



## Landscape scale heterogeneity in the East Turkana ecosystem during the Okote Member (1.56–1.38 Ma)



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### ABSTRACT

Placing the biological adaptations of Pleistocene hominins within a well-resolved ecological framework has been a longstanding goal of paleoanthropology. This effort, however, has been challenging due to the discontinuous nature of paleoecological data spanning many important periods in hominin evolution. Sediments from the Upper Burgi (1.98–1.87 Ma), KBS (1.87–1.56 Ma) and Okote (1.56–1.38 Ma) members of the Koobi Fora Formation at East Turkana in northern Kenya document an important time interval in the evolutionary history of the hominin genera *Homo* and *Paranthropus*. Although much attention has been paid to Upper Burgi and KBS member deposits, far less is known regarding the East Turkana paleoecosystem during Okote Member times. This study pairs spatially-resolved faunal abundance data with stable isotope geochemistry from mammalian enamel to investigate landscape-scale ecosystem variability during Okote Member times. We find that during this period 1) taxa within the East Turkana large mammal community were distributed heterogeneously across space, 2) the abundance of C<sub>3</sub> and C<sub>4</sub> vegetation varied between East Turkana subregions, and 3) the Karari subregion, an area with abundant evidence of hominin stone tool manufacture, had significantly more C<sub>3</sub> vegetation than regions closer to the central axis of the Turkana Basin (i.e., Ileret and Koobi Fora). These findings indicate that the East Turkana paleoecosystem during the Okote Member was highly variable across space and provided a complex adaptive landscape for Pleistocene hominins.

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### 1. Introduction

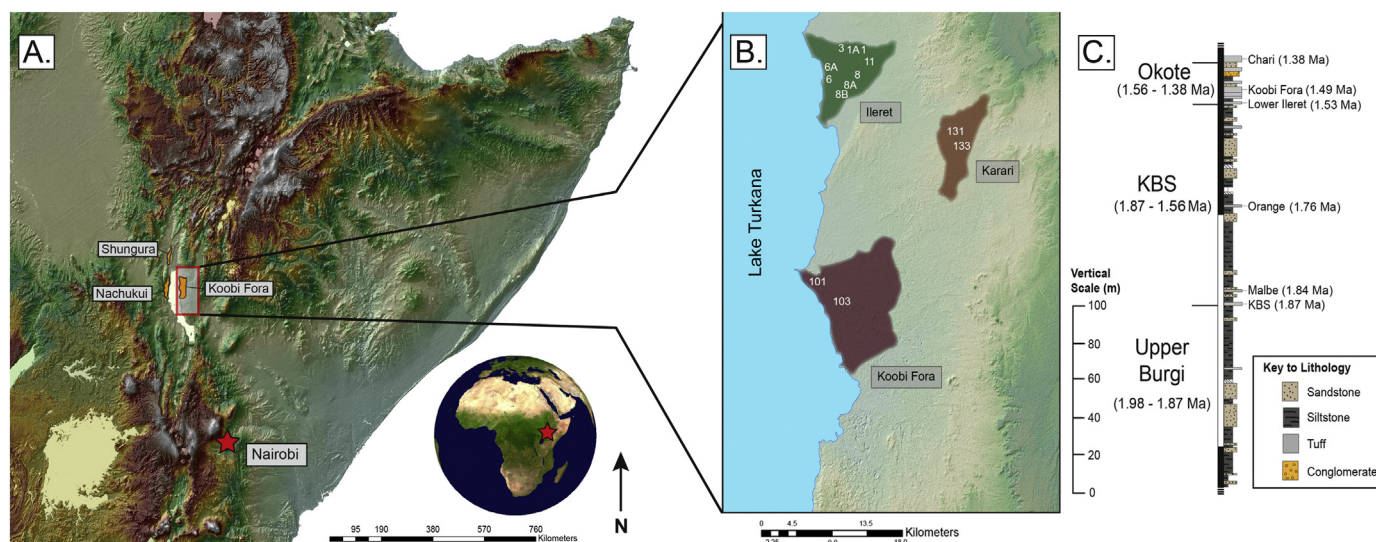
The period between 2.0 and 1.4 million years ago (Ma) in eastern Africa documents many important events in human evolutionary history, including the morphological transition from early *Homo* (i.e., *Homo habilis*, *Homo rudolfensis*) to *Homo erectus/ergaster* (Wood, 1991; Wood and Collard, 1999; Wood and Leakey, 2011; Antón et al., 2014), the synchronic and sympatric existence of the hominin genera *Homo* and *Paranthropus* (Wood, 1991; Wood and Strait, 2004), as well as significant changes in hominin

technology (Harris and Isaac, 1976; Rogers et al., 1994; Isaac and Isaac, 1997; Ludwig and Harris, 1998). Much of the evidence for these events comes from the Upper Burgi (1.98–1.87 Ma), KBS (1.87–1.56 Ma) and Okote (1.56–1.38 Ma) members of the Koobi Fora Formation at East Turkana in northern Kenya (Brown and Feibel, 1991; Brown and McDougall, 2011; Fig. 1). In addition to the hominin record from this period, non-hominin mammal fossils are particularly abundant and have featured prominently in hypotheses related to the tempo and mode of evolutionary and ecological change in eastern Africa during the Pleistocene (Vrba, 1985; Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe, 2011; Patterson et al., 2014, 2017; Bibi and Kiessling, 2015).

Nearly four decades of research into the East Turkana paleoecosystem provides a framework for testing hypotheses about

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**Figure 1.** A) East Turkana (Red Box), the Nachukui and Shungura formations in the context of eastern Africa; B) The Ileret, Karari Ridge and Koobi Fora subregions, and Collecting Areas (indicated by white numerals) from which the carbon isotope dataset is derived; C) Stratigraphic section of Upper Burgi, KBS and Okote deposits (modified from Brown and McDougall, 2011). Paleomagnetic polarity is indicated in the thin column to the left of the lithologic section. Normal intervals shown in white; reversed intervals shown in black. Names to the right of the lithologic column refer to selected tuffs with dates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

landscape-scale ecosystem variability during the Pleistocene. Between 2.0 and 1.4 Ma, the East Turkana record samples primarily lake margin and riverine environments. Early in this sequence (~2 Ma), a large lake (Lorenayang) occupied most of the Turkana Basin. After this phase, the lake retreated and by 1.5 Ma the region was composed of river systems draining into what remained of Lake Lorenayang (Brown and Feibel, 1991; Isaac and Behrensmeyer, 1997; Quinn et al., 2007; Behrensmeyer et al., 2016). The isotopic signature of paleosol carbonates from East Turkana during this period indicates that grassland-dominated ecosystems increased, but at a subregional scale, and that vegetative communities were heterogeneous (Quinn et al., 2007).

Ecosystem dynamism between 2.0 and 1.4 Ma presented a complex landscape context for the East Turkana mammal community, including hominins. This period in the Turkana Basin documents several macroevolutionary changes. These include the appearance of several bovid and suid grazing taxa, the replacement of *Theropithecus brumpti* by the more terrestrial *Theropithecus oswaldi*, and the disappearance of large colobine monkeys and the genus *Paranthropus* from the record (Harris, 1991; Bobe, 2006, 2011; Jablonski and Leakey, 2008). When the stable carbon isotope values from mammalian enamel dating to this period at East Turkana are compared with samples from modern eastern African ecosystems (see Cerling et al., 2015), they indicate an elevated prevalence of mixed-feeding taxa. The stable isotope record from this period also indicates that members of the genus *Homo* show a 20% increase in the ingestion of  $C_4$  resources (i.e., warm growing season grasses and sedges, or the animals that eat these resources), a pattern that is not present in *Paranthropus*, which ingested a high proportion of  $C_4$  resources throughout this period in the Turkana Basin (Cerling et al., 2013a). The archaeological record from East Turkana between 2.0 and 1.4 Ma indicates 1) the first evidence of aquatic resource exploitation by hominins in eastern Africa (Braun et al., 2010), 2) stone tool assemblages associated with the later portion of this sequence occur in greater diversity of depositional environments than early in the sequence (Rogers et al., 1994), and 3) hominin toolmakers selectively transported raw materials to regions distal to their sources on the landscape (Braun et al., 2008). These data indicate that the period

