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Relevance of the eastern African coastal forest for early hominin biogeography

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ABSTRACT

The influence of climate change on hominin evolution is much debated. Two issues hamper our understanding of this process: the limited hominin fossil record, and incomplete knowledge about hominin spatial occupation of Africa. Here, we analyze the presently known hominin fossil distribution pattern and explore the potential geographic distribution of hominins between ~4.5 and ~2.5 Ma. We focus on assessing the relevance of the Coastal Forest of Eastern Africa (CFEA) along the Indian Ocean as a core area for early hominin evolution. Based on biogeographic-phylogeographic data we propose the coastal refuge hypothesis: the CFEA provided a refugium for early hominins in periods of variable climate and strong seasonality during eccentricity maxima. From this refuge, evolved species could disperse inland (e.g. to rift basins) via vegetated humid corridors, whenever onset of stable climate periods with low seasonality during eccentricity minima allowed expansion out of the coastal enclave. We develop a conceptual model in time and space, comparing predictions with climatic and hominin fossil records. The results imply that:

- 1) between ~4.5 and 3 Ma, ongoing (mostly anagenetic) hominin evolution occurred in the CFEA, punctuated by inland dispersal events at ~4.4, 4.2, 3.8, 3.5, and 3.2 Ma;
- 2) before ~3 Ma, the Afar Basin was a (sub)core area often connected to and relatively similar to the CFEA, while other inland areas were more or less marginal for early hominin habitation;
- 3) after ~3 Ma, Northern Hemisphere Glaciation exerted strong influence by causing latitudinal contraction of the CFEA, leading to habitat fragmentation, isolation of hominin populations and possible cladogenetic evolution.

A major challenge for the coastal refuge model is the fact that at present, no (hominin) fossils are known from the CFEA. We consider how this can be explained, and possibly overcome with targeted search efforts. Furthermore we discuss how the model can be tested, e.g. with molecular phylogeography approaches, and used to predict new hominin fossil locations. With this study, we hope to contribute a fresh perspective to the climate–evolution debate, emphasizing the role of climatic stability, length of dry season and vegetation cover to facilitate connectivity between hominin core and marginal habitats.

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1. Introduction

For decades, paleoanthropologists have studied the influence of climatic and environmental change on early hominin evolution in Africa (e.g. Vrba, 1988, 2007; Vrba et al., 1995; Potts, 1998a,b, 2007,

2013; Bobe et al., 2002; Bonnefille et al., 2004; Wynn, 2004; deMenocal, 2004, 2011; Behrensmeyer, 2006; Maslin and Christensen, 2007; Maslin and Trauth, 2009; NRC, 2010; Joordens et al., 2011; Grove, 2012; Potts and Faith, 2015; Levin, 2015; Marean et al., 2015; Cohen et al., 2016; Campisano et al., 2017). Yet, there are two major issues that still obstruct our understanding of factors influencing early hominin evolution (Spoor, 2016). First, we have to face the ugly fact that the fossil record is intrinsically limited, constituting an imperfect representation (on the order of a

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few percent only) of actual species diversity that existed over time (Martin, 1993). Second, the part of this limited hominin fossil record that has been found so far (Fig. 1a) was recovered from areas that cover only a fraction of the African continent (Fig. 1b). The fossils mainly derive from the eastern branch of the East African Rift System (EARS) and from southern African caves, where conditions for fossilization and subsequent exposure are favorable and search efforts by paleoanthropologists have been greatest (Wood, 2002; Spoor, 2016). Maxwell et al. (2018) investigated whether the presently known early hominin fossil record is of sufficient quality to test climate-forcing hypotheses. They found that apparent relationships between early hominin taxonomic diversity and climatic indicators could be largely explained by variation in exposure of suitable sediments and fossil collection effort, instead of climate.

Based on temporal and spatial hominin distribution patterns resulting from this evidently biased fossil recovery, the EARS and southern Africa have often been considered as not only fossil-rich locations, but also “birthplaces” of hominin species and thus the main theater of hominin evolution (e.g. Coppens, 1994; Maslin et al., 2014). However, the discovery of early hominin fossils in the Chad Basin in western-central Africa (Brunet et al., 1995, 2002; Lebatard et al., 2008), 2500 km west of the EARS, served as a reminder that the EARS and southern African sites must represent only a small and perhaps even marginal part of the total possible hominin occupation area in Africa (Joordens, 2011; Joordens et al., 2012, 2017; Spoor, 2016). The recent study on earliest *Homo sapiens* fossils from northwestern Africa also highlights the fact that hominin evolution was not restricted to eastern and southern regions, but must have been a pan-African process (Hublin et al., 2017). These observations on an imperfect fossil record and incomplete knowledge about hominin occupation of Africa demonstrate that paleoanthropologists have only a few pieces of the puzzle, and that it is not even clear how big the puzzle is. Maxwell et al. (2018) concluded that a sustained and major increase in fossil sampling intensity is required before an accurate understanding of links between climate and early hominin diversification can be determined. Unfortunately even such an effort, though helpful, would not be enough to solve the issues of an intrinsically limited fossil record as well as absence of fossiliferous Pliocene deposits in large parts of Africa. For instance, fossils

may never be found in the Congo Basin while it is entirely possible that such a forest area, an ideal primate habitat, played a role in hominin evolution (Spoor, 2016).

The challenge now is to find a way out of this apparent impasse, and to assess what other areas in Africa besides the EARS, southern Africa and Chad Basin may have been relevant for hominin evolution. A new and complementary approach is needed to circumvent the issues outlined above. We maintain that despite shortcomings of the presently known hominin fossil record, the pattern it reflects can provide a wealth of information when placed in a large-scale biogeographical framework encompassing a range of organisms (from insects and birds to large mammals and primates). As Kingdon (2003) pointed out, hominins must have been embedded in the same ecological matrices as other animals in Africa, so insights from recent faunal distribution and phylogeography patterns can be applied to extinct hominins. Also Vrba (2007) observed that with respect to environmental change, evidence from a range of organisms has shown that evolution of taxa does not consist of independent pieces of history but is rule bound, with common rules giving qualitative and temporal coherence to the evolutionary responses across many lineages. In this review, we therefore seek to create fresh perspectives on early hominin evolution by emphasizing the role of African geography, drawing on knowledge of faunal and floral evolution in Africa acquired by different disciplines -notably biogeography and molecular phylogeography. The aim of this study is to explore spatial distributions of early hominins across Africa over time, and ultimately to understand the influence of climatic and environmental change on the evolution and dispersal of early hominin species between ~4.5 and ~2.5 Ma. This is a key period covering the early appearance of bipedal hominins and earliest appearance of the genus *Homo* (Spoor, 2015; Villmoare et al., 2015, Fig. 1a).

We first present and analyze the geographic distribution pattern of known early hominin fossil occurrences over time. Next, we attempt to explain the pattern by 1) comparing it to patterns in non-hominin fossil records, and 2) placing it in a biogeographic context using the insights of Kingdon (2003) on the role of coastal forest along the Indian Ocean, concepts of refugia (Stewart et al., 2010), and results of molecular phylogeography studies. Based on these findings we formulate a working hypothesis and start

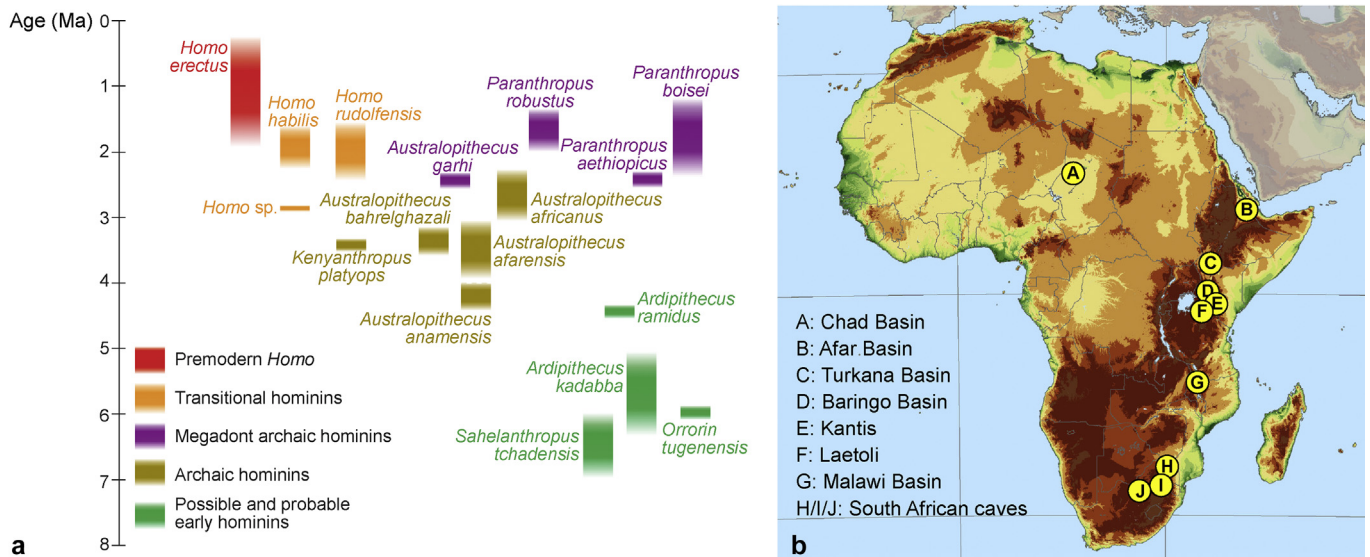


Figure 1. a. Major taxa of the presently known hominin fossil record over the past 7 million years (adapted from Levin, 2015). b. Elevation map of Africa indicating the locations of early hominin fossil sites (adapted from National Research Council (NRC), 2010; courtesy of David Feary).

developing a testable climate-driven biogeographic framework – a conceptual model – for early hominin evolution in Africa. Here we focus on assessing relevance of the coastal forest in eastern Africa (Fig. 2) as a primary refugium for early hominins, while acknowledging that it will be a simplification of the complex actual history of early hominin evolution. Likely, hominins used not one but multiple temporary small and large, secondary and cryptic refugia elsewhere (e.g. eastern montane forests, western-central African forests, northern coastal Africa?) over time. We hope that our study provides an impetus for future studies to focus on the coastal forest, and on evolutionary relevance of additional unexplored parts of Africa.

2. The geographic distribution of early hominin fossils

To investigate hominin biogeography, two basic tasks need to be accomplished (Roebroeks, 2006): identifying the spatial and temporal pattern of hominin presence and absence (in other words ‘getting the pattern right’), and then explaining such a pattern. In

Figure 3 we present an overview of the currently known early hominin fossil record between ~4.5 and 2.5 Ma based on available literature, indicating numbers of fossils found per species, time period, and location. Detecting a meaningful pattern in fossil presence, absence and abundance is not a straightforward exercise (Roebroeks, 2006; Bobe and Leakey, 2009; Patterson et al., 2014; Sauron, 2015). Biased search efforts, absence or paucity of deposits from certain time periods and places, and differential preservation of bones in different environments prevent discovery of species that may have been present, and/or cause failure to capture actual first and last appearance dates of species (Hare, 1980; Signor and Lips, 1982; Roebroeks, 2006; Vrba, 2007; Bobe and Leakey, 2009; Maxwell et al., 2018). Moreover, it is difficult to make taxonomic identifications and infer evolutionary relationships based on few and often partial and/or damaged fossil remains (Grine, 2013). Likewise, occurrences of homoplasy (Wood and Harrison, 2011; Wood and Schroer, 2017) and hybridization (Ackermann, 2011; Popadin et al., 2017; Ackermann et al., 2018) can result in additional confounding factors for interpretation. Dating fossils can also

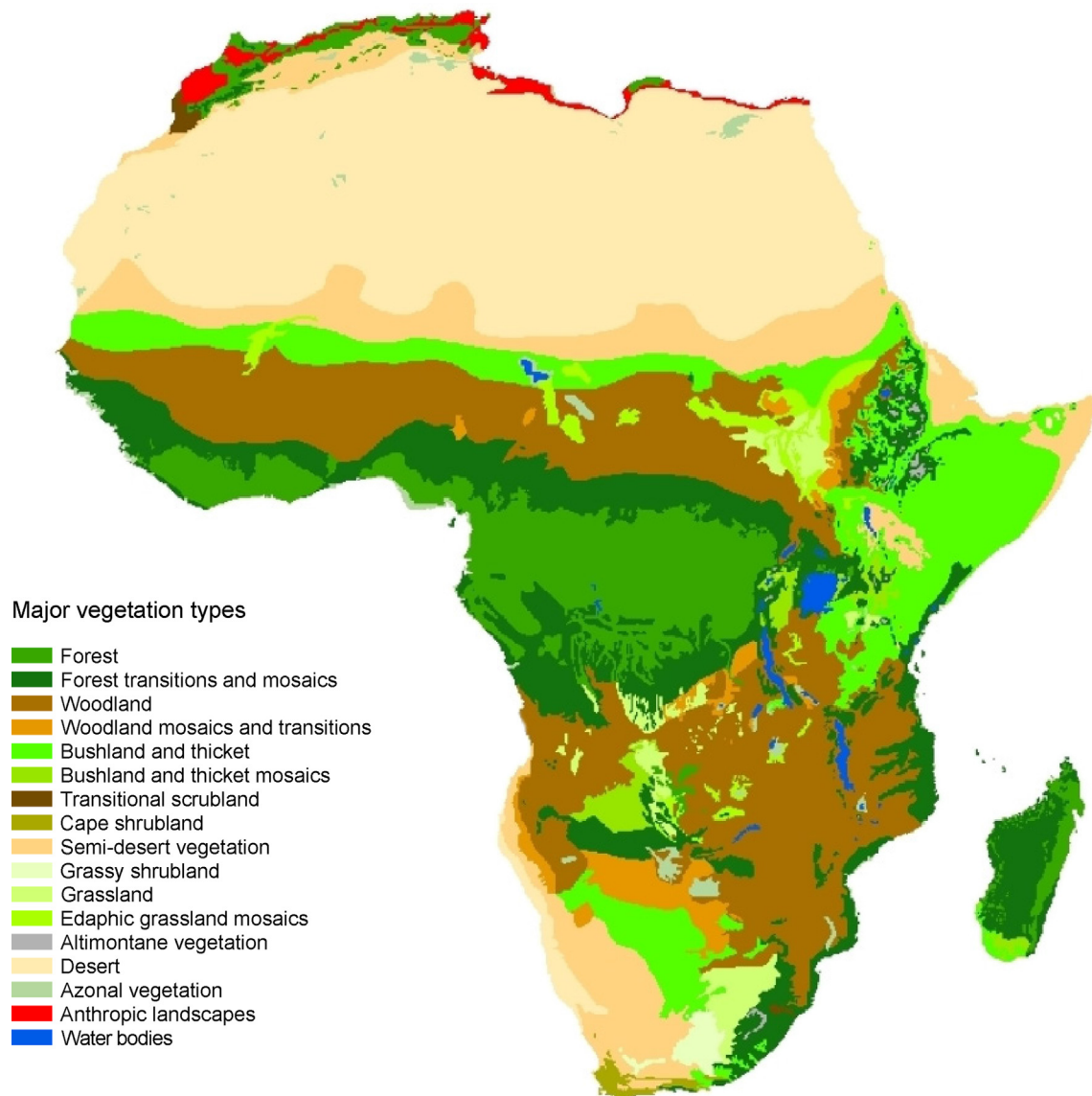


Figure 2. Vegetation map of Africa (White, 1983; UNESCO/AETFAT/UNSO) showing the present-day coastal forest extending along the Indian Ocean coast. Source: <http://geonetwork.grid.unep.ch/geonetwork/srv/en/graphover.show?id=838&fname=gnv031.png&access=public>.

