

RESEARCH PAPER

Edaphic and Topographic Constraints on Exploitation of the Central Kenya Rift by Large Mammals and Early Hominins

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Our aim in this paper is to create a palaeoenvironmental and spatio-temporal framework for interpreting human land use and exploitation of large mammals in the Central Kenya Rift over the past 2 million years, with particular reference to the Nakuru-Elmenteita-Naivasha basin and its adjacent rift flanks on the Kinangop Plateau and Mau escarpment. We pay particular attention to the tectonic and volcanic history of the region, and to the system of lakes that have undergone periodic expansion and contraction during the Pleistocene in response to climatic and tectonic controls. We use this information to reconstruct topographic features as they would have existed at different periods of the past and their likely influence on patterns of large-mammal movements. In addition we present a systematic mapping of variations in the mineral nutrients of soils – soil edaphics – based on 150 analyses of trace elements in modern soil and vegetation samples. Soil edaphics play an important role in animal and human health today, with serious deficiencies in some areas, and would have exerted an important constraint on animal distributions and movements in the past. We show how soil-edaphic properties vary across the region and demonstrate a close relationship between them and the underlying geology and sediments, which allows us to project patterns back into the past and extrapolate them over larger areas. Using this combination of variables, we construct maps that help to place archaeological sites into their wider regional setting. We focus in particular on the Acheulean site of Kariandusi and show that it occupied a unique window of opportunity in place and time for trapping mammals constrained to move through a narrowly defined topographic bottleneck between edaphically-rich areas. We infer that the site was used for a simple form of ambush hunting and briefly explore the implications for differential site use, formation, preservation and visibility.

Keywords: Acheulean; African Mammals; Complex topography; Kariandusi; Kinangop Plateau; Nakuru; Site formation; Soil edaphics; Tectonic landscapes

Introduction

The Kenya Rift is regarded as one of the most important regions for the study of Pleistocene mammals in Africa and the evolution of early hominins, with a notable concentration of fossil and archaeological sites (**Figure 1**). This apparent association between Rift environments and finds of early hominins has given rise to the notion that there may be a causal relationship between the two phenomena, with the distinctive dynamics of rifting acting as a key agent in evolutionary change through one of three

possible processes: (1) directly at a macro-geographical and temporal scale through the introduction of major barriers that have served to isolate populations along divergent evolutionary pathways (vicariance hypotheses, Coppens, 1994; Lewin & Foley, 2004); (2) indirectly by amplifying spatial and temporal variability in climate and vegetation (hypotheses of mosaic environments and variability selection, Potts, 1996, 1998; Kingston, 2007; Maslin et al., 2014; Trauth & Maslin, 2009); or (3) directly but at a more localised spatio-temporal scale by the creation of a complex and dynamic regional topography that afforded opportunities for the evolution of the distinctive human niche with its emphasis on meat-eating, bipedalism and an extended period of juvenile dependency (the complex topography hypothesis or tectonic landscape model, King & Bailey, 2006; Reynolds, Bailey & King, 2011; Winder et al., 2013). However, establishing robust correlations between environmental variables, especially features of the physical landscape, and distributions of

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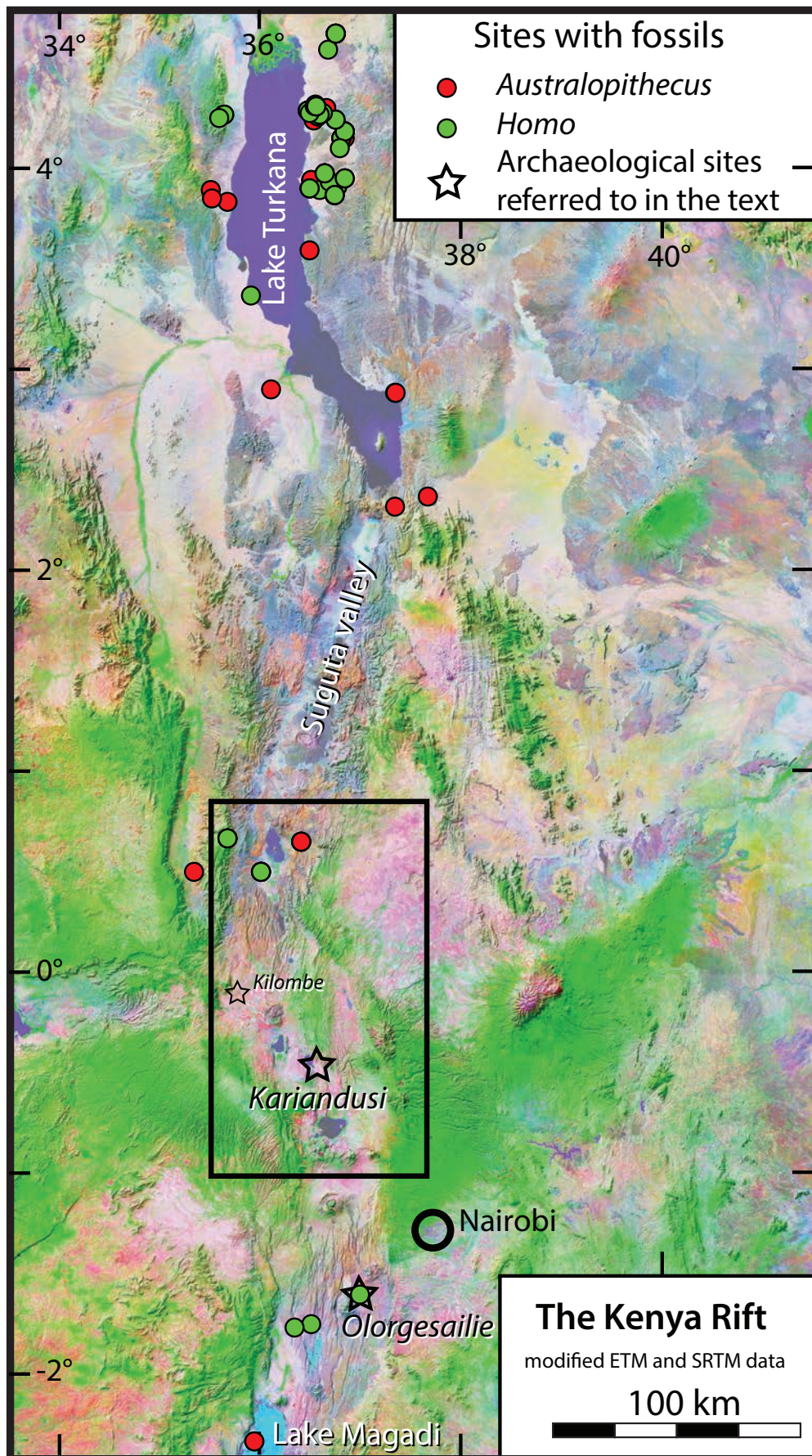


Figure 1: The Kenya Rift and surroundings, showing sites containing hominin fossils and selected archaeological sites referred to in the text. Fossil data are from the Paleobiology database (<https://paleobiodb.org>), and were downloaded on January 21, 2016 using taxa = *Homo erectus*, *Homo habilis*, *Australopithecus*; time interval = Pliocene through Pleistocene; and location = Kenya.

fossil or archaeological sites has well-known difficulties: of accurately reconstructing ancient landscape features in regions subject to ongoing geological change; of biases introduced by differential deposition, preservation, exposure and discovery of bones and stones; of chronological correlation between disparate and stratigraphically unrelated features; and of integrating processes that operate over widely divergent spatio-temporal scales. Faced with difficulties that can seem insuperable, one can either admit defeat, or seek to untangle some of the confounding variables by more detailed investigations of specific regions on a case-by-case basis, aided by known sites of fossil and archaeological remains where available.

In this paper we examine the Central Kenya Rift, in particular the Nakuru-Elmenteita-Naivasha region and its adjacent flanks (**Figures 2 and 3**). We choose this region because it is relatively compact, it is easily accessible for ground-based survey work, it benefits from a number of detailed and already published studies of the geology, tectonics and climate, and it has some record of Lower Pleistocene archaeology, which though not as abundant or detailed as for other regions of the Rift, comprising mainly

the site of Kariandusi, provides a point of departure for examining archaeological material in its wider regional context. We take the complex topography hypothesis as a starting point and present this study as part of an ongoing programme of mapping and research that is intended to extend ultimately to other comparable regions in the Kenyan and Tanzanian Rifts and elsewhere.

We describe our approach as landscape research, but emphasise that it differs in significant ways from the well-established tradition of landscape analysis commonly applied in the study of Plio-Pleistocene deposits in the African Rift (e.g., Isaac, 1977; Isaac & Harris, 1978; Bunn et al., 1980; Kroll, 1994; Stern, 1994; Blumenschine & Peters, 1998; Potts, Behrensmeyer & Ditchfield, 1999; Kingston, 2007; Blumenschine et al., 2012). For the most part, these studies have focused on stone artefacts and faunal materials in relation to their immediately surrounding sediments and surfaces at a spatial scale of hundreds of metres to kilometres, with the emphasis on localised distortions of the record by sediment accumulation and erosion, and on reconstruction of environmental features such as vegetational and palaeoclimatic