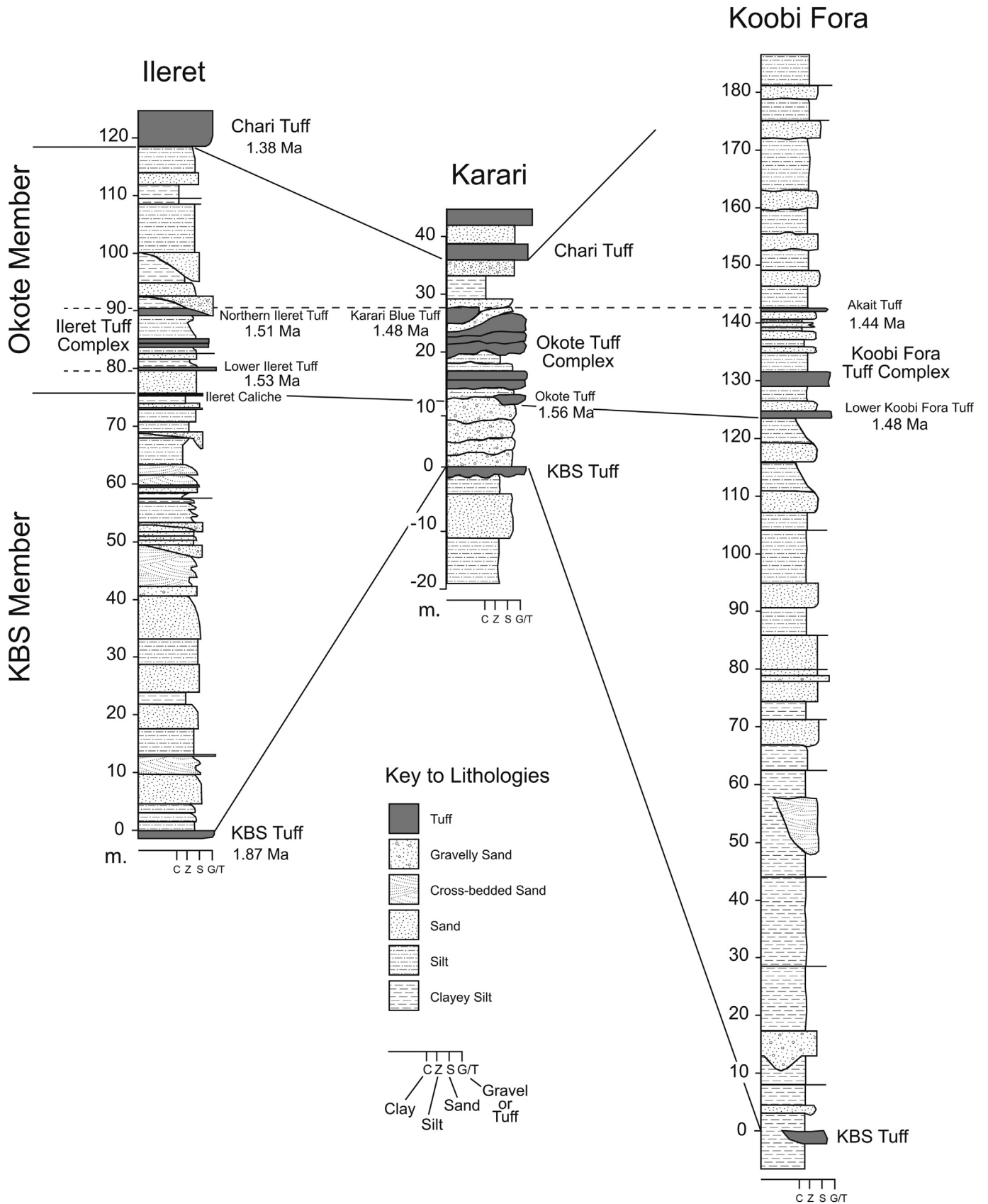
between 2.0 and 1.4 Ma at East Turkana was marked by shifting relationships between environmental change, mammal community dynamics and hominin behavior.

Fossil assemblages relevant to understanding the East Turkana paleoecosystem between 2.0 and 1.4 Ma are largely limited to material from the Upper Burgi and KBS members (Fig. 1C). Earlier work on Okote sedimentology and vertebrate taphonomy (Behrensmeyer and Laporte, 1982; Behrensmeyer, 1985) suggested possible differences in faunal representation across subregions, but intensive paleoecological study of Okote faunas has only recently been undertaken. Renewed focus on this interval provides important new evidence relating to hypotheses about hominin evolutionary history, ecology and behavior in eastern Africa. The objectives of this study are to use new and existing data from the Okote Member to 1) investigate any variation in the distribution of large mammals across the East Turkana paleolandscape, 2) use stable isotope geochemistry to characterize any spatial variation in large mammal diet and paleovegetation, and 3) explore the dietary ecology of the mammals consumed by hominins as resources during this period.

## 2. Background

### 2.1. Geographic and geological context

Okote Member sediments at East Turkana are bounded temporally by the Okote and Chari Tuffs dated to 1.56 and 1.38 Ma, respectively (McDougall and Brown, 2006; Brown and McDougall, 2011; Fig. 2). This sediment package is temporally contemporaneous with parts of the Kaitio and Nattoo members of the Nachukui Formation at West Turkana and members J and K of the Shungura Formation in southern Ethiopia (Brown and McDougall, 2011). Well-dated and widespread tephra correlations between these three regions have made it possible to compare spatial variation in contemporaneous paleoecosystems during the Plio-Pleistocene. Previous authors have suggested regional variability at a larger scale, with more arid conditions in the Koobi Fora and Nachukui formations relative to that of the Shungura (Bobe and Leakey, 2009; Levin et al., 2011), as well as substantial differences in humidity and



**Figure 2.** Correlation of KBS and Okote Member sediments in the three geographic areas referred to in this study. Sections are aligned along the uppermost tuff of the Ileret, Okote, and Koobi Fora Tuff complexes, but the dates on these tuffs are younger from north to south. Sections based on Gathogo and Brown (2006; Ileret) and Brown and Feibel (1991; Karari and Koobi Fora). Dates based on: McDougall and Brown (2006), Bennett et al. (2009), Brown and McDougall (2011). Note: Gathogo and Brown (2006) designate the lower boundary of the Okote Member as the Ileret Caliche rather than the Lower Ileret Tuff.

climate variability between East and West Turkana during this period (Hernández Fernández and Vrba, 2006; Bobe, 2011; Fortelius et al., 2016).

Okote Member strata are spatially extensive and particularly well-exposed in the Ileret, Karari and Koobi Fora subregions (Fig. 1B). Deposits dating to this period were formed under locally variable conditions ranging from fluvial settings in the Karari subregion to low energy alluvial deltas, lacustrine and shoreline deposits in the Ileret and Koobi Fora subregions (Fig. 2; Behrensmeyer, 1985; Brown and Feibel, 1991; Isaac and Behrensmeyer, 1997). Strata from these subregions have received much attention due to the prevalence of archaeological localities (Bunn et al., 1980; Rogers et al., 1994; Isaac and Isaac, 1997; Pobiner et al., 2008), and fossil evidence of hominins (Wood, 1991; Wood and Leakey, 2011), including trace fossils (Bennett et al., 2009). While hominin remains and archaeological localities have been recovered throughout the Ileret, Karari and Koobi Fora subregions, the overall distribution of these traces of behavior is variably distributed during Okote Member times. Specifically, deposits in the Karari subregion have yielded the greatest number of archaeological localities (Isaac and Isaac, 1997). Previous authors have suggested that this concentration was likely a result of proximity to raw material sources (Toth, 1982; Lepre, 2001; Braun et al., 2009), but until now limited attention has been paid to understanding the influence of paleoenvironmental variability on the spatial heterogeneity of the Okote Member archaeological record (Behrensmeyer, 1985).

The complex deposition of tuffaceous sediments during the Okote Member has made precise temporal and stratigraphic correlations between the Ileret, Koobi Fora and Karari subregions particularly challenging (see Vondra et al., 1978; Behrensmeyer and Laporte, 1981; Brown and Feibel, 1985, 1986; Gathogo and Brown, 2006). Nonetheless, it is possible to approximate temporal relationships between fossil-bearing deposits in the Ileret, Koobi Fora and Karari subregions using existing data. In Ileret (Fig. 2), Okote Member fossil-bearing deposits date primarily to between 1.53 and 1.51 Ma, while those of the Koobi Fora subregion are slightly younger and date to between 1.48 and 1.44 Ma. Okote Member fossiliferous deposits of the Karari subregion are 1.56–1.38 Ma, thus including the time spans of the richest sources of fossil evidence in the Okote Member of the Ileret and Koobi Fora subregions (Fig. 2).

## 2.2. Stable isotope geochemistry

Plant physiological diversity can be broadly characterized into three categories based upon the degree to which they fractionate carbon isotopes during photosynthesis: C<sub>3</sub>, C<sub>4</sub> and Crassulacean Acid Metabolism (CAM). In eastern Africa, C<sub>3</sub> plants are primarily trees, bushes and shrubs and have  $\delta^{13}\text{C}$  values ranging from  $-30\%$  to  $-22\%$ , while C<sub>4</sub> plants are grasses and sedges adapted to high temperatures and restricted to low elevations (<3000 m) and have  $\delta^{13}\text{C}$  values ranging from  $-14\%$  to  $-10\%$  (Tieszen et al., 1979; Young and Young, 1983; all isotope ratios are reported relative to the isotope standard Pee-Dee Belemnite [PDB], where  $\delta^{13}\text{C}$  (in ‰) =  $[(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1] \times 1000$ ). Plants that use the CAM pathway primarily consist of succulents like cacti, orchids and bromeliads and have  $\delta^{13}\text{C}$  values intermediate to those of C<sub>3</sub> and C<sub>4</sub> plants, or similar to C<sub>4</sub> plants (Lambers et al., 2008). It is unlikely, however, that CAM plants were significant components of eastern African biomass during the Plio-Pleistocene (Peters and Vogel, 2005) and therefore it is unlikely they contributed substantially to mammalian diet during this period.

The  $\delta^{13}\text{C}$  value of carbonate associated with mammalian bone and tooth apatite can be used to infer proportions of C<sub>3</sub> versus C<sub>4</sub> vegetation in the diet of ancient organisms. The  $\delta^{13}\text{C}$  value of

enamel apatite reflects the  $\delta^{13}\text{C}$  value of ingested foodstuffs, offset by a diet-tissue fractionation factor ( $\epsilon^*_{\text{enamel-diet}}$ ; DeNiro and Epstein, 1978; Vogel et al., 1978; Tieszen et al., 1979). For large herbivores,  $\epsilon^*_{\text{enamel-diet}}$  ranges from 13.3 to 14.6‰ (Cerling and Harris, 1999). Isotopic dietary variation in African mammals is represented as a continuum from C<sub>3</sub>-dominated browsers to C<sub>4</sub>-dominated grazers with C<sub>3</sub>/C<sub>4</sub> mixed feeders having intermediate values between the two endmembers. This scheme has been used extensively in both modern (e.g., Cerling and Harris, 1999; Cerling et al., 2004) and fossil settings (e.g., Kingston and Harrison, 2007; Uno et al., 2011). Most recently, Cerling et al. (2015) used a three-component mixture analysis of a large modern ungulate enamel dataset from eastern and central Africa to establish quantitative boundaries between C<sub>3</sub> browsers ( $<-8\%$ ), C<sub>3</sub>/C<sub>4</sub> mixed-feeders ( $>-8\%$  to  $<-1\%$ ) and C<sub>4</sub> grazers ( $>-1\%$ ).