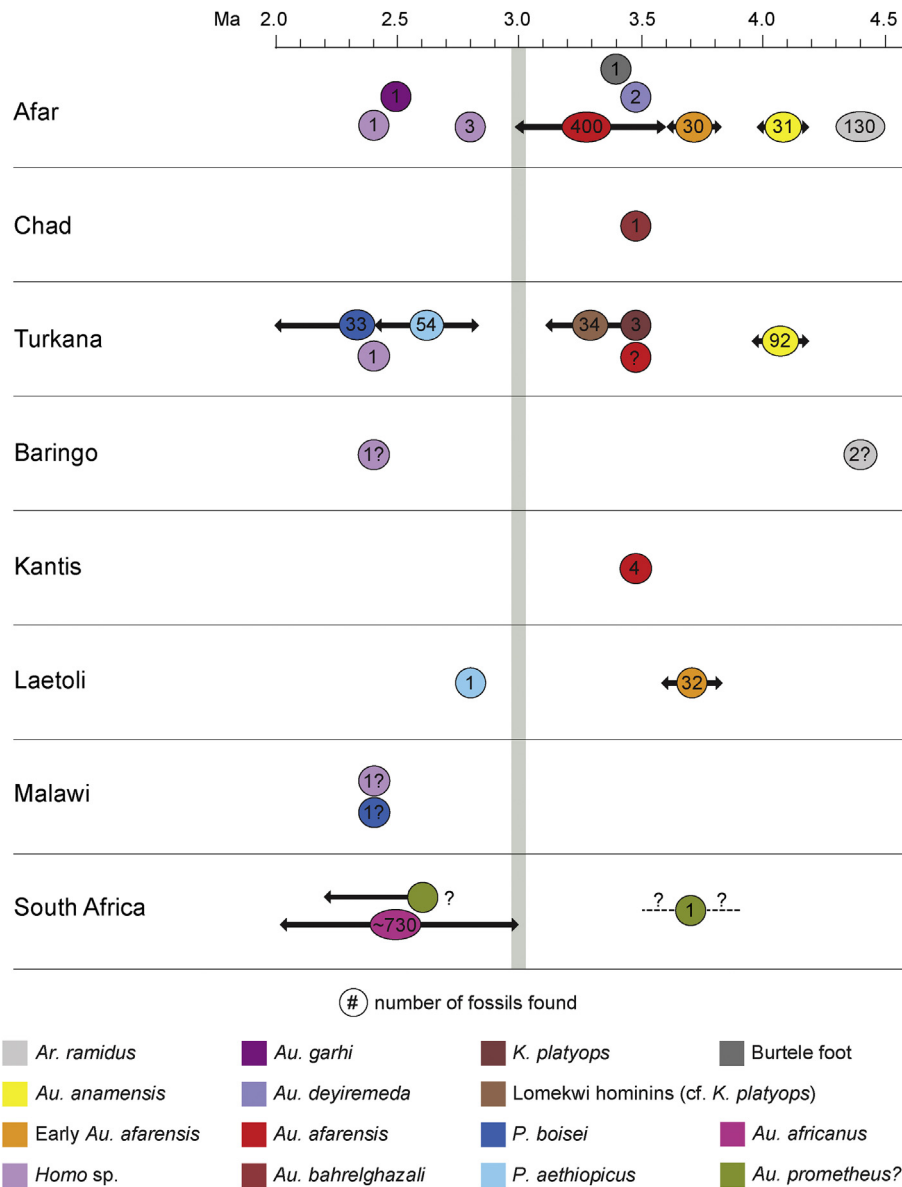


Figure 3. Overview of hominin fossil finds in Africa between 4.5 and 2.5 Ma (based on references in section 2 and additional references: Ward and Hill, 1987; Kimbel 1988, 1997; Hill et al., 1992; Berger et al., 1993; Schrenk et al., 1993, 2002; Leakey et al., 1998, 2001; Asfaw et al., 1999; Haile-Selassie, 2001, 2010; Deino et al., 2002; Partridge et al., 2003; Semaw et al., 2003, 2005; Moggi-Cecchi et al., 2006; Wood and Constantino, 2007; Kimbel, 2009; Kimbel and Delezene, 2009; Harrison, 2011; Wood and Leakey, 2011; Ward et al., 2013; Ward, 2014; Reed et al., 2015; Mckee and Kuykendall, 2016; Daver et al., 2018). Included are published fossils identified to species level, not fossils identified only to genus or family level. The numbers are estimated using the 'modified NISP count' method, if possible lumping all fossil specimens that are clearly part of the same individual (e.g. a partial skeleton), and counting other fossil specimens with unique accession numbers separately (John Rowan, pers. comm.). For *A. africanus* we counted fossil specimen accession numbers from Sterkfontein, Makapansgat, Taung and Gladysvale without lumping. Counting based on accession numbers without lumping overestimates numbers of individuals (Grine, pers.comm.).

be a major challenge, especially in complex depositional settings such as caves in southern Africa (Pickering and Herries, 2017). These difficulties are illustrated here below in a brief review of the hominin fossil record.

2.1. The presently-known hominin fossil record

Recently, Reed et al. (2013), Spoor (2015), Kimbel (2015), Wood and Boyle (2016) and Haile-Selassie et al. (2016) reviewed what is known and what is still debated about early hominin diversity in Africa (Fig. 3). The early hominin species *Australopithecus anamensis* (from 4.2 to 3.9 Ma) is possibly descended from *Ardipithecus ramidus* (4.5–4.4 Ma) or a close relative (Leakey et al., 1995; Ward

et al., 2001; White et al., 2006, 2009a, 2015; Kimbel et al., 2014). At Galili in the Afar Basin, hominin fossils have been found at several levels in deposits aged between 5.4 and 3.9 Ma but so far, their taxonomic attributions and precise ages remain unresolved (Kullmer et al., 2008; Hammond and Ward, 2013; Hujer et al., 2015; Simpson et al., 2017). Next, *Australopithecus afarensis* (~3.8–3.0 Ma; Kimbel, 2015; Haile-Selassie and Su, 2016; Mbua et al., 2016) appeared, based on current fossil evidence, to be a descendent of *A. anamensis*; this relationship could be considered as an example of phyletic gradualism in hominin evolution (Kimbel et al., 2006; Kimbel, 2015). Around 3.5 Ma, *A. afarensis* overlapped in time with no less than four possible other hominin taxa: *Australopithecus bahrelghazali* in Chad (Brunet et al., 1995; Guy et al., 2008),

Kenyanthropus platyops in Kenya (Leakey et al., 2001; Spoor et al., 2010), and *Australopithecus deyiremeda* (Haile-Selassie et al., 2015) in the Afar Basin in Ethiopia. In addition, the *Ardipithecus*-like “Burtele foot” fossil (BRT-VP-2/73; Haile-Selassie et al., 2012) from ~3.4 Ma old deposits in the Afar indicates that another lineage –with adaptations to tree climbing– was present in Africa at the same time as *A. afarensis*. However, due to problems associated with small sample size and lack of anatomical overlap of available fossils, it is not certain that these Pliocene fossils indeed represent four different species; they could represent three or two species only (Spoor, 2015; Haile-Selassie et al., 2016; Spoor et al., 2016). For instance, it has been suggested that *K. platyops* is a regional variant of *A. afarensis* (White, 2003). In contrast, Spoor et al. (2010) concluded that *K. platyops* and *A. afarensis* are different species, but observed that it cannot be ruled out that *A. afarensis* and *A. bahrelghazali* are conspecific. After ~3 Ma, *A. afarensis* disappeared completely from the fossil record and *Australopithecus africanus* first appeared in South Africa (Lockwood, 2013; Grine, 2013; Herries et al., 2013; Kimbel, 2015; Pickering and Herries, 2017). Around ~2.8 Ma two new taxa first appeared in the fossil record, *Homo* sp. in the Afar Basin and the robust *Paranthropus aethiopicus* in eastern Africa (Villmoare et al., 2015; Reed et al., 2015; Spoor, 2015; Kimbel and Villmoare, 2016).

Unresolved taxonomy and dating issues can hamper establishment of a consistent hominin fossil distribution pattern. A case in point is the age and taxonomy of the *Australopithecus* skeleton StW573 from Sterkfontein (South Africa), which has been controversial since its discovery. StW573 has been diagnosed as a possible second (in addition to *A. africanus*) species of *Australopithecus* in southern Africa, named *Australopithecus prometheus* (Clarke, 1998, 2008, 2013, 2019; but see Grine, 2013). Recently StW573 was dated to 3.67 ± 0.16 Ma by Granger et al. (2015), which would make it the earliest hominin in southern Africa and coeval with *A. afarensis* in eastern Africa. However, this date has been challenged by Kramers and Dirks (2017): they argue that the fossil may have a maximum age of only 2.8 Ma, or ~2.6 Ma as suggested by Herries et al. (2013). In Figure 3 we use question marks to keep the taxonomy and age of this particular fossil unassigned until more data become available (Clarke, 2019), and for now exclude it from our pattern analysis. It is clear that even though new hominin fossil finds continue to be made, the fossil record will remain an incomplete and imperfect reflection of original species distribution. Nonetheless, the overview presented in Figure 3 compiles results of more than 50 years of fossil hunting in Africa and for now gives the best possible picture of the hominin distribution pattern.

2.2. Analyzing patterns in the hominin fossil record

While being aware of difficulties and limitations, we are confident that by considering all identifiable early hominin fossils found so far in deposits aged ~4.5 to 2.5 Ma (>1400), we can discern a first approximate pattern that allows us to start the process of analysis. Ideally, fossil records of non-hominin taxa should be established and analyzed in the same way, since these taxa are usually represented by larger numbers of fossils. However, a major difficulty is that such fossils are often not sufficiently well constrained in time. While every hominin fossil is carefully dated, most non-hominin faunal fossils are listed in databases with only a large time-bin or formation member as age indication (e.g. Rannikko et al., 2017), which makes it difficult to obtain a dataset with sufficient time resolution for testing (see also Vrba, 2007). We therefore focus on the hominin record and compare occurrence patterns with other taxa (here below) as far as is possible.

Species distribution Before ~3 Ma, the same (or similar) hominin species occurred in several places in eastern Africa (Fig. 3). For

instance, at 4.4 Ma *A. ramidus* was present in the Afar Basin and likely also in the Baringo Basin (Kissel and Hawks, 2015). *A. anamensis* was present in both Afar and Turkana Basins. Later, *A. afarensis* occurred in the Afar Basin, at Kantis east of the EARS, at Laetoli and possibly also in the northern Turkana Basin (Wood and Leakey, 2011; Mbua et al., 2016). Notably around ~3.5 Ma, *A. afarensis* and other (closely-related or similar) taxa appear to have been remarkably widespread in eastern and western Africa, and perhaps even southern Africa (Granger et al., 2015). In contrast, just after ~3 Ma at ~2.7 Ma, *P. aethiopicus* was present in the Turkana Basin and Laetoli but absent from the Afar Basin and South Africa. The earliest fossils of the genus *Homo* were found solely in the Afar Basin at ~2.8 Ma, and only later (from ~2.3 to 2.4 Ma onwards) also in the Turkana Basin, and possibly Baringo Basin and Malawi. The species *A. africanus* has been found only in South Africa after ~3 Ma.

This distribution pattern suggests that the period before ~3 Ma is characterized by similar hominin species across different fossil localities in Africa, while the period just after ~3 Ma is characterized by regional endemism in hominin species: different species occur in the three separate regions of the Afar Basin, Turkana-Laetoli-Malawi, and South Africa. This is similar to patterns found in fossil hippopotamids (Boisserie et al., 2011; Boisserie, 2017), wherein there is wide distribution of hippopotamid species during the early Pliocene, and from ~2.9 Ma onwards, the occurrence of pronounced endemism even at an intrabasinal scale (Boisserie et al., 2003). Boisserie (2017) pointed out that the paleobiogeographic signal in hippopotamids conflicts with observations performed on other mammalian taxa. The patterns in hippopotamids and hominins are opposite to those identified for fossil bovids: Rowan and Reed (2013) found that bovid communities in eastern Africa were characterized by high degrees of isolation and possible endemism since the late Miocene, and that large geographic ranges evolved only recently from ~2.8 Ma onwards (see also Bibi et al., 2017). This was confirmed in a later study analyzing presence/absence data of ten families of large-bodied fossil mammals in eastern Africa (Afar, Turkana, Laetoli). Rowan et al. (2015) found endemism in the Pliocene (between 4.2 and 2.95 Ma), and increasing species similarity across eastern Africa in the Pleistocene.

Boisserie (2017) concluded that these contrasting distribution patterns indicate that different African mammal taxa had different biogeographical histories, linked to differences in ecological preferences. The distribution of hippopotamids was above all constrained by their dependence on perennial water bodies (Boisserie, 2017) and this may have been also the case, to some extent, for early hominins. The distribution of most bovids was more likely constrained by their dependence on open grasslands for grazing. Hence, we infer that the Pliocene humid and warm climate before onset of Northern Hemisphere Glaciation (NHG) at ~3 Ma (Raymo, 1994; Liddy et al., 2016) produced wooded environments, perennial water bodies, and river and gallery forest connections in Africa, favoring wide distribution of forest/woodland-adapted and water-dependent taxa but causing isolation of more dry-adapted species. After ~3 Ma, the drier cooler climate produced large areas of more open grasslands, favoring opposite distribution patterns: isolation of woodland-adapted permanent water-dependent taxa and wide distribution of dry-adapted taxa such as grazing bovids (Lorenzen et al., 2012).

Fossil abundance In the Afar Basin, deposits older than ~3 Ma yield relatively large numbers (tens to hundreds) of hominin fossils. The Turkana Basin and Laetoli sediments of this time period yield fewer hominin fossils than those of the Afar, and the other EARS basins and the Chad Basin yield few or even no hominin fossils at all (Fig. 3). After ~3 Ma, the number of hominin fossils from the Afar Basin drops sharply, while hominin fossil abundance in the

Turkana Basin remains at the same level. To assess the significance of these numbers and of observed fossil absences at certain times and places, we need to take into account the influence of sedimentology and taphonomy such as absence or rarity of fossiliferous deposits, and poor fossil preservation. Here we focus on the Afar Basin, Turkana Basin and Laetoli, which have a comparably intensive fossil prospecting history. In the Turkana Basin, absence of hominin fossils between 4.5 and 4.2 Ma is not due to absence of fossiliferous deposits, but rather may be due to the fact that available deposits at Lothagam sample open, not wooded, habitats (see section 3.3). The absence of hominin fossils around 3.8 Ma in the Turkana Basin can be explained by an absence of lacustrine deposition (which is favorable for fossilization and preservation) at that time, with the river system leaving only scattered Moiti floodplain sediments that contain few and poorly preserved fossils (Feibel, 2011). At Laetoli, absence of hominin fossils before 3.8 Ma is due to a combination of absence of deposits before 4.3 Ma, and the fact that Lower Laetoli beds aged 4.3–3.8 Ma contain only rare, scattered and fragmentary vertebrate fossils (Kingston and Harrison, 2007).

Both the Afar Basin and Laetoli have well-preserved fossiliferous deposits aged 3.8–3.5 Ma, so numbers of hominin fossils deriving from these sediments can be reliably compared. Su and Harrison (2008) devoted a full paper to discussing rarity of *A. afarensis* at Laetoli compared to its abundance at Hadar in the Afar Basin. They showed that although taphonomic factors may explain part of the discrepancy, the rarity of hominin fossils at Laetoli compared to Hadar is real. Su and Harrison (2008) concluded that Laetoli probably represented a less optimal habitat for *A. afarensis* than the more wooded and mesic Afar Basin. Villaseñor and Bobe (2015) compared hominin fossil abundance in Hadar (Afar Basin) and in East and West Turkana around 3.4 Ma, statistically controlling for taphonomic differences among the sites. Similarly to Su and Harrison (2008), they found that hominins were most abundant at Hadar in the Afar Basin (38%), less common at West Turkana (27%), and East Turkana had the smallest proportion of all samples (11%). We infer that relative difference in hominin fossil abundances between Afar Basin, Turkana Basin and Laetoli before ~3 Ma is a robust characteristic of the hominin fossil distribution pattern, reflecting the exceptional status of the Afar Basin as more optimal early hominin habitat.

The relatively low number of hominin fossils from the Afar Basin after ~3 Ma (Fig. 3) is most likely due to differences in depositional character between the Hadar Formation (3.8–2.9 Ma) and the overlying Busidima Formation (2.7–0.16 Ma). The Hadar Formation is fine-grained, laterally extensive, relatively continuously exposed, and yields abundant vertebrate fossils including *A. afarensis*. In contrast, the Busidima Formation is coarser-grained, poorly preserved, discontinuous, and the density of faunal remains is low (Campisano, 2012). Moreover, because of an erosional unconformity at Hadar, sediments aged 2.9–2.7 Ma are generally lacking (DiMaggio et al., 2015). Exceptions are sedimentary packages aged 2.84–2.58 Ma in Ledi-Geraru that yielded the so far earliest *Homo* fossils (DiMaggio et al., 2015; Reed et al., 2015 and pers. comm. Villmoare et al., 2015), and ~2.5 My old sediments in Bouri Hata where *Australopithecus garhi* fossils were found (Asfaw et al., 1999; De Heinzelin et al., 1999). We conclude that for the period after ~3 Ma, differences in numbers of fossils between the Afar Basin and other regions may not reflect real differences in hominin fossil abundance.

