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Human evolution in a variable environment: the amplifier lakes of Eastern Africa

Martin H. Trauth[a,*], Mark A. Maslin[b], Alan L. Deino[c], Annett Junginger[a,d], Moses Lesoloyia[e], Eric O. Odada[f], Daniel O. Olago[f], Lydia A. Olaka[a,d], Manfred R. Strecker[a], Ralph Tiedemann[g]

[a] *Institut für Geowissenschaften, Universität Potsdam, Potsdam, Germany*
[b] *Geography Department, University College London, London, UK*
[c] *Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, CA 94709, USA*
[d] *DFG Graduate School "Shaping the Earth's Surface in a Variable Environment", University of Potsdam, Germany*
[e] *Milgis Trust, Box 93, Naro Moru 10105, Kenya*
[f] *Department of Geology, University of Nairobi, Nairobi, Kenya*
[g] *Unit of Evolutionary Biology/Systematic Zoology, Department of Biology and Biochemistry, University of Potsdam, Germany*

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ABSTRACT

The development of the Cenozoic East African Rift System (EARS) profoundly re-shaped the landscape and significantly increased the amplitude of short-term environmental response to climate variation. In particular, the development of amplifier lakes in rift basins after three million years ago significantly contributed to the exceptional sensitivity of East Africa to climate change compared to elsewhere on the African continent. Amplifier lakes are characterized by tectonically-formed graben morphologies in combination with an extreme contrast between high precipitation in the elevated parts of the catchment and high evaporation in the lake area. Such amplifier lakes respond rapidly to moderate, precessional-forced climate shifts, and as they do so apply dramatic environmental pressure to the biosphere. Rift basins, when either extremely dry or lake-filled, form important barriers for migration, mixing and competition of different populations of animals and hominins. Amplifier lakes link long-term, high-amplitude tectonic processes and short-term environmental fluctuations. East Africa may have become the place where early humans evolved as a consequence of this strong link between different time scales.

1. Introduction

Numerous hypotheses have been developed to explain the causal linkages between climate, environment and the evolution of mammals including humans in East Africa. After Darwin's (1871) early speculations about the evolution of bipedalism and environmental change, the classic *savanna hypothesis* of Henry Fairfield Osborn and Raymond Dart attempted to link the evolutionary divergence of hominins and other great apes, and the emergence of bipedalism, with the proposed forest–savanna transition in Mio-Pliocene time (e.g., Dart, 1925, 1953). Though largely disproved, the savanna hypothesis and its subsequent modifications has influenced numerous hypotheses that link shifts towards drier climates, and human evolution and migration on all time scales (e.g., deMenocal, 1995; Potts, 1998; Sepulchre et al., 2006; Carto et al., 2009). There were always alternative explanations for the evolution of hominin bipedalism discussed in science, some of them in scientific niches rather than being accepted by a wider scientific audience, but at least having inspired lively discussions over decades (e.g., the *aquatic ape theory* by Hardy, 1977; Morgan, 1982, 1997).

Another, recently challenged hypothesis of climate-evolution linkages is about the onset of the northern hemisphere glaciations near two and a half million years causing a rapid burst of speciation in Africa (e.g., Vrba, 1985, 1993). Elisabeth Vrba used the temporal coincidence of the onset of the northern hemisphere glaciations, a shift towards a drier climate in Africa, and the replacement of forest antilopes by species that graze only in dry, open savannas. According to the *turnover pulse hypothesis*, the spread of the savannas near this event caused the adaptation of bovid species to a new environment and hence the evolution of new species (e.g., Vrba, 1985, 1993). Marine records of Saharan dust seemed to support the hypothesis of a major shift towards a more arid climate during the onset of the northern hemisphere glaciations superimposed on a regime of subdued moisture availability (deMenocal, 1995, 2004). This event also seem to have affected early humans as some favored first occurrences of the genus *Homo* and the earliest

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* Corresponding author. Institut für Erd- und Umweltwissenschaften, Universität Potsdam, Karl-Liebknecht-Str. 24, 14476 Potsdam, Germany. Tel.: +49 331 977 5810; fax: +49 331 977 5700.

E-mail address: trauth@geo.uni-potsdam.de (M.H. Trauth).

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stone tools date back to between 2.4 and 2.6 Ma (e.g., Washbourn, 1960; deMenocal, 1995, 2004).

The challenge for the hypothesis of the 2.5 Ma events arises from many sides. Recent chronologies for the onset of the northern hemisphere glaciations that the build-up continental ice sheets in the northern hemisphere was a gradual process between ca. 3.15–2.5 Ma rather than an abrupt event at 2.5 Ma (e.g., Haug and Tiedemann, 1998; Bartoli et al., 2005). Furthermore, the proposed shift in African climate towards a drier and more variable climate occurs at 2.8 (±0.2) Ma (deMenocal, 1995, 2004) has been challenged by a statistical re-analysis of the terrestrial dust records (Trauth et al., 2009). According to the revised chronologies of terrestrial dust flux an important shift towards a more variable climate fluctuating between extreme wetness and droughts with orbital cyclicities after ca. 1.9–1.6 Ma (Trauth et al., 2009). On the contrary, climate in East Africa has been characterized by significantly wetter, but also variable climate conditions at ca. 2.7–2.5 Ma as indicated by high, fluctuating lakes occurring everywhere in the region (e.g., Trauth et al., 2005, 2007; Deino et al., 2006). An important shift towards increased aridity and variability after approximately 2.2 Ma has also been observed in southwest African palaeovegetation records (Dupont, 2006). It has been suggested that a specific climate reorganization event in the lower latitudes including the development of a stronger Walker Circulation was responsible for this major climate shift in the tropics at around 2.0 Ma (Ravelo et al., 2004).