## 2.3. Faunal abundance

The spatial distribution of mammal taxa across modern (Behrensmeyer et al., 1979; Reed, 1997; Western and Behrensmeyer, 2009) and ancient landscapes (Behrensmeyer and Laporte, 1982; Bobe and Eck, 2001; Patterson et al., 2014) can be used to understand habitat heterogeneity better. Certain groups of mammals (particularly ungulates) have habitat-specific requirements for survival (Vrba, 1992). Thus, their presence in a modern or ancient bone assemblage suggests the presence of a particular type of environment. This scheme is complicated by taphonomic processes that can potentially transport skeletal remains away from the habitat associated with the organism in life (Behrensmeyer et al., 2000). However, if taphonomic biases are understood, the distribution of mammals across space in pencontemporaneous fossil deposits can provide novel insights into the nature of the ancient ecosystems.

## 3. Materials and methods

### 3.1. Faunal abundance analyses

At East Turkana, fossiliferous deposits have been divided into discrete spatial units called “Collecting Areas” that are numbered from 1 to 263 (see Brown and Feibel, 1991 for a detailed description). Data for the analysis of faunal abundance in this study came from three main sources: 1) Okote Member mammal fossils assigned to Collecting Areas in the Ileret, Karari and Koobi Fora subregions, which were sourced from the Turkana Basin Paleontology Database (Supplementary Online Material [SOM] Table S1; [http://naturalhistory.si.edu/ete/ETE\\_Datasets\\_Turkana.html](http://naturalhistory.si.edu/ete/ETE_Datasets_Turkana.html)), 2) fossils collected between 2011 and 2015 in association with the Koobi Fora Research and Training Program (Koobi Fora Field School) by the senior author, and 3) fossils from Okote Member archaeological assemblages ( $n = 101$ ) identified in the National Museums of Kenya (NMK) by the senior author. The paleontological samples presented here were collected using a range of collection methods (e.g., surface surveys, targeted sampling, excavation) designed to record the relative representation of taxa in East Turkana fossil deposits as systematically as possible. Fossils with multiple elements assigned to a single specimen number were counted as a single specimen. Specimens were included only if confidently identified to the generic level (i.e., all cf. taxa were removed). The only exception were bovid fossils identified to the tribal level which is more comparable to genus level identifications in non-bovid taxa. The total dataset was taxonomically diverse and consisted of 763 fossils from 14 mammalian families, dominated by material from the Ileret subregion ( $n = 560$ ) with fewer specimens coming from the Karari ( $n = 97$ ) and Koobi Fora ( $n = 106$ ) subregions. To investigate spatial

heterogeneity in the East Turkana mammal community, we compared the proportional abundance of taxa between the Ileret, Karari and Koobi Fora subregions. Because spatial differences in the composition of the East Turkana mammal community could be due to differences in the taphonomy of fossil assemblages in the three regions, we also compared groups of taxa with similar preservation potential (e.g., within bovid tribes and fossils attributed to the genera *Homo*, *Paranthropus* and *Theropithecus*) using a Chi square analysis in R (R Core Team, 2016) to assess the potential impact of taphonomic biases on the overall faunal abundance data.

Ileret and Koobi Fora Okote sediments include more lake margin and delta depositional settings whereas the Karari is dominantly fluvial (Fig. 2). This raises the possibility that subregional variation in taphonomic processes affected burial and preservation, which in turn could influence taxonomic abundances. For example, fluvial reworking of skeletal remains favor preservation of larger and more robust elements, while marginal lacustrine and deltaic environments typically preserve a wider range of skeletal element and body sizes (Boaz and Behrensmeyer, 1986). To control for these potential biases, fossils from groups with similar preservation probabilities (i.e., similar body sizes) were compared across subregions, but the results still indicate that the East Turkana ecosystem was heterogeneous in terms of faunal abundances.

### 3.2. Stable isotopic analyses

**3.2.1. Sample** We report enamel carbon and oxygen isotope values from 155 new fossils sampling a wide range of mammals (bovids, cercopithecids, proboscideans, equids, giraffids, hippopotamids, hominins, and suids) collected in Okote Member sediments at East Turkana. These new data are supplemented with 98 existing samples compiled from the published literature (SOM Table S2; Cerling et al., 1999, 2011, 2013a, 2013b; Harris and Cerling, 2002; Harris et al., 2008) that also sample this period. Table 1 provides a breakdown of the sample by collection context (archaeological, consisting primarily of excavated material, and non-archaeological, predominantly from surface collections), and subregion (Ileret, Karari and Koobi Fora), to facilitate analyses of spatial variation in  $\delta^{13}\text{C}$  values. We include  $\delta^{18}\text{O}$  enamel values for completeness in SOM Table S2 and discuss them with respect to spatial variation, but the primary focus is on the carbon isotope data for all other analyses presented here.

**3.2.2. Analytical methods** All new enamel samples were photographed and then sampled in the NMK with a high-speed rotary drill fitted with a diamond bit. The analyses were conducted at the Department of Earth and Planetary Sciences at Johns Hopkins University. Enamel powder was treated for 15 min with 3%  $\text{H}_2\text{O}_2$  to remove organic material and rinsed three times with distilled water prior to a 15 min treatment with 0.1 M buffered acetic acid

to remove secondary carbonate. Following this treatment, samples were rinsed three times with distilled water and dried overnight at 60 °C. Samples (typically ranging from between 200 and 600  $\mu\text{g}$ ) were then loaded into silver capsules and digested in a 100% phosphoric acid bath at 90 °C for 10 min. Gases produced from the enamel powders were cryogenically cleaned using a custom-built automated system (Passey et al., 2010) and the resulting  $\text{CO}_2$  was analyzed for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  on a Thermo MAT 253 mass spectrometer. An acid fractionation factor of 1.00725 (90 °C) was used for all enamel samples (Passey et al., 2007; this fractionation factor was also used in existing isotopic data referenced in SOM Table S2). Throughout the analyses, Carrara marble, normalized to the carbonate standard NBS-19, was routinely measured as an internal working standard. Additionally, working internal enamel standards, normalized to NBS-19, were routinely measured during analyses to monitor instrument performance.  $\delta^{13}\text{C}$  standard deviation of internal standards was 0.19‰ and 0.15‰ for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , respectively. We assigned  $\delta^{13}\text{C}$  values of our Okote sample to dietary categories modified from those of Cerling et al. (2015). Specifically, we combine  $\text{C}_3$  closed canopy browsers with  $\text{C}_3$  browsers and  $\text{C}_4$  hyper-grazers with  $\text{C}_4$  grazers (see SOM Table S2). We performed all statistical analyses in R.

## 4. Results

### 4.1. Faunal abundance

The taxonomic distribution of mammal fossils is heterogeneous across space during Okote Member times at East Turkana. This patterning could be related to landscape-scale differences in the East Turkana ecosystem, or to differences in the taphonomic context of the three subregions, or a combination of the two. When the Okote Member subregions are pooled (Fig. 3), reduncin bovids are the most abundant taxon, followed by *Theropithecus*, *Metridiochoerus* and *Hippopotamus*. These four taxa make up ~50% of the Okote sample. Fossils attributed to the genus *Paranthropus* make up ~2%, while those attributed to *Homo* also make up ~2% of the Okote sample. With respect to fossil abundance distributions of the three subregions, fossils from the Ileret subregion constitute ~73% of the entire Okote sample and thus dominate fossil abundance distributions for the Okote Member as whole, with reduncin bovids being most abundant followed by *Theropithecus*, *Metridiochoerus* and *Hippopotamus*. In contrast, in the Karari subregion sample, tragelaphin bovids are the most abundant taxon followed by *Metridiochoerus*, alcelaphin bovids and *Hippopotamus*. Unlike the Ileret sample, reduncin bovids are a minor component of the assemblage from the Karari and make up ~1% of the total sample. In all three subregions of East Turkana the genera *Metridiochoerus* and *Hippopotamus* are abundant, making up greater than 13% of the fossil

**Table 1**  
Summary of Okote Member stable isotopic data included in SOM Table S2.<sup>a</sup>

|                                     | $\delta^{13}\text{C}$ |           |          |        | $\delta^{18}\text{O}$ |           |          |        |
|-------------------------------------|-----------------------|-----------|----------|--------|-----------------------|-----------|----------|--------|
|                                     | n                     | Range (‰) | Mean (‰) | SD (‰) | n                     | Range (‰) | Mean (‰) | SD (‰) |
| <b>Sample by collection context</b> |                       |           |          |        |                       |           |          |        |
| Archaeological                      | 54                    | −6.6–1.4  | −1.7     | 2.1    | 54                    | −4.6–4.6  | 0.3      | 2.1    |
| Non-archaeological                  | 199                   | −12.5–2.8 | −1.1     | 2.6    | 147                   | −6.6–5.3  | −0.3     | 2.3    |
| Total sample                        | 253                   | −12.5–2.8 | −1.2     | 2.5    | 201                   | −6.6–5.3  | −0.1     | 2.3    |
| <b>Sample by subregion</b>          |                       |           |          |        |                       |           |          |        |
| Ileret                              | 147                   | −12.5–2.8 | −1.1     | 2.3    | 138                   | −6.6–5.3  | −0.3     | 2.2    |
| Karari                              | 37                    | −6.6–1.4  | −2.3     | 2.2    | 37                    | −4.6–4.6  | 0.4      | 2.4    |
| Koobi Fora                          | 17                    | −3.4–2.4  | −0.1     | 1.4    | 14                    | −5.7–2.9  | 0.4      | 2.7    |

Note that some specimens, although associated with a Collection Area and assigned to Archaeological / Non-archaeological, are not assigned to any of the subregions (Ileret, Karari and Koobi Fora) analyzed for spatial patterns.

