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Pedogenic carbonate stable isotopic evidence for wooded habitat preference of early Pleistocene tool makers in the Turkana Basin

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ABSTRACT

The origin and evolution of early Pleistocene hominin lithic technologies in Africa occurred within the context of savanna grassland ecosystems. The Nachukui Formation of the Turkana Basin in northern Kenya, containing Oldowan and Acheulean tool assemblages and fossil evidence for early members of *Homo* and *Paranthropus*, provides an extensive spatial and temporal paleosol record of early Pleistocene savanna flora. Here we present new carbon isotopic ($\delta^{13}C_{VPDB}$) values of pedogenic carbonates (68 nodules, 193 analyses) from the Nachukui Formation in order to characterize past vegetation structure and change through time. We compared three members (Kalochoro, Kaitio, and Natoo) at five locations spanning 2.4–1.4 Ma and sampled in proximity to hominin archaeological and paleontological sites. Our results indicate diverse habitats showing a mosaic pattern of vegetation cover at each location yet demonstrate grassland expansion through time influenced by paleogeography. Kalochoro floodplains occurred adjacent to large river systems, and paleosols show evidence of C_3 woodlands averaging 46–50% woody cover. Kaitio habitats were located along smaller rivers and lake margins. Paleosols yielded evidence for reduced portions of woody vegetation averaging 34–37% woody cover. Natoo environments had the highest percentage of grasslands averaging 21% woody cover near a diminishing Lake Turkana precursor. We also compared paleosol $\delta^{13}C_{VPDB}$ values of lithic archaeological sites with paleosol $\delta^{13}C_{VPDB}$ values of all environments available to hominins at 2.4–1.4 Ma in the Nachukui and Koobi Fora Formations. Grassy environments became more widespread during this interval; woody canopy cover mean percentages steadily decreased by 12%. However, significantly more wooded savanna habitats were present in the vicinity of lithic archaeological sites and did not mirror the basin-wide trend of grassland spread. Hominin lithic archaeological sites consistently demonstrated woody cover circa 40% throughout our study interval and were 4–12% more woody than coeval basin environs. We propose that Turkana Basin early tool makers may have preferred a more wooded portion of the savanna ecosystem to reduce heat stress and to gain differential access to potable water, raw materials, animal carcasses, and edible plants.

Introduction

Grassland expansion underpins many environmentally-based hypotheses of human evolution (Brain, 1981; Vrba, 1985, 1995, 1999; Stanley, 1992; deMenocal, 1995, 2004). The origins of the genus *Homo* have long been associated with increasingly more animal products in the diet (Shipman and Walker, 1989; Aiello and Wheeler, 1995), in part, potentially influenced by the biomass transition from plant to animal species with grassland expansion (Bromage and Schrenk, 1995; Leonard and Robertson, 2000; Antón et al., 2002). Scavenging activities of early Pleistocene hominins and increasing abundances of grazing prey have been associated with the rise and increased reliance on lithic technologies (Bunn, 1981, 1994; Potts and Shipman, 1981; Bunn and Kroll, 1986;

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Blumenschine and Selvaggio, 1988; de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005; Pobiner et al., 2008; Braun et al., 2010), although alternative uses of stone tools to process vegetation have been proposed (Keeley and Toth, 1981; Brain, 1985; Schick and Toth, 1993; Toth, 1997; Dominguez-Rodrigo et al., 2001; Hardy et al., 2001; Goren-Inbar et al., 2002; Panger et al., 2002).

Several researchers have demonstrated grassland expansion in Plio-Pleistocene East Africa (Cerling et al., 1988; Cerling, 1992; Bobe and Behrensmeyer, 2004; Levin et al., 2004, 2011; Wynn, 2004; Fernandez and Vrba, 2006; Quinn et al., 2007; Bobe and Leakey, 2009). Recently, all East African hominin-bearing localities spanning the last six million years have been reconstructed with a majority of habitats indicating less than 40% fraction woody canopy cover (Cerling et al., 2011b). This suggests that grassland environments were an important component to the hominin ecological niche, and moreover, that the savanna hypothesis remains a viable selective explanation for evolution of the human lineage (Cerling et al., 2010), perhaps especially of the genus *Homo* (Bobe and Behrensmeyer, 2004). Members of the genus *Homo* have been shown to thrive in diverse habitats (review in Wood and Strait, 2004). Interpretations of early Pleistocene tool-making hominin habitat preference span substantially wooded areas and open grasslands based on environmental reconstructions at hominin paleontological and archaeological localities (e.g., Rogers et al., 1994; Sikes, 1994, 1999; Isaac and Behrensmeyer, 1997; Reed, 1997; Potts et al., 1999; Sikes et al., 1999; Brugal et al., 2003; Plummer et al., 2009).