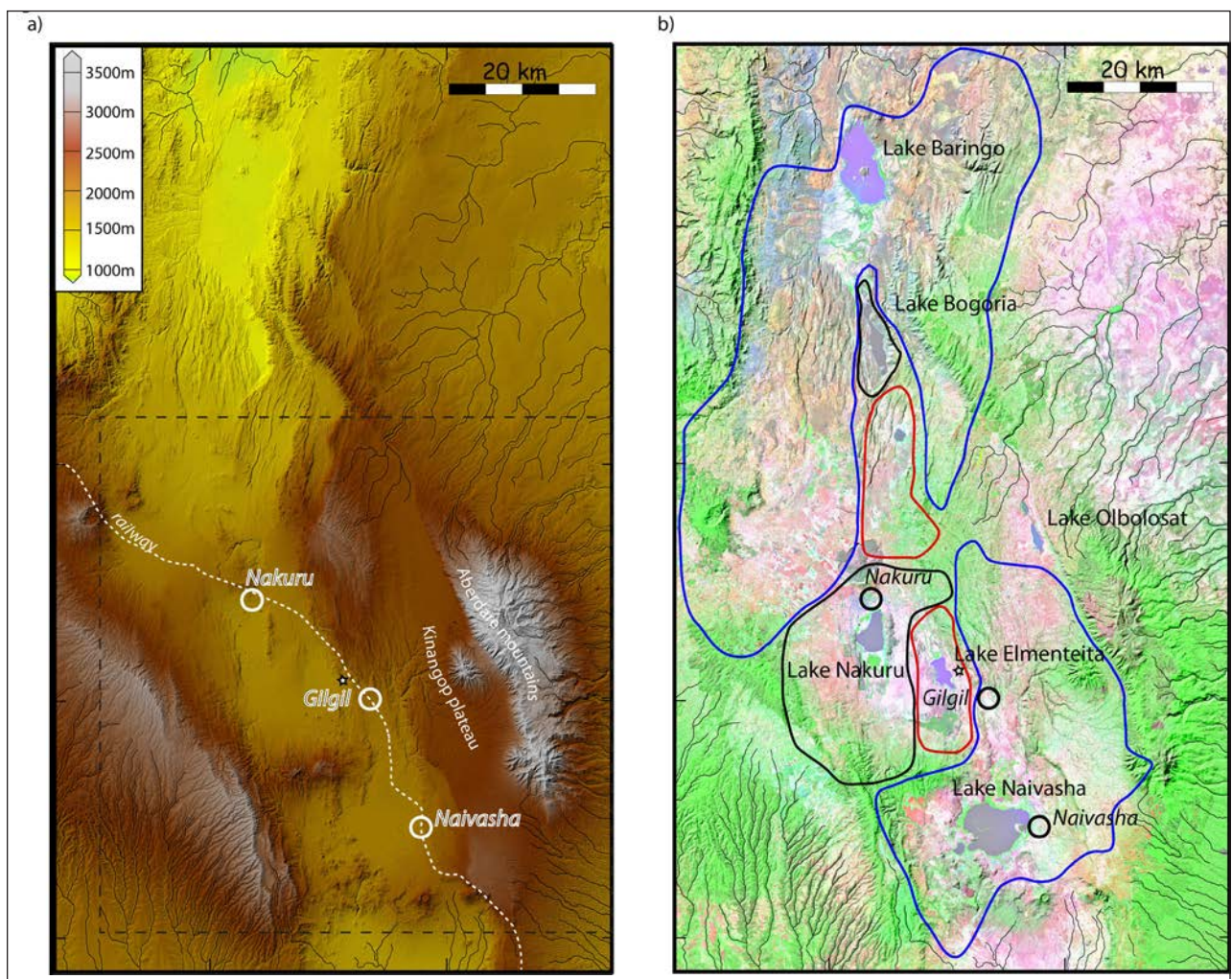


Figure 2: The Central Kenya Rift from Naivasha to Baringo. **(a)** Shaded relief illustrating that the landscape in many regions is topographically complex. **(b)** Modified ETM+ (Earth Thematic Mapper) image of the same region as (a). The many small lakes are identified with their catchments. Rivers within the rift are not shown. All rivers with their origin outside the rift drain away from it. Kariandusi site is indicated by a small star.

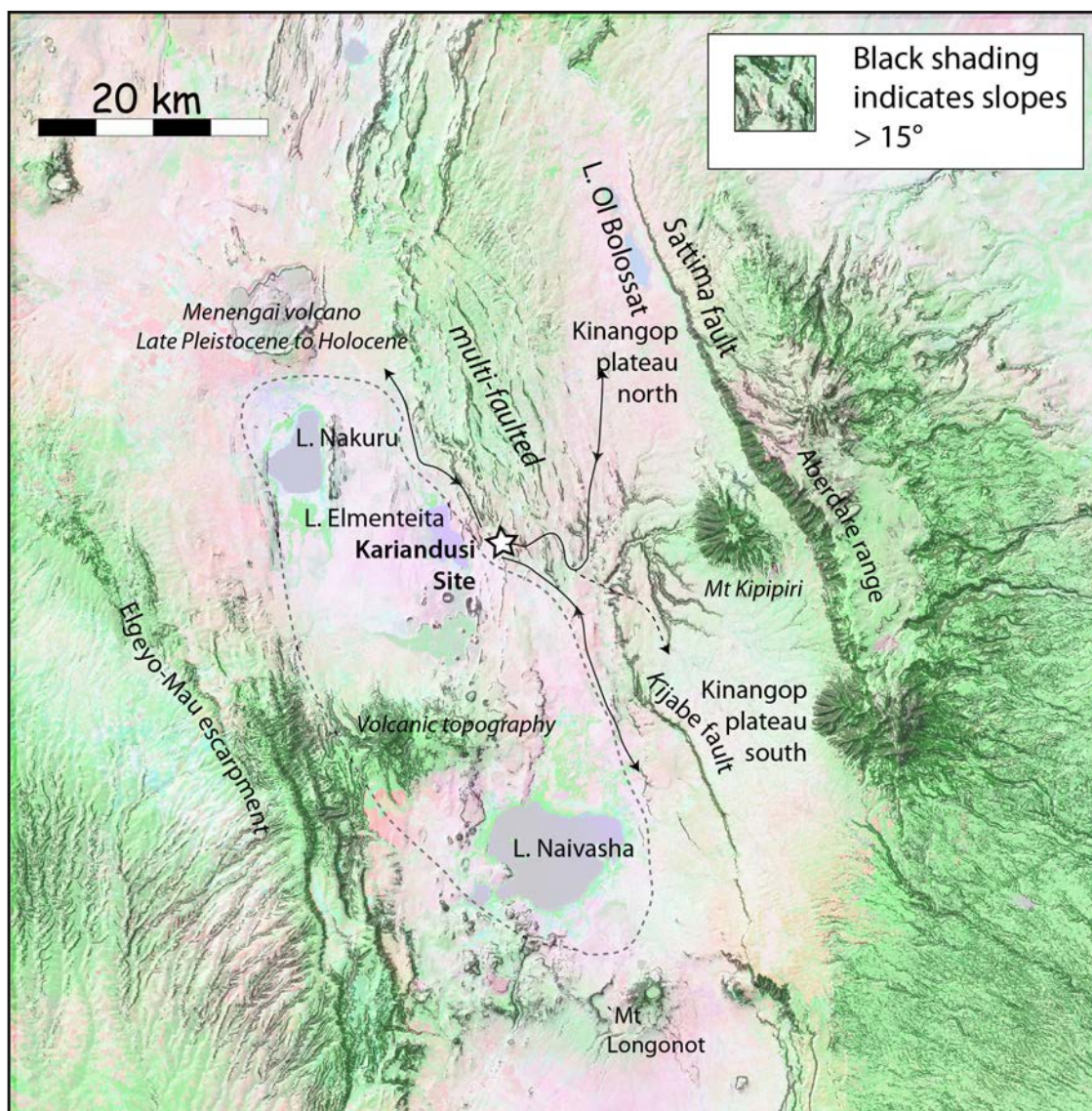


Figure 3: Morphology of the region including Lakes Nakuru, Elmenteita, Naivasha and Bolossat. Slopes greater than 15° are indicated by grey shading. Motor vehicles find such terrain difficult to cross without prepared roads, and large animals would have been restricted by similar factors. At times in the past, Lakes Nakuru, Elmenteita and possibly Naivasha have joined at times of high lake level indicated (See text). The outline is shown approximately by a dashed line. Some earlier features have been masked by volcanism between Elmenteita and Naivasha and around Menengai volcano and Mt. Longonot. See also Figure 4.

indicators. Widening the geographical scale of such an approach has necessarily been hampered by problems of time-averaging, stratigraphic discontinuities between different locations, and the difficulties of extrapolating proxy environmental variables over larger areas. Here, we offer an alternative, and to a large extent a complementary approach that addresses the problems of landscape reconstruction at a larger geographical scale, taking account of geological changes in landforms, but one which is also sensitive to regional and local variability. In this way, we aim to create a different type of framework within which to interpret the distribution of fossil and archaeological remains, and add value to results derived from well-established techniques of lithic, faunal, palaeoclimatic and palaeovegetational analysis.

The aims of this paper, then, are to:

1. Examine the relationship between geology, tectonic activity and topography as it may have constrained the distribution and movements of large mammals and, in turn, their accessibility to hominin predation.
2. Further explore the idea that complex or rough topography affords tactical advantage to hominin populations in accessing large prey animals, using methods for analysing topographic roughness based on DEMs derived from satellite and radar imagery and the use of digital methods to provide visual reconstructions of landscape settings (Bailey, Reynolds & King, 2011)
3. Analyse the edaphic properties of soils as an additional constraint on the distribution of large

mammals, and the extent to which the underlying geology can be used as a reliable proxy for the edaphic properties of the overlying soils. By edaphics, we mean the ability of soils to provide the mineral nutrients necessary for the healthy growth of herbivores, especially young animals, through the plant foods that they eat, particularly soluble phosphates but also other critical trace elements (Devès et al., 2014: 142–4). We distinguish soil edaphics from soil fertility, which is the capacity of soil to support vegetation –vegetation may be abundant but of poor quality for animal grazing or browse if it does not contain the right nutrients. Preliminary research in the Rift has shown that the soils formed on different geological substrates are quite variable in their nutrient potential, being highly deficient in some cases, and that this has important implications for present-day livestock as well as past animal movement (Kübler et al., 2015).

4. Show how mapping of roughness and soil edaphics can help to place fossil and archaeological sites into a wider regional context, and more specifically test the hypothesis that, by the time of the appearance of the genus *Homo* and Acheulean biface manufacture, human groups were actively exploiting topographic barriers and bottlenecks in the landscape for ambush hunting, following the discovery of similar evidence in Acheulean settings elsewhere (Devès et al., 2014; Kübler et al., 2015).

We first provide a general introduction to the geological and tectonic history of the region and its principal environmental and archaeological features. We then describe the methods we use to create maps, with particular emphasis on edaphic analysis, and present an analysis of the key topographic and edaphic features that are relevant to routes of movement and access for large mammals, with particular attention to the impact of fault scarps and the history of changes in lake level. Finally, we discuss the Kariandusi archaeological site within this regional framework, show how its attractions as a locus of repeated hominin activity have varied with changes in topography, especially in relation to changes in lake level, and consider the wider implications of these results.

Tectonic, Geological, Environmental and Archaeological Setting

The region has typical features of an asymmetric rift with progressively uplifted flanks reaching heights of ~4000m asl in the Aberdare Range to the east, and ~3000m asl in the Mau escarpment to the west, and down dropping of the central basin, with its floor at about 1800m asl, accompanied by faulting and volcanic activity. Rifting is aligned on a NNW–SSE axis and was active in the late Miocene, between 12 and 6 Ma BP, with further spells of activity between 5.5 and 3.7 Ma, and again at about 2.6 Ma, when the 30-km-wide Kinangop Plateau and the 40-km-wide inner rift depression were formed (Baker, Mitchell & Williams, 1988; Baker et al., 1971; Baker & Wohlenberg, 1971; Clarke et al., 1990; Roessner & Strecker, 1997;

Strecker, Blisniuk & Eisbacher, 1990). The Aberdare Range is separated from the inner rift by the Sattima fault, and the Kinangop plateau is a major relay ramp bounded by the Sattima fault to the east and the Kijabe fault and multiple faulting to the south-west (Figures 2 and 3).