<sup>a</sup> SD = standard deviation.

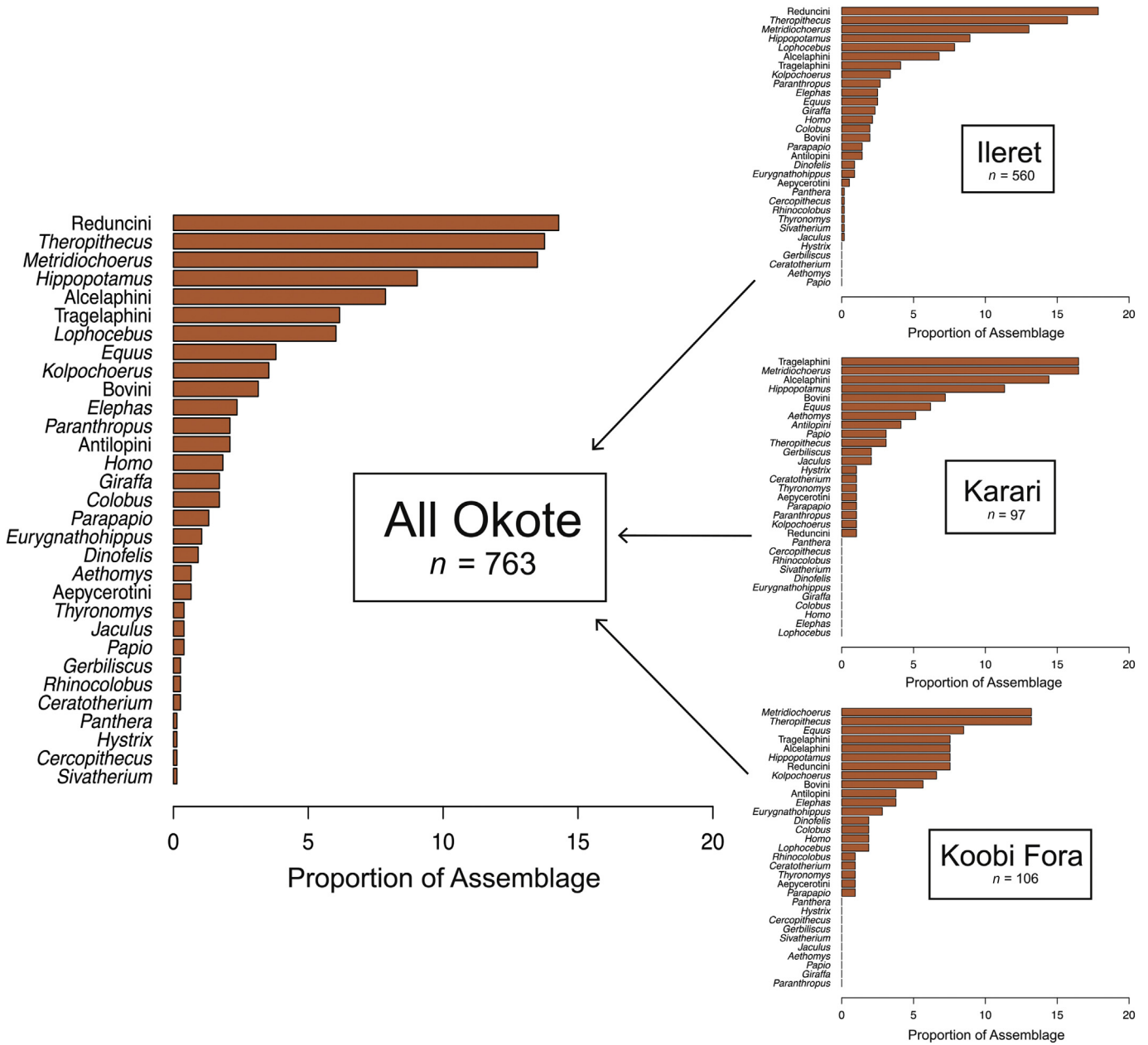


Figure 3. Relative abundance of Okote Member mammal genera and tribes in surface and archaeological fossil assemblages.

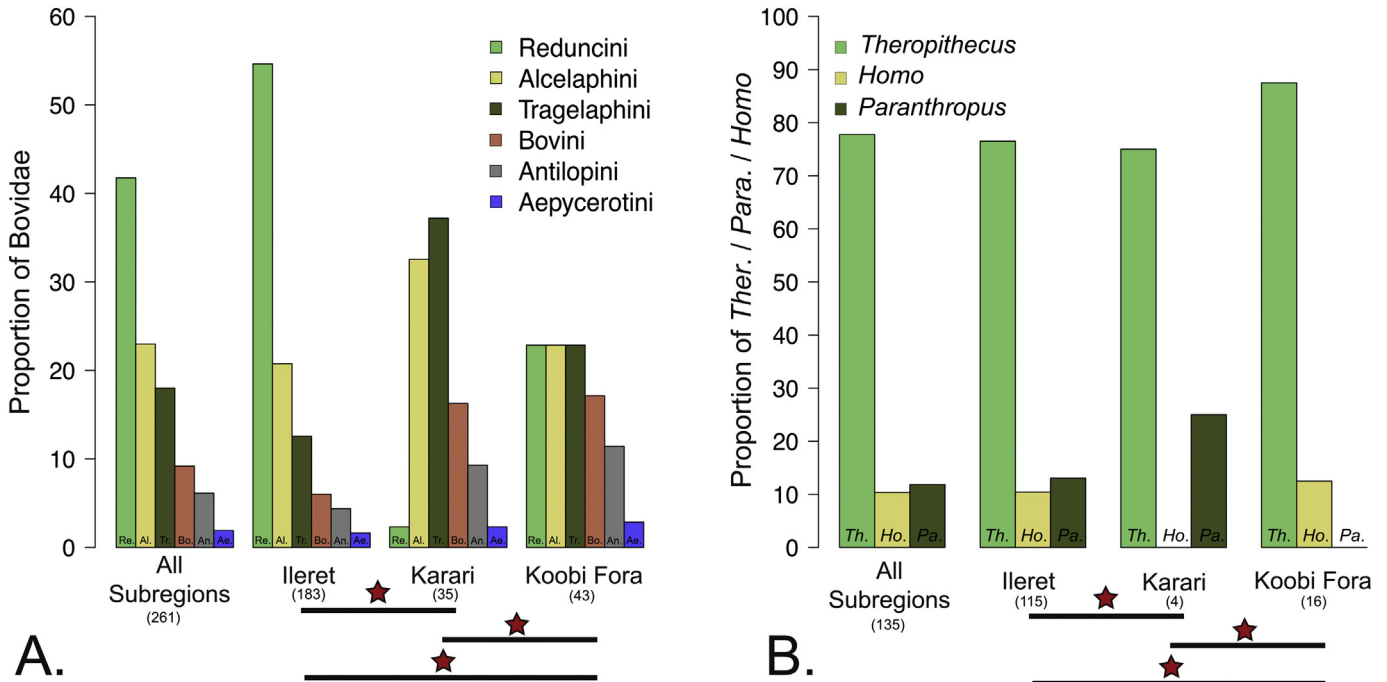
sample in each subregion for the former and greater than 7% for the latter (see Fig. 3). *Theropithecus* fossils are more unevenly distributed, making up more than 13% of the assemblages from Ileret and Koobi Fora subregions, but less than 3% of the sample in the Karari subregion. Fossils from the family Equidae are most abundant in the Koobi Fora subregion and constitute 11% of the total assemblage. Finally, when the fossils attributed to *Homo* and *Paranthropus* are combined they make up ~5% of the Ileret sample and less than 2% of the Koobi Fora and Karari subregions.

