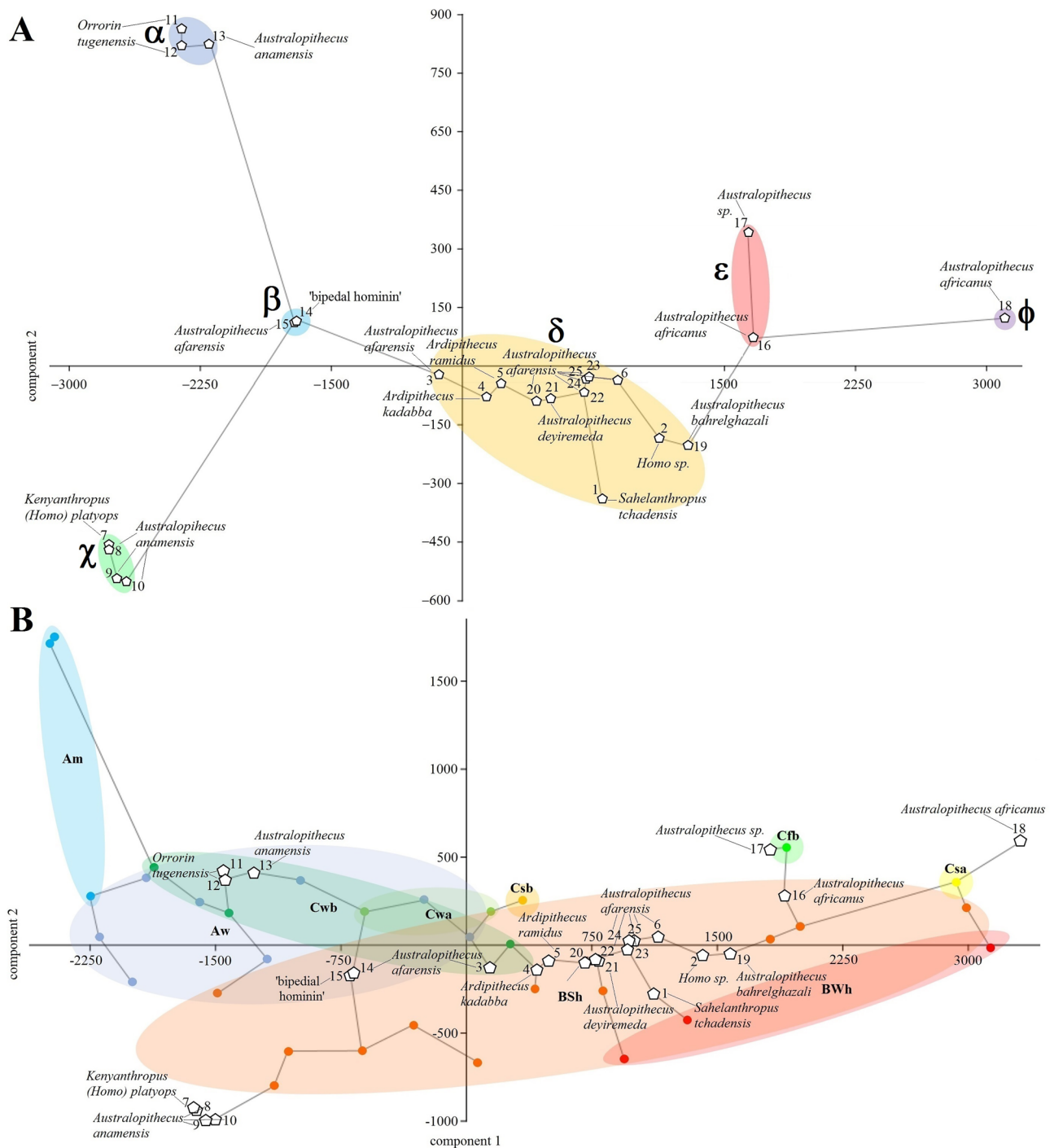
It can be concluded that among the four species, *Australopithecus afarensis* inhabited regions where, due to the generally high temperatures, low precipitation sums and high precipitation seasonality, the risk of drought (relative water scarcity) might have been greatest, and *O. tugenensis* arguably lived in the most balanced, humid, equatorial-like climatic conditions. Furthermore, based on the wide environmental tolerance of the species, *A. afarensis* could have been the most resistant of the four species against large-scale climatic fluctuations (Supplementary Table 6).