The inner rift was subsequently covered by trachytic, basaltic and rhyolitic lavas and tuffs and continues to be cut by normal faulting around a central axis (McCall, 1967; Clarke et al., 1990; Strecker, Blisniuk & Eisbacher, 1990). A change in the direction of extension in the middle Pleistocene has been proposed, with the development of NNE striking normal faults linked by complex transfer zones, and reactivation of some older faults on the new alignment (Bosworth & Strecker, 1997; Strecker, Blisniuk & Eisbacher, 1990; Zielke & Strecker, 2009). The young structures of the inner rift are accompanied by late-Pleistocene to Holocene volcanoes, such as Menengai, Eburru, and Longonot, and some smaller rhyolitic domes and basaltic lava flows. As a consequence, the present-day inner rift has become compartmentalized into smaller lake basins, principally the Nakuru-Elmenteita and Naivasha basins, separated by normal faults and intervening volcanic structures.

The region is dominated by volcanic rocks, and volcanoclastic and lacustrine sediments (Figure 4). The volcanic rocks are predominately lavas and pyroclastic deposits from the Late Miocene to the present (McCall, 1967; Baker et al., 1971; Baker, Mitchell & Williams, 1988). The oldest volcanic units are Late Miocene plagioclase-rich basalts of the Aberdares and Mount Kipipiri. Early Pliocene basalts and phonolites outcrop along the Sattima fault escarpment and the northern part of the Aberdare range. The Kinangop plateau is mostly Pliocene and Pleistocene tuffs and ignimbrites with trachytes to the south and north. The Mau escarpment to the west mainly comprises welded and non-welded ignimbrites of the upper and lower Mau sequences, the source of which is probably in the inner rift, buried by younger deposits (McCall, 1967; Leat, 1991). Basalts dominate the Sattima fault, Mount Kipipiri, and the Aberdare range. South of Lake Elmenteita small rhyolitic to basaltic volcanic cones and Late Holocene basalt flows form the most recent volcanic complex of the area.

The present-day topography is dominated by the tectonic history of the region. Principal pathways of movement mainly run parallel to these major faults, around and across the rift floor and on the Kinangop plateau, with major barriers to east–west movement in most places. The Kenya-Uganda railway although now of little importance, had a vital role in developing the present-day economy of the region and the growth of the towns of Nakuru, Gilgil and Naivasha, and its route across the edge of the rift flanks and the inner rift indicates some of the easiest pathways of movement on the eastern side of the basin. Also, an eastern branch line of the railway used to extend eastwards up onto the flank to near Lake Ol Bolosat giving access to the Kinangop plateau.

The region hosts many small lakes ranging from fresh water to highly alkaline, a variability determined by catchment size (Figure 2b). The fresh water lakes of Baringo

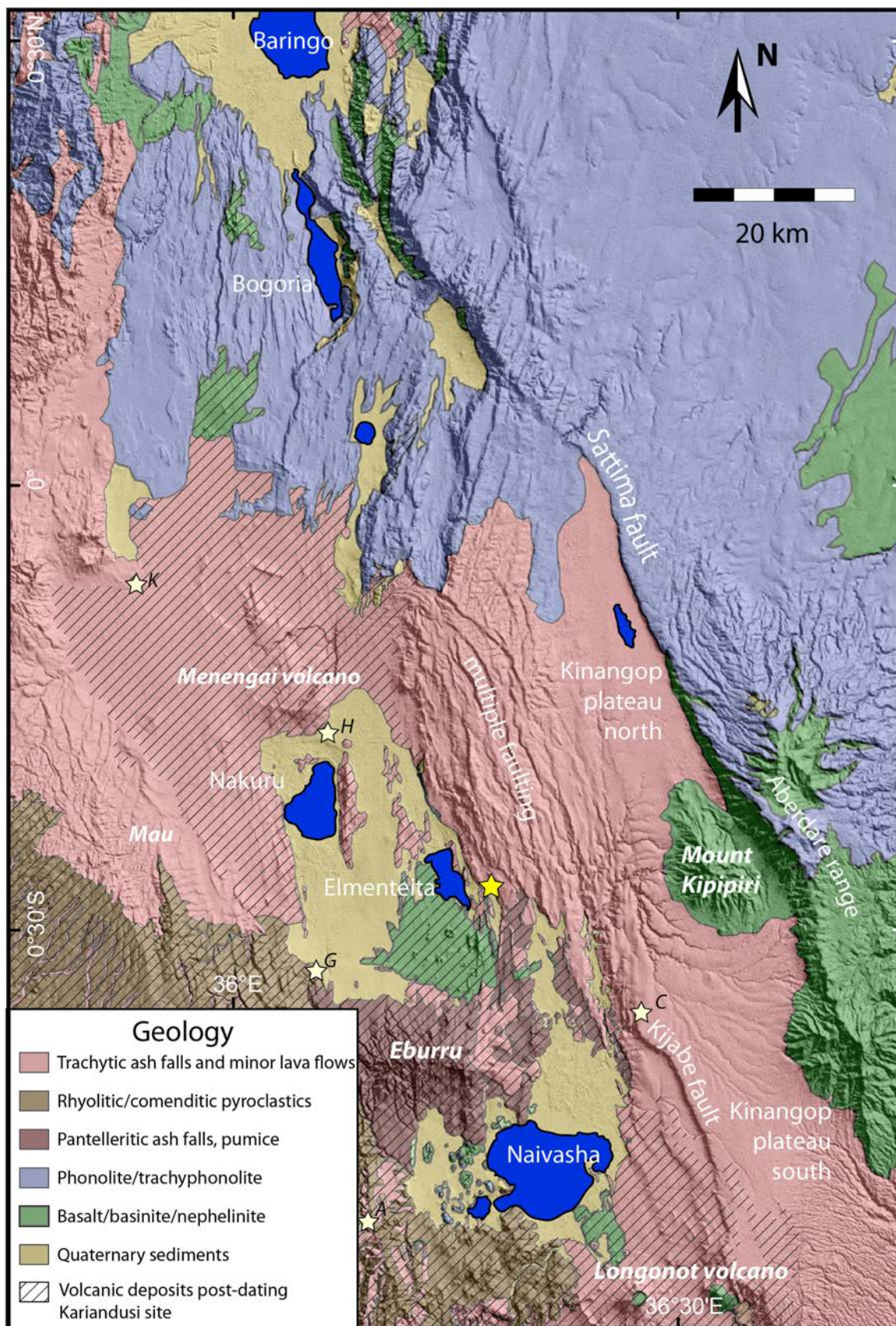


Figure 4: Geological map of the rift and flanks from Lake Naivasha to Lake Baringo. The Kariandusi site location is indicated by a star. Cross hatching indicates volcanic deposits c. 700ka – postdating the Kariandusi site (Bergner et al., 2009; Clarke et al., 1990; McCall, 1967; Scott & Skilling, 1999). Younger sites are indicated by small stars: H = Hyrax hill; G = Gamble’s cave; C = Cartwright’s site; E = Ekapune Ya Muto (Leakey, 1931; Leakey et al., 1943; Ambrose, 1998; Waweru, 2002).

and Naivasha have large catchment areas, while those of alkaline Bogoria and Elmenteita are very small. At present the lakes have no outlets and are sensitive to even small changes of climate, exposing towns like Naivasha and Nakuru to risk of flooding. Nowhere within the rift receives water from outside, with rivers flowing away to the east or west down the outer rift-shoulders of the Aberdare and Mau escarpments respectively.

The lakes have a complex history of variations in size, lake level and water composition, determined in part by climate change and partly by tectonic movements (Bergner et al., 2009). Over the past 1 million years, there have been periods when lake levels were substantially higher than present, with important implications for the interpretation of animal movements, considered in more detail below.

Lacustrine sediments occur predominantly in the Nakuru-Elmenteita, the Naivasha and the Baringo basins, and to a smaller extent around Lake Ol Bolosat in the NE part of the Kinangop plateau. The basin fill usually consists of Mid-Pleistocene to Holocene lake sediments interbedded with volcanic ash and pyroclastic deposits (McCall, 1967; Bergner et al., 2009).

Because of the sharp variations in altitude and geology, the Rift exhibits marked variations in climate, vegetation, and land use (Bergner et al., 2009; Hesslerová & Pokorný, 2010; Were, Dick & Singh, 2013). Land at high altitude on the rift flanks is characterized by a perennially cool and humid climate with annual rainfall of up to 3000 mm per year. This climate supports forest cover and the development of thick soils, but much of the forest has been cleared for agriculture and settlement (Hesslerová & Pokorný, 2010), and a major part of Kenya's agricultural output occurs in these regions, particularly tea and coffee. Conversely, the rift floor is characterized by an arid climate with a short rainy season, poor soil development and an annual rainfall of about 500 mm, particularly in the southern part of the inner rift. Other cash crops include, fruit, vegetables, cotton and flowers, including a concentration of intensive production in the Naivasha basin with huge poly-tunnels and artificial irrigation. Maize and beans are grown for local consumption, and the principal livestock are cattle, sheep and goats.

There are almost no Plio-Pleistocene fossil remains from the immediate region, and details about large-mammal populations before the agricultural era can be inferred only approximately by analogy from adjacent regions of the Kenya Rift (Maglio & Cooke, 1978; Potts, 1994; Turner & Antón, 2004; Bobe, Alemseged & Behrensmeyer, 2007; Bobe & Leakey, 2009), from Late Pleistocene and Holocene rockshelter-deposits on the Mau escarpment (Marean, 1992), and from historical and present-day observations. Hippo still live in the basin today and elephants were present within living memory, while the occurrence of buffalo, zebra, eland, hartebeest, gazelle, klipspringer, antelope and reedbuck in the Hell's Gate National Park gives some indication of what was once more widely available (Kenya Wildlife Service, 2015). We infer that a full suite of African large mammals would have been available as prey for hominin exploitation, subject to variations in

topography, climate and forest cover, but do not attempt a more detailed analysis, since our aim here is to identify general topographic and edaphic constraints on large mammal movements rather than to attempt detailed habitat reconstructions and biogeographic distributions for specific taxa that cannot be corroborated by any currently available evidence.

Only one archaeological site from the Lower-Middle Pleistocene is known in the region we are considering, and that is the Acheulean biface site of Kariandusi with an age bracketed between 0.73 and 0.98 Ma (Gowlett & Crompton, 1994; Leakey, 1931a; Shipton, 2011). The nearest comparable Acheulean site is Kilombe, but that lies further north, where much of the surrounding terrain is blanketed by volcanic material that post-dates the occupation of the site (**Figure 4**), limiting what can be said about its original landscape setting (Bishop, 1978). Other material of significance but of very much later date is a series of MSA sites and LSA rockshelters on the Kinangop Plateau, full details of which remain unpublished (Lahr, 2015; Waweru, 2002), and the rockshelter of Ekapune Ya Muto above the Mau escarpment, with a long stratified sequence extending from MSA through LSA, including some of the earliest dates, estimated at ~50,000, for the LSA in Africa, and later deposits of Neolithic and Iron Age date (Ambrose, 1998). Another group of sites on or close to the rift floor includes Gamble's Cave and Hyrax Hill, where the cultural material is mainly post-Pleistocene in age, belonging variously to the Later Stone Age (LSA), Neolithic or Iron Age.