When we compared bovid fossils, most of which are from taxa >50 kg in body mass, across subregions, reduncin bovids are more abundant in the Ileret and Koobi Fora subregions relative to the Karari subregion, which was dominated by tragelaphin bovids ( $\chi^2$ ,  $p < 0.05$ ; Fig. 4A). Similar differences were found when the sample was restricted to the large-bodied primates (e.g., *Homo*,

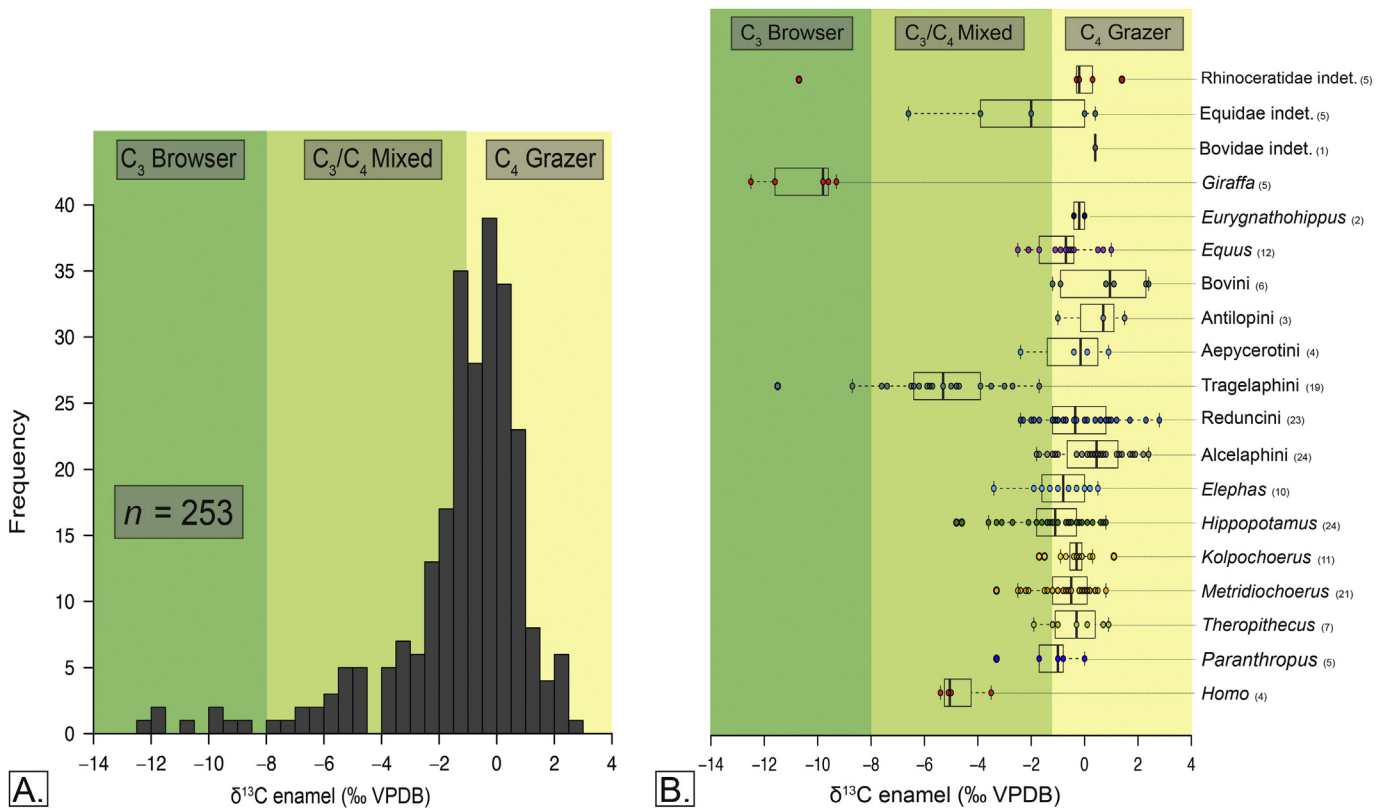
*Paranthropus* and *Theropithecus*) in the three subregions ( $\chi^2$ ,  $p < 0.05$ ; Fig. 4B). In all three subregions, hominin abundances were low relative to those of *Theropithecus*, but it is difficult to assess the influence of sample size on these differences.

#### 4.2. Stable isotopes

**4.2.1. Okote  $\delta^{13}C$  values**  $\delta^{13}C$  values in our Okote Member enamel sample encompass the full spectrum from strictly C<sub>3</sub> to strictly C<sub>4</sub> diets (Fig. 5). In this dataset,  $\delta^{13}C$  values average  $-1.2\text{‰} \pm 2.5\text{‰}$  ( $1\sigma$ ) and range from  $-12.5\text{‰}$  to  $+2.8\text{‰}$  (Table 1), with browsers (e.g., *Giraffa*) yielding lower  $\delta^{13}C$  values than contemporaneous grazers (e.g., *Alcelaphini*, *Equus*, *Hippopotamus*, *Kolpochoerus*, *Metridiochoerus*, *Reduncini*; SOM Table S2). The  $\delta^{13}C$  values from archaeological localities are significantly depleted (Table 2; Fig. 6)



**Figure 4.** Relative abundance of taphonomically similar groups across the Ileret, Karari and Koobi Fora subregions. Sample size presented in parentheses under each subregion. Significant differences ( $\chi^2$ ,  $p < 0.05$ ) denoted with red star. A) comparison of bovid tribe distribution, B) comparison of fossils attributed to *Theropithecus*, *Homo* and *Paranthropus*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Figure 5.** A) Distribution of  $\delta^{13}\text{C}$  values from Okote Member enamel samples; B) Taxonomic distribution of Okote Member  $\delta^{13}\text{C}$  values. Median  $\delta^{13}\text{C}$  values represented by horizontal line within the box, edges of box represent quartile ranges, vertical lines represent the range, outlier values plotted as circles. Raw  $\delta^{13}\text{C}$  data presented as circles superimposed on the box plots. Dietary classifications in both plots based upon Cerling et al. (2015). Sample size for each taxon in parentheses.

**Table 2**  
Statistical comparisons of subsample values (collection context and subregions).<sup>a</sup>

|                              | Carbon   |                 | Oxygen   |                 |
|------------------------------|----------|-----------------|----------|-----------------|
|                              | <i>p</i> | TS              | <i>p</i> | TS              |
| Arch × Non-arch              | 0.02     | W = 4228.5      | 0.13     | W = 4519.5      |
| Ileret × Karari × Koobi Fora | 0.0001   | Chi Sq. = 17.77 | 0.13     | Chi Sq. = 4.095 |
| Ileret × Karari              | 0.0004   | W = 3737        | 0.11     | W = 2115        |
| Ileret × Koobi Fora          | 0.05     | W = 886         | 0.15     | W = 739.5       |
| Karari × Koobi Fora          | 0.0004   | W = 502.5       | 0.7      | W = 278         |

<sup>a</sup> TS = test statistic; Arch = archaeological; Non-arch = non-archaeological.

relative to those from a non-archaeological context, while the  $\delta^{18}\text{O}$  values show no significant differences (Fig. 6; Table 2).  $\delta^{13}\text{C}$  values are significantly different (Fig. 7; Table 2) among the Ileret, Karari and Koobi Fora subregion samples, while the  $\delta^{18}\text{O}$  values show no significant differences (Fig. 7; Table 2). Karari subregion  $\delta^{13}\text{C}$  values overall are significantly depleted relative to those from the Ileret and Koobi Fora subregions (Table 2).

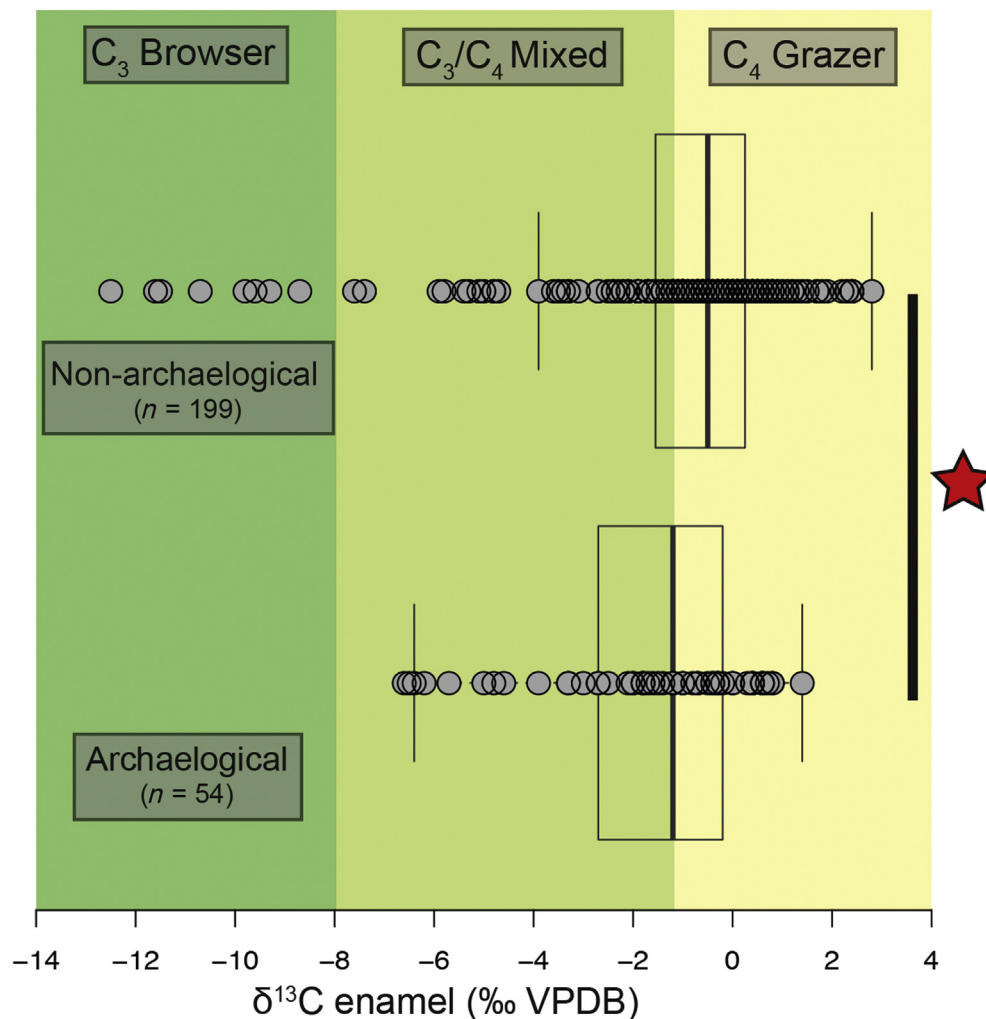
Due to relatively small sample sizes from the Karari and Koobi Fora subregions, taxonomic analyses of spatial variation in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values were limited to the genera *Metridiochoerus* and