## Discussion

The model results indicate geographic variation among the effects of Pliocene glacial episodes on the range of early hominins. In Northern Africa, cooler and drier climatic conditions caused the fragmentation and almost the total disappearance of the areas inhabited by early hominins. In Southern Africa, the glacial stages resulted in the shift of

habitable territories. In Northern and Southern Africa, the geographical barriers to the migration of early hominins may have been fewer. Naturally, large rivers, tropical rainforests, and deserts formed as much as barriers for ancient hominin movement as the seas and mountain ranges.

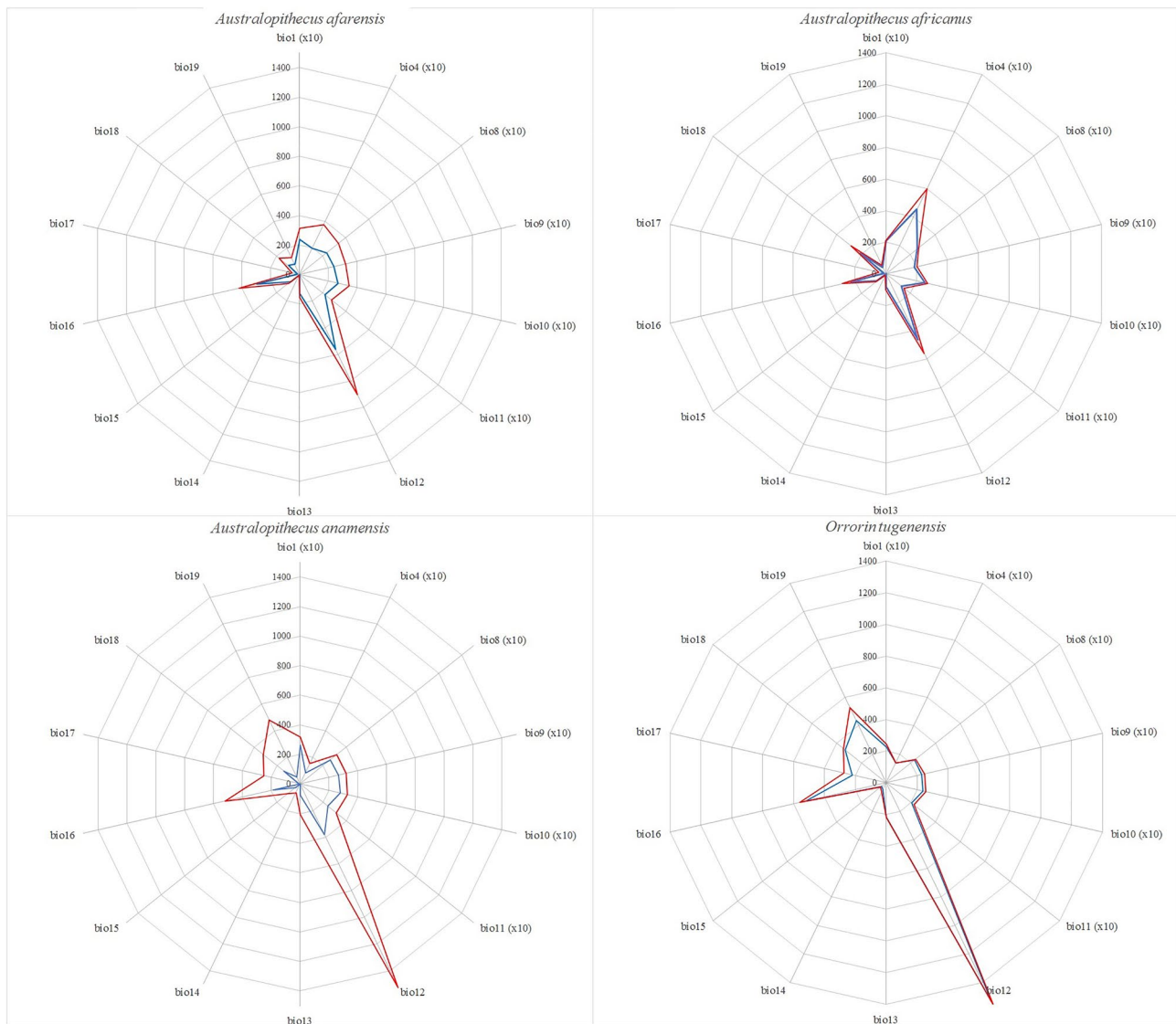
It is important to distinguish between the northern and the central parts of Eastern Africa in terms of the variability of the mean level and, in several periods, the extent of the suitability fluctuations in the northern and central parts of Eastern Africa during the Middle and Late Pliocene. The cooling periods may have negatively impacted the habitability of several important fossil site areas in general, such as Lake Turkana, the Olduvai Gorge, and Laetoli, where the increase in the suitability values could have been specially marked after 2.883 Mya. However, great habitat contraction might have also occurred before this in the 3.398–3.339 Mya BP period. These results directly match the findings of Robinson et al. (2017), who found that the climate of the two regions was largely similar throughout the Plio–Pleistocene epoch. They may indicate that important environmental differences