Preservational biases, however, potentially confound differentiation of primary depositional environments of skeletal and dental elements representing habitat preference(s) in life from secondary deposition in potentially non-preferred environments. For example, in many of the Plio-Pleistocene Turkana Basin paleolandscapes, past and present hydrological systems have reworked and redeposited fossil material some distance from the original source (Feibel, 2011b), potentially resulting in significant time-averaging (e.g., Behrensmeyer and Kidwell, 1985; Behrensmeyer, 1991; Kidwell and Behrensmeyer, 1993). Discoveries of relatively complete skeletons provide rare evidence for little to no reworking (e.g., KNM-WT 15000, KNM-ER 1808). Lithic assemblages are susceptible to similar hydrological redeposition forming palimpsets that encapsulate 10^3–10^4 years (Stern, 1993, 1994). However, through lithic refitting, relative abundances across paleogeography and burial in fine-grained sediments, numerous archaeological sites in the Turkana Basin have been demonstrated to be in primary contexts and thus meaningful to reconstructing aspects of hominin behavioral ecology (Isaac, 1978, 1980, 1981, 1986, 1997; Bunn et al., 1980; Shick, 1987; Bunn, 1994; Kroll, 1994; Rogers et al., 1994; Roche et al., 1999, 2003; Delagnes and Roche, 2005).

In an effort to link hominins to specific habitats and test for potential habitat preference, we reconstruct structural categories of African vegetation by estimating fraction woody canopy cover (f_{wc}) from $\delta^{13}C_{VPDB}$ values of paleosol carbonates (after methods of Cerling et al., 2011b) adjacent to West Turkana archaeological and paleontological sites preserving Oldowan and Acheulean technologies and encompassing the fossil evidence of early *Homo* and *Paranthropus* from sedimentary sequences dated between 2.4 and 1.4 Ma (millions of years ago). We also compare vegetation structure derived from paleosol $\delta^{13}C_{VPDB}$ values and estimated f_{wc} at lithic archaeological sites preserved in the Koobi Fora and Nachukui Formations (data from Quinn et al., 2007; Levin et al., 2011; this study) with those of all environments present throughout the Turkana Basin during the rise of early Pleistocene tool makers (2.4–1.4 Ma) (data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011).

Paleogeographic and paleoenvironmental setting

The Turkana Basin of northern Kenya and southern Ethiopia (Figs. 1 and 2a) lies within the eastern branch of the East African Rift System between the Kenyan and Ethiopian plateaus (Ebinger et al., 2000; Pik, 2011). The basin presently contains one of the largest rift lakes, Lake Turkana, with an area of 7500 km^2 (Frostick, 1997). Today, this is a saline-alkaline and closed-basin lake that receives over 90% of its water from rainfall over the Ethiopian Highlands, via the Omo River, with minor inputs from the Turkwell and Kerio river systems (Yuretich, 1979). However, during the early Pleistocene the basin was a dynamic landscape containing large meander belts, lakes of varying sizes, and alternating open- and closed-hydrological systems (Fig. 2b–f). At the start of our sample interval (~2.4–2.2 Ma), there was likely no lake present in the basin, although a small, rather short-lived lake was present on the west side from 2.39 to 2.35 Ma (Feibel et al., 1991; Feibel, 1997, 2011a). For the majority of the interval, the large meander belt of the Omo River flowed through the region. Within the interval 2.2–2.0 Ma, a large Lake Lorenyang fed by the Omo River and basin margin rivers was present (Feibel et al., 1991; Feibel, 1997, 2011a). Notably during this interval, there is a depositional hiatus on the east side (Brown and Feibel, 1991). At 2.0–1.8 Ma lobes of the Omo delta migrated through the region near the present-day Koobi Fora spit, and the Omo River extended through the Il Dura and Karari regions on the east side of the basin (Feibel et al., 1991; Feibel, 1997). During this interval, Lake Lorenyang was slightly smaller than at 2.2–2.0 Ma (Feibel, 1997) and was connected to the Indian Ocean via the Turkana River (Feibel, 1993). During the interval from 1.8 to 1.6 Ma, Lake Lorenyang had an open-basin configuration and maintained its connection to the Indian Ocean via the Turkana River (Feibel, 1993, 2011a). At this time, lake levels fluctuated potentially due to climatic forcing (Lepre et al., 2007). The Omo delta was likely located near its present-day position in the northern part of the basin; marginal river systems were present along the east and west lake shores (Feibel et al., 1991). At 1.6–1.4 Ma, the Lake Turkana precursor was relatively small or absent from the basin and continued to be connected to the Indian Ocean via the Turkana

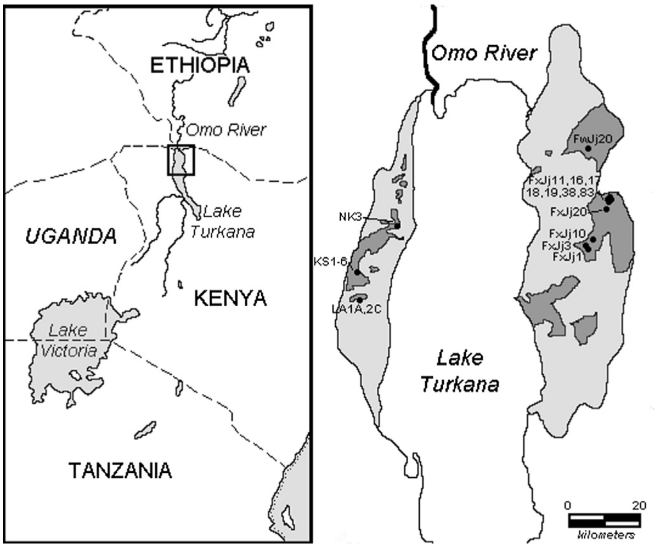

Figure 1. Left: location map of the Turkana Basin in northern Kenya, East Africa; right: map of Nachukui and Koobi Fora Formations in the Turkana Basin. Shaded areas denote collecting locations of all sampled paleosols for isotopic analysis in the basin (data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study). Dots show locations of paleosols sampled for isotopic analysis at lithic sites (data from Quinn et al., 2007; Levin et al., 2011; this study).