Methods

Palaeotopographic analysis

The mapping of roughness provides a method to identify and map barriers of greater or lesser extent such as fault scarps and cliffs that would have constrained patterns of movement and access for large mammals. For this region, we derive roughness from DEMs making use of SRTM30 data and ASTER GDEM (a product of METI and NASA) (Bailey, Reynolds & King, 2011), figure 19). This is supplemented by field observations. For the mapping of lake palaeoshorelines, we draw on the published literature on changes of lake level (Trauth et al., 2005; Bergner et al., 2009), supplemented by our own field observations

Edaphic analysis

For the edaphic analysis, we have selected soil and vegetation samples from a representative selection of different lithological and sedimentary units, basing our selection on field observation and geological maps. We excluded regions with an agricultural overprint and severe recent deforestation such as the southern Mau escarpment and Eburru forest to avoid disturbance from agricultural fertilizers and other anthropogenic modifications to the soil composition. We took soil samples using standard protocols provided by KALRO (Kenya Agricultural and Livestock Research Organisation). For thin soils, we generally sampled the uppermost horizon (<25cm). Soil and plant tissue analysis was carried out at the KALRO laboratories (Kübler et al., 2015).

During two field seasons in 2013 and 2014, we collected a total of 163 soil samples and 160 plant tissue samples (Figure S1) in the Kenya Rift from Lake Magadi in the south to Lake Baringo in the north. In this paper, we show results for 75 soil samples and 75 plant tissue samples for the Nakuru-Elmenteita-Naivasha basin and the Kinangop plateau (Figures 2 & 3, Appendix Figure S1). All samples were tested for concentration of the following trace elements and nutrients: calcium (Ca), copper (Cu), iron (Fe), manganese (Mn), magnesium (Mg), nitrogen (N), potassium (K), sodium (Na), phosphorus (P), and zinc (Zn). Further, soil samples were tested for pH-value, electrical conductivity, and total organic carbon (Table S1. Sample locations and coordinates are shown in Figure S1 and Table S2, respectively). We additionally took water samples from springs and boreholes around Lake Elmenteita to test for fluoride (Table S3) since excess fluoride can be a major problem, resulting in widespread tooth fluorosis (Moturi, Tole and Davies 2005) and bone deformation (rickets) in humans and cattle (Thacher et al., 2006).

Results

Palaeotopography

A map of roughness, with slopes greater than 15° indicated by dark shading (Figure 3), highlights the constraints on access, whether for large animals or modern

motor vehicles. The multiple faulting, especially on the Kijabe and Sattima fault escarpments, presents major barriers to such movements. The Kinangop Plateau is an extensive area of smoother terrain confined to east and west by these fault scarps; its north-western border is also dissected by deeply incised rivers, and its south-eastern border comprises complex faulting and rough topography, making the plateau an enclosed area with very limited points of easy access, the easiest route to and from the rift floor being via the Kariandusi River (Figure 5). According to information from the heads of pastoral families in the area, female hippo are reported to migrate today along this route between Lake Elmenteita and Lake Ol Bolosat to protect their young from aggressive males. In the past, elephants are also reported to have found a route to reach Kinangop. On the western side of the rift the Elgeyo-Mau escarpment represents a barrier to movement as do north-south incised valleys further west on the flank. Apart from these obstacles, movement within the lake basins is largely unrestricted.

There is abundant evidence for higher lake levels. Lake beds can be readily identified on satellite images (e.g. Figure 2b) or Google Earth, and have been extensively studied by Trauth et al. (2005) and Bergner et al. (2009). These authors are mainly interested in climate change rather than palaeotopographic reconstruction and

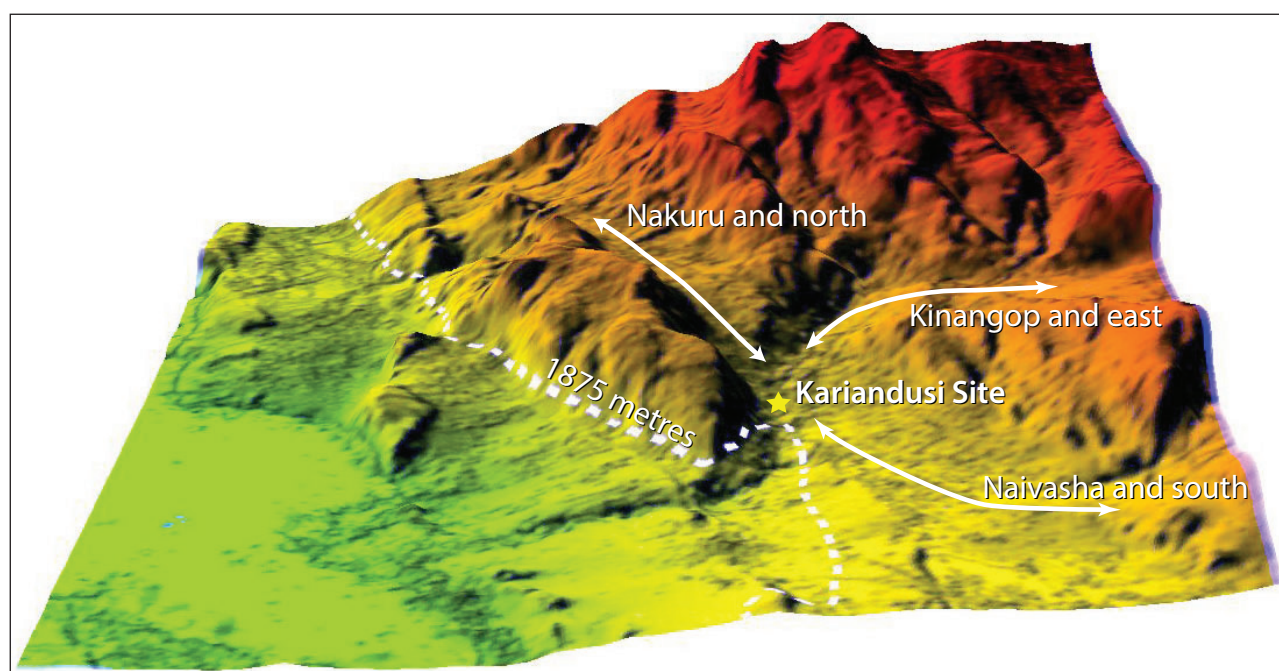


Figure 5: Routes for large animals when the level of Lake Elmenteita is high. Bergner et al. (2009) quote 1900m to be overall the highest level. Our observations suggest that at the Kariandusi site highest lake level should have been 10m lower. Lake levels of greater than 1875m completely block access along the lake-shore. For lower lake levels movements along the lake shore would have been straightforward and the lake sediments would also have provided good grazing or browsing. At high lake-levels, animals moving to or from Nakuru and the north would have to pass along a valley bounded by fault scarps and cliffs. The railway today follows this route. The artefacts indicate an ideal location for intercepting animals crossing the river, regardless of whether they are in primary position or were subsequently moved by fluvial action over distances which are in any case thought to be quite short (see text for discussion). The DEM used for this figure is a product of two World View 2 scenes processed with “Stereo Pipeline” software. Data was available through collaboration with Ryan Gold, USGS.

therefore pay most attention to identifying high lake stands. However, they suggest that semi-quantitative information about intermediate levels can be determined from sediment cores. Interpretation of these is complicated by tectonic controls as well as climatic ones, but they indicate at least three episodes of highest lake levels associated with wetter climate over the past one million years: at ~1 ma, 150–60 ka, and 15–4ka. It is possible that Lake Nakuru, Elmenteita and Naivasha formed one lake during times of high lake level but volcanic topography separates them today and conceals any clear evidence that they were once joined (**Figure 4**).

High lake levels greatly reduce the area of easily accessible grazing or browsing land but do not block movement along lake edges. A major exception is near to the Kariandusi River when the lake reaches a level of 1880m or higher. The steep slopes and cliffs north of the Kariandusi River make any movement along the shoreline impossible (**Figure 5**). Movement remains difficult until the level has dropped to 1860m and below, when full access is restored. Any movement to and from the north during high lake levels would have to use an inland route as indicated in the Figure. Only one route is possible and is today followed by the railway line and crosses the Kariandusi River close to the Kariandusi archaeological site.

Edaphics

Soils in the study area form on volcanic bedrock (basalt, phonolite, trachyte), volcanic ash and pyroclastic deposits (trachytic, pantelleritic, rhyolitic) and on fluvial and lacustrine sediments. Soil mapping and sampling revealed that on lake beds and trachytic tuffs of the Kinangop plateau, soils are mainly thin (thicknesses above regolith < 50cm). Deep red soils occur on the basalts of Mount Kipipiri, and in the foothills of the Aberdare Range, along the Sattima escarpment, as well as on volcanic ash and pyroclastics of the Mau escarpment and the Eburru forest. Most of the places with deep soils were previously forested but are now associated with intensive agriculture (Hesslerová & Pokorný, 2010; Were, Dick & Singh, 2013). Deep red but strongly weathered and acidified soils dominate the normal faulting complex north and northeast of Kariandusi as well as the edges of the Sattima fault and Mount Kipipiri (Mireri, 2005; Muchena & Gachene, 1988).

The results show that the nutrient distribution in soils of the study region is very heterogeneous. Whereas levels for Fe, Mn, and K are moderate to high in almost all soil and vegetation samples (Figures S2a, S2b, Table S3), other nutrient levels show strong variations throughout the study area. Calcium levels in all soil samples are moderate to high. In vegetation samples, however, Ca is mainly deficient except in samples from basaltic soils south of Mount Kipipiri, river sediments downstream of Mount Kipipiri and on some tuff soils of the Kinangop plateau and the Rongai region (**Figure 6a**, Table S3). Magnesium levels are moderate to high in all soil samples. Vegetation samples, however, reveal mainly low Mg levels, with the exception of some samples taken from Mount Kipipiri and Sattima basalts, and Kinangop tuffs (**Figure 6a**). Copper levels are low in a large number of soil samples from lake

beds around Elmenteita, and tuffs from Eburru and south of Rongai. In vegetation samples, Cu levels are high in all samples (**Figure 6b**). Soluble phosphate levels are low in almost all soil samples and moderate in most vegetation samples (**Figure 6b**). Exceptions are high phosphate levels in soil samples from the Sattima escarpment on basaltic soils and on the foothills of Mount Kipipiri on soils that consist of a mixture of basaltic rocks and ignimbrites. Nitrogen (N) levels are moderate in most soils, except in some soils around Elmenteita and Naivasha with low N levels. In almost all vegetation samples N occurs in moderate levels (Figure S2b). Sodium (Na) is low in most vegetation samples and moderate only in some samples from the Kinangop and Rongai tuffs. High Na levels in vegetation occur in lake beds north of Lake Elmenteita, on Mount Kipipiri basalts and on Mau tuffs. In soil samples Na levels are mainly moderate (Figure S2c). Zinc (Zn) occurs in moderate to high levels in all plant samples. Some soils from the Kinangop tuffs are deficient in Zn (Figure S2c). Fluoride levels were very high in all samples (Figure S3) and for Lake Elmenteita 26.44mg/l, exceeding the recommended upper limit of 1.5mg/l by more than 17 times (WHO, 2004, Table S3).