A significant rise in environmental instabilities rather than distinct shifts in climate has been suggested as the driver for contemporaneous emergence of mammals and hominins by the *variability selection hypothesis* (Potts, 1998). Potts (1998) identifies intervals of enhanced variability on relatively long time scales, e.g., variability in the Milankovitch frequency band (10^5–10^4 yrs) but does not explain how these long-term variations may have an effect on species individuals, groups or populations having life times of $<10^2$ years. This theory has been modified to take account of the new data on the appearance and disappearance of large lakes in East Africa (Trauth et al., 2005, 2007) and has been referred to as the *pulsed climate variability hypothesis* (Maslin and Trauth, 2009). According to this hypothesis, Plio-Pleistocene African climate was characterized by pulses of a significantly wetter and more variable climate fluctuating at precession/half precession cycles unrelated to the onset and amplification of high-latitude glacial cycles (Trauth et al., 2003, 2005, 2007; Maslin and Trauth, 2009).

Hypotheses on environment-evolution linkages are typically tested in East Africa because of the frequency of hominid remains and the ability to data fossil bearing strata and environmental records. Most of these hypotheses, however, are not considering the particularity of East Africa as a tectonically active and climatically sensitive region (e.g., Trauth et al., 2003, 2005). One of the few hypotheses considering this aspect is the one by Geoffrey King and collaborators (e.g., King and Bailey, 2006). According to this hypothesis, the evolutionary stimulus lies not in the savanna but in broken, hilly rough country where the early hominins could hunt and hide. Such surface roughness, generated by tectonic and volcanic movements characterizes not only the African rift valley but probably the whole route of early hominin dispersals (King and Bailey, 2006). Here, the rift valley provides the necessary geographic barriers through lava flows and fault scarps (King and Bailey, 2006). On the other hand, rift valleys have also been discussed as corridors for migration, expansion and dispersals of mammals and hominins (e.g., Peltenburg et al., 2001).

In this context, the environmental conditions and causes of major migrations events such as the one of *Homo ergaster/erectus* out of Africa and *Homo sapiens* are also intensely discussed (deMenocal, 1995; Trauth et al., 2005, 2007, 2009; Carto et al., 2009; Castañeda et al., 2009). According to the established view, early hominins tried to escape unfavorable environmental conditions during severe droughts (deMenocal, 1995; Carto et al., 2009), whereas recent work suggests that humans dispersed and expanded during pulses of wetter climates, the emergence of larger hominin populations and conditions with sufficient food to provide the necessary energy for migration (Trauth et al., 2005, 2007, 2009; Castañeda et al., 2009). As an example for a hypothesis favoring the arid scenario, it has been suggested that global cooling events, such as Heinrich events, which occurred episodically throughout the last glacial cycle, led to abrupt changes in climate that may have rendered large parts of North, East, and West Africa unsuitable for hominin occupation, thus compelling early *Homo sapiens* to migrate out of Africa (Carto et al., 2009). Accordingly as a result of a drier climate, Cowling et al. (2008) suggested the reduction of tropical forest across Central and East Africa during glacial period may have allowed migration. On the contrary, Castañeda et al. (2009) proposed that changes in variability in the strength of Atlantic meridional overturning circulation influenced North African climate and, at times, contributed to wetter conditions in the central Sahara/Sahel, allowing humans to cross this otherwise inhospitable region.

Here, we propose a hypothesis that links both tectonic processes and climate change as major drivers for evolution and migration in East Africa. The new hypothesis both explains speciation according to the classic allopatric model and natural selection in a variable, diverse and challenging environment: the *hypothesis of amplifier lakes*. It explains how relatively moderate global/regional/local climate shifts are amplified by (1) the specific geometry/geomorphology of the rift valley with steep walls and flat graben floors and (2) the distinct climate/environmental gradient/contrast between high rainfall on the rift shoulders and volcano peaks on one hand and extreme heat/high evaporation in the rift lowlands. We believe that this hypothesis fits well into the family of hypothesis that either focus on the particularity of the rift topography or on climate/environmental changes. The incompleteness of the fossil and the inaccuracy of the paleoclimate/environmental records will probably never provide the degree of detail that would be required to prove or disprove any of these hypotheses as the ones describe above or the one proposed here. It will, however, provide a valuable scenario to be tested, challenged, or even falsified in the sense of Karl Popper's epistemology of critical rationalism (Popper, 1959).