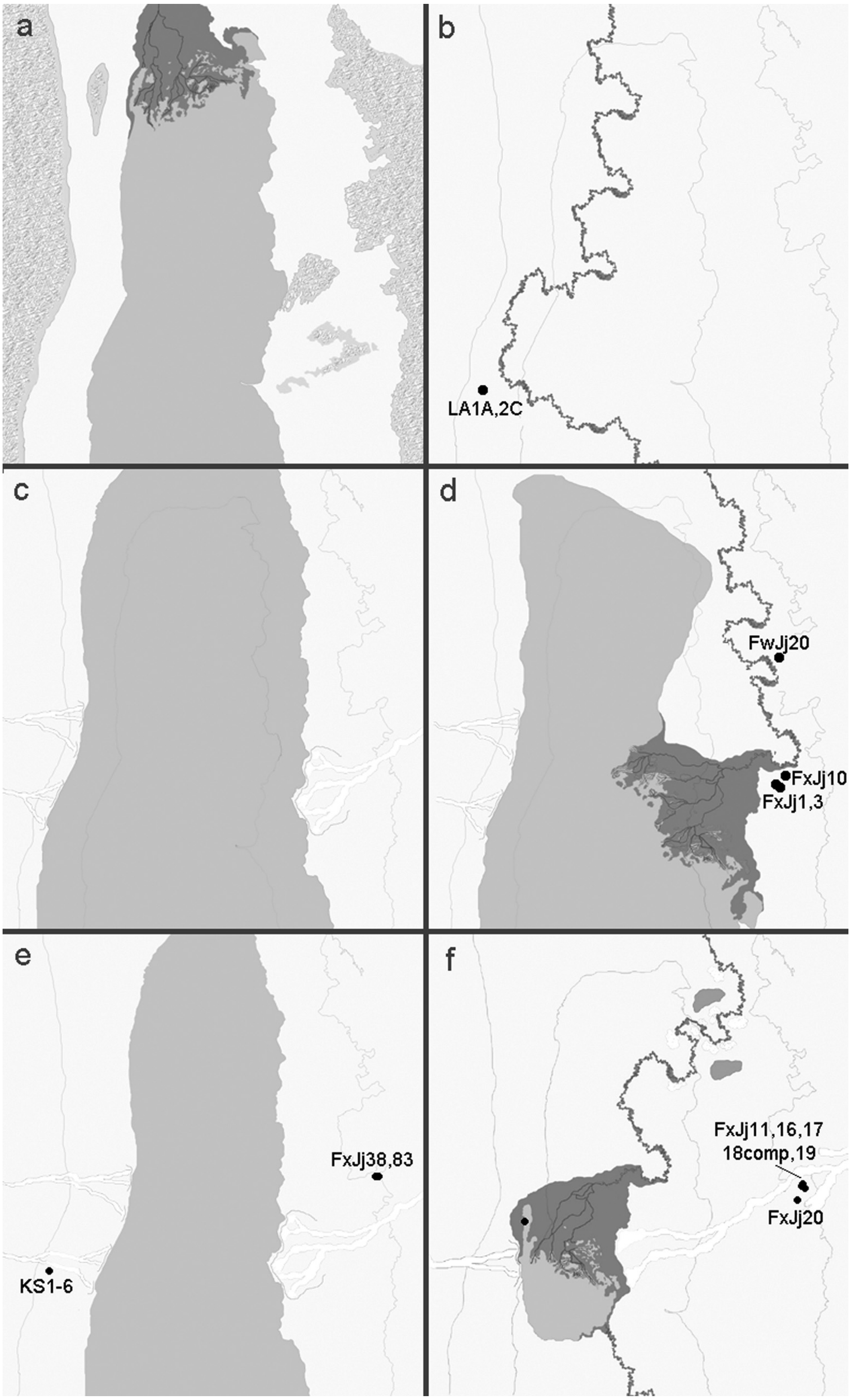

Figure 2. Paleogeographic reconstructions of the Turkana Basin across five temporal intervals (a: present day; b: 2.4–2.2 Ma; c: 2.2–2.0 Ma; d: 2.0–1.8 Ma; e: 1.8–1.6 Ma; f: 1.6–1.4 Ma). Dots denote locations of paleosols sampled for isotopic analysis at lithic sites in corresponding time period and paleogeographic setting [b: LA1A, LA2C (this study); c: no sites present/analyzed; d: FwJj20 (Quinn et al., 2007; Levin et al., 2011); FxJj1, FxJj3, FxJj10 (Quinn et al., 2007); e: KS1-6 (this study); FxJj38 (Quinn et al., 2007); FxJj83 (Quinn et al., 2007; Levin et al., 2011); f: FxJj 11, FxJj16, FxJj17, FxJj18 complex, FxJj19, FxJj20 (Quinn et al., 2007)].