It is noteworthy that, for both Ca and Mg, levels are moderate to high throughout but almost all samples of vegetation lack both nutrients in many places. A reason for this may be that successful uptake of these nutrients is only possible if they are present in the soil in the right ratio (Schulte & Kelling, 1985).

Interpretation of animal distributions

The results of the edaphic analysis are combined with topographic information to highlight in a more detailed way those areas that can be exploited by large animals, particularly those moving in large groups or herds (**Figure 7**).

The most striking feature is the patchy distribution of the most favourable categories, with areas characterized by rough topography and poor edaphics dominating the region. These areas would not necessarily have been devoid of animals but are likely, at best, to have been used intermittently, by smaller numbers of animals, or in transit between edaphically and topographically more attractive areas. The best edaphics are confined to the upper rift flanks of the Kinangop Plateau and the Mau escarpment, with smaller patches on the rift floor near Lake Baringo and Lake Elmenteita. The latter is the result of recent (mostly Holocene) volcanic activity and cannot be extrapolated to earlier periods. Areas of moderately good, but variable, edaphics are on the rift floor and on the Kinangop Plateau.

Today, the lake shores provide the most topographically accessible grazing over wide areas. Soils are potentially attractive for animals, with high Ca, Mg, Ca and K contents, but these advantages are offset by other factors. The vegetation growing on these soils often has low Ca and Mg levels, as noted earlier, and geophagia (the practice of eating soil-like substrates) is common today in this part of the Kenya Rift for both humans and animals (Davies, 2008). 'Salt licks' at places where lake beds are

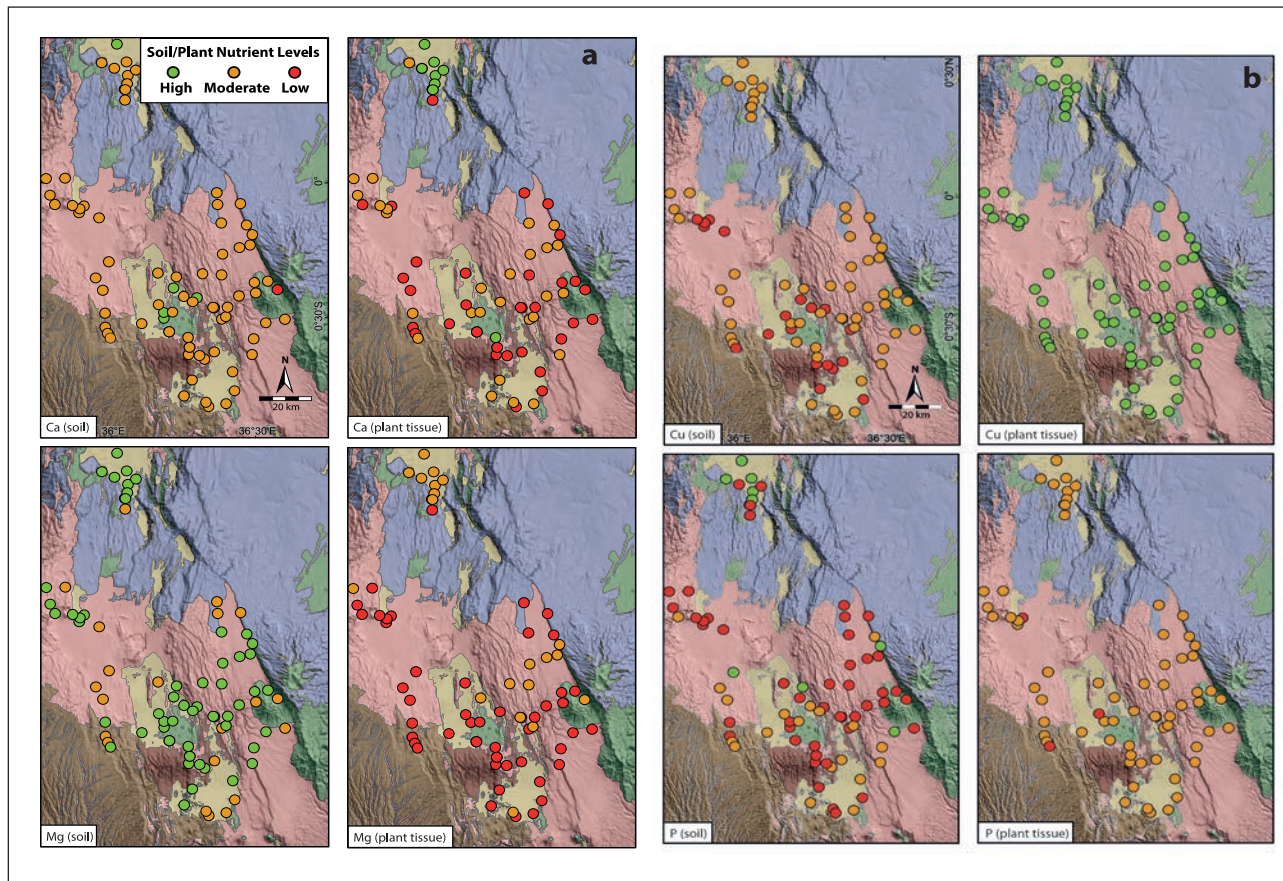


Figure 6: Maps showing the results for some important trace nutrients. The supplementary material (Table S1, Figure S2) contains complete data. The base map is shown in Figure 5, which also shows the Kariandusi site location. Not many soil and vegetation samples were taken on Phonolite or Trachyphonolite. The soils in these regions were not easy to access, vegetation was thin and there were few animals. **(a)** Sites of soil and plant material samples. The sample sites are colour-coded for Calcium (upper row) and Magnesium (lower row). Green indicates good or adequate mineral levels and red low levels. Orange shows intermediate levels. Information for latitude and longitude and a key are shown in the upper left figure. **(b)** Sites of soil and plant material samples. The sample sites are colour coded for Copper (upper row) and Phosphorus (lower row). Green indicates good or adequate mineral levels and red low levels. Orange shows intermediate levels. Information for latitude and longitude and a key are shown in the upper left panel of Figure 6a.

exposed are an important alternative source of nutrients, and sacks of mineral salt are extracted from these lake-bed outcrops, notably in the quarry below the Kariandusi site, and distributed to farmers more widely in the region to supplement cattle feed. Soils formed on the lake sediments are also usually shallow and sensitive to erosion and have reported low copper and cobalt content (Maskall & Thornton, 1996). This is a particular problem for ruminants as the bacteria exploited by their digestive systems depend on these minerals. Without them, the animals cannot process food and starve. Such cases are reported repeatedly by cattle farmers of the Nakuru region where the disease is known as Nakurutitis.

Lakes Nakuru and Elmenteita are now highly saline and are not a suitable freshwater source for animals. Some drinkable water comes from hot springs in the multi-faulted region to the east of the basin (Figure 3). However, our measurements show very high fluoride levels around Lake Elmenteita (Figure S3).

In summary, the areas around the lake basins of the inner rift provide moderate edaphic properties suitable mainly as short-term grazing for animals. The disadvantages, mainly due to the lack of certain nutrients, excessive fluoride and thin, saline soils, make it likely that vegetation growing on soils in these areas would only be exploited by animals for part of the year, with movement elsewhere at other times. At times of high lake levels, fresh water would have been available in the basin but grazing and browsing areas on the rift floor would have been much reduced.

To the east, the Kinangop plateau provides extensive areas of relatively smooth and accessible topography, circumscribed by steep faults or inaccessible areas of rough topography, and moderate nutrient content for most of the tested soils. Lake Ol Bolosat is a fresh water source and the lake shores and associated wetlands provide easy grazing or browse. Mount Kipipiri and the Sattima fault escarpment provide one of the few larger areas of basalt

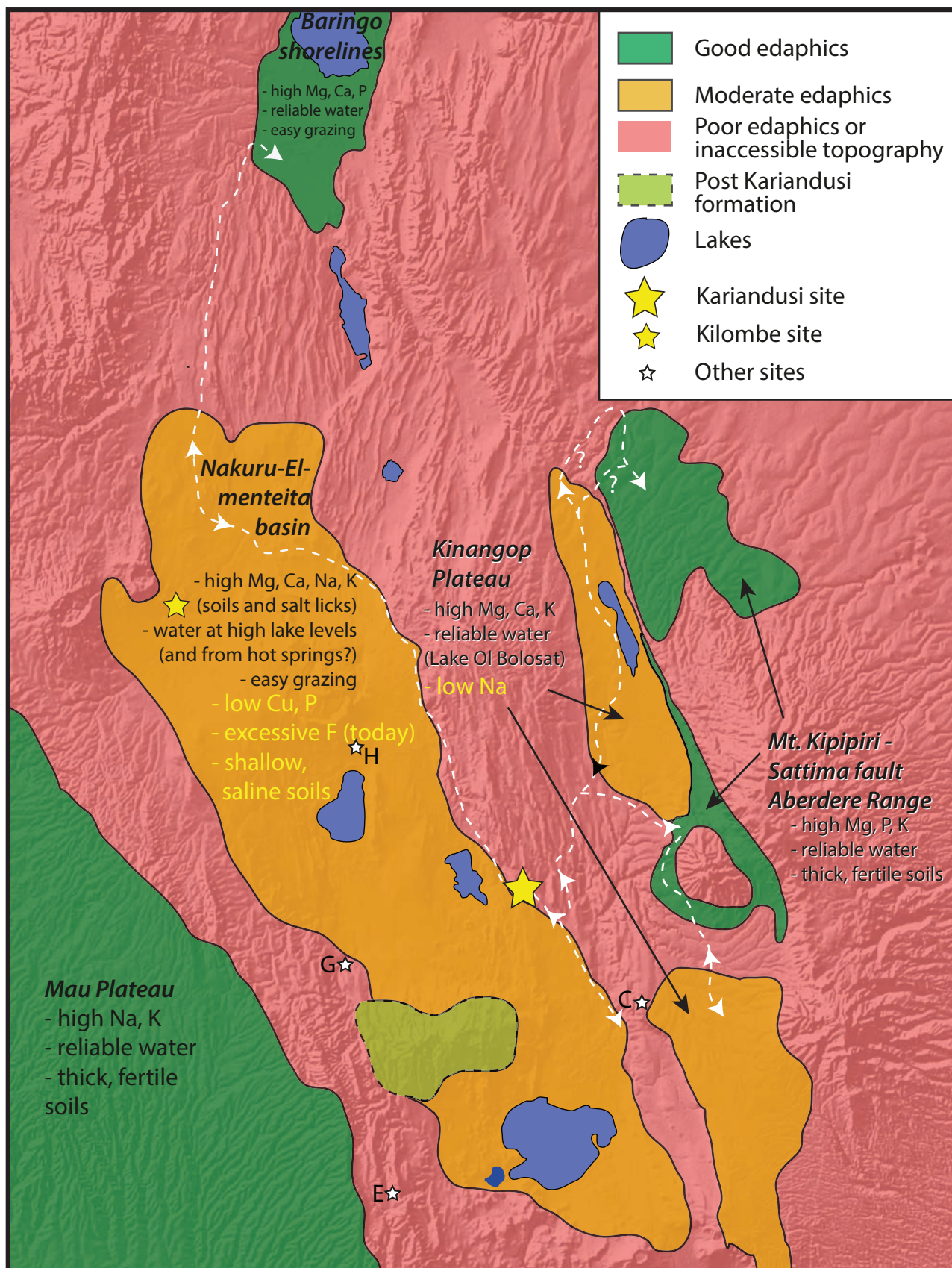


Figure 7: Edaphic sub-regions between Lake Naivasha and Lake Baringo. Areas of good edaphics attractive to animals are shown in green. Moderately good areas are indicated in orange. Elsewhere either the edaphics are very poor or topographic complexity makes the area inaccessible to large animals. Possible routes for animal movements are shown. At very high lake levels, large animals have to pass the Kariandusi site. At other times animal movements would have been less constrained and ambush hunting might not have been a viable way to access fat-rich protein.