With caveats taken into account we can distill the following pattern from the early hominin fossil record (Fig. 3): before ~3 Ma, there was hominin species similarity across different regions in Africa reflecting dispersal and wide distribution, with highest hominin abundance in the Afar Basin, somewhat lower abundance

in the Turkana Basin and lowest abundance at Laetoli. After ~3 Ma, *A. afarensis* went extinct followed by the appearance of new regionally endemic hominin taxa reflecting regional isolation and evolution, and diminished dispersal options. The discontinuity after ~3 Ma likely resulted from major climatic and environmental change starting between ~3.15 and 2.95 Ma, associated with onset of NHG and global cooling and drying (deMenocal, 2004). Importantly, the pattern of regional hominin species similarity before ~3 Ma followed by endemism after ~3 Ma, testifies to adaptation of early hominins to forest/woodland conditions and permanent water availability. This confirms the interpretation of Rowan and Reed (2015) who posit that there is now accumulating evidence that early hominins preferred to live in a mesic wooded habitat, rather than a dry open habitat (see also Forrest et al., 2018).

Next, our objective is to understand and explain the hominin distribution pattern by developing a testable biogeographic framework for early hominin dispersal and evolution. We are aware that geographic ranges of hominins are influenced by a multitude of factors: abiotic and biotic factors (e.g. physical barriers, water and other resource availability, presence or absence of predators), population dynamics of a species, and genetic characteristics (e.g. Gaston, 2003). Moreover, these interconnected factors and their relative impact change over time (Roebroeks, 2006). While acknowledging complexity, we here take a first simple step and focus on climatic and environmental factors influencing hominin dispersal and evolution.

3. Biogeographic framework

3.1. A biogeographic perspective

Our premise is that in order to evaluate climatic and environmental drivers of early hominin evolution, much can be learned from African faunal and floral biogeography. Hominins are African mammals that must have been embedded in the same ecological matrices that other African animals are, and have been (Kingdon, 1971–1982, 1990, 2003). Jonathan Kingdon, zoologist and artist specialized in African natural history, used biogeographic patterns of present-day eastern African mammalian sibling species to derive an evolutionary mechanism of climate-induced isolation of ancient ape populations in Indian Ocean coastal forests, with evolution of bipedality followed by inland dispersal and subsequent evolution (formation of new species) in different inland river basins (Kingdon, 2003). In his book, he provided a detailed conceptual model for human evolution with many novel ideas but also some inaccuracies, which resulted in ambiguous reception by the paleoanthropological community. While Kingdon's thoughtful biogeographic perspective, intimate knowledge of African mammals and landscapes, and out-of-the-box thinking was appreciated, not all of his ideas were fully embraced (Kimbel, 2004; Wood, 2004; Kingston, 2007). We feel that it is timely now to reconsider his contribution, using it as a source of inspiration for a fresh look at hominin evolution. Firstly, Kingdon draws humans firmly back to their place in nature, as “a very peculiar and special one, true, but in essence just one more African mammal”. Secondly, he directs our attention to the ecological and evolutionary significance of an often overlooked but important vegetation zone in eastern Africa, the coastal forest zone along the Indian Ocean (Fig. 2; White, 1983; Mayaux et al., 2004; Groves, 2015). Kingdon proposed that for mammalian – including hominin – evolution this coastal forest zone has played a major role as an isolated refugium during adverse climatic-environmental conditions, and as a source area for new species (Kingdon, 2003). In the next subsections, we review what is now known about the eastern African coastal forest, and assess if

Kingdon's postulation of the coastal forest as refugium and source area is valid and applicable to hominin evolution studies.

3.2. The coastal forest as refugium

The concept of refugia stems from recognizing (e.g. by Darwin, 1859) that geographical ranges of species have expanded and contracted according to cyclic climate change during the Quaternary (Birks, 2015). The value of this concept has been challenged, because it can be argued that species respond to climatic and environmental changes in different and complex ways (Bennett and Provan, 2008). However, Stewart et al. (2010) pointed out that the refugium concept, if well-defined and delimited, remains relevant for species-level evolution. We follow definitions by Stewart et al. (2010): a refugium is the geographic location that a species inhabits during the part of the climate cycle that represents the species' maximum contraction in geographic range. This implies that a refugium is at a certain moment the relatively best place to be for certain taxa. It does not mean that it is absolutely the perfect place to be. We use 'core area' (or source area) for locations where a species' habitat preferences are largely met and population size will be relatively large, as is the case in a refugium. We use 'marginal area' for locations where a species preferred habitat is only temporarily present, degrades over time, or no longer exists, as is the case in expansion areas when the climatic conditions swing from stable to strongly variable again. In marginal areas, population size will be relatively small and/or decreasing (Stewart et al., 2010). During favorable climate conditions, core and marginal areas are connected while during adverse climate conditions they are isolated from each other (Vrba, 2007; Stewart et al., 2010).

Traditionally, refugia relate to temperate zone glacial-interglacial warm-cold climate cycles (e.g. Hublin and Roebroeks, 2009) but in this study we focus on tropical climate (wet-dry) cycles that are orbitally forced by changes in insolation. In general, "latitude rules" in biogeography whereas the often longitudinal dimension of the coastal–continental axis is mostly—and unjustly—ignored (but see Cohen et al., 2012). Stewart et al. (2010) is one of the first studies (after e.g. Fortelius et al., 2003 and Kingdon, 2003) to recognize the importance of this axis. They distinguish a 'continental' adaptation to a drier climate with greater difference (in temperature and precipitation) between the seasons in inland areas, and an 'oceanic' adaptation to a more humid and stable, less seasonally different climate along the coast. In this paper we focus mainly on the oceanic–continental axis (in this case West–East), while also taking the longitudinal axis (North–South) into account.

The present-day eastern African coastal forest zone is one of six well-defined forest floristic clusters associated with particular environmental conditions: Moist West Africa, Dry West Africa, Wet Central Africa, Moist Central Africa, Upland East Africa, and Coastal East Africa (Fayolle et al., 2014). These different forest types, now isolated from each other, resulted from complex climatically and tectonically driven fragmentation processes operating on the original single continuous equatorial forest that covered Africa during the Early and Middle Miocene (Burgess and Clarke, 2000; Plana, 2004; Bryja et al., 2017). The Late Miocene timing of this major environmental restructuring in Africa is supported by climate data from Herbert et al. (2016) who identified, based on sea surface temperature records, an increasing aridification of Africa starting between ~7 and 5 Ma. The central and eastern African forests are partitioned by a dry region that—analogue to Wallace's Line (Mayr, 1944)—is called "Kingdon's Line": this division crossing eastern Africa represents the optimal separation of overlapping central and eastern forest faunal elements (Grubb et al., 1999; Kingdon, 2003, Fig. 4). The eastern African coastal forest zone

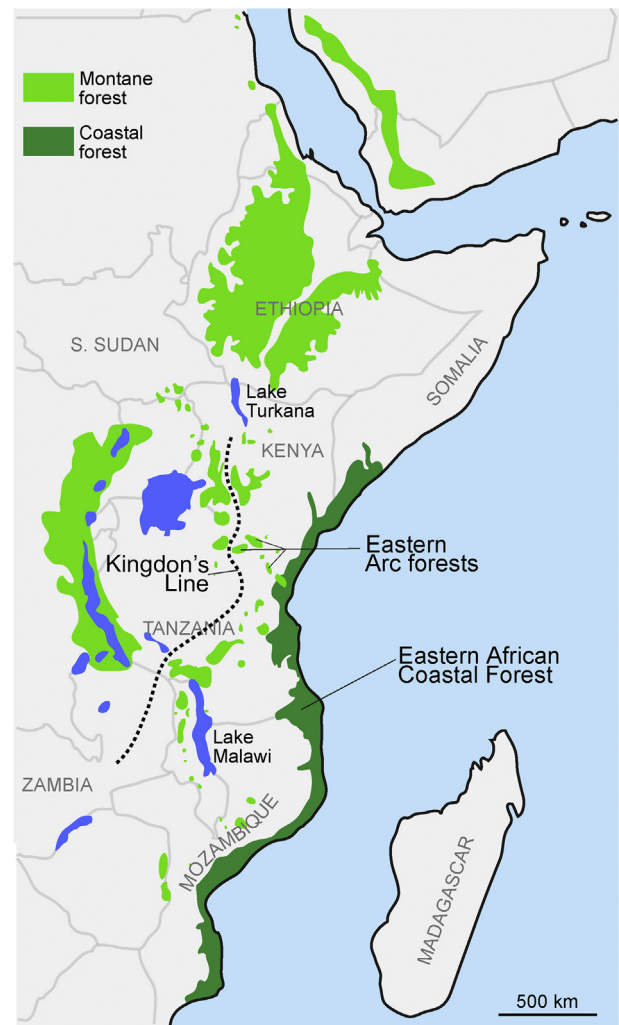


Figure 4. Map of eastern Africa, showing the modern distribution of the northern part of the Coastal Forest of Eastern Africa (CFEA) and eastern African montane forests. Kingdon's Line represents the optimal separation of overlapping central and eastern forest faunal elements (Grubb et al., 1999; Kingdon, 2003).

comprises the narrow (width ~50–100 km) longitudinally aligned vegetation zone presently stretching along the Indian Ocean from southern Somalia to southern South Africa (White, 1983; Grubb et al., 1999; Burgess and Clarke, 2000, Fig. 4). More inland at higher elevation are eastern African montane forests such as the Eastern Arc Forests in Kenya and Tanzania, that were in the initial phase of Miocene forest fragmentation still linked to the coastal forest (Bryja et al., 2017).

Clarke (2000) formally defined the Indian Ocean coastal forest zone as "Coastal Forests of Eastern Africa" (henceforth referred to as CFEA or coastal forest; see also Barratt, 2017; Barratt et al., 2018) and described the composition as a mosaic of halophytic mangrove forest, lowland mixed rain forest, *Brachystegia* woodland, swamp and scrub forest, and riverine gallery forest. The coastal forest zone is further characterized by the presence of estuarine wetland areas, shallow-water tidal creeks with sea-grass fields, and seasonal freshwater ponds with water lilies and other aquatic vegetation (Fig. 5). Jurassic, Cretaceous and Eocene limestone formations occur widely along the Indian Ocean coast, forming karstic hills and caves within the coastal forest (Schlüter, 2006; Helm et al., 2012; Carvalho et al., 2017; Habermann et al., 2018). In terms of present-day terrestrial ecoregions in Africa, the northern part from

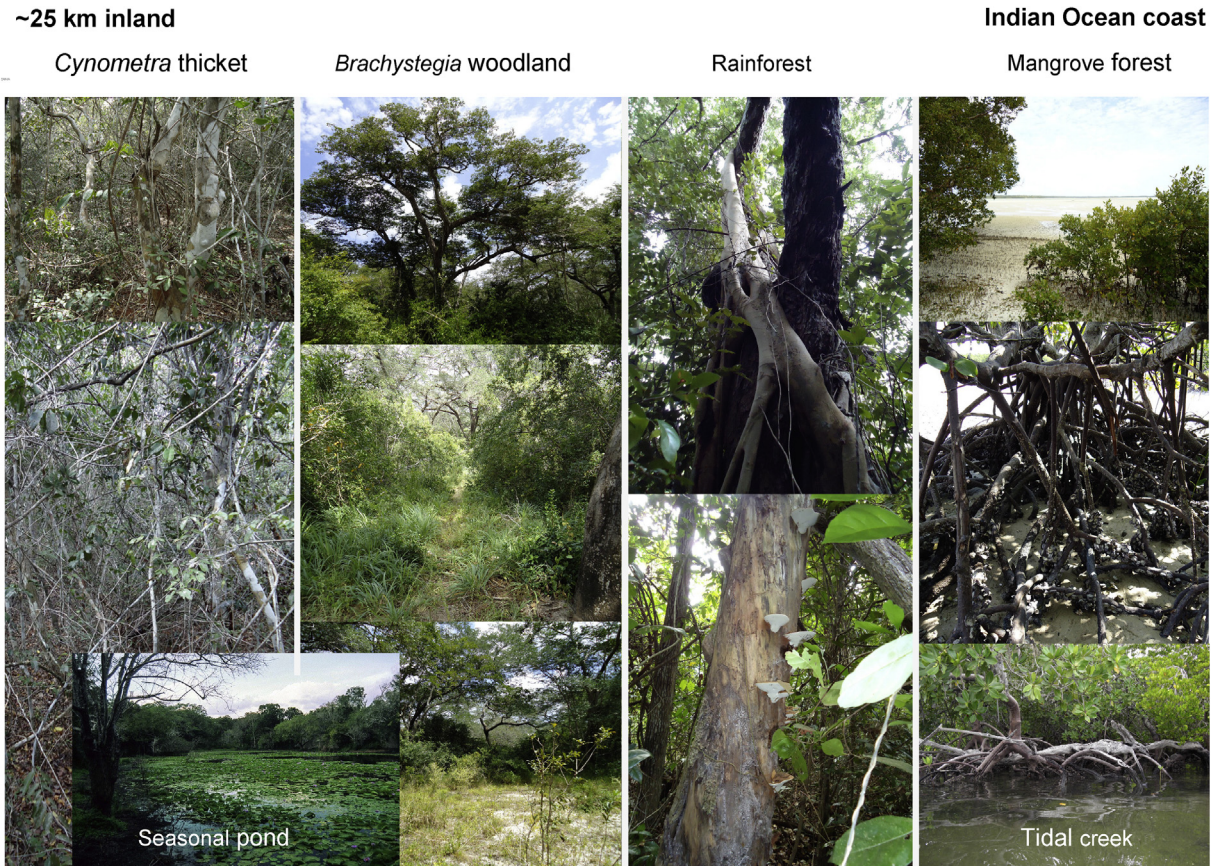


Figure 5. Characteristic vegetation zones of the Arabuko-Sokoke coastal forest, a present-day part of the Coastal Forest of Eastern Africa situated in Kenya.

southern Somalia to northern Mozambique is classified as Zanzibar-Inhambane coastal forest mosaic. This part grades southward into Maputoland and KwaZulu-Cape coastal forests that continue until Cape St. Francis in South Africa (Burgess et al., 2004). Coastal gallery forests extending along rivers can reach far inland, up to 200–400 km (Burgess and Clarke, 2000; Kingston et al., 2007). The coastal region has, since the Late Miocene, benefited from climatic stability (Kingdon, 1990, 2003; Burgess et al., 1998; Burgess and Clarke, 2000; Azeria et al., 2007). Even during cyclic occurrences of severely fluctuating and dry global climate conditions, the buffering influence of the Indian Ocean maintained a relatively stable warm and humid climate in this zone, providing a vegetated and water-rich refugium for permanent-water adapted forest-woodland organisms (Kingdon, 1990, 2003; Lovett and Wasser, 1993; Burgess and Clarke, 2000).

Recent molecular phylogeography studies on a range of extant forest-dwelling organisms (trees, birds, mammals, and insects) confirm a Late Miocene (~7–5 Ma) separation of West, Central, Upland and Coastal East African forests (e.g. Johansson et al., 2007; Couvreur et al., 2008; Johnston and Anthony, 2012; Mikula et al., 2016; Bryja et al., 2017). Notably the phylogenetic positions of typical CFEA species like Ader's duiker (Johnston and Anthony, 2012) and Sombre greenbul (Johansson et al., 2007), as Late Miocene sister species of both western and other eastern branches of their respective lineages, demonstrate antiquity and relative stability of the coastal forest zone as a separate forest habitat.

3.3. Hominin evolution along the Indian Ocean coast?

The main question now is: was the CFEA indeed relevant for hominin evolution, as Kingdon proposed? Fossil finds indicate that

between ~11 and 8 Ma, Africa was populated by hominoids (apes) such as *Samburupithecus*, *Nakalipithecus* and *Chororapithecus* (Harrison, 2010; Turner and O'Regan, 2015; Kunitatsu et al., 2016; Katoh et al., 2016). Kingdon (2003) suggested that before ~8 Ma, apes were spread over practically the whole of Africa from the Atlantic to the Indian Ocean. The climatic drying in Africa that led to forest fragmentation after ~7–5 Ma must have fragmented these ape populations as well, restricting some to west and central Africa and others to eastern Africa, east of Kingdon's Line. Coppens (1994) remarked that geographic distributions of African great apes, together with molecular phylogeny and tectonic-climatic data, indicate that ancestors of present-day clades of *Gorilla*, *Pan* and *Homo* split in the Miocene: gorilla and chimpanzee lineages remained tied to western and central Africa, while the hominin lineage was present in eastern Africa. Based on this, Coppens (1994) –and many others before and since (see reviews by Potts, 1998a,b; Bender et al., 2012; Dominguez-Rodrigo, 2014)– concluded that the birth of the bipedal hominin lineage must have resulted from evolution in relatively dry open savannas of the EARS, where today hominin fossils are mostly found.