River (Feibel, 1993, 2011a). Floodplain landscapes along distributaries of the Omo River show evidence of crevasse splays (Quinn et al., 2007).

The Nachukui Formation lies along the western margin of modern Lake Turkana and spans portions of the Plio-Pleistocene from 4.1 to 1.2 Ma (Harris et al., 1988). It is the temporal complement of the Koobi Fora Formation located on the east side of Lake Turkana (Brown et al., 1985a; Brown and Feibel, 1986, 1991) and the Shungura Formation to the north in the Omo River Valley (Brown et al., 1985a; de Heinzelin, 1983). An established geochronological framework affords temporal comparisons of past environments within and between formations in the basin (Feibel et al., 1989; Brown et al., 2006; McDougall and Brown, 2006, 2008; Feibel et al., 2009; Lepre and Kent, 2010; Lepre et al., 2011). Our new paleosol $\delta^{13}C_{VPDB}$ data presented here were sampled at five locations from three members in the Nachukui Formation: the Kalochoro, Kaitio, and Natoo Members.

The Kalochoro Member is bounded by the Kalochoro and KBS Tuffs (2.33–1.87 Ma) (Harris et al., 1988; McDougall et al., 2012) and contains at its base the Lokalalei site complex (Roche et al., 1999; Brown and Gathogo, 2002; Tiercelin et al., 2010), which has provided fossil and lithic evidence for earliest *Homo* and Oldowan technologies in the Turkana Basin (Kibunjia et al., 1992; Kibunjia, 1994; Roche et al., 1999, 2003, Brugal et al., 2003; Prat et al., 2005; Delagnes and Roche, 2005; Harmand, 2005, 2007, 2009b). Lokalalei site complex paleosols (Fig. 3a) are well-developed, thick vertisols with preserved B_K horizons occupying the proximal floodplain of the axial, meandering Omo River with adjacent marginal systems (Roche et al., 1999). Faunal remains indicate woodlands and grasslands including grazing mammals (*Hipparion ethiopicum*, *Equus* sp., and diverse body-sized bovids as alcelaphines, antilopines), mixed feeders (Reduncini, suids), browsers (*Elephas recki*, *Deinotherium*, giraffids) and different species of primate (cercopithecids, *Galago* sp.); aquatic fauna indicating large axial and marginal river systems include siluriforms and *Crocodylus* sp. (Roche et al., 1999; Brugal et al., 2003). The Lokalalei site complex represents tool making and shows evidence of food processing (LA1). At Lokalalei 2C, the level of knapping skill according to raw material properties has been interpreted to indicate unusually organized core reduction patterns compared with other early Pleistocene sites (Roche et al., 1999; Delagnes and Roche, 2005; Harmand, 2009a). Proximity of terrestrial tortoise remains and ostrich eggshell fragments are reportedly in close association with lithic artifacts and may represent to some extent food selection/acquisition (Roche et al., 1999; Brugal et al., 2003).

The Kaitio Member, defined by the KBS and Lower Koobi Fora Tuffs (1.87–1.48 Ma) (Harris et al., 1988; McDougall et al., 2012), includes the Kokiselei site complex (Kibunjia et al., 1992; Roche et al., 2003; Lepre et al., 2011), which has yielded Oldowan technologies and fossil evidence of early *Homo* (possibly *Homo ergaster*) and *Paranthropus boisei* (Kibunjia et al., 1992; Kibunjia, 1994; Brugal et al., 2003; Prat et al., 2003; Roche et al., 2003; Harmand, 2007; Roche, 2011). Kokiselei 4 contains one of the world's oldest known Acheulean assemblage (Lepre et al., 2011), and Kokiselei 6 is one of the largest Oldowan accumulations (Harmand, 2007). Kokiselei site complex environments (Fig. 3b) were dynamic as the basin transitioned from fluvial to lacustrine. Kokiselei paleosols are well-developed but have a larger proportion of sand than observed at Lokalalei. During this time a large, fluctuating Lake Lorenyang occupied the region; Kokiselei shows sedimentological facies evidence for beach, back beach/lagoonal, and marginal rivers feeding the lake (Lepre et al., 2011). Bovids are the most numerous with respect to specimens and taxa: Bovini (aff. *Pelorovis*), small to large Reduncini (*Kobus* sp.), Aepycerotini (*Aepyceros melampus*), Antilopini (*Gazella*), and small- to medium-sized Tragelaphini and Alcelaphini, suggesting both grassy and wooded components were present (Harris et al., 1988; Brugal et al., 2003; Lepre et al., 2011). The large-sized hippopotamus, *Hippopotamus gorgops* (adult and juvenile) is also abundant, indicating a perennial water source and the presence of grassy environments along the riverbanks and lake margin. Suids (*Kolpochoerus*, *Metridiochoerus*, *Notochoerus*?), rhinoceros (*Ceratotherium* sp.), equids (*Equus* and *Hipparion*) and a few