(Sattima basalt). Here, soils tend to be thick and fertile and have very high phosphorus levels in some of the samples tested. In general, most nutrients tested were available in sufficient levels on the soils sampled in this region. The best soils are located in a narrow ring around Mount Kipipiri and a thin strip where the Sattima fault exposes basalt. No soil samples were taken from the Aberdare Range. However, the lithological similarities of the uppermost part of the range to Mount Kipipiri and the thick forest cover suggest thick and fertile soils for this region comparable to Mount Kipipiri.

To the west, the Mau Escarpment presents a significant barrier to east–west movement but there is easy passage from the Nakuru basin through the escarpment to extensive areas of relatively accessible topography at higher altitude, originally covered with dense forest but now extensively cleared for production of tea, coffee and maize, with good soil edaphics.

To the south, the situation is less clear. The Eburru forest today is characterised by a dense forest cover, and thick red, fertile soils with high Ca, Mg, and P levels. However, the onset of volcanism at Eburru is of Holocene age (Bergner et al., 2009; Clarke et al., 1990; Scott & Skilling, 1999) and these high values cannot therefore be extrapolated to earlier times.

When lake levels were high, it is clear that the only feasible pathway for animals to pass along a north–south axis or between the rift floor and the extensive and relatively attractive grazing territory of the Kinangop Plateau would be to cross the Kariandusi River (**Figure 5**). The distance over which the river can be crossed is in fact only a few hundred metres because of the obstructions on either side. No alternative route is possible. This places the Kariandusi site at a critical point to intersect animals moving along a highly predictable migration route during high lake levels. Conversely, when lake levels were low, at or close to present-day levels, extensive grazing territory would have been available around the lake margin, and the Kariandusi site would have lost its strategic importance, being more easily bypassed.

Discussion

The combination of edaphic and topographic analysis reveals important features about the palaeoenvironment of the wider region and the location of individual archaeological sites in relation to large-mammal movements that would not otherwise have been apparent. Here, we concentrate on the site of Kariandusi, and consider how far the location of the site can be explained in terms of its unusually advantageous position in relation to the topographic and edaphic variables identified above, as opposed to other factors such as access to water supplies or lithic raw materials, and whether we can infer some form of ‘ambush hunting’ from its location, following the identification of similar combinations of edaphic and topographic features elsewhere, notably at Gesher Banat Yaqov in Israel (Devès et al., 2014), and at Olorgesailie in the southern Kenyan Rift (Kübler et al., 2015).

The Kariandusi site comprises a palimpsest of artefacts, representing an unknown number of depositional

episodes (Shipton, 2011). There are two groups of finds, an upper site first excavated by the Leakeys in the 1930s and 1940s on the right bank of a small tributary of the Kariandusi River, and a nearby concentration of stone tools on its left bank excavated by John Gowlett in 1974, with an age bracketed between 0.73 and 0.98 Ma (Gowlett & Crompton, 1994; Shipton, 2011). The material was originally deposited on the river bed or the adjacent banks of the river not far from where it entered an expanded Lake Elmenteita during a period of high lake level. The stone artefacts could have been subsequently re-deposited by river bank erosion though they were probably not moved very far from their original position (Walter & Trauth, 2013), and were later buried in fluvial sediments stratified between underlying lake sediments and overlying lavas. There is no evidence that archaeological or human fossil material was deposited in the nearby lake or lake shore deposits. Some of the archaeological material from both the Leakey and Gowlett excavations has been preserved and protected *in situ* and is perched on the sides of a more recently formed shallow gorge incised by the Kariandusi River as it cut down to a lowered lake level (**Figure 8**). The artefact material is dominated by bifaces made of locally available lava, or obsidian possibly obtained from sources up to 30 km to the south on the rift floor and the Kinangop Plateau (Shipton, 2011). Flake debitage is under-represented, suggesting that many bifaces were made elsewhere and discarded at Kariandusi. Faunal remains are very rare, comprising only Equid teeth, most probably all that has survived the effects of post-depositional destruction.

Source material for making artefacts is readily available in the volcanics of the region, and though a lava outcrop is present some 90m to the north, the site has no particular advantage in respect of raw material availability. Similarly, freshwater would have been widely available along river courses, in springs along fault lines, and from an expanded Lake Elmenteita that would have contained freshwater at high lake levels in contrast to the saline conditions that prevail today. Neither of these variables uniquely determines the attractiveness of the Kariandusi location, though they could have been added attractions.

Rather, the key factor is the combination of topographic features further constrained by high lake levels during a limited time window of opportunity that allowed animals to be easily and predictably intercepted. The important features here are the date of the site, which coincides with a period of high lake levels, and the location of the site on the only accessible pathway between the attractive upland soils and topography of the Kinangop Plateau and the resources of the rift floor in the Nakuru-Elmenteita and Baringo basins (**Figure 7**). If, as is now widely accepted, meat-eating played a significant role in the development and expansion of the *Homo* lineage (Ben-Dor et al., 2011; Cordain et al., 2000; Aiello & Wheeler, 1995), then availability of such features would have been of critical advantage, providing easy opportunities for hunting or scavenging the meat of large mammals.

This raises two further questions for discussion: what sort of methods of exploiting large mammals are implied



Figure 8: View of the Kariandusi site taken from the present-day valley floor looking east. The tin-roofed structure above the cliff marks the location of the John Gowlett excavation. Below it are thick accumulations of lake sediment that have been extensively quarried (Photo by G. Bailey February 2012).

by these site locations? And why, in the current state of knowledge, are these sites apparently so rare?

With regard to the first question, ‘ambush hunting’ seems an intuitively obvious interpretation in the circumstances we describe, and we see no reason to deny such abilities to early hominins simply because of their great antiquity (see also Pickering, 2013). However, we note that, when talking about the whole span of human evolution, ‘ambush hunting’ may cover a wide spectrum of possibilities, ranging from high levels of social cooperation and planning at one extreme, involving large groups of people, investment in artificial aids and additional technologies such as the construction of artificial barriers for channelling animal movements, to simpler techniques, at the other extreme, that depend mainly on being in the right place at the right time in a landscape constrained by natural traps that animals are forced to move through during the course of their normal patterns of movement (see Marean 1997, for further discussion). In the absence of evidence at Kariandusi for human population size, details of the material culture, the duration, timing or frequency of individual episodes of activity, or even any direct information about prey animals or evidence from

their bone remains, there is a limit to how much we can infer about the social organization, technology and hunting techniques involved other than to highlight the opportunities afforded by the local topography at the time of occupation.

This, in its turn bears on the question of why such sites are not more commonly found. One possibility is that the sites are not rare at all, but are simply a tiny and unrepresentative sample of a much larger distribution of material, most of which has been eroded away, buried under later deposits, or simply has not yet been discovered. In a region of active tectonics, with ongoing volcanic activity and changing lake levels, it is possible that some sites in lake-edge and river-bank locations have been eroded away and buried under later sediments, or have been buried under later volcanic deposits, especially on the floor of the inner rift. On this argument, Kariandusi might be just one of a range of sites involving different patterns of activity and land use, different environmental and topographic associations, different tactics for exploiting animal prey, and quite possibly other facets of economic subsistence involving exploitation of non-mammalian, aquatic or plant resources.

Another possibility is that the surviving pattern of sites has been biased by variations in hominin behaviour with respect to the discard of material. Isaac (1981) was among the first to emphasise the tendency of early African archaeological 'sites' to represent clusters or patches of material surrounded by a more widely distributed background scatter of individual artefacts – the 'scatters and patches' approach to spatial analysis (see also Isaac & Harris, 1978; Kroll, 1994; Stern, 1994). Isaac further pointed out that the clusters might not be functionally different from the scatters, simply representing the same sort of individual depositional episode repeated many times in the same place – a 'cumulative palimpsest' of more recent terminology (Bailey, 2007) – and therefore with a higher probability of achieving a threshold of archaeological visibility. On this argument, there might be more sites scattered across the landscape representing the same sorts of activities as at Kariandusi, but consisting of a single artefact or a small group of artefacts deposited in a given location only once and therefore more likely to have escaped preservation or discovery. According to this hypothesis, any putative differences in visibility of evidence would be the result of pre-depositional variations in hominin behaviour rather than post-depositional variations in exposure or preservation of discarded bones and stones, but the outcome would be the same, namely to compromise any interpretation that sees significance in the relationship between Kariandusi and its local topographic features.

We do not rule out the operation of factors of differential visibility and preservation, but we prefer to look for patterns of association in the evidence that we do have rather than to speculate about the possible meaning of data that may never have existed. We may not be able to say with much confidence precisely what activities were carried out at Kariandusi – hunting, scavenging, sleeping, making tools, caching of raw materials, finding shade and protection in trees, or any of a range of other possibilities, perhaps any or all of these, or different ones at different times. Rather, the significance of Kariandusi lies exactly in the fact that it was the scene of repeated visits and discard of material, and that the main episodes of activity coincide with strikingly advantageous topographic opportunities for the exploitation of large mammals at about the period of time when these opportunities would have been most obviously available.

A final possibility is that sites like Kariandusi are genuinely rare, and that the pattern we see is indeed broadly representative of the distribution of past hominin activities, with their main concentration in widely-spaced locations with unusual combinations of topographic and edaphic features that facilitated easy access to large mammals. Raw material distributions and other features of the artefact assemblage indicate that the makers of the Kariandusi bifaces may have ranged more widely in the area, but that is not inconsistent with a pattern of land use focused on limited and widely spaced nodes of subsistence activity. If correct, this interpretation carries the further implication that hominin populations 1 million years ago were small and concentrated in limited areas of the wider landscape, consistent with recent inferences of

small population size from genetic analyses (Sherry et al., 1997; Huff et al., 2010), or that they lacked the skills, motivation or technology to hunt mammals or exploit other food resources more widely in less constrained topography. In this context we note the presence of MSA and LSA material on the Kinangop Plateau and the Mau escarpment in locations that do not seem to have been any less available at earlier periods, and where concentrations of Acheulean bifaces, had they been discarded there, might be expected to have remained just as visible to discovery as the stone artefacts from later periods.