**Fig. 10** **A:** The results of the principal component analysis of the reconstructed Pliocene hominin fossils-related site's bioclimatic values with the minimum spanning tree; **B:** the results of the PCA analysis of the reconstructed bioclimatic values of the Pliocene hominin fossil specimens and the climatic values of 33 African cities with the minimum spanning tree; components 1 and 2 are the values of first and second principal components. Fossil specimens: 1: TM 266–01-060–1 (*S. tchadensis*), 2: LD 350–1 (*Homo sp.*), 3: AL 288–1 (*A. afarensis*), 4: ALA-VP 1/20 (*Ar. kadabba*), 5: ARA-VP-6/500 (*Ar. ramidus*), 6: DIK-1/1 (*A. afarensis*), 7: KNM-WT 40000 (*H. platyops*), 8: KNM-KP 29287 (*A. anamensis*), 9: KNM-LT 329 (*A. anamensis*), 10: KNM-KP 271 (*A. anamensis*), 11: BAR 1000 (*O. tugenensis*),

12: BAR 1215 (*O. tugenensis*), 13: KNM-TH 13150 (*A. anamensis*), 14: LH 4 (*A. afarensis*), 15: Laetoli Footprints (bipedal hominin), 16: MLD 46 (*A. africanus*), 17: Stw 573 (*Australopithecus sp.*), 18: Taung Child 1 (*A. africanus*), 19: KT-12/H1 (*A. bahrelghazali*), 20: KSD-VP-1/1 (*A. afarensis*), 21: BRT-VP-3/14 (*A. deyiremeda*), 22: NFR-VP-1/29 (*A. afarensis*), 23: AL 200–1 (*A. afarensis*), 24: AL 129–1 (*A. afarensis*), 25: AL 444–2 (*A. afarensis*). Köppen-Geiger climate categories: *Am*: tropical monsoon climate, *Aw*: tropical savanna climate, *BSh*: semi-arid climate, *BWh*: arid climate, *Cfb*: oceanic climate, *Csa*: hot dry-summer Mediterranean climate, *Csb*: cool dry-summer Mediterranean climate, *CWa*: humid subtropical climate, *CWb*: subtropical highland oceanic climate)





**Fig. 11** Radar chart of the distribution-limiting climatic extrema of *A. anamensis*, *A. afarensis*, *A. africanus* and *O. tugenensis*

existed during the emergence of *Homo* around 2.8 Mya BP between the northern and central parts of Eastern Africa.

In examining the consequences of current climate change, I identified that the shift of the climatic belts in the last two decades has resulted in either notable habitat losses or gains of hominin species (Hume et al., 2016; Klausmeyer & Shaw, 2009). Currently, mainly the primates of the rainforest ecosystems seem to be the species most endangered by human-induced climate change (Graham et al., 2016). Many Afro-Arabian primates became extinct near the Eocene–Oligocene boundary due to the increasing continentality of the climate and the decline of the rainforest ecosystems (Seiffert, 2007). In the Tortonian period, rich hominoid fauna inhabited the former humid and warm temperate climate regions of West, Central and South Europe. However, it became extinct due