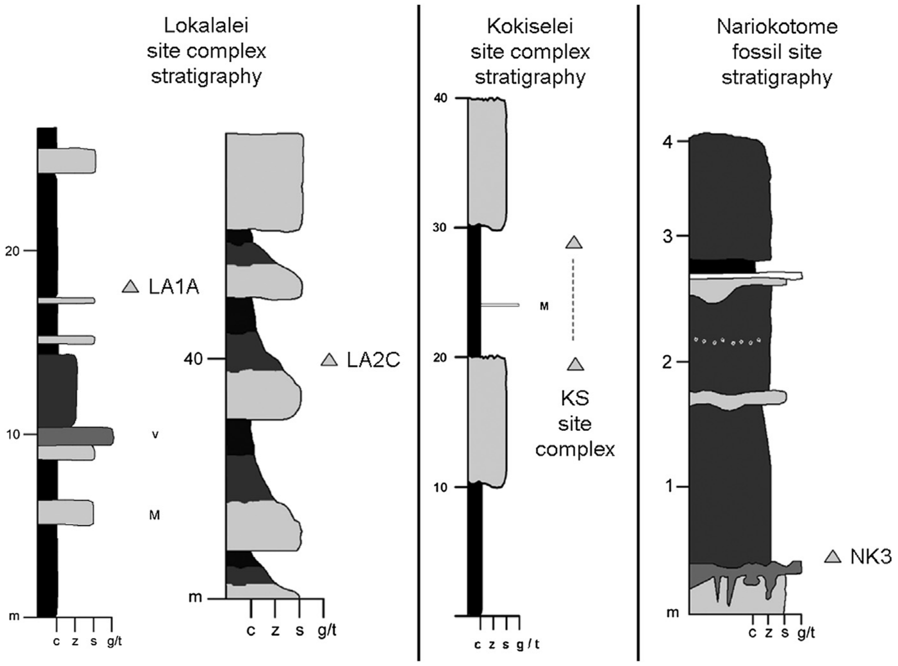

Figure 3. Stratigraphic sections of the Lokalalei (LA1A, LA2C) and Kokiselei (KS1-6 Complex) lithic archaeological sites and the Nariokotome (NK3) paleontological site. Key: M, molluscan fauna; V, tuffaceous; c, clay; z, silt; s, sand; g/t, gravel, tuff; black, clay/paleosol; dark gray, silt; medium gray, tuff; light gray, sand; white, carbonate.

carnivores (*Panthera*, Hyaenidae aff. *Crocuta*) are also present, indicating grasslands and bushlands (Brugal et al., 2003; Lepre et al., 2011).

The Natoo Member is bounded by the Lower Koobi Fora and the Chari Tuffs (1.48–1.39 Ma) (Harris et al., 1988; McDougall et al., 2012) and contains the Nariokotome fossil site (NK3), which yielded KNM-WT 15000 ('Turkana boy') (Brown et al., 1985b; Walker and Leakey, 1993). Nariokotome site paleosols (Fig. 3c) are not well-developed and can be interpreted as inceptisols with preserved B_K horizons. Overall the environment in this area was a distal floodplain of a substantially smaller lake susceptible to short-term flooding events, which were responsible for deposition of aquatic invertebrate assemblages (Feibel and Brown, 1993). The lake at that time was fed by the axial river system located to the north and by smaller basin margin rivers from the west. The presence of sponge spicules indicates a strong substrate (e.g., branches and large grasses) and potentially aquatic vegetation such as reeds. Ostracod assemblages indicate that lake waters were well oxygenated with a reduced alkalinity, categorized as oligohaline, possibly due to proximity to fresh basin margin river deltas (Feibel and Brown, 1993).