Recent molecular phylogenetic studies have indeed corroborated that *Pan* and *Homo* last shared a common ancestor around ~7–5 Ma (e.g. Moeller et al., 2017 and references therein), and that the lineages then split. However as explained in section 2.2, in contrast to Coppens (1994) and decades of associating the origin of bipedal hominins with the expansion of grasslands during the late Miocene, current understanding is that early hominins inhabited forests and woodlands rather than open grassland savanna environments (e.g. Rowan and Reed, 2015). This is exemplified by the site of Lothagam (SW of present-day Lake Turkana) with deposits aged between 7.4 and 4.2 Ma. It is considered to be one of the oldest

known examples of an open savanna biome in Africa (Leakey and Harris, 2003). The site samples a rich and diverse Late Miocene fauna with over 9000 fossil specimens collected. However, hominin/hominoid fossils are extremely rare: two hominoid teeth aged ~6.5–5 Ma, and one hominoid/hominin mandible (KNM-LT 329, constrained between ~4.9 and 4.2 Ma) have been found so far (McDougall and Feibel, 1999; Leakey and Harris, 2003; Wood and Leakey, 2011; Kissel and Hawks, 2015). The rarity of hominoids and hominins in this savanna biome supports the current interpretation that early hominins preferred forest and woodland environments. We therefore infer that after Late Miocene forest fragmentation, a population of “eastern apes” ended up isolated in eastern African montane and coastal forests east of Kingdon’s Line, instead of in savanna areas between the western-central and eastern forest blocks.

Kingdon (2003) reasoned that, following the isolation of ape populations in their coastal forest enclave, they adapted to the specifics of their finite and confining environment. The CFEA habitat differs from west-central African forests in terms of size, shape, rainfall, seasonality, biodiversity, availability of food resources and intense resource competition from, for example, monkeys. Due to the relatively small ape gene pool in an isolated habitat experiencing different selection pressures, genetic drift and selection would have accelerated evolution in the coastal forest zone, leading to genetic separation from ape populations in the more extensive rainforests and woodlands west of the arid barrier separating west-central and eastern forests (Kingdon, 2003). Kingdon (2003) further suggested that during this isolation, adaptation to foraging for small plant and animal food items on the coastal forest floor in squatting position (the apes being largely forced out of the trees by monkey competition) led to pelvic reorganization and ultimately to bipedality. This is one of the many more or less speculative hypotheses on the origin of hominin bipedality, which so far remains elusive. We therefore merely suggest that, given the documented locomotor changes in *A. ramidus* at 4.4 Ma and *A. kaddaba* at 5.8–5.5 Ma (see section 6.),

the evolution of changes in locomotion may have been favored in this coastal forest habitat. Kingdon (2003) predicted the existence of a Late Miocene to Early Pliocene bipedal, omnivorous ape living in the CFEA: the “coastal ground ape”. Based on present-day typical distributions of CFEA species, such as certain birds, monkeys, elephant-shrews, squirrels, duikers (Kingdon, 1971–1982), we expect that this coastal ground ape would have colonized the entire CFEA along the Indian Ocean from north to south. So far, there are no reports of Pliocene hominin fossil finds from the coastal forest zone. This can be explained by the fact that, generally, conditions in forests are less suitable for fossilization and subsequent fossil discovery than conditions in arid regions (Hare, 1980; Vrba, 2007); also, there has been only limited search effort in this eastern African coastal area (Szymanski, 2018). Recent exploratory research at Gorongosa Park in the coastal zone of Mozambique yielded, for the first time, Miocene animal and plant fossils from riverine forest/woodland and estuarine environments, beginning to fill in an important gap in the paleobiogeography of Africa (Carvalho et al., 2017; Habermann et al., 2018). Therefore, absence of evidence cannot be seen as evidence of absence in this case. In summary, we conclude that there are sufficient grounds for assuming that the CFEA could have been a relevant area for hominin evolution.

3.4. A coastal refuge hypothesis

We hypothesize that the CFEA provided an isolated refugium for early hominins, conducive to evolution during orbitally forced climatically variable episodes (at 400–100 ky timescales) when extremely dry conditions alternated (at 20 ky timescales) with extremely wet conditions. From this coastal refuge, newly evolved hominin species could disperse inland to montane forests and rift basins via humid (riverine/vegetated/groundwater-fed) corridors, whenever onset of climatically stable episodes allowed expansion from the coastal enclave (Fig. 6). Three premises underlie this ‘coastal refuge hypothesis’:

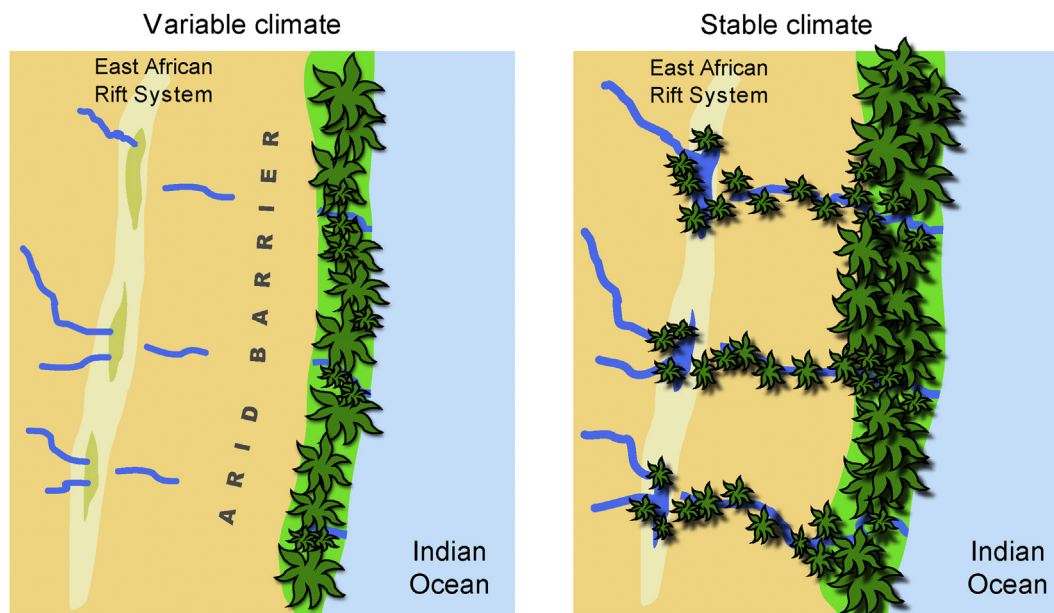


Figure 6. Cartoon illustrating the coastal refuge hypothesis. During a variable climate episode (eccentricity maximum) basins in the Eastern African Rift System (EARS) generally do not contain lakes and rivers do not reach the Indian Ocean. During a stable climate episode EARS basins may contain lakes surrounded by forest/woodlands. Vegetated humid corridors connect the EARS with the Coastal Forest of Eastern Africa (CFEA). Due to the oceanic influence that buffers climate fluctuations in the coastal zone, the CFEA is always present providing a relatively stable forest–woodland environment along the coast, but its extent and floral/faunal composition may vary somewhat (less than in inland areas) under different climate conditions.

- 1) since its origin in the Late Miocene, the CFEA has always been climatologically buffered by the warm ocean and was an evolutionary source (core) area of many woodland/forest-adapted organisms needing permanent water (see examples below) – likely including early hominins (Kingdon, 2003; Leakey et al., 2008; Carvalho et al., 2017; Habermann et al., 2018);
- 2) the ~100 and ~400 ky Earth' eccentricity maxima episodes are characterized by climate variability with alternating extremely wet and dry conditions at precession (~20 ky) timescales, strong seasonality, and high dust production. In contrast, eccentricity minima episodes are climatically stable, characterized by relatively constant moderate rainfall intensity, moderate seasonality and low dust production (Vallé et al., 2016), promoting and sustaining vegetated/riverine/spring-fed connecting corridors between CFEA, eastern montane forests and other inland areas (e.g. EARS basins); and
- 3) the existence of recurrent humid connecting corridors during climatically stable episodes facilitated hominin dispersal from refugial core area(s) such as the CFEA to marginal areas (e.g. inland rift basins), while climatically variable episodes lead to contraction, isolation, endemism and evolution in core area(s).

Support for validity of the premises underlying the coastal refuge hypothesis is provided by the following examples. Hemp et al. (2015) studied biogeographical patterns of the forest-dwelling flightless grasshopper *Parepistaurus* and specifically addressed the questions: a) are the old coastal forests of Kenya and Tanzania the source for inland taxa in *Parepistaurus*? and b) did river systems serve as corridors for the spread of *Parepistaurus* into the hinterland? Indeed, based on molecular phylogeography they found that coastal *Parepistaurus* taxa belonged to ancestral lineages from which evolved the high diversity of species found in montane forests of the Eastern Arc Mountains of Kenya and Tanzania. They concluded that riparian vegetation along rivers draining into the Indian Ocean probably served as corridors for dispersal of coastal taxa to the hinterland. These findings are corroborated by a molecular phylogeography study demonstrating that in arboreal rats of the genus *Grammomys*, upland taxa (e.g. in Usambara Mountains, Tanzania and Mulanje Mountains, Malawi) are closely related to eastern African coastal taxa, which points to an inland spread of coastal taxa via riverine gallery forests (Bryja et al., 2017). Recently, Cuthbert et al. (2017) modeled networks of groundwater “hydro-refugia” in eastern Africa through a wet-dry precession cycle, further substantiating the occurrence of climate-modulated coastal-inland humid dispersal corridors (perpendicular on the N–S axis of the EARS) for permanent-water adapted fauna.

The next step in our study is to develop the coastal refuge hypothesis into a biogeographic conceptual model for hominin evolution and dispersal in Africa between ~4.5 and 2.5 Ma. First, we set up tectonic-climatic (section 4) and geographic frameworks (section 5) by reviewing available literature on these subjects. Next, we establish “initial conditions” of the model by choosing, based on biogeographic and fossil information, the stem hominin in this conceptual model (section 6). We define the “algorithm” (a sequence of instructions) that makes the model “run”, producing predictions on hominin evolution and dispersal (section 7). In sections 8 and 9, based on combination of available climate and hominin fossil records, we test predictions following from the coastal refuge model and explore impacts of climatic and environmental change. Finally, we discuss examples of how to further test the conceptual model and start using it as a predictive tool, hopefully inspiring novel research directions (section 10).

4. The tectonic-climatic framework

4.1. Rifts and east-west connectivity

Tectonic processes such as volcanism, uplift and rifting played a key role in shaping topography, local climate and hominin environments in Africa (e.g. Veldkamp et al., 2004; Sepulchre et al., 2006; Wichura et al., 2010; Veldkamp et al., 2012; Claessens et al., 2016; Ring et al., 2018). Two large rift systems can be distinguished: 1) the branches of the EARS both situated along a largely north-south axis, and 2) the interconnected Anza, Sudan and Central and West African Rifts running along an east-west axis between the Indian Ocean and western Africa. The two rift systems cross each other at the location of present-day Lake Turkana (Turkana Basin) in Kenya (Fig. 7; Winn et al., 1993; Bosworth and Morley, 1994; Bruhn et al., 2011; Macgregor, 2015). Development of the E-W oriented rift systems started in the Cretaceous (Winn et al., 1993) and while these rifts were progressively filled up over time, they still constitute relatively low-lying areas.

Aquatic faunal evidence (reflected e.g. in ichthyological provinces) indicates that during the Mio-Pliocene, western and eastern Africa were hydrographically connected at least up to ~7 Ma (Otero et al., 2009). After ~7 Ma this connection was lost due to aridification in Africa (Zhang et al., 2014; Herbert et al., 2016) but intermittently re-established during recurring orbitally forced humid climate cycles (Larrasoana et al., 2013). Indeed, malacological evidence suggests that Chad and Turkana Basins were from time to time connected via the Central African Shear zone and Sudan Rift (Van Bocxlaer et al., 2008; Van Damme and Van Bocxlaer, 2009; Van Bocxlaer, 2017, Fig. 7). Bruhn et al. (2011) also drew attention to evidence reflecting ancient west-east connections and faunal dispersal along these interconnected rift systems, such as an isolated eastern African population of *Cercocebus* that is distributed principally in forests of west and central Africa—the extant Tana River mangabey (*Cercocebus galeritus*) that inhabits gallery forests near the Indian Ocean coast. Leakey et al. (2008) concluded, based on sudden appearances and disappearances of monkey species in the fossil record of the Turkana Basin, that many species of fossil cercopithecoid monkeys that first appeared in the Turkana Basin without obvious local predecessors are likely to have migrated into the basin while having evolved elsewhere. The authors inferred that waterways linking the Turkana Basin with habitats elsewhere would have been critical in facilitating dispersals into and out of the basin, and recognized that the central African forests and particularly the Coastal Forest of Eastern Africa, as proposed by Kingdon (2003), would have provided ideal habitats for evolution of primates. For instance, the ancient Turkana River, which flowed from the southern Turkana Basin via Lamu Embayment to the Indian Ocean (Feibel, 1993; Bruhn et al., 2011), may have been a crucial link to coastal forest habitats and thus to a possible source of some of the primate species that appeared in the Turkana Basin (Leakey et al., 2008; Joordens et al., 2013).

4.2. Global climate change

Global climate evolution over the past 5 million years is characterized by several major climate transitions, together with ongoing regular orbitally driven climate cyclicity. Overall, the Pliocene (5.33–2.58 Ma; Gradstein et al., 2012) was a warm period with higher sea levels than today (Rovere et al., 2014), punctuated by several short-lived glaciations at ~4.9, 4.0, 3.6 and 3.3 Ma (De Schepper et al., 2014) with concomitant sea level low stands (Toomey et al., 2016) and minima in sea surface temperatures (Herbert et al., 2010) at those times (Fig. 8). A major climatic transition occurred at the end of the Pliocene warm period, caused

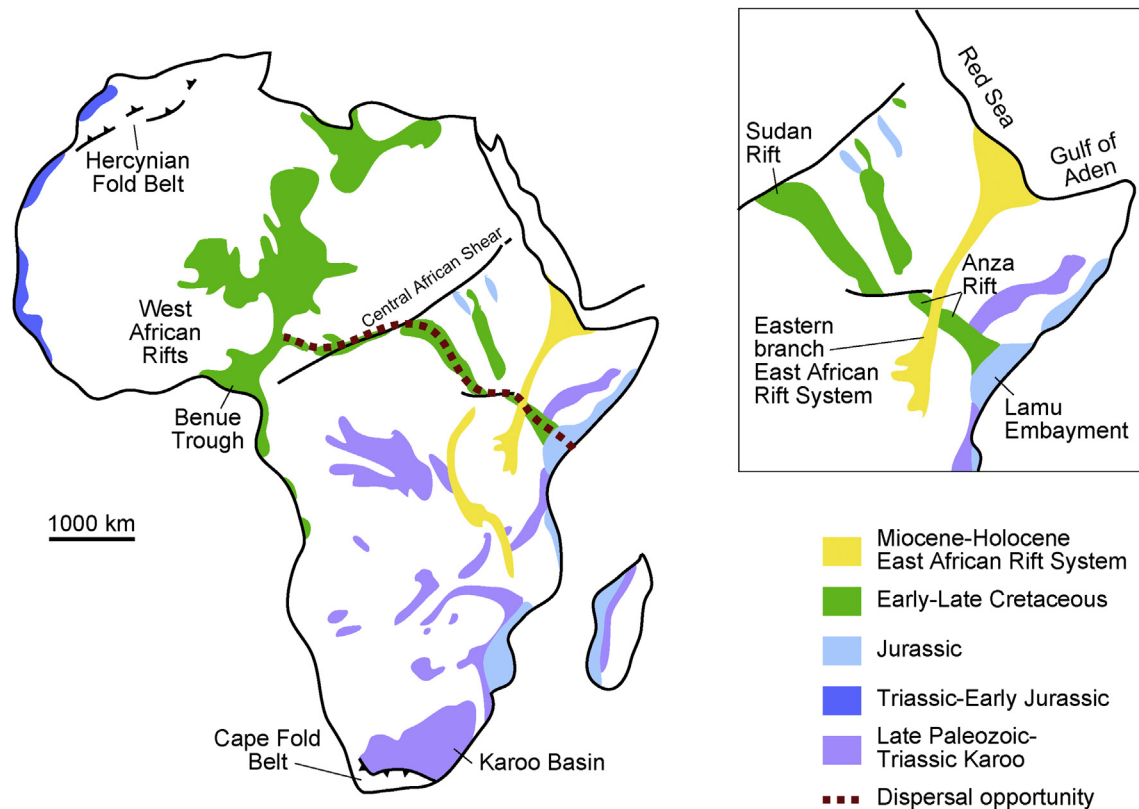


Figure 7. Rift systems in eastern, central and western Africa (adapted from Winn et al., 1993). Red dots indicate east-west connection (crossing the eastern branch of the East African Rift System) from Lamu Embayment via Anza Rift, Sudan Rift and Central African Rift to the West African Rift that contains the Chad Basin.

by geological events such as changing ocean circulation, changing atmospheric carbon dioxide levels, and intensification of NHG between ~3 and 2.6 Ma (Ravelo et al., 2004; Bartoli et al., 2005; Liddy et al., 2016). The transition from global warmth up to ~3 Ma to markedly cooler and more variable climate conditions is demonstrated by sea surface temperature records (Martínez-García et al., 2010; Liddy et al., 2016; Herbert et al., 2010, 2016) and benthic foraminifera $\delta^{18}\text{O}$ records reflecting ice volume and bottom sea water temperatures (Lisiecki and Raymo, 2005; Zachos et al., 2011; Bell et al., 2015, Fig. 8a,b).