Conclusion

The landscape of the Central Kenya rift is the product of cumulative rifting, tectonic faulting and volcanic activity over a period of more than 5 million years. In this paper we have concentrated on the Nakuru-Elmenteita-Naivasha region. The basic morphology of this region as it appears today had become established by about 2.5 Ma, but ongoing faulting and volcanic activity has continued to transform local features up to the present day, rejuvenating fault scarps and covering some earlier land surfaces with volcanic lavas. Superimposed on these processes are changes in lake level, jointly determined by climate change and tectonic activity. These processes have exerted major controls on the ways in which large mammals were distributed and their accessibility to hominin predation. They have also probably had an impact on the preservation, exposure and discovery of archaeological material, which may account in part for the apparent rarity of sites in this region. No Plio-Pleistocene hominin fossils have yet been discovered, and that may be due to similar factors of preservation, although we note that alkaline lake sediments good for preserving fossil material and formed at higher lake levels are well exposed in parts of the basin, with extensive quarrying below the Kariandusi site, and we might expect fossil material to have been recovered here if it had been available for discovery (**Figure 8**).

Collecting and analysing nutrients of the soils (soil edaphics) and vegetation provides a key to reconstructing how animals could have used the region prior to the impact of modern agricultural development. Relating this to the mineralogy of the underlying rock (regolith) in a systematic way has not previously been carried out, and the results presented here offer the prospect of producing satellite-based soil and geological maps that can apply to a wider region than the one examined here. The edaphic analysis shows that the distribution of soil nutrients is patchy, with the best conditions on some of the basaltic rocks of the rift flanks and some areas of lake sediment, but with significant deficiencies in many other areas. This feature would have prompted movements of animals in the past and also has important modern social implications because a lack of trace elements has serious consequences for human and animal health today.

Contrary to initial expectations, the rift floor, despite the presence of extensive lakes, is not the most obviously attractive place for human exploitation of mammal-resources. When lake levels were low, the microclimate was generally hot and dry with a short rainy season compared

to the rift flanks, and the lakes with small catchments would have become alkaline and unsuitable for drinking water. In wetter climatic intervals with high lake levels, freshwater would have been more widely available in an extended lake region, but the lakes would have flooded extensive areas of previously available animal habitat.

Combining the analysis of topographic and edaphic features has enabled us to produce maps of the region that highlight the areas where hominin predators would have had the best opportunities for targeting large mammals, and a framework for the interpretation of archaeological sites more generally. The site of Kariandusi is especially well placed to capture animals moving between the extensive and attractive upland grazing territories of the Kinangop Plateau to the east and southeast of the site and the Nakuru and Baringo basins to the north and west, especially during periods of high lake level. We interpret the site as an ideal location where simple ambush hunting could have been practised, taking advantage of the natural trap-like features of the local topography in relation to the wider distribution and pattern of movements of large mammals. We cannot rule out the distorting effects of differential preservation and exposure in removing or obscuring archaeological sites elsewhere, but we regard it as significant that the unusual combination of features at the Kariandusi location is associated with the only Acheulean site complex so far discovered in the region, and consider this evidence of some form of ambush hunting. If patterns of Acheulean land use were limited by the availability of natural features like those we have identified at Kariandusi, this might explain the relative rarity of substantial and repeatedly used Acheulean sites in this region and elsewhere, and this has further implications for assessments of hominin population density and hunting skills at this early stage in the hominin evolutionary trajectory.

Supplementary Material

Data from this research has been published in an open repository and can be found at Kübler et al (2016), <http://dx.doi.org/10.7910/DVN/1AN9GO>

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Competing Interests

The authors declare that they have no competing interests.

References

- Aiello, L C and Wheeler, P** 1995 The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology*, 36(2): 199–221. DOI: <http://dx.doi.org/10.1086/204350>
- Ambrose, S H** 1998 Chronology of the Later Stone Age and food production in East Africa. *Journal of Archaeological Science*, 25: 377–392. DOI: <http://dx.doi.org/10.1006/jasc.1997.0277>
- Bailey, G N** 2007 Time perspectives, palimpsests and the archaeology of time. *Journal of Anthropological Archaeology*, 26: 198–223. DOI: <http://dx.doi.org/10.1016/j.jaa.2006.08.002>
- Bailey, G N, Reynolds, S C and King, G C P** 2011 Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. *Journal of Human Evolution*, 60: 257–280. DOI: <http://dx.doi.org/10.1016/j.jhevol.2010.01.004>
- Baker, B, Mitchell, J and Williams, L** 1988 Stratigraphy, geochronology and volcano-tectonic evolution of the Kedong-Naivasha-Kinangop region, Gregory Rift Valley, Kenya. *Journal of the Geological Society*, 145: 107–116. DOI: <http://dx.doi.org/10.1144/gsjgs.145.1.0107>
- Baker, B, Williams, L, Miller, J and Fitch, F** 1971 Sequence and geochronology of the Kenya rift volcanics. *Tectonophysics*, 11: 191–215. DOI: [http://dx.doi.org/10.1016/0040-1951\(71\)90030-8](http://dx.doi.org/10.1016/0040-1951(71)90030-8)
- Baker, B and Wohlenberg, J** 1971 Structure and evolution of the Kenya Rift Valley. *Nature*, 229: 538–542. DOI: <http://dx.doi.org/10.1038/229538a0>
- Ben-Dor, M, Gopher, A, Hershkovitz, I and Barkai, R** 2011. Man the fat hunter: the demise of *Homo erectus* and the emergence of a new hominin lineage in the Middle Pleistocene (ca. 400 kyr) Levant. *PLoS One*, 6(12): e28689. DOI: <http://dx.doi.org/10.1371/journal.pone.0028689>

- Bergner, A, Strecker, M, Trauth, M, Deino, A, Gasse, F, Blisniuk, P and Dühnforth, M** 2009 Tectonic and climatic control on evolution of rift lakes in the Central Kenya Rift, East Africa. *Quaternary Science Reviews*, 28: 2804–2816. DOI: <http://dx.doi.org/10.1016/j.quascirev.2009.07.008>
- Bishop, W W** 1978 Geological framework of the Kilombe Acheulian archaeological site, Kenya. Geological Society, London, Special Publications, v. 6, pp. 329–336. DOI: <http://dx.doi.org/10.1144/GSL.SP.1978.006.01.23>
- Blumenschine, R J and Peters, C R** 1998 Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. *Journal of Human Evolution*, 34: 565–607. DOI: <http://dx.doi.org/10.1006/jhev.1998.0216>
- Blumenschine, R J, Stanistreet, I G, Njau, J K, Bamford, M K, Masao, F T, Albert, R M, Stollhofen, H, Andrews, P, Prassack, K A and Mchenry, L J** 2012 Environments and hominin activities across the FLK Peninsula during Zinjanthropus times (1.84 Ma), Olduvai Gorge, Tanzania. *Journal of Human Evolution*, 63: 364–383. DOI: <http://dx.doi.org/10.1016/j.jhev.2011.10.001>
- Bobe, R, Alemseged, Z and Behrensmeyer, A K** (eds.) 2007 Approaches to the analysis of faunal change during the East African Pliocene. *Hominin environments in the East African Pliocene: an assessment of the faunal evidence*. Dordrecht, Springer. DOI: <http://dx.doi.org/10.1007/978-1-4020-3098-7>
- Bobe, R and Leakey, M G** 2009 Ecology of Plio-Pleistocene Mammals in the Omo-Turkana Basin and the Emergence of Homo. In: Grine, F E, Fleagle, J C & Leakey, R E (Eds.) *The First Humans: Origin and Early Evolution of the Genus Homo*. Dordrecht, Springer, pp. 173–184. DOI: http://dx.doi.org/10.1007/978-1-4020-9980-9_15
- Bosworth, W and Strecker, M R** 1997 Stress field changes in the Afro-Arabian rift system during the Miocene to Recent period. *Tectonophysics*, 278: 47–62. DOI: [http://dx.doi.org/10.1016/S0040-1951\(97\)00094-2](http://dx.doi.org/10.1016/S0040-1951(97)00094-2)
- Bunn, H, Harris, J W, Isaac, G, Kaufulu, Z, Kroll, E, Schick, K, Toth, N and Behrensmeyer, A K** 1980 FxJj50: an early Pleistocene site in northern Kenya. *World Archaeology*, 12: 109–136. DOI: <http://dx.doi.org/10.1080/00438243.1980.9979787>
- Clarke, M, Woodhall, D, Allen, D and Darling, G** 1990 Geological, volcanic and hydrological controls on the occurrence of geothermal activity in the area surrounding Lake Naivasha, Kenya. *Ministry of Energy, Nairobi*.
- Coppens, Y** 1994 East side story: the origin of humankind. *Scientific American*, 270: 88–95. DOI: <http://dx.doi.org/10.1038/scientificamerican0594-88>
- Cordain, L, Miller, J B, Eaton, S B, Mann, N, Holt, S H and Speth, J D** 2000 Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *The American Journal of Clinical Nutrition*, 71: 682–692.
- Davies, T** 2008. Environmental health impacts of East African Rift volcanism. *Environmental Geochemistry and Health*, 30: 325–338. DOI: <http://dx.doi.org/10.1007/s10653-008-9168-7>
- Devès, M, Sturdy, D, Godet, N, King, G C and Bailey, G N** 2014 Hominin reactions to herbivore distribution in the Lower Palaeolithic of the Southern Levant. *Quaternary Science Reviews*, 96: 140–160. DOI: <http://dx.doi.org/10.1016/j.quascirev.2014.04.017>
- Gowlett, J A J and Crompton, R H** 1994 Kariandusi: Acheulean morphology and the question of allometry. *African Archaeological Review*, 12: 3–42. DOI: <http://dx.doi.org/10.1007/BF01953037>
- Hesslerová, P and Pokorný, J** 2010 Effect of Mau forest clear cut on temperature distribution and hydrology of catchment of Lakes Nakuru and Naivasha: preliminary study. In: Vymazal, J (Ed.) *Water and Nutrient Management in Natural and Constructed Wetlands*. Dordrecht: Springer, pp. 263–273. DOI: http://dx.doi.org/10.1007/978-90-481-9585-5_19
- Huff, C D, Xing, J, Rogers, A R, Witherspoon, D and Jorde, L B** 2010 Mobile elements reveal small population size in the ancient ancestors of Homo sapiens. *Proceedings of the National Academy of Sciences*, 107: 2147–2152. DOI: <http://dx.doi.org/10.1073/pnas.0909000107>
- Isaac, G L** 1977 *Ologesailie: Archaeological studies of a Middle Pleistocene Lake Basin in Kenya*. Chicago: University of Chicago Press.
- Isaac, G L** 1981 Stone Age visiting cards: approaches to the study of early land use patterns. In: Hodder, I, Isaac, G and Hammond, N (Eds.) *Pattern of the Past*. Cambridge: Cambridge University Press, pp. 131–155.
- Isaac, G L and Harris, J W K** 1978 The archaeological context of the hominid fossils. In: Leakey, M G and Leakey, R E F (Eds.) *Koobi Fora Research Project, Volume 1. The Fossil Hominids and an Introduction to their Context* Oxford. Clarendon Press, pp. 64–85.
- King, G and Bailey, G** 2006 Tectonics and human evolution. *Antiquity*, 80: 265–286. DOI: <http://dx.doi.org/10.1017/S0003598X00093613>
- Kingston, J D** 2007 Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Yearbook of Physical Anthropology*, 50: 20. DOI: <http://dx.doi.org/10.1002/ajpa.20733>
- Kroll, E M** 1994 Behavioral implications of Plio-Pleistocene archaeological site structure. *Journal of Human Evolution*, 27: 107–138. DOI: <http://dx.doi.org/10.1006/jhev.1994.1038>
- Kübler, S, Owenga, P, Reynolds, S C, Rucina, S M and King, G C** 2015 Animal movements in the Kenya Rift and evidence for the earliest ambush hunting by hominins. *Nature Scientific Reports*, 5: 14011. DOI: <http://dx.doi.org/10.1038/srep14011>
- Kübler, S, Rucina, S, Reynolds, S, Owenga, P, Bailey, G and King, G** 2016 Edaphic and Topographic Constraints on Exploitation of the Central Kenya Rift by Large Mammals and Early Hominins,