Stable carbon isotopic ($\delta^{13}C$) analyses of paleosol carbonates

The C_3 (Calvin–Benson) and C_4 (Hatch–Slack) photosynthetic pathways of plants can be differentiated by $\delta^{13}C_{VPDB}$ values (O'Leary, 1981; van der Merwe, 1982; Ehleringer, 1989). Woodland vegetation (trees, shrubs) and temperate grasses utilizing the C_3 pathway discriminate against the heavier and kinetically slower isotope of carbon, ^{13}C, whereas tropical grasses using the C_4 pathway allow some incorporation of ^{13}C. The resulting distribution in global vegetation shows clear separation: C_3 flora yields an average $\delta^{13}C_{VPDB}$ value of −27.1‰, and C_4, −12.1‰ (Cerling and Quade, 1993). East African vegetation also shows a clear carbon isotopic separation. C_3 dicots from closed and open canopy forests average −31.4‰ and −27.8‰, respectively, and from savanna and bushlands, −27.0‰ (Cerling et al., 2003). Mesic C_4 grasses (NADP subpathway) average −11.8‰ and xeric C_4 grasses (NAD and PCK subpathways) range from −13.1 to −12.9‰ (Cerling et al., 2003). Pedogenic carbonates at depths greater than 30 cm in soils with relatively high respiration rates incorporate CO_2 of decaying organic matter derived from surface vegetation during soil development (Cerling, 1984; Quade et al., 1989; Cerling and Quade, 1993). We assume that fluctuations in atmospheric CO_2 were minimal during the early Pleistocene (Cerling, 1991), thus the main source of variation of CO_2 to carbonate nodule formation was derived from decaying organic matter from surface vegetation (e.g., Cerling et al., 1988; Levin et al., 2004; Wynn, 2004). In the savanna biome, characterized by C_4 grasses with varying proportions of woody vegetation, $\delta^{13}C_{VPDB}$ values of pedogenic carbonates may be used to quantitatively measure the percentage of grasses present on the land surface during soil formation (Cerling, 1992; Sikes, 1999; Sikes et al., 1999; Wynn, 2000). Recently, Cerling et al. (2011b) derived a regression equation to calculate the fraction of woody canopy cover from paleosol carbonate $\delta^{13}C_{VPDB}$ values in order to categorize structure based on UNESCO classifications of African vegetation. These categories were taken from White (1983) and have the following $\delta^{13}C_{VPDB}$ value ranges of pedogenic carbonates (Cerling et al., 2011b): 1) *forest*: continuous stand of trees at least 10-m tall with interlocking crowns ($\delta^{13}C_{VPDB}$: >−11.5‰), 2) *woodland/bushland/shrubland*: woodland is an open stand of trees at least 8-m tall with woody cover exceeding 40% and a field layer dominated by grasses; bushland is an open stand of bushes usually between 3- and 8-m tall with woody cover exceeding 40%; and shrubland is an open or closed stand of shrubs up to2-m tall ($\delta^{13}C_{VPDB}$: −11.5 to −6.5‰), 3) *wooded grassland*: land covered with grassland and has 10–40% tree or shrub cover($\delta^{13}C_{VPDB}$: −6.5 to −2.3‰), and 4) *grassland*: land covered with herbaceous plants with less than 10% tree and shrub cover ($\delta^{13}C_{VPDB}$: <−2.3‰).

Materials and methods

Paleosol carbonate field sampling

We sampled a total of 68 nodular pedogenic carbonates within observable calcic horizons at >30 cm below contact with the paleosurface from five locations in three members of the Nachukui Formation. From the Kalochoro Member, we sampled 8 pedogenic carbonate nodules from 8 locations adjacent to the Lokalalei archaeological site complex (scaled to interval 2.4–2.2 Ma) across an area of 0.20 km^2. From the Kaitio Member, we sampled 23 nodules from 20 sample locations near the Kokiselei archaeological site complex across an area of 0.20 km^2 (scaled to interval 1.8–1.6 Ma). The following two sample locations are not adjacent to known lithic archaeological sites. From the Kalochoro Member, we sampled 11 nodules at 9 locations across an area of 0.20 km^2 between the Ekalalei and KBS Tuffs (scaled to interval 2.2–2.0 Ma). From the Kaitio Member, we sampled 18 nodules from 18 locations across an area of 0.10 km^2 between the KBS and Lower Koobi Fora Tuffs (scaled to interval 1.8–1.6 Ma). From the non-lithic bearing paleontological site containing KNM-WT 15000 ('Turkana boy'), we sampled 8 nodules from 8 locations adjacent to the Nariokotome fossil site (NK3) in the Kaitio and Natoo members across an area of 0.03 km^2 (scaled to interval 1.6–1.4 Ma).

Carbonate laboratory sampling and mass spectrometry

We cross-sectioned pedogenic nodules and sampled microcrystalline calcite with a 0.5 mm carbide drill bit (Foredom Series). We subsampled nodules two–four times depending on size in order to account for internal nodular variability and averaged the subsample values (193 total isotopic analyses). All analyses were conducted at the Stable Isotope Laboratory at Rutgers University on a Micromass Optima Mass Spectrometer with an attached multiprep device. Carbonate samples were reacted in 100% phosphoric acid at 90 °C for 13 min. Ratios are reported in standard delta notation in parts per thousand (per mil, ‰) $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$ where $R = {}^{13}C/{}^{12}C$, relative to Vienna-Pee Dee Belemnite ($\delta^{13}C_{VPDB}$) through the analysis of NBS-19. Analytical error is ±0.05‰.

Data comparisons

We combined our new Nachukui Formation paleosol $\delta^{13}C_{VPDB}$ dataset with previously published datasets from the Nachukui (Cerling et al., 1988; Wynn, 2004; Levin et al., 2011) and Koobi Fora (Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011) Formations to characterize all environments potentially available in the Turkana Basin over the time period of early Pleistocene (~2.4–1.4 Ma) tool makers. Utilizing methods of Cerling et al. (2011b), we subtracted 14‰ from the $\delta^{13}C_{VPDB}$ values of pedogenic carbonate to convert to the isotopic equivalent of organic carbon ($\delta^{13}C_{om}$) and used the equation $f_{wc} = \{\sin[-1.06688 - 0.08538(\delta^{13}C_{om})]\}^2$ to generate estimates of fraction woody cover canopy for classification into UNESCO categories of African vegetation. We compared the paleosol $\delta^{13}C_{VPDB}$ and estimated f_{wc} from the basin with those adjacent to lithic archaeological sites in the Nachukui (Kibunjia et al., 1992; Roche and Kibunjia, 1996; Roche et al., 2003) and Koobi Fora (Isaac and Harris, 1978; Isaac, 1997) Formations.