to the disappearance of the subtropical forests during the drier and cooler Pliocene epoch (Rook et al., 2000). It is also possible that a somewhat similar climatic change resulted in the extinction of *A. afarensis*, the appearance of the *Paranthropus* species in a period of increasingly extreme climate in 2.9–2.7 Mya, and the emergence of *Homo* (de Menocal, 2011) about in 2.6 Mya (first appearance calculator data of Fossilworks.org, based on assuming continuous sampling method of Strauss & Sadler, 1987, 1989). As the models I present here show, during the cooler and more continental climate episodes of the mid-Pliocene, the Eastern African distribution of the early hominins could have been smaller than in the warmer and more balanced periods. This result confirms that ecological stress situations may have led to the partial extinction of early hominins and the emergence

of new groups in Eastern Africa in the Pliocene glacial episodes.

Although the exact reconstructions of former paleoclimatic conditions were the focus of this study, my results show good correlations with the bioclimatic reconstructions. The multi-model simulations of Prescott et al. (2017) showed that in the mid-Pliocene warm period, the south Sahel belt and the northern areas of Southern Africa were covered by tropical xerophytic shrublands, and Eastern Africa (depending on elevation) had xerophytic shrublands, tropical savannas, and tropical deciduous forests. These are the regions where Pliocene hominin remains were found. The PCAs also showed that most of the Pliocene hominins preferred the semi-arid and tropical savanna-like (open, mixed, or forested) climate areas of Africa but did not inhabit arid and expressly humid tropical climatic areas. It was also found that these conditions rapidly changed in the second half of the Pliocene. The results indicate that the climatic fluctuations in varying ways and to different degrees affected the suitability patterns of the regions. In general, the colder eras had a parallel negative effect on both the general suitability values of Northern and Eastern Africa but were not always the case. For example, the global cooling in 3.296–3.289 or 3.141–3.047 Mya could have resulted in the clear decline of the Northern African hominin populations, although a less dramatic change in East Africa, and no change in the Southern African area. I identified an increasing trend in continent-wide habitat fluctuations in the period of 3.5–2.5 Mya.

The PCA data suggest that Pliocene hominins did not favour the tropical rainforest and tropical monsoon areas. Interestingly, in the Middle Palaeolithic era, archaic humans also avoided the equatorial hot and humid climate regions of Africa (Trájer et al., 2020). One possible explanation is that semi-arid and tropical savanna environments provided the most congenial habitats, notably sufficient food resources for Pliocene hominins. Under a tropical savanna climate, much of the plant biomass can be found in the carbon store of the soil and the rhizomes of the savanna grasses. It is a monocotyledons and bush-size dicotyledons-based ecosystem engineered and maintained by episodic fires, large herbivores, and termites (Schuurman, 2005; van Langevelde et al., 2003) limits vegetational succession. Henry et al. (2012) found that *Australopithecus sediba* (Lee et al. 2010), like modern savanna chimpanzees, consumed C3 dicotyledons, including leaves, fruits, woods, barks, grass species, and sedges. In contrast, Quinn (2019), found that the diet of present-day savanna-dwelling common chimpanzees cannot be a direct dietary analogue of *A. anamensis* from the Pliocene Omo-Turkana Basin. The enamel carbon isotope data from *A. afarensis* within the Hadar Formation indicate that this species consumed significant amounts

of 13 carbon-enriched foods, e.g., C4/CAM plants and/or the meat of herbivores that consumed these such plants (Wynn et al., 2013). Based on the carbon isotope data and the accompanying fossil fauna of *Australopithecus bahrelghazali* findings from Koro Toro in Chad (Brunet et al. 1995), Lee-Thorp et al. (2012) claimed that this species lived in open-to-wooded grasslands and stream channels associated with a greatly enlarged Lake Chad.

These findings indicate that while Pliocene hominins occupied various environments, they might have fallen within the range of the tropical climates of Africa I present here. However, based on isotopic evidence, Wynn et al. (2020) showed that ca. 2.37 Mya, the diet of both robust and gracile hominins shifted toward C4-plants like grasses and sedges. This dietary and habitat shift may have resulted from rapid climatic changes in about 2.816–2.500 Mya BP, whose effects I described. The rapid but notable cooling periods could have resulted in the extension of grasslands to the detriment of the forests. Furthermore, isotopic dietary studies of early hominins showed a great dietary gap between *H. habilis* and *Paranthropus boisei* (e.g., Broom, 1938 in Tanzania). In variable environments, competition among similar niche-occupying species can frequently lead to dietary opportunism and segregation (Rotenberry, 1980), which may have led to greater specialization among early hominin populations in Eastern Africa.