- Harvard Dataverse*, DOI: <http://dx.doi.org/10.7910/DVN/1AN9GO>.
- Lahr, M M** 2015 Available at: <http://in-africa.org/fieldwork/central-rift/> (last accessed 23 January 2016).
- Leakey, L S B** 1931 *The Stone Age Cultures of Kenya Colony*. Cambridge: Cambridge University Press.
- Leakey, M D, Leakey, L S B, Game, P and Goodwin, A** 1943 Report on the excavations at Hyrax Hill, Nakuru, Kenya Colony, 1937–1938. *Transactions of the Royal Society of South Africa*, 30: 271–409. DOI: <http://dx.doi.org/10.1080/00359194309519847>
- Leat, P T** 1991 Volcanological development of the Nakuru area of the Kenya rift valley. *Journal of African Earth Sciences (and the Middle East)*, 13: 483–498. DOI: [http://dx.doi.org/10.1016/0899-5362\(91\)90111-B](http://dx.doi.org/10.1016/0899-5362(91)90111-B)
- Lewin, R and Foley, R A** 2004 2nd ed. *Principles of Human Evolution*. Malden, MA and Oxford: Blackwell.
- Maglio, V J and Cooke, H B S** 1978 *The Evolution of African Mammals*. Cambridge, MA: Harvard University Press. DOI: <http://dx.doi.org/10.4159/harvard.9780674431263>
- Marean, C W** 1992 Hunter to herder: large mammal remains from the hunter-gatherer occupation at Enkapune ya Muto rock-shelter, Central Rift, Kenya. *African Archaeological Review*, 10: 65–127. DOI: <http://dx.doi.org/10.1007/BF01117697>
- Marean, C W** 1997 Hunter-gatherer foraging strategies in tropical grasslands: model building and testing in the East African Middle and Later Stone Age. *Journal of Anthropological Archaeology*, 16: 189–225. DOI: <http://dx.doi.org/10.1006/jaar.1997.0309>
- Maskall, J and Thornton, I** 1996 The distribution of trace and major elements in Kenyan soil profiles and implications for wildlife nutrition. In: Appleton, J D, Fuge, R and McCall, G J H (Eds.) *Environmental Geochemistry and Health*. London: Geological Society Special Publication, 113: 47–62. DOI: <http://dx.doi.org/10.1144/gsl.sp.1996.113.01.05>
- Maslin, M A, Brierley, C M, Milner, A M, Shultz, S, Trauth, M H and Wilson, K E** 2014 East African climate pulses and early human evolution. *Quaternary Science Reviews*, 101: 1–17. DOI: <http://dx.doi.org/10.1016/j.quascirev.2014.06.012>
- McCall, G J H** 1967 *Geology of the Nakuru-Thomson's Falls-Lake Hannington Area: Degree Sheet No. 35 SW Quarter and 43 NW Quarter (with Coloured Maps)*. Geological Survey of Kenya.
- Mireri, C** 2005 Challenges facing the conservation of Lake Naivasha, Kenya. *FWU Topics of Integrated Watershed Management-Proceedings*, 3: 89–98.
- Moturi, W K, Tole, M P and Davies, T C** 2005 The contribution of drinking water towards dental fluorosis: a case study of Njoro Division, Nakuru District, Kenya. *Environmental Geochemistry and Health*, 24: 123–130. DOI: <http://dx.doi.org/10.1023/A:1014204700612>
- Muchena, F and Gachene, C** 1988 Soils of the highland and mountainous areas of Kenya with special emphasis on agricultural soils. *Mountain Research and Development*, 8: 183–191. DOI: <http://dx.doi.org/10.2307/3673446>
- Pickering, T R** 2013 *Rough and Tumble: Aggression, Hunting and Human Evolution*. Oakland, CA: University of California Press.
- Potts, R** 1994 Variables versus models of early Pleistocene hominid land use. *Journal of Human Evolution* 27: 7–24. DOI: <http://dx.doi.org/10.1006/jhev.1994.1033>
- Potts, R** 1996 Evolution and climate variability. *Science*, 273: 922. DOI: <http://dx.doi.org/10.1126/science.273.5277.922>
- Potts, R** 1998 Environmental hypotheses of hominin evolution. *American Journal of Physical Anthropology* 107: 93–136. DOI: [http://dx.doi.org/10.1002/\(SICI\)1096-8644\(1998\)107:27+<93::AID-AJPA5>3.0.CO;2-X](http://dx.doi.org/10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X)
- Potts, R, Behrensmeier, A K and Ditchfield, P** 1999 Paleolandscape variation and early Pleistocene hominid activities: Members 12 and 7, Ologesailie Formation, Kenya. *Journal of Human Evolution*, 37: 747–788. DOI: <http://dx.doi.org/10.1006/jhev.1999.0344>
- Reynolds, S C, Bailey, G and King, G C P** 2011 Landscapes and their relation to homin habitats: case studies from *Australopithecus* sites in eastern and southern Africa. *Journal of Human Evolution*, 60: 257–280. DOI: <http://dx.doi.org/10.1016/j.jhevol.2010.10.001>
- Roessner, S and Strecker, M R** 1997 Late Cenozoic tectonics and denudation in the Central Kenya Rift: quantification of long-term denudation rates. *Tectonophysics*, 278: 83–94. DOI: [http://dx.doi.org/10.1016/S0040-1951\(97\)00096-6](http://dx.doi.org/10.1016/S0040-1951(97)00096-6)
- Schulte, E E and Kelling, K A** 1985 *Soil Calcium to Magnesium Ratios—Should You be Concerned?* Bulletin G2986. University of Wisconsin Extension Service. Madison, Wisconsin.
- Scott, S C and Skilling, I P** 1999 The role of tephrochronology in recognizing synchronous caldera-forming events at the Quaternary volcanoes Longonot and Suswa, south Kenya Rift. In: Firth, C R and McGuire, W J (Eds.) *Volcanoes in the Quaternary*. London: Geological Society Special Publication, 161: pp. 47–67. DOI: <http://dx.doi.org/10.1144/gsl.sp.1999.161.01.05>
- Sherry, S T, Harpending, H C, Batzer, M A and Stoneking, M** 1997 Alu evolution in human populations: using the coalescent to estimate effective population size. *Genetics*, 147: 1977–1982.
- Shipton, C** 2011 Taphonomy and behaviour at the Acheulean site of Kariandusi, Kenya. *African Archaeological Review*, 28: 141–155. DOI: <http://dx.doi.org/10.1007/s10437-011-9089-1>
- Stern, N** 1994 The implications of time-averaging for reconstructing the land-use patterns of early tool-using hominids. *Journal of Human Evolution*, 27: 89–105. DOI: <http://dx.doi.org/10.1006/jhev.1994.1037>
- Strecker, M, Blisniuk, P and Eisbacher, G** 1990 Rotation of extension direction in the central Kenya Rift. *Geology*, 18: 299–302. DOI: [http://dx.doi.org/10.1130/0091-7613\(1990\)018<0299:ROEDIT>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1990)018<0299:ROEDIT>2.3.CO;2)

- Thacher, T D, Fischer, P R, Strand, M A and Pettifor, J M** 2006 Nutritional rickets around the world: causes and future directions. *Annals of tropical paediatrics*, 26: 1–16. DOI: <http://dx.doi.org/10.1179/146532806X90556>
- Trauth, M H and Maslin, M A** 2009 Comment on “Diatomaceous sediments and environmental change in the Pleistocene Ologesailie Formation, southern Kenya Rift” by RB Owen, R Potts, AK Behrensmeier and P Ditchfield (*Palaeogeography, Palaeoclimatology, Palaeoecology* 269 (2008) 17–37). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 282: 145–146. DOI: <http://dx.doi.org/10.1016/j.palaeo.2008.06.021>
- Trauth, M H, Maslin, M A, Deino, A and Strecker, M R** 2005 Late cenozoic moisture history of East Africa. *Science*, 309: 2051–2053. DOI: <http://dx.doi.org/10.1126/science.1112964>
- Turner, A and Antón, M** 2004 *Evolving Eden: an Illustrated Guide to the Evolution of the African Large-Mammal Fauna*, New York: Columbia University Press.
- Walter, M J and Trauth, M H** 2013 A MATLAB based orientation analysis of Acheulean handaxe accumulations in Ologesailie and Kariandusi, Kenya Rift. *Journal of Human Evolution*, 64: 569–581. DOI: <http://dx.doi.org/10.1016/j.jhevol.2013.02.011>
- Waweru, V** 2002 New excavations at the Middle Stone Age Cartwright’s site, Kenya. *Nyame Akuma*: 26–33.
- Were, K, Dick, Ø and Singh, B** 2013 Remotely sensing the spatial and temporal land cover changes in Eastern Mau forest reserve and Lake Nakuru drainage basin, Kenya. *Applied Geography*, 41: 75–86. DOI: <http://dx.doi.org/10.1016/j.apgeog.2013.03.017>
- WHO** 2004 *Guidelines for drinking-water quality: recommendations*. *WHO Library Cataloguing-in-Publication Data*, 1: 375–377.
- Winder, I C, King, G C P, Devés, M and Bailey, G N** 2013 Complex topography and human evolution: the missing link. *Antiquity*, 87: 333–349. DOI: <http://dx.doi.org/10.1017/S0003598X00048985>
- Zielke, O and Strecker, M R** 2009 Recurrence of large earthquakes in magmatic continental rifts: insights from a paleoseismic study along the Laikipia–Marmanet Fault, Subukia Valley, Kenya Rift. *Bulletin of the Seismological Society of America*, 99: 61–70. DOI: <http://dx.doi.org/10.1785/0120080015>

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