Our sampling regime of all environments and those in the vicinity of lithic sites is by no means comprehensive. For instance, we (nor the authors of previously published data that we used here) did not sample paleosols equally across time and space. The occurrence and preservational issues of paleosols and their mineral precipitates do not permit such a sampling method. Paleosols do not occur at regular temporal and spatial intervals; soils do not always form carbonate nodules, and paleosols do not always preserve B_K horizons. Additionally, we did not sample paleosols in the vicinity of every lithic archaeological site in the Turkana Basin. In some cases, paleosols with carbonate nodules were not present at or near lithic sites. We also are aware of the time-averaging of paleosol carbonate formation (10^1–10^3 years) and Paleolithic archaeological sites (10^3–10^4 years). We attempt to mitigate mixing scales (e.g., Behrensmeyer, 2006) by sampling paleosols adjacent to (0–500 m) and stratigraphically above and below lithic sites and collapsing paleosol $\delta^{13}C_{VPDB}$ values into large temporal bins (200 kyr [thousand years]). In this study, we focused our analysis on lithic sites in the Turkana Basin for which there exists paleosol carbonate isotopic data and did not consider archaeological sites with only cutmarked faunal remains (e.g., GaJi5, GaJi14; Bunn, 1994; Pobiner et al., 2008). Moreover, we did not re-evaluate each lithic site for taphonomic bias (e.g., Potts et al., 1999). Paleosol carbonate isotopic data in the vicinity of lithic archaeological sites were taken from Quinn et al. (2007), Levin et al. (2011) and this study (Figs. 1 and 2b–f; Table 1).

During our study interval, the Turkana Basin shows a drying trend that is climatically driven, tectonically mediated, and potentially influenced by paleogeography and hydrology (Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Levin et al., 2011). We therefore compared paleosol $\delta^{13}C_{VPDB}$ values and resulting f_{wc} data in five intervals that are characterized by different geographic and hydrologic regimes (Fig. 2) (after Brown and Feibel, 1991; Feibel et al., 1991). Each interval is approximately 200 kyr in duration. We did not include paleosol data from the Shungura Formation since we do not have samples from locations adjacent to lithic sites. Moreover, due to paleogeography along the axial Omo River, these paleosol $\delta^{13}C_{VPDB}$ values record primarily one depositional regime through time, and therefore, Shungura environments may have responded differently to climatic, tectonic, and/or paleogeographic influences than those preserved in the Koobi Fora and Nachukui Formations (Levin et al., 2011).

Results

Nachukui Formation paleosol $\delta^{13}C_{VPDB}$ values

Our new Nachukui Formation pedogenic carbonate samples averaged from five different sample locations from ~2.4 to 1.4 Ma yielded a mean $\delta^{13}C_{VPDB}$ value of −6.1‰ and range from −12.3 to 0.8‰ (Table 2). These $\delta^{13}C_{VPDB}$ values represent four UNESCO structural categories of African vegetation (after White, 1983; Cerling et al., 2011b) including: 1) forest, 2) woodland/bushland/shrubland, 3) wooded grassland, and 4) grassland. Hydrological systems include large meander belts, axial rivers, large and small, open- and closed-basin lakes. Each time period and paleogeographic setting supported plant communities spanning C_3- and C_4-vegetation, yet show statistical evidence for significant increases in paleosol $\delta^{13}C_{VPDB}$ values through time. Below we detail the results of each of the five sample locations.

Table 2
Nachukui Formation $\delta^{13}C_{VPDB}$ values (‰) and estimated f_{wc} (methods after Cerling et al., 2011b) through time (this study).

	Lokalalei Lithic Sites	Kalochoro Member	Kokiselei Lithic Sites	Kaitio Member	Nariokotome Fossil Site
N paleosols, analyses	8, 24	11, 37	23, 57	18, 43	8, 32
Mean $\delta^{13}C_{VPDB}$	−7.7	−7.3	−6.0	−5.6	−3.6
$\delta^{13}C_{VPDB}$ St dev	0.9	2.0	1.3	1.8	2.7
Mean f_{wc}	0.50	0.46	0.37	0.34	0.21
Median f_{wc}	0.47	0.42	0.37	0.34	0.23
f_{wc} St dev	0.09	0.15	0.10	0.13	0.14

Lokalalei archaeological site complex (2.4–2.2 Ma) Paleosols from the Lokalalei lithic sites (LA1A, LA2C) yielded the lowest average $\delta^{13}C_{VPDB}$ value of −7.7‰ and range from −9.9 to −6.2‰, indicating that woodland/bushland/shrubland was the dominant vegetation structural category (f_{wc} mean = 50%) (Table 2). Notably, the wooded grassland category was also present in abundance. Riparian woodlands near a large, perennial river system may have provided shade, protection, floral food resources, and drinkable water to hominins.