2. The amplifier lakes of East Africa

The established drivers of environmental instability in East Africa are volcano-tectonic phenomena associated with the East African Rift System (EARS) and associated plateaus (time scales of 10^6–10^5 years), orbitally-driven changes in insolation (10^5–10^4 years), and variations in total solar irradiance (10^3–10^0 years) (Kutzbach and Street-Perrott, 1985; Verschuren et al., 2000, 2009; Trauth et al., 2003, 2005; Barker et al., 2004; Sepulchre et al., 2006) (Fig. 1). In addition to these direct influences, remote drivers of East African environmental changes include the uplift of the Tibetan plateau and the establishment of the African-Asian monsoon system (10^6 to 10^5 years), orbitally-driven glacial–interglacial cycles (10^4 to 10^3 years), and sea-surface temperature variations driven by the Indian Ocean Dipole and the El Niño/Southern Oscillation (10^2–10^0 years) (e.g., Kutzbach and Street-Perrott, 1985; Saji et al., 1999; Maslin and Christensen, 2007) (Fig. 2).

Drivers of environmental changes acting on relatively long time scales have the greatest amplitudes and therefore should have the greatest effect on the habitats of animals and hominins. For example, growth of the East African and Ethiopian plateaus are considered to be major influences in the dramatic vegetation change on the continent during the last twenty million years (e.g., Sepulchre et al.,

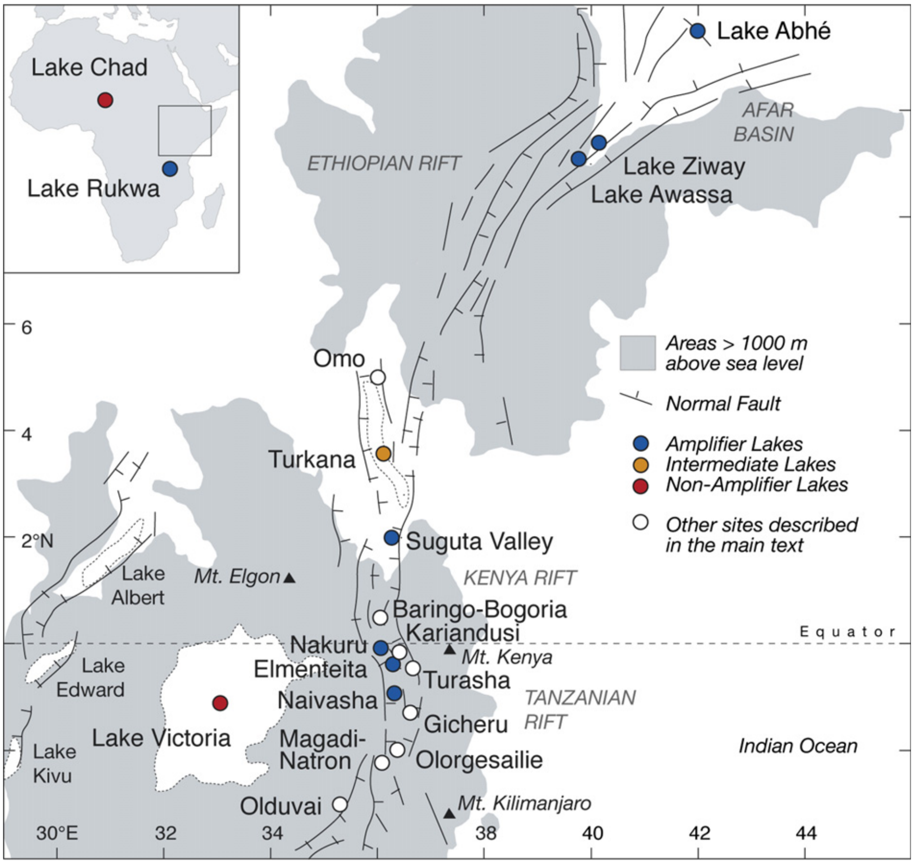

Fig. 1. Map of East Africa showing topography, faults and lake basins (modified from Trauth et al., 2005). Note the location of amplifier, intermediate and non-amplifier lakes. All amplifier lakes are located in a rift environment and respond sensitively to relatively moderate climate variation.

2006). The effects of such long-term tectonic displacements, however, can also have an influence on the magnitude of short-term environmental instabilities, thus leading to a more direct impact on the biosphere. Ancient shorelines of East African lakes, most of them reduced to salty puddles today, document orbitally-driven lake-level fluctuations of tens or hundreds of meters as a response to only moderate climate shifts (e.g., Washbourn-Kamau, 1970, 1975; Street-Perrott and Harrison, 1985; Trauth et al., 2003; Bergner et al., 2003; Garcin et al., 2009) (Fig. 1). In the early '80s, Street (1980) and Street-Perrott and Harrison (1985) introduced the term *amplifier lake* to explain the exceptional sensitivity of rift lakes to climate change by a combination of the water balance in rifts, the basin relief and the interaction between climate and local hydrological factors. Olaka et al., 2010 furthered this concept by including a detailed hypsometric and climatological analysis of East African lake basins and concluded that a lake basin with a hypsometric integral of between 0.23 and 0.30 and a UNEP aridity index that is above unity is an amplifier lake that responds sensitively to climate changes. According to this concept, the amplification effect of a lake is the result of a tectonically-formed graben morphology in combination with an extreme contrast between high precipitation in the elevated parts of the catchment and high evaporation in the lake area (Olaka et al., 2010).