Superimposed on such “unique” climatic transitions are regular Milankovitch climate cycles due to orbital forcing, causing cyclicity in insolation and thus in monsoonal rainfall and seasonality in Africa, at different timescales ranging from ~10 ky to 1.2 Ma (Kingston et al., 2007 and references therein). Of particular importance are Earth eccentricity cycles (with a frequency of ~100 and ~400 ky; Fig. 8c) as they modulate the precession cycle, determining the amount of insolation and thereby the amplitude of monsoonal intensity in Africa (Rossignol-Strick, 1983, 1985; Kutzbach and Liu, 1997). During eccentricity maxima the amplitude of insolation values is greatest (Fig. 8d), resulting in extremes in high rainfall and low rainfall periods at precession (~20 ky) timescales in Africa, and also extremes in seasonality (largest difference between wet and dry seasons) at these points in time (Berger et al., 2006; Wang, 2009).

In some studies, eccentricity maxima (characterized by peaks in monsoonal rainfall) are correlated to major lake phases in Africa and considered to be “wet periods” (e.g. Trauth et al., 2005, 2007; Maslin and Christensen, 2007, Maslin and Trauth, 2009). Here, however, we emphasize that eccentricity maxima result not so much in overall wet periods but rather in periods of large climate variability with high-amplitude extremes in wet and dry conditions

(example indicated with **v** in Fig. 8d). In contrast, 400 ky and 100 ky eccentricity minima are periods of climate stability, characterized by relatively constant (low-amplitude variation) moderate rainfall intensity and moderate seasonality over a time span of ~20–150 ky (example indicated with **s** in Fig. 8d). We consider such stable moderate rainfall conditions to be beneficial for promoting and sustaining vegetation cover, and decreasing erosion and continental dust production. Indeed, eccentricity minima correlate with minima in continental dust percentages in marine cores drilled off the West African coast (ODP 659, Fig. 8e; Tiedemann et al., 1994) and in the Gulf of Aden (ODP 721/722, Fig. 8f; deMenocal, 1995, Wang, 2009; Vallé et al., 2016). Dust reduction strengthens vegetation-albedo feedbacks of precipitation, further stabilizing vegetation cover (Pausata et al., 2016). Stable moderate amounts of rainfall may be sufficient and even optimal to nourish vegetation and forest cover, while extreme amounts of rainfall – as seasonally occurring during eccentricity maxima – are not necessarily advantageous for vegetation. Moreover, it is notably the absence of extreme and prolonged dry spells (and long dry seasons) during eccentricity minima that may contribute to ensuring a critical amount of vegetation to maintain a humid self-propagating microclimate, thus enhancing forest ecosystem resilience to cope with climatic and other perturbations (Hirota et al., 2011).

In Figure 8, green dashed lines represent stable periods of moderate rainfall and seasonality, coinciding with low dust percentages in marine cores drilled off the African coast. They generally occur every ~400 ky (or 100 ky) when eccentricity is lower than ~0.01. These stable periods indeed coincide with “forest phases” as characterized by peaks in tree pollen and lows in “desert pollen” in marine core DSPD Site 231 (Gulf of Aden) at ~4.4 Ma, 3.8 Ma, 3.5 Ma, 3.15 Ma, 2.8 and 2.45 Ma (Bonnefille, 2010; NB no data are available for the time period 3.9–4.4 Ma). The stable periods also coincide

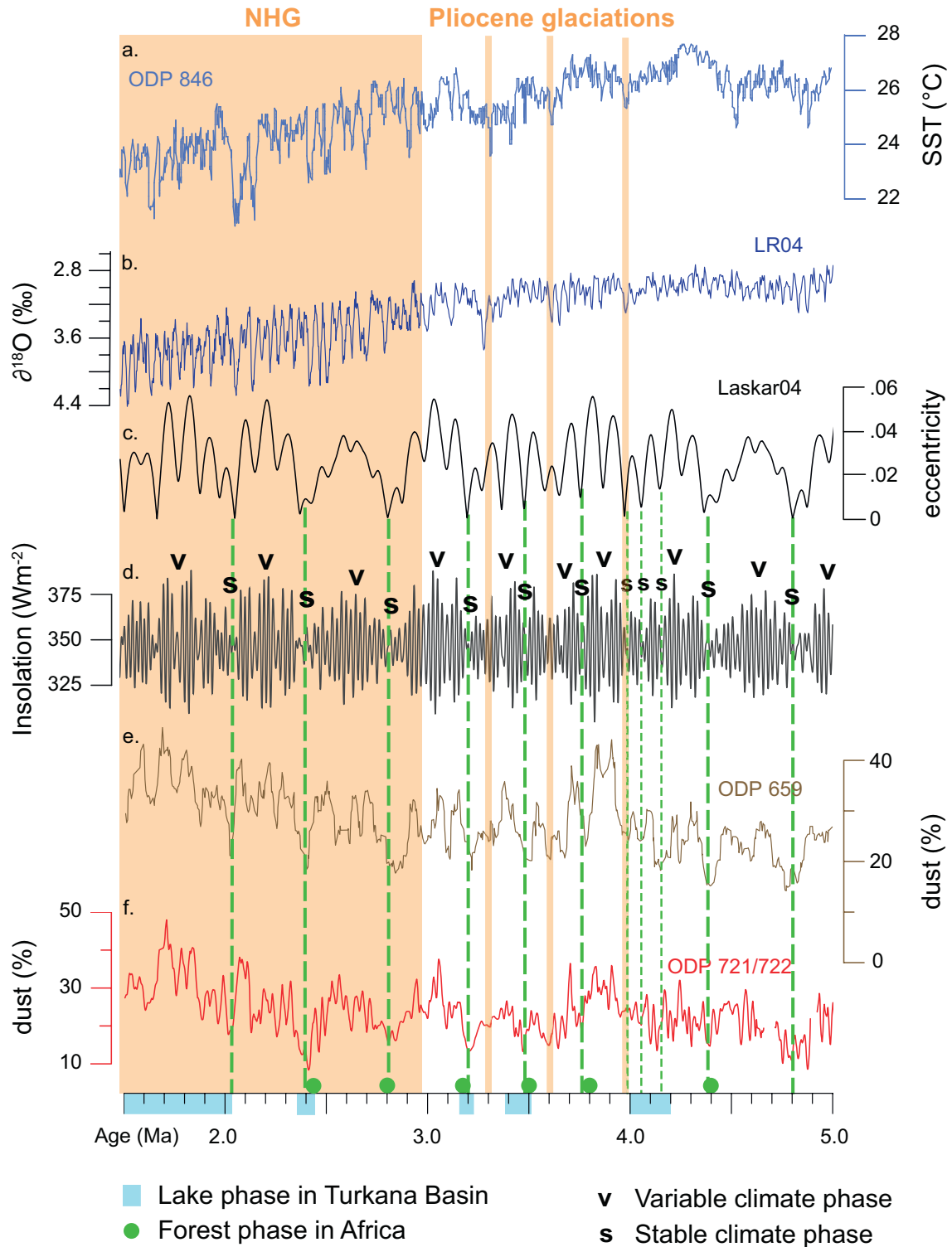


Figure 8. Global climate change between 4.5 and 2.5 Ma. a. Sea surface temperatures (SST) in marine core ODP Site 846 (Herbert et al., 2010). b. $\delta^{18}\text{O}$ of benthic foraminifera (Lisiecki and Raymo, 2005). c. Eccentricity values (Laskar et al., 2004). d. Insolation values (Laskar et al., 2004). e. Dust percentages in core ODP Site 659. f. Dust percentages in core ODP Site 721/722 (Tiedemann et al., 1994; deMenocal, 1995; Wang, 2009). Forest phases from Bonnefille (2010); Lake phases from Feibel (2011).

with onset of lake phases in the Turkana Basin at ~4.2 Ma, ~3.5 Ma, ~3.15 Ma and ~2.4 Ma (Feibel, 2011; Joordens et al., 2013, Fig. 8). However, lakes are not always unequivocal indicators of climatic conditions, since the formation of lakes is contingent also on local tectonics and on basin thresholds. In case accommodation space (e.g. through basin subsidence) is not available, a lake phase will

not occur even when climatic conditions for lake formation are favorable. This was the case in the Turkana Basin at ~3.8 Ma and 2.8 Ma (Feibel, 2011). Formation and characteristics of lakes also depend on sensitivity of basins, determined by e.g. basin shape and geographic location. For instance, the Baringo Basin has a different threshold for lake formation than the Turkana Basin: the Baringo

Basin needs relatively high rainfall amounts, as caused by peak insolation values during eccentricity maxima (but not during eccentricity minima), to form relatively short-lived deep lakes at 20 ky timescales (Deino et al., 2006; Kingston et al., 2007; Wilson et al., 2014); during eccentricity minima, lakes also formed in the Baringo Basin but they were not as deep and well developed (John Kingston, pers. comm.).

Notably the period around ~3.5 Ma appears to have been wet and wooded in Africa. For instance, Feibel (1988) found, based on paleosol types, that at ~3.5 Ma the Turkana Basin was characterized by enhanced local rainfall conditions, possibly related to high sea level and marine transgression into the low-lying Lamu Embayment providing more moisture at that time. This observed increased humidity signal is supported by Hernández-Fernández and Vrba (2006) who inferred a paleoprecipitation of 1100 mm/yr in the Turkana Basin at 3.5 Ma, based on taxonomic analysis of macromammalian faunas. In conclusion, we deduce that during eccentricity minima, low dust values coincided with (and are causally connected with) increased vegetation cover, forest expansion, onset of lake phases in the Turkana Basin and occurrence of vegetated/riverine corridors. Conversely, during eccentricity maxima high dust values coincided with (and resulted from) vegetation contraction, causing disruption of connective vegetated/riverine corridors.

An interesting point of discussion is the question: why were mesic corridors suitable for inland dispersal only established –as we infer– during 100 and 400 ky eccentricity minima, and not every 20 ky during insolation maxima as for instance suggested by Larrasoña et al. (2013) and Grant et al. (2017)? Larrasoña et al. proposed the occurrence of over 230 “Green Sahara Periods” within the last 8 million years, with savanna and gallery forest expansion throughout most of the desert in northern Africa. While we cannot exclude the possibility that connectivity and to some extent also hominin dispersal may have occurred at 20 ky timescales, we argue that conditions were not always sufficiently suitable for successful establishment of viable long-lasting populations in marginal areas. We base this on the observation that before ~3 Ma, habitat requirements of hominins were more strictly limited to woodland and forest conditions, rather than to savanna/floodplain conditions. Establishment of woodland/forest conditions in marginal areas would have been adversely affected by extreme variability and seasonality associated with high insolation maxima. The length of the dry season especially must have been a crucial threshold factor, not only for hominin dispersal opportunities but also for establishment of suitable habitats and viable populations in marginal areas (see e.g. Eronen et al., 2017). Consequently, we assume that 100 ky and 400 ky eccentricity minima, clearly coinciding with forest and lake phases, provided the most optimal conditions for mesic corridors, attractiveness of inland areas, and dispersal and successful inland settlement of hominin populations.

5. Towards a conceptual model: the geographic framework

5.1. The coastal forest of Eastern Africa: core area

When developing the coastal refuge hypothesis into a conceptual model for African hominin evolution (“coastal refuge model”), it is vital to acknowledge the particular climatic and environmental characteristics associated with geographic position and elevation of presently proposed key areas for early hominin evolution: the CFEA, several basins in the EARS, and the Chad Basin (Fig. 9). Nowadays, the coastal forest zone stretches along the Indian Ocean coast from southern Somalia in the north to southern South Africa (Figs. 2, 4). In the warm Mio-Pliocene before ~3 Ma, sea levels were higher (Rovere et al., 2014) and more humid conditions prevailed in

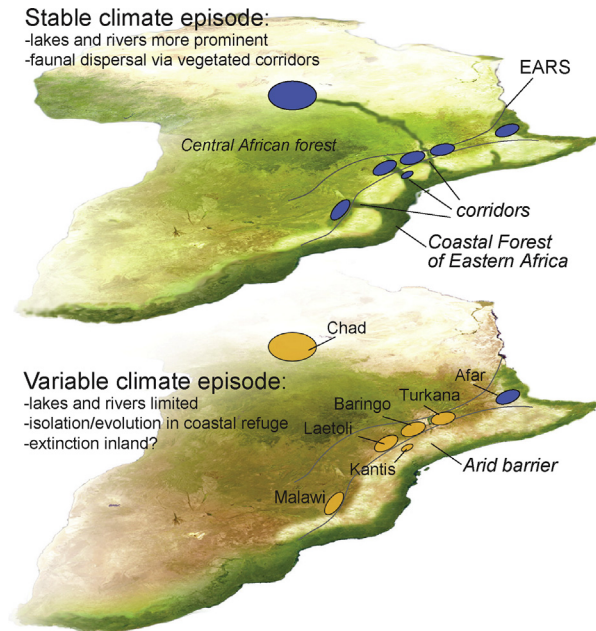


Figure 9. Schematic representation of the environmental setting in Africa during a stable climate episode with low seasonality (upper panel) and a variable climate episode with strong seasonality (lower panel).

eastern Africa (Bonnefille et al., 2004; Neumann and Bamford, 2015), thus it can be expected that the coastal forest extended further northward than its present-day limits. Marine pollen records from the offshore Niger Delta and Gulf of Aden corroborate presence of forest and woodland conditions in NE Africa between ~5 and 3 Ma, including the typical *Brachystegia* woodland/forest in the Afar Basin (Bonnefille, 2010); *Brachystegia* woodland forms an important vegetation zone in the coastal forest of Kenya (Burgess and Clarke, 2000, Fig. 5). Hence we assume that during the early part of our study interval up to ~3 Ma, the CFEA reached along the coast northward all the way around the Horn of Africa into what is now Djibouti, Eritrea and Ethiopia, and southward into South Africa.

5.2. The Afar Basin: climatologically buffered until at least ~3 Ma

The Afar Basin, the northernmost EARS basin situated in Ethiopia, differs from other EARS basins with respect to its unique tectonic setting, local volcanic activity and relative coastal proximity (Fig. 9). The Afar marks the subaerial triple junction between Nubian, Somali and Arabian plates, which are diverging from each other due to extension in the Red Sea, East African and Gulf of Aden Rifts (Keir et al., 2013). The rifts in the Afar area contain numerous smaller graben structures that host sedimentary basins, often filled with sediments (runoff from the adjacent uplifted Ethiopian Highlands; Kalb, 1995) and volcanics (numerous thin tuff layers and thick basalt packages; e.g. Alene et al., 2017; Campisano et al., 2017). At present, distances between Afar Basin hominin sites and Red Sea coast are only ~200 km; in contrast, other early hominin sites in the EARS are situated much further from the Indian Ocean coast, at least ~500–700 km. During the Pliocene, up to at least ~3 Ma when sea levels were higher than today, the coast may regularly even have been as close as 100 km to Afar Basin sites. Assuming that the coastal forest extended all around the Horn of Africa, this would bring sites in the Afar Basin (e.g. Middle Awash Valley, Gona, Hadar,

Ledi-Geraru, Woranso-Mille) relatively easily within the typical inland extent of the CFEA. Hence, we propose that up to ~3 Ma the Afar Basin was regularly, more often than other EARS basins, part of or connected to the CFEA. Importantly, we consider fossiliferous sediments deposited in the Afar Basin during the latter conditions as a “proxy” of, or a “window” into, the coastal forest ecosystem at that time.