*Hippopotamus* and the family Equidae (Fig. 8). These taxon-specific analyses are important given that lumping multiple taxonomic groups into a single assemblage from each of the three subregions could produce spurious patterns related to sampling of the original community. We found that Karari subregion  $\delta^{13}\text{C}$  values in *Metridiochoerus* ( $n = 29$ ;  $p = 0.01$ ; Wilcoxon rank sum test:  $W = 39$ ) and Equidae ( $n = 11$ ;  $p = 0.04$ ; Wilcoxon rank sum test:  $W = 0$ ) are significantly depleted relative to those from the Ileret subregion. *Metridiochoerus*  $\delta^{18}\text{O}$  values are significantly lower ( $n = 13$ ;  $p = 0.01$ ; Wilcoxon rank sum test:  $W = 0$ ) in the Karari relative to those from Koobi Fora, while Equidae  $\delta^{18}\text{O}$  values are significantly lower ( $n = 11$ ;  $p = 0.05$ ; Wilcoxon rank sum test:  $W = 2$ ) in the Karari subregion relative to those from Ileret. *Hippopotamus* shows no significant variation in  $\delta^{18}\text{O}$  across the three areas.

## 5. Discussion

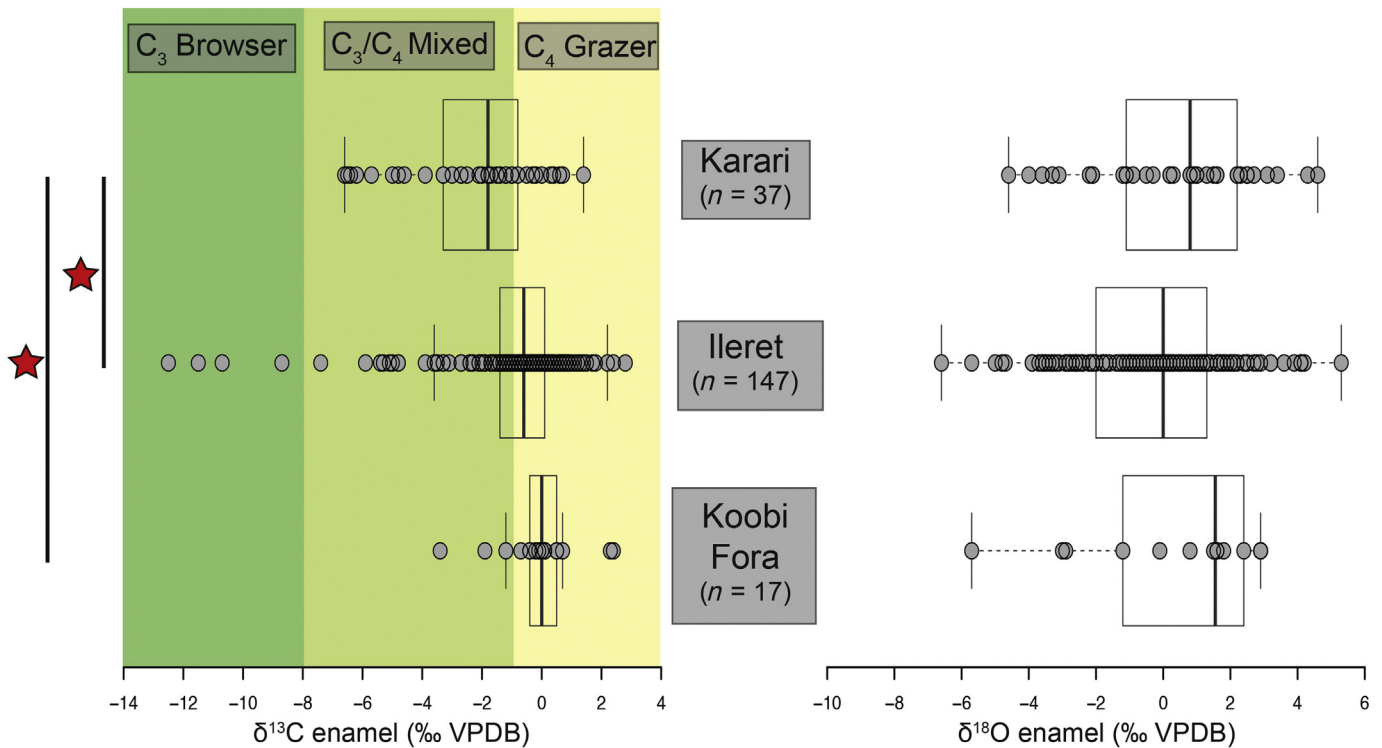
### 5.1. Spatial heterogeneity in the East Turkana mammal community

Our analyses support the hypothesis that the composition of the East Turkana large mammal community varied across the East Turkana landscape during Okote Member times. The overall Okote



**Figure 6.** Comparison of Okote Member non-archaeological and archaeological enamel  $\delta^{13}\text{C}$  values. Median  $\delta^{13}\text{C}$  values represented by horizontal line within the box, edges of box represent quartile ranges, vertical lines represent the range, outlier values plotted as circles. Raw  $\delta^{13}\text{C}$  data presented as circles superimposed on the box plots. Dietary classifications in both plots based upon Cerling et al. (2015). Red star indicates significant difference at  $p < 0.05$  level, Wilcoxon rank sum test. VPDB = Vienna Pee Dee Belemnite. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)





**Figure 7.** Okote Member enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values by East Turkana subregion. Median  $\delta^{13}\text{C}$  values represented by horizontal line within the box, edges of box represent quartile ranges, vertical lines represent the range, outlier values plotted as circles. Raw  $\delta^{13}\text{C}$  data presented as circles superimposed on the box plots. Dietary classifications in both plots based upon Cerling et al. (2015). Red star indicates significant difference at  $p < 0.05$  level, Kruskal-Wallis rank sum test. VPBD = Vienna Pee Dee Belemnite. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sample is dominated by reduncin bovids, but these taxa are unevenly distributed across the East Turkana subregions. Modern reduncins are most often found in marshes and floodplains and are rarely found away from permanent water sources (see Bobe et al., 2007). In combination with the prevalence of  $\text{C}_4$  vegetation in the diet of the individuals sampled here (Fig. 5B), the abundance of reduncin bovids in the Ileret and Koobi Fora subregions suggests the presence of well-watered grasslands. This is consistent with existing geological interpretations that indicate that these regions sample low energy alluvial deltas, lacustrine and shoreline deposits (Brown and Feibel, 1991; Isaac and Behrensmeyer, 1997). These depositional environments likely existed along the shoreline of Paleolake Lorenyang and would have provided abundant marshy grasslands to support sizable populations of reduncins. The prevalence of reduncins in the Ileret subregion contrasts with their low abundance in the Karari subregion. The fossil assemblage from the Karari is dominated by tragelaphin bovids, indicators of the presence of mixed  $\text{C}_3/\text{C}_4$  vegetation, and hypsodont (i.e., high crowned) taxa like *Metridiochoerus* and alcelaphin bovids. This combination of taxa indicates that the Karari region was characterized by a more arid grassland-brushland setting than the well-watered western subregions (i.e., Ileret and Koobi Fora) nearer the central axis of the Turkana Basin.