The recent lake-level history of Lake Naivasha, and adjacent lakes in the Kenya Rift, highlights the extreme sensitivity of such amplifier lakes to climate changes (Fig. 3). As shown exemplarily for Lake Naivasha, amplifier lakes in the EARS typically vary between 0 and 1.5 m on time scales of 10^0–10^1 years (USDA/NASA/Raytheon/UMD; Ministry of Water and Irrigation of Kenya, 2008), whereas lake-level fluctuations on a time scale of 10^2–10^3 years are on the order of tens of meters (Verschuren et al., 2000). In contrast, water-level variations reach amplitudes of up to one hundred meters during the last 10^3–10^4 years (Washbourn-Kamau, 1970, 1975; Hastenrath and Kutzbach, 1983; Bergner et al., 2003), and the lake-level varied by ~150 m on a time scale of 10^4–10^5 years (Bergner et al., 2003; Trauth et al., 2003). Even greater water depths of more than 250 m are documented for a time scale of 10^5–10^6 years, after about three million years ago (Trauth et al., 2005, 2007). Essentially, the prominent water-level changes follow a power law where larger lake-level variations occur on longer time scales (Fig. 3). Compared to Lake Naivasha, other African lakes such as Lake Chad (Leblanc et al., 2006) and Lake Victoria (Hastenrath and Kutzbach, 1983) respond with significantly lower lake-level variations over similar time scales, whereas some lakes, e.g., Lake Ziway (Gillespie et al., 1983), Lake Nakuru (Washbourn-Kamau, 1970) and Lake Suguta (Garcin et al., 2009) demonstrate even more extreme lake-level variations than Lake Naivasha. Importantly, all amplifier lakes occur in the tectonically-controlled environments of the Kenyan and Ethiopian rifts (Fig. 1). Since both basin morphology and precipitation–evaporation contrasts in the catchment areas of the amplifier lakes result from extensional tectonic processes, our compilation of lake-level variations highlights the relevance of long-term tectonic processes to short-term climate fluctuations and environmental instability.

When did the amplifier lakes evolve in East Africa? Clearly, the intrusion of an asthenospheric plume causing the uplift of the East African and Ethiopian plateaus initiated the Cenozoic East African continental break-up (Strecker et al., 1990; KRISP Working Party, 1991). Subsequent faulting after ~20 Ma created half-graben morphologies that were subsequently faulted antithetically between about 5.5 and 3.7 Ma generating a full-graben morphology in most