During highly variable climate episodes in eccentricity maxima, rivers draining the Ethiopian Highlands and running into the Afar Basin would not always supply enough water to sustain permanent lacustrine conditions in the basin, as evidenced by the temporary nature of its lake deposits (Campisano and Feibel, 2007). However, due to the relative proximity of the coast we expect that the Afar Basin would –just like the coastal forest along the Indian Ocean– suffer less from extremely dry conditions through the buffering, humidifying influence of the warm Red Sea/Gulf of Aden water body. Indeed, it has been found that from ~3.3 to 3.23 Ma a lake was present at Hadar (Campisano and Feibel, 2007) while lakes were then absent in other lake basins in the EARS (Trauth et al., 2005, 2007; Feibel, 2011). Furthermore, in the Middle Awash Valley relatively wet and wooded conditions prevailed between at least ~5.8 and 3.2 Ma (WoldeGabriel et al., 2001; Haile-Selassie et al., 2004; White et al., 2009a,b; Louchart et al., 2009; WoldeGabriel et al., 2009; Haile-Selassie et al., 2010a,b; Bonnefille, 2010). For instance, the habitat of *A. ramidus* at ~4.4 Ma was characterized as woodland to grassy woodland (White et al., 2009a,b). While this interpretation was challenged by Cerling et al. (2010, 2014), White et al. (2010, 2014) maintained that *A. ramidus* fossils are associated with woodland to grassy woodland habitat indicators and riparian forests. This reconstruction is confirmed by a recent review of available independent lines of evidence (Rowan and Reed, 2015).

Palynological evidence from Hadar also indicates that conditions there were wetter in the past: Pliocene rainfall (~800–1200 mm/year) was about twice that of today (Bonnefille et al., 2004). Throughout the Hadar sequence between ~3.4 and 2.95 Ma, humidity coefficients oscillated around 60%, which is only slightly below the 65% threshold for forest biome worldwide today (Bonnefille et al., 2004). Reed (2008) provided a multi-proxy habitat reconstruction for the Hadar Formation: between 3.42 and 3.25 Ma, closed wooded environments prevailed, followed by wet edaphic grasslands between 3.25 and 3.2 Ma. After that, a transition occurred to increasingly more open and arid grasslands at 2.95 Ma (Dupont-Nivet et al., 2008). Woodland habitats also prevailed at Woranso-Mille, Dikika and Maka (Rowan and Reed, 2015). Based on the documented permanent high humidity and presence of wooded conditions even during highly variable climate episodes, we propose that before ~3 Ma the Afar Basin was almost continuously habitable for woodland-forest-adapted and permanent-water-dependent fauna.

5.3. EARS rift basins and Chad basin: marginal areas?

Among inland EARS basins, the Turkana Basin (Fig. 9) occupies a unique position. This is due to its low elevation (now ~360 m above sea level) in the Turkana Depression, its permanent riverine connection to the vast Omo River drainage area in the Ethiopian Highlands (Feibel, 1993; 2011), and its location at the intersection of two rift systems (Bosworth and Morley, 1994). The Turkana Basin is connected via the Anza Rift to the near-coastal Lamu Embayment (Fig. 7) that flooded during periods of high sea level. Such marine incursions periodically brought the Indian Ocean coastline much closer to the Turkana Basin: ~300–400 km instead of 700 km (Oosterom, 1988), increasing the amount of moisture carried inland from the Indian Ocean to the Turkana Basin by the monsoon (e.g. at ~3.5 Ma; Feibel, 1988). The Turkana Basin was effectively a

“stepping-stone” on the recurrently available dispersal route between CFEA, EARS and central-western Africa. Turkana Basin paleohydrology over time was characterized by alternating lacustrine and riverine conditions (Feibel, 2011, Fig. 8), ensuring permanent water availability throughout climate cycles. As such, the Turkana Basin can be considered as a potential regional refugium for hominins (Hernández-Fernández and Vrba, 2006; Vrba, 2007; Joordens et al., 2011; Fortelius et al., 2016).

In contrast, other early hominin find areas such as the Baringo Basin, Laetoli and Kantis are located in upland eastern Africa at much higher elevations of ~1000 m, ~1600 m and ~1750 m respectively. These areas did not have a permanent major riverine input and were therefore, despite the occurrence of seasonal orographic rainfall, less buffered against recurrent variable and arid climate conditions. The Karongo Basin in the Malawi rift is different again, situated further South at ~500 m elevation. It is located at the southernmost seasonal reach of the Intertropical Convergence Zone (ITCZ; Ivory et al., 2018) and currently falls in a different vegetation zone than the more northerly EARS basins (White, 1983). Lüdecke et al. (2016) found, based on carbon isotope ratios of soil carbonates and suid teeth, a consistently closed wooded (C₃ vegetation) environment over the last 4.3 Ma, with regional patches of more dry-adapted C₄ vegetation. These differences highlight the spatial heterogeneity of inland EARS basins, which influences how different environments responded to climate change over time.

In summary, we infer that before ~3 Ma:

- the CFEA can be considered as a possible refugium for hominins and core (source) area for hominin evolution;
- the Afar Basin likely fulfilled an almost similar role as refugium and core area, due to its buffered climate and its regularly being part of or connected to the CFEA;
- inland EARS basins (Turkana, Baringo, Kantis, Laetoli, Malawi) and Chad Basin can be considered as marginal areas for hominin evolution, while the Turkana Basin due to its permanent water availability was less marginal and more refugial (providing more favorable living conditions) than other inland EARS basins.

6. Initial conditions of the conceptual model: who, when, where?

Next, we need to establish the “initial conditions” of the conceptual coastal refuge model: choosing the stem hominin, starting time, and source area. So, which known species or genus could possibly be considered as (similar to) Kingdon’s “coastal ground ape”? Between ~7 and 5 Ma, at least three alleged hominins were present in Africa: *Sahelanthropus tchadensis* at ~7 Ma in the Chad Basin (Brunet et al., 2002), *Orrorin tugenensis* at ~5.7–6 Ma in Kenya (Senut et al., 2001) and *Ardipithecus kadabba* at ~5.8 Ma in the Afar Basin, Ethiopia (Haile-Selassie et al., 2004). The skull characteristics of *Sahelanthropus* can be interpreted as indicating bipedality (Zollikofer et al., 2005). Anatomical analysis indicated that *O. tugenensis* was a habitual biped (Richmond and Jungers, 2008), and also *A. kadabba* was bipedal (Haile-Selassie et al., 2004, 2009; Haile-Selassie et al. (2016). Kingdon (2003) proposed that possibly one (or more) of the taxa above, and/or the younger ~4.4 My old *A. ramidus* from the Afar Basin, could be closely related to his hypothetical coastal ground ape. The recent detailed description of *A. ramidus* (White et al., 2009a,b; 2015) suggests that it indeed resembles Kingdon’s predicted ape: *A. ramidus* was a bipedal, omnivorous denizen of woodland with small patches of forest, and likely foraged both in trees and on the ground. Kingdon (2003) remarked that the find area of *Ardipithecus* in the Middle Awash Valley (Afar Basin) was too far from the coast for this genus to represent a “coastal ground ape”. However, the

assumed Mio-Pliocene (up to ~3 Ma) far northern extent of the coastal forest around the Horn of Africa places find localities of *Ardipithecus* in a wooded habitat connected to (or being part of) the coastal forest zone, supporting Kingdon's prediction of a bipedal coastal ground ape being similar to *A. ramidus*.

Based on the hominin fossil record (and notably the discoveries of *Sahelanthropus* and *Orrorin*) we conclude that the geographic origin (or multiple origins?) of hominin bipedality remains an open question (see also Strait, 2013). It is possible that bipedality first arose around paleolake Chad, or even more northward along the ancient Sahabi river and delta system in Libya, instead of in the CFEA as proposed by Kingdon (2003). However, in view of the continuous forest cover and East-West connectivity prior to ~7 Ma (Otero et al., 2009), it does not matter where the origin was, since it can be expected that the earliest bipedal hominins could rapidly spread to colonize accessible habitats. Based on abundant fossil presence of *A. ramidus* in the wooded Afar Basin (White et al., 2009b, 2015) and observed distribution of typical CFEA species (Kingdon, 1971–1982), we propose that this bipedal hominin inhabited the whole CFEA. Hence, as initial conditions for the conceptual model we suggest that *A. ramidus* serves as a good candidate for a “stem hominin”. The start time then is ~4.4 Ma, and start location is the coastal forest extending along the Red Sea/Indian Ocean coast from Eritrea and the Horn of Africa down to southern Africa (Fig. 9).

7. Defining the model “algorithm”

During variable climate episodes lasting several hundred thousand years, isolation of populations in the geographically confined refugium along the coast would be particularly conducive for ongoing evolution (Lister, 2004; Stewart et al., 2010; Martínez-Freiría et al., 2015). During climatically stable episodes that follow, evolved populations could expand and disperse via riverine/vegetated corridors to inland areas (such as Chad and EARS basins). Lakes in some of these rift basins then provided well-watered habitats with abundant terrestrial and aquatic food resources (Braun et al., 2010; Joordens et al., 2011; Archer et al., 2014) and must have formed attractive destinations for permanent-water dependent fauna dispersing from the coast. What is generally the fate of populations trapped outside their refugium in marginal (expansion) areas, when the climate changes again from stable to variable conditions? The results from genetic studies (e.g. Dalén et al., 2007 and references therein) suggest that expanded populations outside refugia often become extinct instead of tracking their retreating habitats by physically moving back into the refugium (Roebroeks et al., 2011). According to Stewart et al. (2010) this implies that populations in long-term refugia are descended from those individuals that remained in these refugia during dispersal phases, and consequently that expanded populations outside refugia make little or no contribution to long-term evolution of the species. In this case, the refugium can be termed a ‘source area’ and the expansion areas ‘sink areas’ for populations. However, it is also possible that populations in marginal areas manage to persist and even adapt to new environmental conditions (e.g. river floodplains in the Turkana Basin) when climate changes from stable to highly variable again. Rapidly fluctuating environments are often associated with increased phenotypic and behavioral plasticity that can be targeted by selection, resulting in new adaptive traits (Grove, 2012, 2014). In that case these populations find themselves on a new evolutionary trajectory, and as a consequence the previously marginal area is no longer a marginal area for them, but a relatively optimal area (and a possible future source area for a new lineage).

An additional possibility that should be taken into account is interbreeding and hybridization between populations (Ackermann, 2011; Abbott et al., 2016; Popadin et al., 2017; Ackermann et al., 2018). These processes could have taken place for instance if newly immigrated evolved hominin populations from the coastal forest met with local hominin populations that persisted in an inland area, after dispersal from the coast during the previous stable period.

In summary, we posit that hominin populations arriving from the CFEA in inland areas either go locally extinct at the end of climatically stable episodes when climatic-environmental conditions change again, or hybridize with local hominins that were there already, or persist and do not evolve, or persist and evolve into a new species. Thus, we define as “algorithm” of the conceptual model:

- During a climatically variable episode: isolation and ongoing evolution of hominin populations in the CFEA (Step 1);
- At the onset of and during a stable episode: expansion and dispersal of evolved hominin species to inland areas; and in case of establishment of a viable population: Step 2a) continuation of species as is, or 2b) meet local hominin population and interbreed, leading to hybridization. During stable episodes, the coastal forest remains populated with hominins;
- At the beginning of and during a variable climate episode in inland areas: Step 3a) local extinction, or 3b) persistence of species as is, or 3c) adaptation and evolution, or 3d) persistence of hybrid population, or 3e) adaptive evolution of hybrid population; and Step 1) again: isolation and evolution of hominin populations in the CFEA.

In Figure 10 we present one possible example (starting with a fictive hominin species during a variable climate phase in the coastal forest) of how this algorithm could play out. It is clear that even with simple climate forcing and this algorithm, the many degrees of freedom associated with multiple combinations of steps can produce bushy complex speciation and distribution patterns in a multitude of ways, approximating the levels of actual complexity and hominin species richness that must have existed but that we may never truly know (Martin, 1993; Spoor, 2016). However, we can derive predictions from the coastal refuge model, and evaluate how they compare with the observed pattern in hominin and climate records (Figs. 3, 8) that we have combined into one figure (Fig. 11).

8. Comparing model predictions with the hominin fossil record before ~3 Ma

We consider the following model predictions for the time period before ~3 Ma:

8.1. Prediction a): hominin dispersal events should coincide with (onset of) stable climate episodes

Onset of a stable episode reflects a major climatic-environmental transition, resulting in rivers and/or vegetation corridors connecting previously isolated regions (Fig. 9). As a consequence, plant and animal species (including hominins) can disperse from the coastal source area and colonize marginal inland habitats e.g. in the EARS and Chad basin. Hence, the coastal refuge model predicts that onset timing of stable episodes should coincide with timing of dispersal events, reflected in first appearance/presence of species dispersing from the source area. Indeed, *A. ramidus*

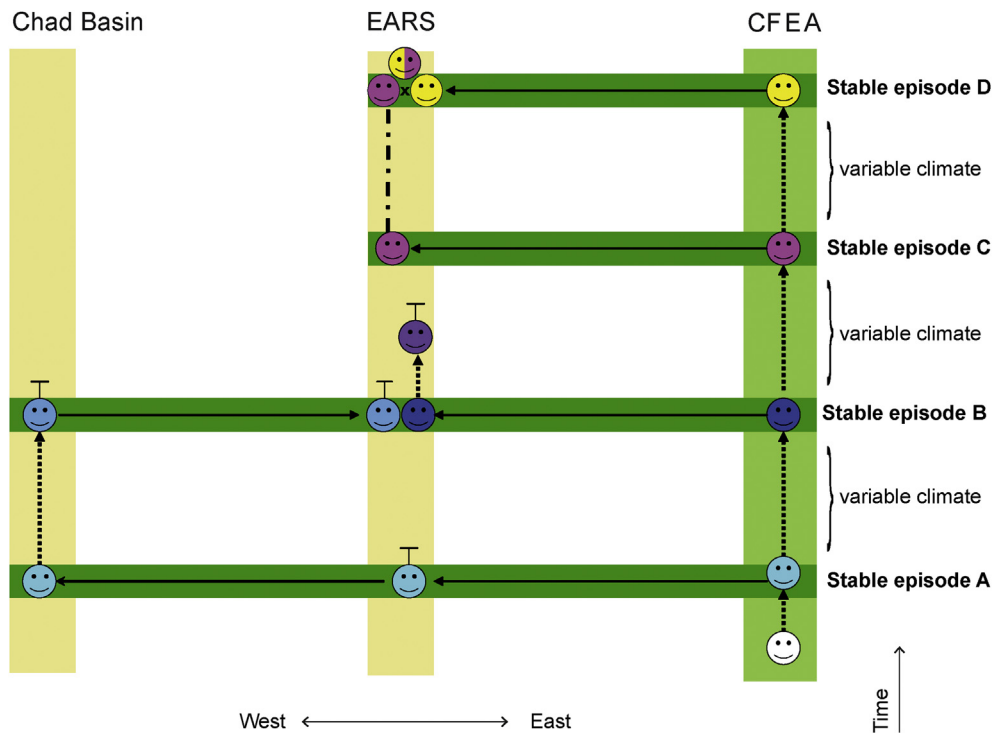


Figure 10. Conceptual model of possible dispersal and evolutionary processes (e.g. speciation, hybridization, extinction) over time. The generalized East African Rift System (EARS) basin is subjected to alternation between variable (beige) and stable (green) environmental conditions. Characters A-D indicate consecutive stable climate episodes in Africa. Horizontal green bars indicate recurrent temporary connections between the Coastal Forest of Eastern Africa (CFEA) and inland areas such as rift basins. Line arrow: hominin dispersal. Dotted arrow: evolution. Dash-dot line: persistence of species. Line with end: (local) extinction.

is present during a stable climate episode at 4.4 Ma in the Afar Basin and possibly in the Baringo Basin (Fig. 11). At the onset of the next stable climate episode at 4.2 Ma, *A. anamensis* first appears in the Afar and Turkana Basins. At the onset of the stable climate episode at 3.8 Ma, an early form of *A. afarensis* with affinities to *A. anamensis* first appears at Laetoli (Leakey et al., 1995; Lockwood et al., 2000) while the “Woransse-Mille hominins” (intermediate between *A. afarensis* and *A. anamensis*; Haile-Selassie 2010) are then present in the Afar Basin. Next, at the onset of the major stable climate episode around 3.5 Ma, *A. afarensis* and similar taxa like *A. bahrelghazali* and *K. platyops* appear in Kantis, Chad Basin and Turkana Basin respectively, and, *A. deyiremeda* appears in the Afar Basin (Fig. 11). We conclude that prediction a) is consistent with the combined hominin and climate records.