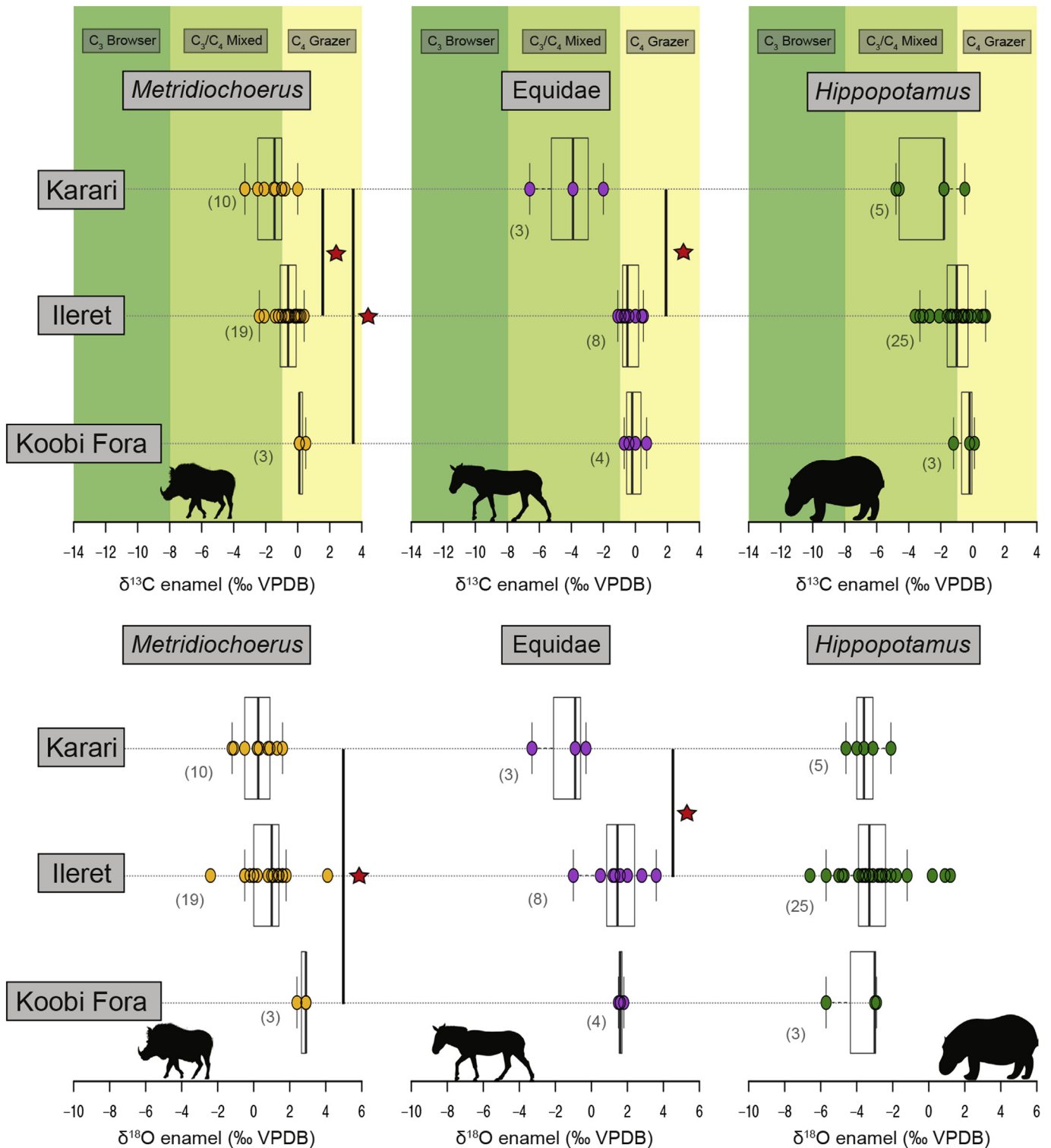
The ubiquity of *Metridiochoerus* across the Ileret, Karari and Koobi Fora subregions is intriguing. Fossils attributed to *Metridiochoerus* from the Okote Member are typically extremely hypsodont, which has been suggested as an adaptation to water-stressed environments (Liu et al., 2009). *Metridiochoerus* fossils, however, make up approximately 13% of both the Ileret and Koobi Fora sample. Sedimentological data as well as the prevalence of reduncin bovids suggest that these areas were well-watered (i.e., a persistently high water table) during the Okote Member

(Behrensmeyer, 1975). This spatial patterning of *Metridiochoerus* fossils could indicate that 1) the taxon's diet was more flexible than indicated by their dental morphology alone, 2) factors other than diet controlled their spatial distribution, 3) semi-arid grassland environments also occurred in the Ileret and Koobi Fora subregions, 4) *Metridiochoerus* dental elements are more taphonomically durable and thus there is a taphonomic bias towards their preservation. As these specimens are also easily identifiable relative to those from other Okote Member mammals this may represent a further collection bias. A combination of these different factors could explain this patterning, and further studies are needed to tease out their relative contribution to the abundance pattern of *Metridiochoerus*.

## 5.2. Isotopic evidence of East Turkana paleoenvironments

### 5.2.1. Diet in the East Turkana mammal community

Our enamel sample indicates that  $\text{C}_4$  grazing taxa were the most prominent component of the East Turkana mammal community during Okote Member times. This finding is consistent with the contemporaneous carbon isotope record from Turkana Basin paleosol carbonates that indicate a paleolandscape dominated by  $\text{C}_4$  vegetation, particularly in floodplain settings (Levin et al., 2011). However, 40% of our  $\delta^{13}\text{C}$  enamel sample is composed of  $\text{C}_3/\text{C}_4$  mixed feeding taxa, which suggests that the vegetation community of East Turkana included a significant quantity of  $\text{C}_3$  plants. Previous work indicates that due to their specific environmental requirements for formation and preservation, paleosol carbonates may not capture the full range of  $\delta^{13}\text{C}$  variation in vegetation on a paleolandscape (Levin et al., 2004), so it is possible that the paleosol carbonate record underestimates the frequency of  $\text{C}_3$  environments. Our enamel



**Figure 8.** *Metridiochoerus*, Equidae and *Hippopotamus*  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values by East Turkana subregion. Median  $\delta^{13}\text{C}$  values represented by horizontal line within the box, edges of box represent quartile ranges, vertical lines represent the range, outlier values plotted as circles. Raw  $\delta^{13}\text{C}$  data presented as circles superimposed on the box plots. Dietary classifications in both plots based upon [Cerling et al. \(2015\)](#). Red star indicates significant difference at  $p < 0.05$  level, Wilcoxon rank sum test. Sample sizes in parentheses. VPBD = Vienna Pee Dee Belemnite. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sample reflects a wide range of dietary adaptations, which suggests a broader range of  $\delta^{13}\text{C}$  variation in the Okote Member plant community. This interpretation depends on how accurately the enamel sample records the proportions of grazing, mixed feeding, and browsing taxa in the original East

Turkana mammal community. Given that teeth are relatively durable elements across all large mammal taxa, it is unlikely that there are significant taphonomic biases for or against the three dietary categories. Additional sampling and taphonomic analysis of the East Turkana mammal community, as well as

further analysis of the paleosol carbonate record, are needed to fully evaluate potential disparities in these paleoecological proxies.

**5.2.2. Spatial variation in East Turkana  $\delta^{13}\text{C}$  values**  $\delta^{13}\text{C}$  values from fossil herbivores in the Ileret, Koobi Fora and Karari subregions at East Turkana suggest a heterogeneous distribution of vegetation across space during Okote Member times (Fig. 7). For the overall samples,  $\delta^{13}\text{C}$  values from the Karari sample are significantly depleted relative to those from the Ileret and Koobi Fora subregions, indicating more  $\text{C}_3$  vegetation in the Karari subregion. This pattern potentially could relate to differential preservation and sampling of mixed feeders and browsers relative to grazers in the Karari mammal community. However, where it is possible to sample individuals belonging to the same taxa, (i.e., *Metridiochoerus* and Equidae) these taxa have significantly lower  $\delta^{13}\text{C}$  values in the Karari subregion relative to the Ileret and Koobi Fora subregions (Fig. 8). This is consistent with the hypothesis that spatial variation in vegetation influenced herbivore distribution in the different subregions.

We recognize two scenarios that could explain the elevated quantity of  $\text{C}_3$  vegetation in the Karari subregion. First, geologic evidence indicates that much of the Karari landscape was composed of fluvial environments draining the eastern basin margin (Feibel, 1988). These types of depositional environments possess abundant  $\text{C}_3$  vegetation around river channels and  $\text{C}_4$  grasses in adjacent flood plains (Levin et al., 2004). Areas adjacent to water courses are also more likely to preserve fossils due to rapid sedimentation rates (Behrensmeyer, 1982). It is important to consider that  $\text{C}_3$ -indicative  $\delta^{13}\text{C}$  values do not necessarily correspond to an abundance of trees, as such  $\delta^{13}\text{C}$  values in the Karari subregion are also consistent with the presence of arid-adapted shrubs. The presence of this type of vegetation in the Karari may be expected given the prevalence of arid-adapted taxa like *Metridiochoerus* and alcelaphin bovids. We propose that  $\text{C}_3$  vegetation associated with the combination of wooded river-proximal settings and bushland-shrubland environments is a viable explanation for the overall  $\delta^{13}\text{C}$  depletion in the Karari enamel sample. These findings are consistent with the paleosol carbonate  $\delta^{13}\text{C}$  values of Quinn et al. (2013) that indicate archeological localities in the Karari subregion frequently occur in habitats interpreted as bushland environments with elevated quantities of  $\text{C}_3$  vegetation relative to other portions of the East Turkana paleolandscape. Although our findings indicate that the localities analyzed by Quinn et al. (2013) occurred in environments with  $\text{C}_3$  vegetation, hominins in the Karari subregion butchered taxa with both  $\text{C}_3$ - and  $\text{C}_4$ -dominated diets.

Depleted  $\delta^{18}\text{O}$  values in *Metridiochoerus* and Equidae could indicate these taxa were more water dependent in the Karari subregion. However, given the complex environmental and behavioral influences on the  $\delta^{18}\text{O}$  signal in enamel (Sponheimer and Lee-Thorp, 1999), particularly in obligate drinking taxa such as suids and equids, the underlying biological factors contributing to these patterns are difficult to interpret. Due to their semi-aquatic habitat, *Hippopotamus* oxygen isotope values are frequently used as an indicator of source water for a particular region (Levin et al., 2006; Cerling et al., 2008). Although sample sizes are particularly small from the Karari and Koobi Fora subregions, *Hippopotamus*  $\delta^{18}\text{O}$  values in our sample are not spatially distinct at East Turkana (Fig. 8). These data could indicate that these subregions had similar water input and similar environmental aridity, which is inconsistent with our hypothesis of increased environmental aridity in the Karari subregion relative to that of Ileret and Koobi Fora. Additional *Hippopotamus* enamel isotopic data are needed to evaluate this trend.

### 5.3. Spatial variation in the East Turkana ecosystem

The combination of faunal abundance and stable carbon isotope data provides novel insights into ecosystem variability during Okote Member times at East Turkana. In the Ileret subregion, our analyses show a prevalence of reduncin bovids, which is consistent with independent evidence of  $\text{C}_4$  vegetation from pedogenic carbonates from East Turkana during this same period. This combination indicates moist, open  $\text{C}_4$  grasslands and serves as a cautionary tale to interpretations that link the spread of  $\text{C}_4$  grasslands in eastern Africa with increased environmental aridity (deMenocal, 2004; Sepulchre et al., 2006; Maslin et al., 2014; see Levin, 2015 for summary). Specifically, moist grassland environments, like those indicated for the Okote Member in the Ileret subregion, are characterized by virtually identical  $\delta^{13}\text{C}$  distributions as those of more arid-adapted grasslands. Thus, this study demonstrates that when interpreting variation in local paleoecosystems, it is important to draw upon both carbon isotope and faunal abundance data as well as contextual evidence from sedimentary environments.