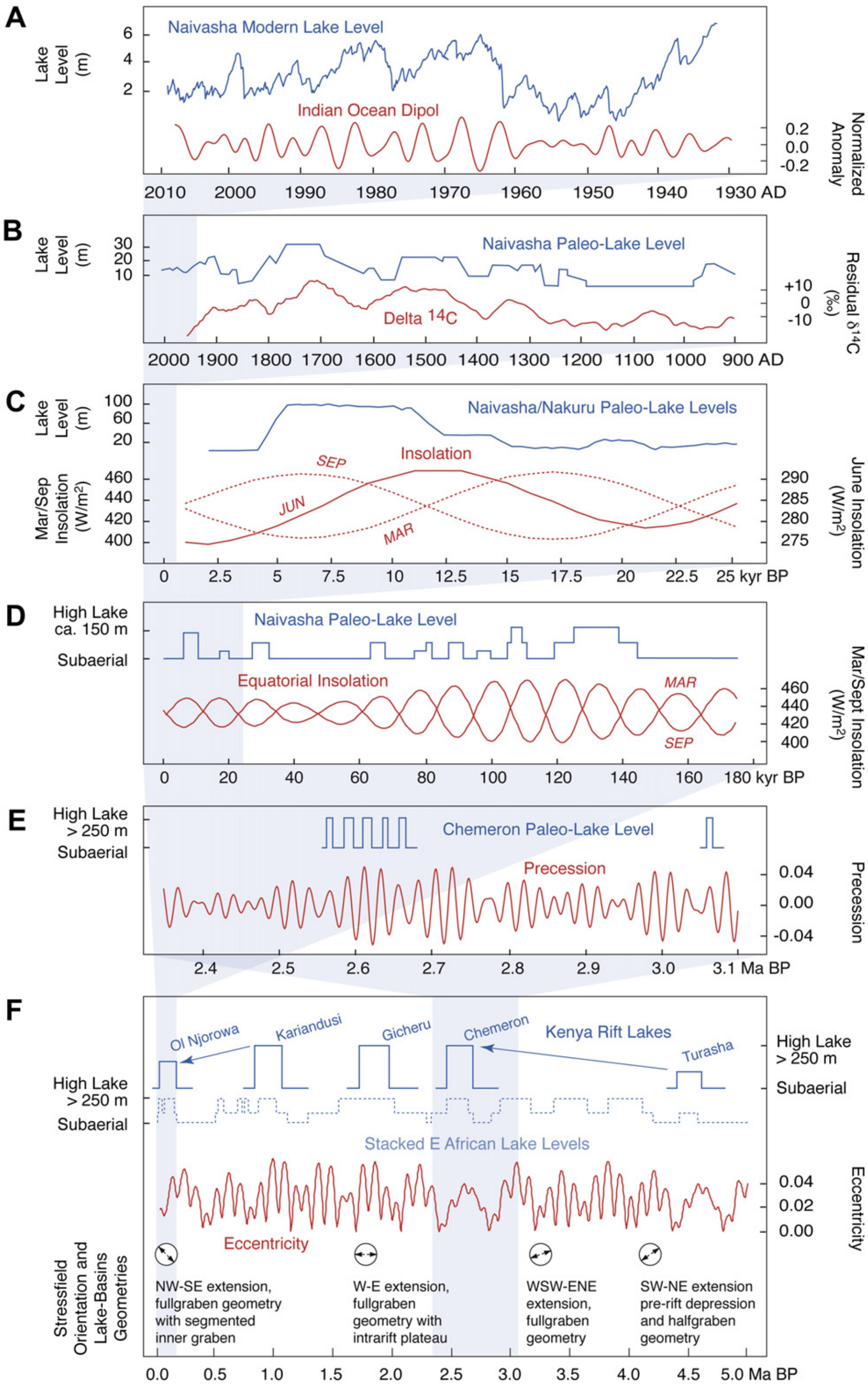

Fig. 2. (A–F) Lake-level variations in the Kenya Rift; (A) modern lake-level fluctuations based on satellite altimetry and observations (Data from Ministry of Water and Irrigation of Kenya, 2008; and Vincent et al., 1979; Åse, 1987). Indian Ocean Dipole data from Saji et al. (1999); (B) Lake Naivasha short cores (Verschuren et al., 2000); (C) Lakes Naivasha and Nakuru-Elmenteita sediment cores (Richardson and Dussinger, 1986; Dühnforth et al., 2006); (D) Ol Njorowa Gorge Formation (Trauth et al., 2001, 2003; Bergner et al., 2003); (E) Chemeron Formation (Deino et al., 2006; Kingston, 2007); (F) Stacked lake-level record for East Africa (dashed line) (Trauth et al., 2005, 2007), major lake episodes in the Kenya Rift (solid line) (Trauth et al., 2001, 2007; Deino et al., 2006; Kingston et al., 2007) and major tectonic events and stressfield change in the Kenya Rift (Strecker et al., 1990). Whereas before ca. 3 Ma, large, but shallow lakes existed in the Kenya Rift prior to the devopment of full-graben geometries, the lakes after ca. 3 Ma are generally large and deep (>250 m) based on silica algae (diatom) assemblages (Trauth et al., 2007). After ca. 0.5 Ma, the tectonic separation of the inner graben significantly reduced the amplitude of lake-level variations in most basins of the Kenya Rift (Richardson and Dussinger, 1986; Trauth et al., 2001, 2003; Bergner et al., 2003). Orbital forcing and insolation variations from Berger and Loutre (1991) and Laskar et al. (2004); residual atmospheric $^{14}CO_2$ production from Stuiver and Reimer (1993).