It is important to address the methodological bias stemming from the nature of the fossil record. Fossil remains of Pliocene mammals have been found in the same regions in Africa as hominin remains, including Eastern Africa, Chad, and Southern Africa (Fig. 1). It is clear that knowledge of non-hominin mammalian remains is partly a consequence of the search for human ancestors. The scarcity of Pliocene hominin fossils in West and Central Africa makes it difficult to evaluate the model results related to these areas. Maxwell et al. (2018) also warned that due to the sporadic occurrence of ancient hominins, a highly cautious approach is needed before testing hypotheses about the impact of climatic alternations on human evolution. However, there is no theoretical reason for the lack of early hominin fossils in West and Central Africa. It is plausible that weather conditions strongly influence the possibility of fossilization of the skeletal remains of mammals. Although it is a common assumption that the decomposition of skeletal remains in rainforest environments is especially rapid, Tappen (1994) has demonstrated that this is not necessarily so. Ross and Cunningham (2011) showed that the process could be much more rapid in a savanna environment than in shaded rainforests due to animal predation and intense solar radiation. Further, it is well-recognized that karst-filling sediments are suitable for preserving skeletal remains. Hollingsworth et al. (2006) document notable karst regions in West, Central, and Northern Africa, indicating that there could have been no

obstacle to the fossilization of early hominin remains in these areas.

The role of climatic factors cannot be interpreted separately from the geographic conditions and effects. Palaeogeographic events also play an important role in determining where primates occurred (Thompson, 2003). In addition, local topography and hydrology can influence the genetic structure of ape populations (Eriksson et al., 2004), possibly may indicating that habitat shifts due to climate changes combined with various geographic barriers may have influenced the evolution of the ancestors of the *Homo* species in complex ways. In Eastern Africa, the Great Rift Valley, the East African volcanic chain, the distribution of the large lakes in tectonic trenches, and the coastline of the Indian Ocean have a clear north-to-south alignment. The oldest part of the East African Rift Valley in Kenya dates to around 20–25 Mya BP; the most recent in Malawi is dated ca. 9 Mya BP (Zwaan & Schreurs, 2020). The strong north–south geographical asymmetry in Africa has been related to the degree of climatic specialization of large mammals, including primates (Fernández & Vrba, 2005). According to the Rapoport effect, which is now agreed not to be universal, the most important predictor of latitudinal variability in biomic specialization in northern-hemisphere Africa is temperature variability. In contrast, the continental area is the primary predictor of biomic variability in the southern hemisphere. This observation warns that similar climatic differences in the southern and northern hemispheres did not necessarily trigger the same evolutionary events among early hominins, even in the case of widely distributed, identical, or closely related species.

## Conclusions

Mid-late Pliocene climatic fluctuations resulted in notable habitat contraction–expansion events of early African hominins. The South Sahel region of Northern Africa was inhabited in the interglacial phases and depopulated during the glacial periods. Although the coldest glacial periods could also strongly reduce habitable territories in the present-day territories of Ethiopia, Kenya, and Tanzania, the long-term environmental conditions of Ethiopia seem to have been more stable for early hominins compared to other regions on the continent. In Southern Africa, the effect of cold phases could have been advantageous for early hominins in a climatic suitability sense. On the other hand, interglacial phases in this region generally could negatively influence hominin populations of the western regions of Southern Africa (e.g., Namibia). While the early bipedal hominin *O. tugenensis* possibly lived in regions that resembled the present-day climate of the apes' habitats in equatorial Africa,

*A. afarensis* tolerated dry, relatively hot regions of Northeast Africa, where precipitation seasonality was notable.

## Data Availability Statement

The author confirms that all data generated or analysed during this study are included in this published article.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10745-023-00415-y>.

**Author contributions** The author is solely responsible for this research.

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## Declarations

**Conflict of Interest** The author declares he has no conflict of interest.

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