The carbon isotope data indicate that the Karari ecosystem had more  $\text{C}_3$  vegetation than the Ileret and Koobi Fora subregions. We propose that this pattern was driven by a combination of  $\text{C}_3$  vegetation adjacent to fluvial settings and arid-adapted shrubland vegetation lateral to floodplain environments. This hypothesis is supported by the lack of reduncin bovids in the Karari, combined with the dominance of tragelaphin and alcelaphin bovids. These data, particularly the low numbers of reduncin bovids, suggest that moisture availability that would sustain moist/edaphic grasslands in the Karari subregion was significantly reduced relative to areas that were closer to the central axis of the Turkana Basin. This could be explained by differences in physical geography. The modern Karari subregion is approximately 300 m higher in elevation than the Ileret and Koobi Fora subregions. Although this difference in elevation was almost certainly different in the past, paleoenvironmental reconstructions indicate that the Karari ecosystem was dominated by a fluvial sedimentary regime, while Ileret and Koobi Fora were characterized by lacustrine and shoreline environments with frequent standing water. Thus, water to support moist  $\text{C}_4$  grasslands and reduncin bovids was less overall, and likely linked to seasonal drainage of the eastern basin margin in the Karari subregion compared to regions closer to lacustrine environments (i.e., Ileret and Koobi Fora) and a more persistently high water table nearer the rift axis.

### 5.4. Temporal variation in the East Turkana ecosystem

It is possible, and plausible, that some of the subregional environmental variation we describe here is related to temporal (rather than spatial) differences in the fossil assemblages collected from the Ileret, Koobi Fora and Karari subregions. East Turkana depositional environments were dynamic during the Okote Member and although these assemblages are broadly contemporaneous, collections from each subregion could reflect slightly different periods of ecosystem evolution between 1.56 and 1.38 Ma (Fig. 2). In particular, the fossiliferous portions of the strata in the three subregions represent variable sampling of the paleocommunities over time. There is also mixing of fluvial and lake margin source deposits at Ileret and Koobi Fora compared with only fluvial channel and floodplain source deposits in the Karari subregion.

Our stratigraphic interpretation of the temporal relationship between the three subregions (Fig. 2) indicates that most fossils from the Koobi Fora subregion are slightly younger than those collected from Ileret, while assemblages from the Karari subregion span the entire interval represented at Ileret and Koobi Fora. Our

documentation of prevalent C<sub>3</sub> vegetation in the Karari subregion is supported by the paleosol carbonate record from East Turkana from this period. The work of Quinn et al. (2013) indicates that hominin sites yielding lithic artifacts dating to the Okote Member occurred in the more wooded portions of the East Turkana landscape. All six localities included in the analysis of Quinn et al. (2013) were derived from the Karari subregion sediments. Paleosol carbonates can potentially take 10<sup>2</sup>–10<sup>5</sup> years to form (Jenny, 1980; Machette, 1985; Retallack, 2005) therefore their isotopic signature represents a much longer temporal interval than that represented by the enamel of a terrestrial mammal (i.e., a single lifetime). The Karari subregion data indicate the prevalence of C<sub>3</sub> vegetation (~40–50% of the vegetation community; Quinn et al., 2013) during the same interval sampled by our enamel isotope assemblage, supporting the persistence of C<sub>3</sub> vegetation in that region throughout the Okote Member.

### 5.5. Implications for hominin paleobiology

Hominin remains make up approximately 4% of the fossil mammal assemblage from the Okote Member at East Turkana (Fig. 3). Previous work in the Shungura Formation of southern Ethiopia indicates that hominins were uncommon components of Plio-Pleistocene mammal communities (i.e., <1%; see Bobe and Leakey, 2009). There are several possible explanations for their slightly elevated prevalence in our fossil sample. First, depositional environments in the Shungura Formation are primarily fluvial (de Heinzelin et al., 1976) and as a result hominin remains are dominated by isolated dental elements (Wood and Leakey, 2011). The East Turkana record samples low energy depositional environments that often preserve more fragile skeletal elements such as complete crania (Wood, 1991; Leakey et al., 2012). Second, fossil collecting at East Turkana over the past five decades has emphasized the collection of hominin remains, whereas the strategies employed in the Shungura Formation have involved more systematic techniques for sampling the fossil mammal community (Bobe and Eck, 2001; Alemseged, 2003). The possibility remains, however, that the East Turkana ecosystem, and the resources available within it, were more attractive to hominins during this period and their elevated abundance could be a genuine ecological signal. Further systematic investigations are needed to evaluate the combination of taphonomic and ecological factors responsible for the different abundance of hominin remains across different parts of the Turkana Basin during this period.

The  $\delta^{13}\text{C}$  values from fauna preserved in Okote Member archaeological localities are significantly depleted relative to those from non-archaeological contexts (Fig. 6). This is consistent with the hypothesis that hominins consumed a greater proportion of particular types of organisms, specifically C<sub>3</sub>/C<sub>4</sub> mixed feeding taxa, from within the larger East Turkana mammal community. This could simply reflect the fact that most of the archaeological sites are in the Karari subregion, where mixed feeding taxa were more common than in the other two subregions. The majority of non-archaeological  $\delta^{13}\text{C}$  values are derived from the Ileret and Koobi Fora subregions and include more C<sub>4</sub>-feeding taxa. Thus, although it is also possible that hominins were selectively consuming mixed-feeding taxa, we cannot at present distinguish this from landscape-scale sampling differences between the archaeological and non-archaeological  $\delta^{13}\text{C}$  values.

Finally, research suggests that the time period represented by the Okote Member documents substantial changes in the way that hominins used lithic resources across the broader paleolandscape. Rogers et al. (1994) indicate that Okote Member hominins used a broader range of depositional settings for the manufacture of stone tools than in the KBS Member at East Turkana. A behavioral

transition is also supported by the work of Braun et al. (2009), which shows that during the Okote Member hominins utilized a different set of raw material sources for the manufacture of stone artifacts. Although depositional setting and raw material availability influenced the distribution of lithic artifact manufacture and discard, the results of the research presented here suggests also that differences in the distribution of large mammals and paleovegetation, reflecting a heterogeneous paleolandscape in East Turkana, offered hominins a range of habitats and tool-assisted foraging opportunities.

### 5.6. Future directions

Although this study indicates several intriguing patterns related to ecosystem variability and hominin behavior at East Turkana during Okote Member times, future studies should focus on 1) increasing systematic faunal collections in the Karari and Koobi Fora subregions, with careful documentation of the source lithofacies (e.g., fluvial channel, floodplain, delta or lake margin), 2) testing our hypotheses related to spatial variation in vegetation with other paleoenvironmental proxies, and finally 3) establishing robust connections between the hominin behavioral record and ecosystem heterogeneity. Our data indicate differences in the distribution of mammals across the Okote Member landscape at East Turkana. Faunal samples from the Koobi Fora and Karari subregions, however, are limited relative to those from the Ileret subregion. It is imperative to test further the impact of sample size on our interpretations of spatial heterogeneity in the East Turkana mammal community. The differences in spatial heterogeneity that we interpret as ecologically likely are affected to some extent by depositional and taphonomic (e.g., collection biases) disparities between the Ileret, Karari and Koobi Fora subregions which could be tested with additional carefully controlled faunal sampling. The currently available samples show depleted  $\delta^{13}\text{C}$  values in the Karari sample and are indicative of more C<sub>3</sub> vegetation in that subregion relative to the Ileret and Koobi Fora subregions. We hypothesize that this pattern is related to the combination of woody vegetation in delimited fluvial settings as well as arid-adapted bushlands adjacent to these floodplains. Our hypotheses should be tested with other paleovegetation proxies such as isotopic data from paleosol carbonates and plant waxes (Uno et al., 2016a, 2016b). This research adds to previous studies proposing spatial variation in hominin behavior and ecology during Okote Member times (Rogers et al., 1994; Quinn et al., 2013). These patterns should be placed within the context of the ecosystem heterogeneity described here to understand better how ecological factors contributed to the spatial distribution of the hominin behavioral record.

## 6. Conclusion

Understanding how paleoecosystems vary across space is crucial to testing hypotheses related to hominin ecology and behavior (Blumenshine and Peters, 1998). Okote Member deposits at East Turkana in northern Kenya present the rare opportunity to construct a spatially resolved ecological context for testing hypotheses relating to hominin adaptation. Based upon the combination of faunal abundance and stable isotopic data, our findings indicate that 1) taxa within the East Turkana mammal community were distributed heterogeneously across space, 2) subregions closer in proximity to the Basin axis (i.e., Ileret and Koobi Fora) had more C<sub>4</sub> vegetation based on faunal abundance and stable isotopic evidence, and 3) the Karari subregion, which has abundant evidence of hominin stone tool manufacture and discard, had significantly more C<sub>3</sub> vegetation than the Ileret and Koobi Fora subregions, although the exact nature of the vegetation in this area is still an open question. These lines of

evidence indicate that during the Okote Member the East Turkana ecosystem was highly variable across space. This setting would have undoubtedly contributed to the ecological pressures experienced by hominins during this period and could have been a primary factor in shaping the disparate evolutionary trajectories of the genera *Homo* and *Paranthropus*.

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### Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.06.007>.

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