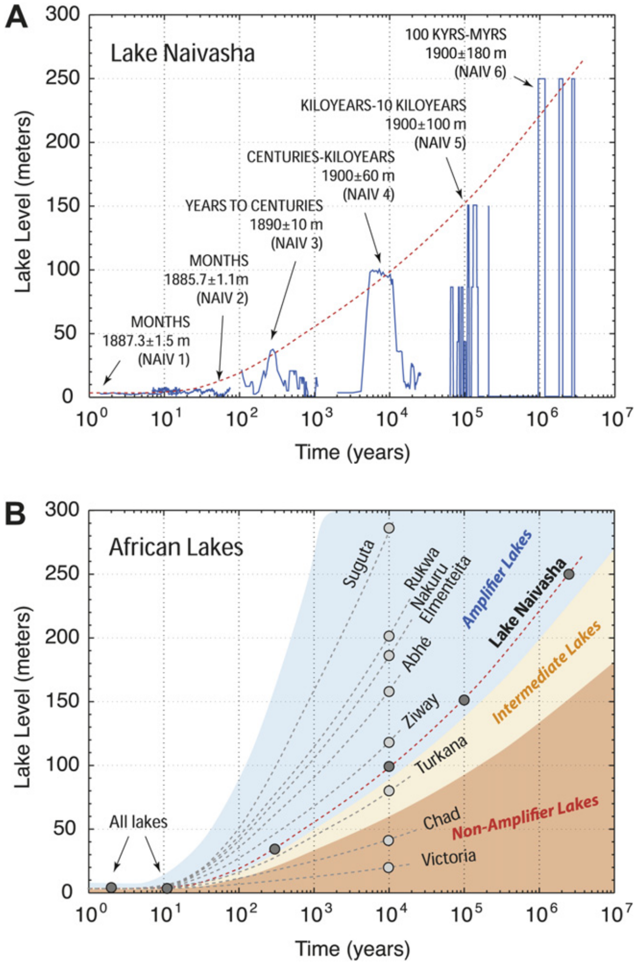

Fig. 3. (A) Lake-level change in the Naivasha basin in the Central Kenya Rift based on lake sediments and paleo-shorelines; (NAIV 1) observations (Ministry of Water and Irrigation of Kenya, 2008), (NAIV 2) satellite altimetry (USDA/NASA/Raytheon/UMD), (NAIV 3) sediment characteristics (Verschuren et al., 2000), (NAIV 4) sediment characteristics and paleo-shorelines (Washbourn-Kamau, 1970, 1975), (NAIV 5) sediment characteristics, authigenic mineral phases, diatom assemblages (Trauth et al., 2003), (NAIV 6) sediment characteristics, diatom assemblages (Trauth et al., 2005). (B) Compilation of lake-level variations in Africa at time scales from 10^0 to 10^7 years based on lake sediments and paleo-shorelines; Lake Victoria (Hastenrath and Kutzbach, 1983), Lake Chad (Leblanc et al., 2006), Lake Turkana (Owen et al., 1982; Hastenrath and Kutzbach, 1983), Lake Naivasha (Washbourn-Kamau, 1975; Hastenrath and Kutzbach, 1983; Bergner et al., 2009; Trauth et al., 2003, 2005; USDA/NASA/Raytheon/UMD; Ministry of Water and Irrigation of Kenya, 2008), Lake Ziway (Gillespie et al., 1983), Lake Abhé (Gasse, 1977), Lake Nakuru-Elmenteita (Washbourn-Kamau, 1970), Lake Rukwa (+200 m) (Kervyn et al., 2006), and Lake Suguta (Garcin et al., 2009).

parts of the rift (Strecker et al., 1990). The internal drainage conditions were caused by the conspiring effects of magmatic activity centered along the volcano-tectonic axis and the formation of central volcanoes during the Plio-Pleistocene. These processes were augmented by the formation of horst and graben structures that fundamentally influenced the fluvial network of the rift. The timing of these processes coincides with a re-orientation of the extension direction from an earlier E-W to a neotectonic ESE-WNW orientation between 3.6 and 2.7 Ma (Strecker et al., 1990). The conditions for the establishment of large lakes existed by approximately 3.7 Ma, whereas the modern complex relief, the shape of the amplifier lake basins and drainage systems was established after 2.7 Ma. The hallmark of these young extensional processes is the formation of presently isolated sub-basins that coalesced multiple times in the past during episodes of climatic changes when East Africa must have experienced greater amounts of precipitation. The combination of these tectonic movements and the existence of earlier volcanic edifices results in the distinct precipitation–evaporation contrast between the rift shoulders receiving more than 2000 mm/year rainfall and graben areas with up to 4000 mm of potential evapotranspiration today (e.g., Dunkley et al., 1993; Garcin et al., 2009).

The development of amplifier lake systems after circa three million years is also manifested in a distinct change in the paleo-lake character in different rift basins in East Africa. Whereas the ∼4.6–4.5 Ma old paleo-Lake Turasha in the central Kenya Rift was a relatively stable, large and shallow freshwater lake as documented by a ∼90 m thick sequence of diatomites in the Naivasha basin, the younger paleo-lakes Gicheru (∼1.9–1.6 Ma) and Kariandusi (∼1.0–0.9 Ma) were characterized by water depths of >250 m that varied significantly on all time scales and may thus present the transition to the amplifier-lake conditions (Trauth et al., 2005, 2007). Sensitivity alone, however, does not alter the local environment as an initial climate change is required for an environmental response to occur. There is growing body of evidence for precession-forcing of moisture availability in the tropics, both in East Africa and elsewhere during the Plio-Pleistocene (Bush et al., 2002; Deino et al., 2006; Trauth et al., 2003, 2007). The precessional control on tropical moisture has also been clearly illustrated by climate modeling of Clement et al. (2004), which demonstrated that a 180° shift in precession could change the annual precipitation in the tropics by at least 180 mm/year and induce a significant shift in seasonality, but has no influence on global or regional temperatures.

3. Environmental significance of amplifier lakes

The synopsis of lake-level histories in the EARS suggests that precessional forcing of moisture availability fundamentally influences the expansion and shrinkage of lakes in the amplifier rift basins (Trauth et al., 2005, 2007) (Fig. 4). The first possible environmental state occurs at minimum precession and maximum insolation in the Northern Hemisphere, inducing a wetter climate over East Africa (Kutzbach and Street-Perrott, 1985) (Fig. 4, Panel A). Once a critical evaporation/precipitation threshold is passed, the amplifier lakes respond rapidly (within less than 200 years) and become very large and deep (Kutzbach and Street-Perrott, 1985; Bergner et al., 2003; Garcin et al., 2009). The presence of large lakes in different areas of East Africa affects the local environment by altering the adiabatic lapse rates leading to generally moister conditions, local vegetation changes and forest expansion. Response times between climate and major vegetation changes can be as short as 50 years (Hughen et al., 2004).