8.2. Prediction b): fossil abundance differs in the various rift basins

In this biogeographical context the Turkana Basin –and other inland rift basins even more so – is considered to be a relatively marginal area while the Afar Basin is regarded as a (sub-)core area for hominin habitation. Hence, the coastal refuge model predicts a higher number of hominin fossils in the Afar Basin than in the Turkana Basin and other rift basins. As already discussed in section 2.2 there is a difference in hominin fossil abundance between the Afar Basin, the Turkana Basin and Laetoli before ~3 Ma (Fig. 11): tens to hundreds of hominin fossils in the Afar Basin, tens of fossils in the Turkana Basin and Laetoli, and the other areas yield fewer or even no hominin fossils at all. As suggested by Su and Harrison (2008) and Villaseñor and Bobe (2015) this difference can be explained by environmental and ecological differences between the areas, with the Afar Basin then providing the most optimal habitat for early hominin occupation. We conclude that prediction a) is consistent with the hominin fossil records.

8.3. Prediction c): hominin presence in the Afar Basin is largely continuous and similar to the CFEA

Since in the biogeographical framework the Afar basin is regarded as being regularly part of or connected to the coastal forest (hence a (sub-)core area for hominin evolution), we expect that the hominin fossil record in the Afar basin is largely similar to that assumed for the CFEA. The coastal refuge hypothesis holds that before ~3 Ma, there is continuous hominin presence and ongoing evolution in the coastal forest, notably during variable climate phases (see Fig. 10). When we “run” the model algorithm in its most simple form (just evolution and migration of one lineage), starting with an *A. ramidus*-like species as the basal “coastal ground ape”, we obtain a predicted continuous hominin presence in the coastal forest (Fig. 12), that can be compared with observed hominin presence in the Afar Basin (Fig. 11). There appear to be gaps in hominin presence in the Afar Basin between 4.4–4.2 Ma and 4.0–3.8 Ma. However, ongoing studies indicate that these gaps may become “filled” by hominin fossil finds from deposits aged 5.4–3.9 Ma in Galili (Hujer et al., 2015; Simpson et al., 2017) and fossils from deposits aged 4.8–4.3 Ma in Gona (Simpson et al., 2019). Between ~3.8 and 3 Ma, the fossil record indeed reflects continuous presence of hominins belonging to the early to late *A. afarensis* lineage (Figs. 11, 12). We conclude that prediction c) is consistent with the hominin fossil record.

9. The impact of climate and environmental change between 3 and 2.5 Ma

The hominin fossil record between ~3 Ma and 2.5 Ma (Figs. 3, 11) is characterized by:

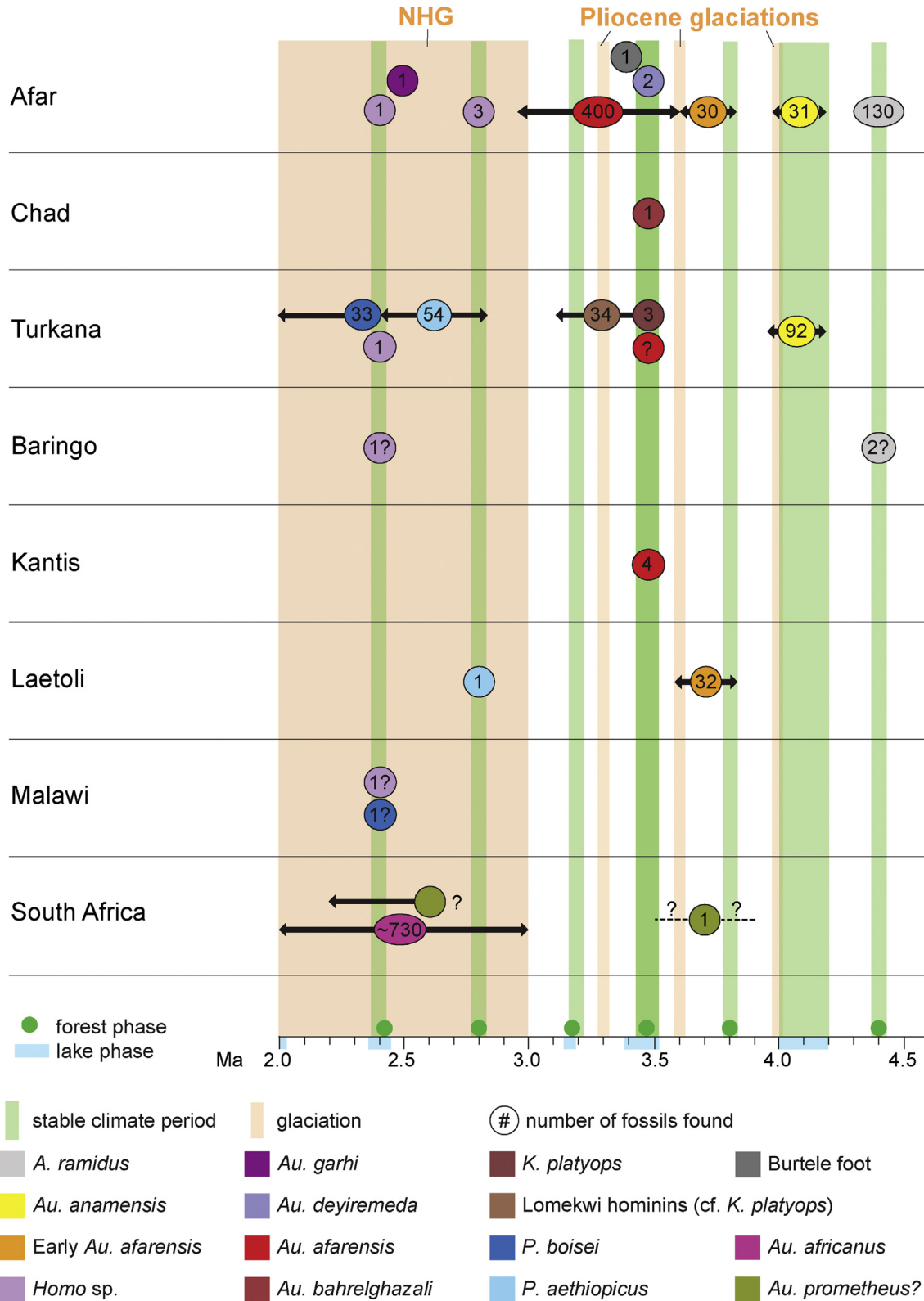


Figure 11. Combination of global paleoclimate records and early hominin fossil record in Africa between 4.5 and 2.5 Ma (see captions Figs. 3 and 8).

- the observed last appearance of the widespread and long-lasting species *A. afarensis* at ~2.95 Ma (Kimbel and Deleuzene, 2009; Kimbel, 2015);
- the observed first appearance of *Homo* sp., in the Afar Basin at ~2.8 Ma (Villmoare et al., 2015; DiMaggio et al., 2015; Reed et al., 2015);

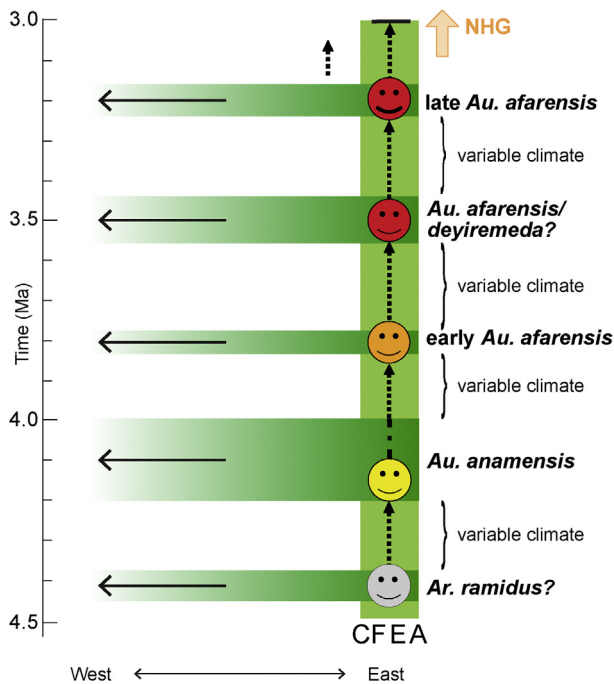


Figure 12. Example of application of the coastal refuge model for the time period between 4.5 and 3 Ma: ongoing evolution in the Coastal Forest of Eastern Africa (CFEA), with regular inland dispersals during stable climate periods.

- the observed first appearance of *P. aethiopicus* in the Turkana Basin, Laetoli and Malawi Basin by ~2.7 Ma (Wood and Constantino, 2007; Harrison, 2011);
- the observed first appearance of *Australopithecus africanus* at ~3 Ma in southern Africa (Herries et al., 2013).

Together, these last and first appearances suggest occurrence of a major regional change in hominin taxa between ~3 and 2.8 Ma, resulting in at least three new lineages (Kimbel, 1995; Reed, 2008; Rowan and Reed, 2015; Robinson et al., 2017). Where, why and how were these changes in hominin evolution brought about? Between ~3 and 2.6 Ma, onset and intensification of NHG resulted in increasing climatic cooling and drying in Africa (Fig. 8) and globally increased seasonality (Hennissen et al., 2015), which influenced vegetation cover in Africa. This is demonstrated by a pronounced decline in tree pollen density at ~2.7 Ma indicating an abrupt retreat of rain forests to an area of the same extension as today (Bonnefille, 2010). This is also shown in pollen records from ODP Site 659 off the western African coast (Leroy and Dupont, 1994). A pronounced shift in $\delta^{13}\text{C}$ of soil carbonates in the Turkana Basin at ~2.7 Ma (Bonnefille, 2010; Levin et al., 2015) and in dietary $\delta^{13}\text{C}$ in herbivores in the Omo Valley at ~2.8 Ma (Bibi et al., 2013) indicates a change from woodland to more open conditions, and/or a shift from C_3 to more C_4 grasses at that time. Robinson et al., 2017 provided a detailed multi-proxy analysis of the environmental shift at ~2.8 Ma the Lower Awash Valley of the Afar Basin, showing consistent changes from wooded towards more open and arid conditions. Interestingly, they found that after ~2.8 Ma the Turkana Basin was more mesic than the Lower Awash Valley, confirming its status as a continuously well-watered environment thanks to the Omo River.

Between ~3 and 2.5 Ma, progressive climatic cooling and drying in Africa adversely influenced vegetation of the coastal forest. Moreover, from ~3 Ma onwards, weakening of the rain-bearing summer monsoon and strengthening of the cold and dry winter

monsoon (Zhisheng et al., 2001; Xu et al., 2015; Vallé et al., 2016) may have contributed to drying out the Horn of Africa. Hence, for the CFEA this would mean a latitudinal retreat of the forest area, with its northern and southern borders moving in the direction of the equator, approximately to their present-day locations in southern Somalia and southern Mozambique respectively. Extensive dry coastal areas would occur to the north and south of the CFEA borders, respectively the Horn of Africa, and part of the flat river-less coastal lowland between the mouths of the Zambezi and Limpopo Rivers (Kingdon, 2003). However, we assume that some areas in the northeast and southeast of Africa remained relatively humid due to orographic rainfall. Part of the Afar Basin still received water from the Awash River draining the Ethiopian Highlands, and the southernmost part of eastern Africa still received water via rivers flowing to the coast from the Drakensberg mountain chain. We infer that global climate change around ~3 Ma caused fragmentation of the coastal forest, resulting in the emergence of three geographically isolated relatively humid hominin occupation areas along the north–south axis of eastern Africa: the Afar Basin, the contracted CFEA along the coast of Southern Somalia, Kenya, Tanzania and northern Mozambique, and the coastal forest in southeastern Africa (Fig. 13). Environmental conditions in these isolated areas, arguably each containing populations of *A. afarensis* at that moment, would differ due to different rainfall, river water input and air temperatures associated with their particular geographical position. Especially in the Afar Basin where local rainfall decreased dramatically between ~3 and 2.7 Ma (Zhisheng et al., 2001; Bonnefille et al., 2004), woodlands would disappear to be replaced by more arid open conditions (Campisano and Feibel, 2007, 2008; Reed, 2008; Robinson et al., 2017) with gallery forests forming a narrow verdant strip along the Awash River. The contracted CFEA likely became dryer compared to conditions before ~3 Ma, but coastal woodlands and rivers with gallery forests and floodplains continued to exist throughout orbital wet-dry climate cycles (Kingdon, 2003; Dupont and Kuhlmann, 2017). The humid area in southern Africa, consisting of a narrow coastal strip (~10–20 km) with mountains rising abruptly out of the plain, differs physically and ecologically from equivalent coastal habitats further up the coast (Kingdon, 2003). Due to its southern position, it experiences a strong seasonality with short cold winters and long hot summers, possibly driving seasonal faunal migration between lowland and highland (inland) environments. The arid areas north and south of the contracted coastal forest would inhibit spread of forest and water-dependent species along the coast and thus act as a barrier to gene flow between populations on either side of it (Kingdon, 2003), ensuring genetic isolation of separated hominin populations.

In summary, environmental change in eastern Africa has likely led to a tripartite habitat fragmentation slightly after ~3 Ma. We propose that this resulted in a tripartite cladogenetic split into three different taxa (X, Y and Z; Fig. 14). The northern population of *A. afarensis* that became isolated in the Afar Basin gave rise to taxon X (and/or possibly *Homo* sp. at 2.8 in the Afar Basin; Villmoare et al., 2015), and the southern population that became isolated in southeastern Africa evolved into taxon Z (possibly *A. africanus* at ~3 Ma in Makapansgat; Herries et al., 2013). The “central” population isolated in the contracted CFEA gave rise to taxon Y. No fossil remains are known from possible descendants of this isolated CFEA population, which is not surprising since the coastal forest has a poor vertebrate fossilization potential. However, the presence of *P. aethiopicus* fossils at ~2.7 Ma in the Turkana Basin and Laetoli (Kimbel and Delezene, 2009; Harrison, 2011) could suggest the identity of hominin inhabitants of the contracted coastal forest at that time. Within the constraints of the coastal refuge model outlined above, regular connections between contracted CFEA and

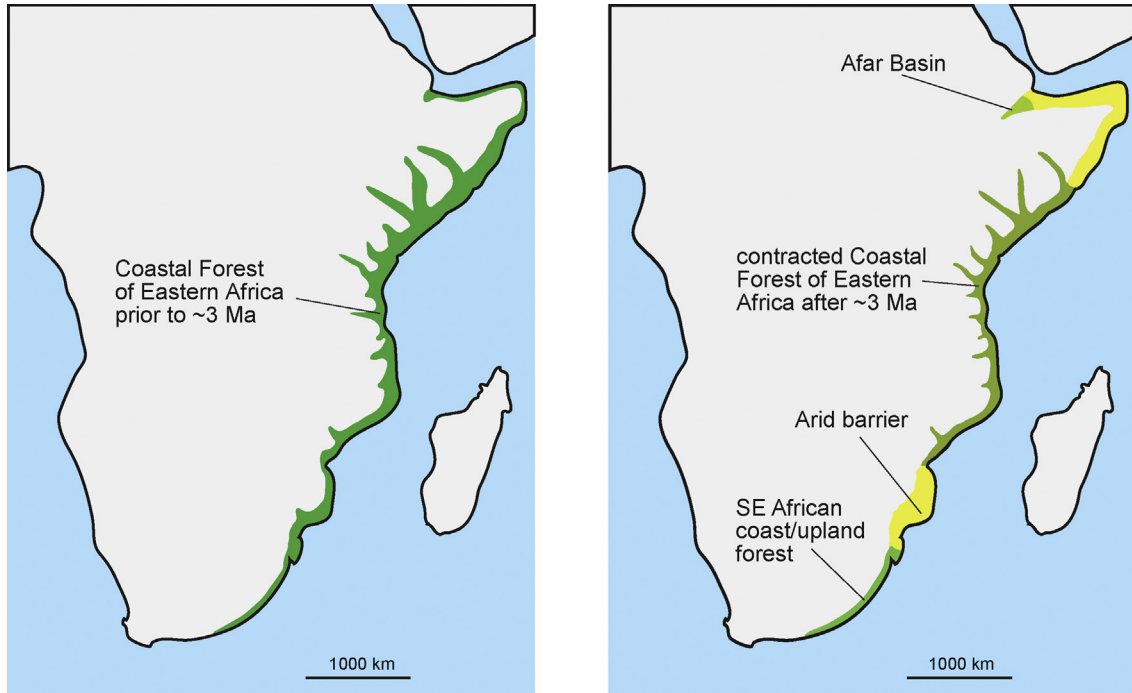


Figure 13. a. Schematic representation of the continuous Coastal Forest of Eastern Africa (CFEA)/hominin habitat before 3 Ma. b. Fragmented hominin habitats: Afar Basin, contracted EAFC, and southeastern African coastal/upland forest.