Once the maximum extent of rift lakes is established during such a *Wet Period*, they serve on a regional basis as an east-west barrier to the migration of animals and early hominins. North-south movement between the different lake systems would be relatively unimpeded, but with rich fertile woody environments surrounding lakes and on the rift shoulders, there would be little or no environmental pressure for extensive dispersal. As the precession cycle progresses and the insolation maximum moves towards the Southern Hemisphere, moisture availability in EARS would be reduced. The lakes initially have a muted response as their presence maintains a relative wet environment in the rift valley, until increased aridity overcomes inertia and the lakes shrink (Fig. 4, Panel B). Modeling results and field observations suggest that East African lakes require up to 2000 years to disappear during a wet-to-dry climate transition (Bergner et al., 2003; Garcin et al., 2009).

The reduced rainfall and lake shrinkage during such a *Transitional Period* has a dramatic effect on the adjacent vegetation mosaic, with forest retreat from lakeshore environments to the rift shoulders. This facilitates both north-south and east-west migration of biota. As the

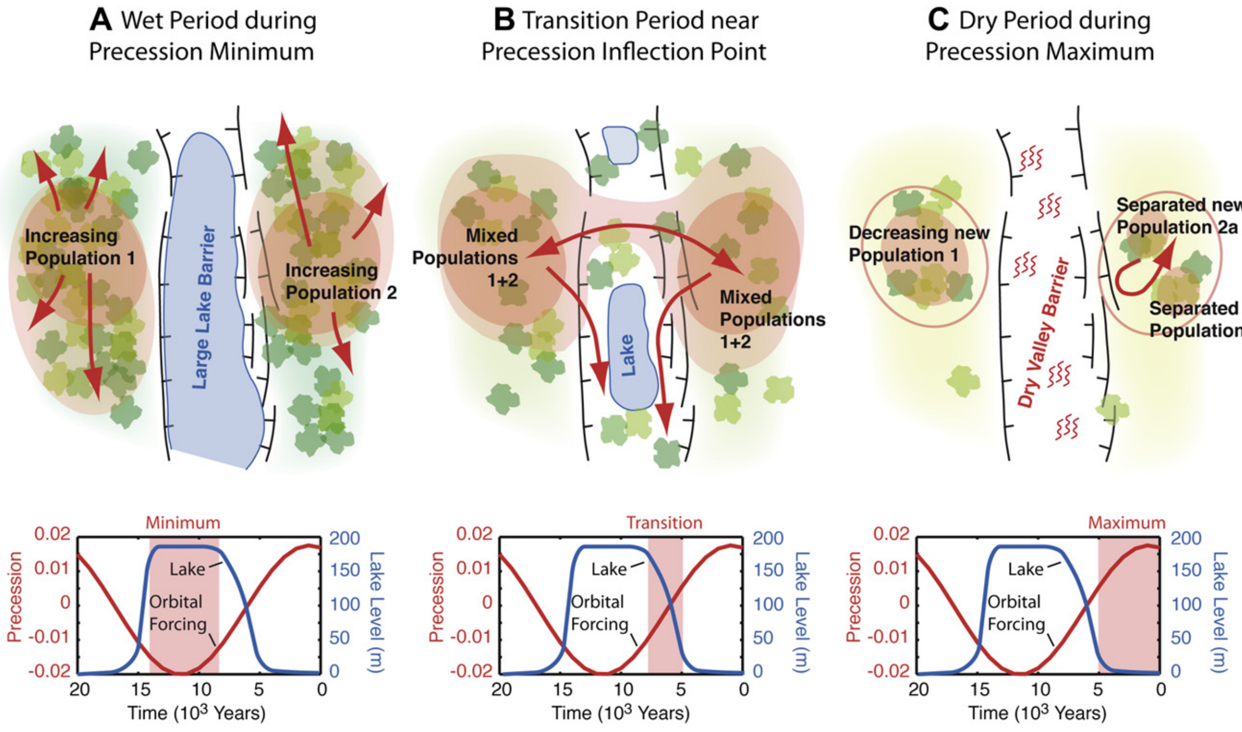

Fig. 4. (A–C) Conceptional model of orbitally-induced climate variation, environmental change, and population speciation and radiation in a rift environment. (A) During precessional minima, hence Northern Hemisphere insolation maxima, large rift lakes form natural barriers that inhibit mixing of the two separate populations 1 and 2 of animals and hominins. New species evolve independently in geographic isolation according to the model of allopatric speciation. Due to favorable environmental conditions during a wetter climate, population sizes increase, the larger populations split, and sub-populations migrate to other regions with favorable conditions. (B) Near the precession inflection point, favorable but deteriorating conditions foster migration of portions of the population along a corridor through the fading barrier. The populations 1 and 2 meet and compete during a gradually drying climate with limited availability of water and food. The populations utilize the margins of lakes to migrate southwards following favorable conditions in course of latitudinal climate shifts. (C) During the precession maximum, severe aridity creates a dry valley as a new barrier for migration of animals and early hominins forming two new populations 1 and 2. The limited availability of water and food results in a reduction of population size, and a tendency to migrate toward uplands where favorable conditions persist. Isolation of sub-populations 2a and 2b fosters allopatric speciation in small refugia with favorable environmental conditions.

insolation maximum reaches the Southern Hemisphere, the rift valley becomes extremely arid (Fig. 4, Panel C). Small refugia of forest survive only in the rift shoulder areas or on isolated volcanic edifices during this *Dry Period*. This causes fragmentation of homogeneously distributed organisms into allopatrically separated populations. Such vicariance is a potential driver of speciation, as has been elucidated, e.g., in flightless bush crickets, which were forced into shrinking forest refugia on the rift shoulders during dry intervals, and subsequently evolved into separate species (Voje et al., 2008). We therefore also postulate that a dry rift valley acts as a major barrier, isolating animals and hominins periodically during the Plio-Pleistocene, resulting in small populations trapped in higher altitude refugia with the possibility of allopatric divergence and, eventually, speciation.

Consequently, alternating wet and very dry conditions superposed on a changing tectonically active environment in the EARS may have resulted in the formation of efficient barriers to animal and hominin migration, both east-west and north-south. We can also speculate on the relative durations of the three periods based on the timing of the precessional cycle (Fig. 4). Precession is sinusoidal, with intervals of little or no change in insolation, followed by intervals of a much increased rate of changes. Sinusoidal forcing results in intervals of ~8000 years when relatively little change in daily insolation occurs (Maslin et al., 2005), representing the *Wet Period* and *Dry Period* intervals described above. These are followed by rapid transition of about 2500 years during which 60% of the total variation in daily insolation and seasonality occurs. These intervals of rapid change correspond to the *Transitional Periods* described above. The *Transitional Periods* are most sensitive to extreme global climate influences, for example extreme Indian Ocean Dipole and El Niño/Southern Oscillation intervals or millennial-scale Heinrich or Dansgaard-Oeschger events because the water balance of the amplifier lakes will react strongly to small changes in moisture availability. In contrast, the large and deep lakes during the *Wet Period* buffer against extreme rainfall events or short episodes of increased precipitation, similar to Lake Turkana today. The extreme aridity during the *Dry Period* also reduces the influence of heavier rains through its extreme evaporation, as in the modern Suguta Valley. Nevertheless, without the tectonically created topographic boundary conditions, these rapid and extreme changes associated with the amplifier lakes could not have occurred in local environments.

Although hypothetical, the close relationship between tectonics, climate, topography and superposed oscillating environmental changes on all time scales repeatedly caused vicariance for prolonged periods of time in a variety of organisms and hence must have fundamentally influenced evolutionary processes in this tropical environment. Even today and on short time scales, the modern Lake Turkana acts as an effective natural barrier for *H. sapiens* between nilotic tribes to the west and cushitic tribes to the east (Lewis, 2009). Towards the south, the adjacent hot and dry Suguta Valley was not as efficient as a natural barrier as the nilotic people migrated across the valley towards the east. The valley, however, nowadays splits the Turkana and Samburu tribes, both of nilotic origin (Lewis, 2009) and only during wetter years some migration of Turkana people occurs eastward into the Samburu territory, causing competition about pastures and cattle, and tribal clashes in some years.

The Plio-Pleistocene position, extent, timing and effectiveness of specific paleo-barriers such as large lakes and dry valley, however, are difficult to document. Undoubtedly, none of these large, but fluctuating lakes were infinitely long in a north-south direction along the rift. Corridors might have existed through these barriers such as volcanoes, horsts and ridges crossing the graben structures. Why did populations not meet by walking around the end of the lakes or dry valleys? How do these imperfect barriers prevent contact and interbreeding, and hence permit (classic allopatric) speciation? Again, we use the modern situation in the northern Kenya rift to explain the effectiveness of morphologically imperfect barriers. Today, historical, cultural and political factors intensify the efficiency of a natural barrier such as Suguta Valley, as it also might be true for the past. As an example, generations back the Turkana and Samburu tribes were intensely mixed as the dressing was the same indicating culture mix, whereas today cultural differences such as circumcising men only by Turkana people, the change from darker to brighter colors of Turkana dressing, holes in earlobes and mud put on their heads separate the two tribes on both sides of the Suguta Valley. All these cultural differences intensify the efficiency of the dry valley as a natural barrier today and we therefore speculate that similar effects might have be acting in the past.

4. Conclusions

The proposed model of amplifier lakes serving as natural barriers, aggravated by cultural differences between highly mobile organisms such as humans living on both sides of the barrier might have contributed to habitat fragmentation, to reducing migration, expansion and dispersals of animals including humans and therefore increase biodiversity in the surroundings of the rift valley. The East African amplifier lakes are therefore a keystone in this scenario and may help explain why East Africa eventually became the place where early humans evolved.

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