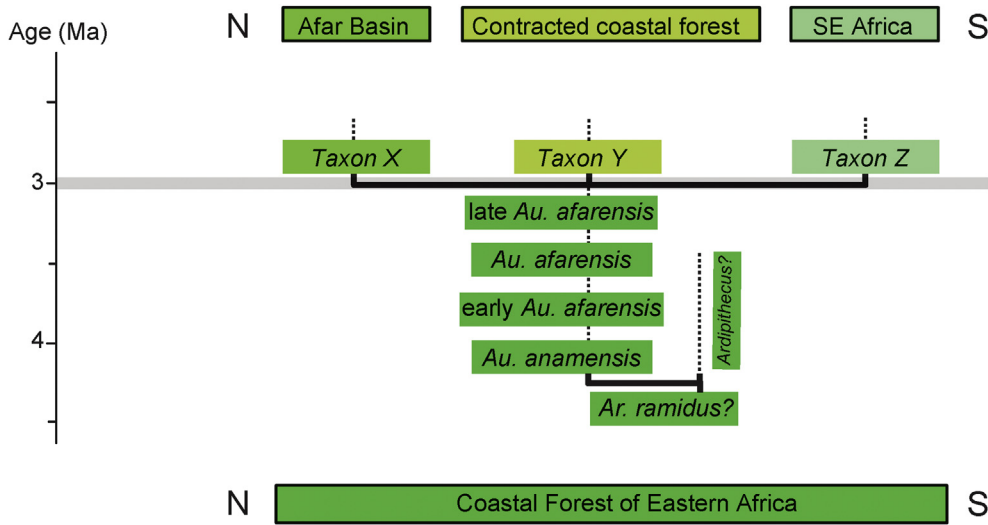


Figure 14. Proposed schematic phylogenetic tree of early hominin taxa in the biogeographic framework of the coastal refuge model. The dotted line alongside the *Australopithecus* lineage indicates the postulated presence of a contemporaneous *Ardipithecus*-like lineage persisting until at least 3.4 Ma, as suggested by the discovery of the “Burtele foot” fossil (Haile-Selassie et al., 2012).

inland EARS basins indicate that *P. aethiopicus* may have evolved from *A. afarensis* after ~3 Ma in the contracted CFEA, and then during a stable episode migrated inland via humid corridors. This mechanism would explain the presence of *P. aethiopicus* fossils in Turkana Basin and Laetoli (and the later presence of its descendant *Paranthropus boisei* in the Turkana, Baringo, and Malawi Basins; Wood and Constantino, 2007), and its absence in the Afar Basin and southern Africa. However, we have to bear in mind that an alternative explanation for presence of *P. aethiopicus* could be that it locally descended from an as yet unknown robust hominin in an

inland area (c.f. the dark blue hominin evolving into the purple hominin in an EARS basin, Fig. 10).

We conclude that the proposed climate-forced habitat fragmentation at ~3 Ma provides an ecological mechanism that could explain patterns of observed taxon change in one of the lineages of the presently known hominin record (Figs. 11 and 14). Other, presently less well-understood taxa such as *K. platyops*, “Burtele foot”, *A. deyiremeda* and *A. prometheus* (and future discoveries of new taxa) are tantalizing indicators of the possible existence of additional lineages in the hominin evolutionary record,

reminding us of its daunting complexity and species richness (Martin, 1993).

10. Discussion

We present a new view on geographic patterns in early hominin presence over time, placing the core area of early hominin evolution not in the EARS or southern Africa, but in the Coastal Forest of Eastern Africa (with the Afar Basin, notably before 3 Ma, being regularly part of this core). We concede that this would not necessarily be the one and only core area: possibly the forests in the central and western parts of Africa (and perhaps even the Atlantic and Mediterranean coasts) played an as yet unknown role as well. It can be expected that during stable climate periods when east-west connectivity existed, hominins were present in (some of) these areas. For instance, occasional interfingering of separated western-central and eastern biomes led to occasional spatial overlap and secondary contact between early hominin and chimpanzee lineages at the fringes of ranges (Grubb et al., 1999; McBrearty and Jablonski, 2005), as demonstrated by interbreeding and hybridization between these lineages after their initial split (Patterson et al., 2006). Similarly, research on ape and human body lice genetics has shown that there must have been a secondary meeting (probably predator-prey contact) between early hominin and gorilla lineages at some time in the Pliocene (Light and Reed, 2009).

We have presented supporting evidence for the assumptions underlying the coastal refuge model, and concluded that several predictions following from the coastal refuge model are consistent with the observed hominin fossil and paleoclimate records. However, we have not yet rigorously tested the model. Vrba (2007) pointed out that is difficult to test hypotheses on environmental causes of hominin and other biotic evolution, because the data come from different subdisciplines each with their own set of biases and errors. A major challenge for the coastal refuge model is the fact that at present there is not a single Pliocene hominin fossil known from the Coastal Forest of Eastern Africa. The primary test of the coastal refuge hypothesis would be to find early hominin fossils in east coastal deposits, thus corroborating the model. Or alternatively, a good test would be to find a rich and diverse fossil fauna in east coastal deposits aged ~4.5–2.5 Ma, containing no hominin fossils (cf. Lothagam, section 3.3), thus rejecting the model.

Since fossilization potential in the CFEA is very low, extra efforts are required to identify and explore possibly fossiliferous areas near former Indian Ocean coastlines and in specific places within the coastal zone. Fortunately, there is increasing scientific interest in the coastal area. For instance, as mentioned before, the new project at Gorongosa in Mozambique conducted by Susana Carvalho and colleagues (Carvalho et al., 2017; Habermann et al., 2018) is starting to find evidence of forested conditions in a coastal setting in the Mio-Pliocene Mazamba Formation, with so far limited but encouraging presence of vertebrate fossils. Habermann et al. (2018) state that absence or presence of primates in the fossil record from Gorongosa will be key for testing paleobiogeographic hypotheses of primate evolution in coastal forests. We are hopeful that their continuing work in Gorongosa will yield such fossils.

Other examples of promising fossil exploration areas would be sediments trapped in limestone caves located in the Indian Ocean coastal areas, notably along the coasts of Kenya (e.g. Vipingo and Similioni caves; Kilifi area), Tanzania (e.g. Matumbi and Amboni caves) and Mozambique (Marean and Shea, 1996; Younge et al., 2002; Helm et al., 2012; Pickford, 2012; Gonçalves et al., 2016). Recently, Shipton et al. (2018) excavated to 3 m depth in the Panga ya Saidi cave in the coastal forest north of Mombasa (Kenya), and found a record of human activity back to ~78 ka. This inspires confidence that it would in principle not be impossible to find

evidence of hominin occupation in the CFEA. It could be worth while to dig deeper than 3 m in caves such as Panga ya Saidi in order to look for older deposits containing signs of hominin presence, analogous to the discoveries made in deep trenches in the cave Liang Bua on Flores in Indonesia (Sutikna et al., 2018).

In addition to the hominin fossil record, non-hominin faunal and floral fossil records are particularly useful for testing the coastal refuge model. For example, the model posits that hominins (especially before ~3 Ma) were predominantly associated with the humid forest/woodland biome, instead of with a more open savanna biome. Hence, we can infer that mammals constituting a forest/woodland faunal community would show a similar distribution pattern in space and time as hominin fossils before ~3 Ma. Providing there is sufficient age control and temporal resolution in the dataset, this can be tested by quantitatively analyzing presence/absence/abundance of typical “forest” and “non-forest” (and “water-dependent” and “dry-tolerant”) species over time in a similar way as we did for hominin fossils, by plotting numbers of fossils (or preferably percentages of total fauna) per basin over time (as in Fig. 11). Since relatively large numbers of non-hominin mammal fossils are (and will become) available for this (Bobe et al., 2007; Bobe and Leakey, 2009; Rannikko et al., 2017), it should be possible to use statistical analyses to test significance of the patterns found (e.g. Rowan et al., 2015). It would also be worthwhile to apply ecometric analysis to fossil mammal teeth of different time periods in order to detect possible evidence of the variable-stable climate periodicity and associated periodicity in seasonality, notably the role of long dry seasons (Žliobaitė et al., 2016). The more fossils become available for study, and the better constrained in time, the more feasible it will be to discern statistically significant patterns in time and space that can be interpreted in terms of environmental change, evolution and dispersal.

Another way of testing the model is to conduct genetic/genomic analyses on extant flora and fauna in different parts of Africa. The molecular phylogeographic work of Hemp et al. (2015), Bryja et al. (2017) and Barratt et al. (2017, 2018), resolving evolutionary relationships and timing of separation/connection events between coastal and inland populations of forest-dwelling insects, rats, and amphibians, has already been mentioned. Such approaches could also be applied to test Kingdon's predictions on the coastal-inland sister-species complexes, such as squirrels of the genus *Paraxerus* (Kingdon, 2003; see also; Grubb, 1978) and bushbabies of the genus *Paragalago* (Groves, 2015; Masters et al., 2017). Presently, we are using comparative genetic analyses (mitochondrial genomes in combination with several nuclear genes) on the extant fish species *Synodontis schall* and *Hydrocynus forskahlli*, in combination with occurrence data from the fish fossil record in Africa (see e.g. Pinton et al., 2013), to calculate phylogenetic trees and estimate timing of the last gene flow (as proxy for drainage connection) between populations of these species in the Turkana Basin and the Chad Basin (Otero et al., 2016). These approaches provide powerful tools to interpret evolutionary patterns and to test hypotheses and models, by linking biogeography, climate, and development of drainages (connection-disconnection) and environments (e.g. forest expansion-contraction) over time.

10.1. The coastal refuge model as predictive tool

The coastal refuge model can be used to predict the occurrence of hominin fossils in deposits of certain ages in certain places. For instance, based on the model and the pattern in the hominin fossil record (Fig. 11), it would be expected to find fossils of early *A. afarensis* in ~3.8 My old deposits in the Turkana Basin, similar to fossils of that age in the Afar Basin and Laetoli. The absence of such hominin fossils from the Turkana Basin observed so far could be

explained by geomorphology and taphonomy: through lack of accommodation space, there was no lacustrine deposition at 3.8 Ma in the Turkana Basin, only scattered Moiti floodplain sediments that contain few and mostly badly-preserved fossils (Feibel, 2011). This decreases the chance of finding hominin fossils. However, we predict that with more intense prospecting specifically targeting these deposits, hominin fossils aged around ~3.8 Ma may be found. In addition, we predict that such early *A. afarensis*-like populations could adapt to then prevailing floodplain conditions and over time evolve locally into a new taxon (see Fig. 10, the dark blue hominin evolving into the purple hominin in an EARS basin). Furthermore, based on the model we can predict that it should be possible to find fossils of *P. aethiopicus* in the younger part of the Chemeron Formation (dated to 3.3–2.6 Ma) in the Baringo Basin where this species has not been encountered so far.

The coastal refuge model can also point toward locations of promising new exploration areas for hominin fossils. For example, the model holds that in the stable episode around 3.5 Ma, *A. afarensis*-like populations were widespread in Africa and thus could potentially be found in many different areas far away from –but then temporarily connected to – the EARS and CFEA. Based on the occurrence of ~4–3 My old fossil proboscideans in Bethlehem showing affinities to Afar Basin taxa (Rabinovich and Lister, 2016), it would not be unreasonable to predict finding *A. afarensis*-like populations as far north as the Levant –technically “out of Africa”. The extensive fossil finds over the past 50 years have demonstrated that ‘marginal’ areas (inland areas such as Chad Basin, Turkana Basin, Laetoli) are suitable for fossil hunting, especially so when sediments deposited during stable climate episodes are targeted. The coastal refuge model predictions now also make the connecting zones between marginal areas and coastal forest worthy of examination. This is exemplified by the new hominin locality Kantis, which is situated on the eastern shoulder of the EARS (Mbua et al., 2016), along the Kantis River that flows from the EARS via the Athi-Galana-Sabaki River system into the CFEA and Indian Ocean. Other promising areas between EARS basins (for instance Turkana Basin) and coastal forest would be the Chalbi Basin just east of the Turkana Basin (e.g. Algas and Equid Tooth Sites, see Ferraro et al., 2012), the area around Mt. Marsabit, and areas along the flanks of the Lamu Embayment (Kenya, Somalia).

11. Conclusions

We have explored the relevance of the Coastal Forest of Eastern Africa in hominin biogeography and proposed that the coastal forest served as a core area for early hominin evolution and dispersal. From this hypothesis, we developed the conceptual coastal refuge model that combines dimensions of time and space to investigate how climatic and environmental changes are reflected in the presently known hominin fossil record. The most striking temporal feature of the pattern in the hominin fossil record is the dividing line that can be drawn at ~3 Ma (Fig. 11).

Before ~3 Ma, the Afar Basin appears to have been a hominin (sub-)core area, and in that respect similar to (and/or part of) the CFEA. The other inland fossil sites then were marginal areas for hominin habitation, with the Turkana Basin being relatively less marginal than the other inland EARS basins. Between ~4.5 and 3 Ma, the 100 and 400 ky eccentricity cycles were main climatic drivers of evolution and dispersal. Hominin evolution occurred notably during variable climate episodes in Earth’s eccentricity maxima (as proposed by Maslin and Trauth, 2009; Potts, 2013). We add an important component to the existing viewpoint: hominin dispersal from the coast to (and between) inland basins occurred via vegetated humid corridors notably during stable climate episodes in eccentricity minima. Seasonality, especially the length of

the dry season, must have been a critical factor constituting a threshold for establishment and persistence of vegetated conditions and viable hominin populations in inland areas.

After ~3 Ma, when NHG intensified, increasingly arid and cool conditions resulted in latitudinal contraction of the CFEA. We infer that this forest contraction and habitat fragmentation caused a tripartite geographic split of the hominin population then residing in the coastal forest zone along Indian Ocean and Red Sea coasts. As a consequence, three separated populations found themselves isolated from each other in different ecological conditions, which resulted in different evolutionary trajectories (Figs. 13 and 14). We conclude that between ~3 and 2.5 Ma, NHG exerted the all-important climatic influence on hominin evolution, likely causing a major cladogenetic event in the hominin lineage. We posit that also after ~3 Ma, the 100 ky and 400 ky climate cycles will have continued to affect the dispersal and evolution patterns of hominin populations by recurrently, during stable climate episodes, connecting the contracted coastal forest with inland EARS basins.

A major challenge for the coastal refuge model is the fact that so far, no (hominin) fossils have been found in the CFEA. We have provided explanations for the lack of fossils, and indicated how this could be remedied with targeted search efforts in the coastal area. Furthermore we have discussed how the model can be tested, e.g. with molecular phylogeography approaches, and used to predict new hominin fossil locations. The coastal refuge model recognizes and includes the influence of climatic and environmental variability as drivers of early hominin evolution (Potts, 1996, 1998a, b, 2013; Kingston, 2007; Maslin and Trauth, 2009), and significance of climatic stability and mesic corridors to facilitate hominin dispersal (Castañeda et al., 2009; Drake et al., 2011; Larrasoana et al., 2013; Grove, 2014; Grove et al., 2015; Cuthbert et al., 2017). Also, it agrees with deMenocal (2004, 2011) who invoked major global climate change related to onset and intensification of NHG as driver for hominin evolution. Our model integrates the spatial component into these accumulated insights and proposes a unifying testable climate-forced ecological mechanism explaining distribution of early hominin taxa in Africa. Even so, we realize that such a conceptual model will at best be a mere approximation of actual complexity in hominin taxic diversity and evolution. We hope that this study will provide food for thought and lead to new avenues in hominin evolution research.

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