Kalochoro Member (2.2–2.0 Ma) Kalochoro Member (no archaeological lithic sites) paleosol $\delta^{13}C_{VPDB}$ values were comparable with those of the Lokalalei archaeological site complex, averaging −7.3‰, but show a larger range of −12.3 to −5.9‰ (Table 2). These values indicate that the woodland/bushland/shrubland structural category was most abundant (f_{wc} mean = 46%), however, the wooded grassland category is also indicated. Notably, this is the only sample location that recorded a $\delta^{13}C_{VPDB}$ value lower than −11.5‰, which indicates a forest structural category (after Cerling et al., 2011b).

Kokiselei archaeological site complex (1.8–1.6 Ma) Paleosols from the Kokiselei lithic sites (KS1-6) yielded a mean $\delta^{13}C_{VPDB}$ value of −6.0‰ and range from −9.0 to −2.2‰, suggesting that the wooded grassland structural category was dominant (f_{wc} mean = 37%), but the woodland/bushland/shrubland and grassland categories were also present (Table 2). Wooded grasslands near the lake margin may have served as an active location for tool making and use.

Kaitio Member (1.8–1.6 Ma) Paleosol $\delta^{13}C_{VPDB}$ values from the Kaitio Member (no archaeological lithic sites) were slightly higher than those from the Kokiselei archaeological site complex, although both sets of paleosols show similar depositional environments of near shore, back beach, and small river floodplains. Paleosol carbonates gave a mean $\delta^{13}C_{VPDB}$ value of −5.7‰ and range

Table 1
Archaeological lithic sites of the Nachukui and Koobi Formations adjacent to paleosol samples for this study.

	2.4–2.2 Ma	2.2–2.0 Ma	2.0–1.8 Ma	1.8–1.6 Ma	1.6–1.4 Ma
Nachukui Formation	Lokalalei site complex (LA1A, LA2C)[a]	No known sites	Unsampled	Kokiselei site complex (KS1-6)[a]	Unsampled
Koobi Fora Formation	No known sites	Depositional hiatus	FxJj 1[b] FxJj 3[b] FxJj 10[b] FwJj 20[b,c]	FxJj 38[b] FxJj 83[b,c]	FxJj 11[b] FxJj 16[b] FxJj 17[b] FxJj 18 site complex[b] FxJj 19[b] FxJj 20 site complex[b]

Paleosol $\delta^{13}C_{VPDB}$ values taken from a: this study; b: Quinn et al. (2007); c: Levin et al. (2011).

from −8.7 to −2.5‰, which indicates that the wooded grassland category was most abundant (f_{wc} mean = 34%) (Table 2).

Nariokotome fossil site (1.6–1.4 Ma) Nariokotome fossil site (NK3) paleosols displayed $\delta^{13}C_{VPDB}$ values between −9.8 and 1.3‰ and averaged −3.6‰ indicating that they primarily supported not only the wooded grassland structural category (f_{wc} mean = 21%) but also woodland/bushland/shrubland and grassland categories (Table 2). Overall, we interpret the Nariokotome fossil site to have been a seasonally indurated C_4 marshy riverine grassland with few woody components. The lack of stone tools and few fragmentary specimens of terrestrial mammalian fauna, other than KNM-WT 15000 may indicate that this area was not necessarily conducive to terrestrial food resources and/or tool-making activities. The presence of a nearly complete hominin individual may indicate a high preservation potential at this locality rather than a habitation/foraging area.

All Turkana Basin versus lithic site paleosol $\delta^{13}C_{VPDB}$ values and estimated f_{wc}

All paleosol $\delta^{13}C_{VPDB}$ values ($n = 444$) from the Nachukui and Koobi Fora Formations in the Turkana Basin from 2.4 to 1.4 Ma (data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study) yielded a mean value of −5.6‰, which give an estimated f_{wc} mean of 34% (Fig. 4; Table 3). Notably, although all four structural categories (forest, woodland/bushland/shrubland, wooded grasslands, grasslands) were indicated, only one paleosol in the combined sample ($n = 444$) from 2.4 to 1.4 Ma yielded $\delta^{13}C_{VPDB}$ values indicating a forest category ($f_{wc} = 86\%$). Excluding this one paleosol, the combined dataset yielded a f_{wc} range from 0 to 75%. Across the five paleogeographic intervals, basin paleosol $\delta^{13}C_{VPDB}$ mean values significantly increased through time from 42% at 2.4–2.2 Ma to 30% at 1.6–1.4 Ma (Figs. 5 and 6; Tables 3 and 4). Although we reproduced the grassland expansion trend of Cerling et al. (1988), Wynn (2004), Quinn et al. (2007), and Levin et al. (2011) with the combined Koobi Fora and Nachukui datasets, the lithic archaeological site paleosol $\delta^{13}C_{VPDB}$ values ($n = 68$) (data from Quinn et al., 2007; Levin et al., 2011; this study) do not mirror this pattern (Figs. 5 and 7; Tables 5 and 6). Early Pleistocene hominin sites yielding lithic artifacts in the Turkana Basin were significantly more wooded than what was available in the basin from 2.4 to 1.4 Ma. The median of all lithic site paleosol $\delta^{13}C_{VPDB}$ values is 6% more woody than that of all basin environment paleosols (Table 7). When separated by paleogeographic/temporal intervals, the pattern is maintained with one exception; that is, lithic site paleosol $\delta^{13}C_{VPDB}$ values at 2.4–2.2 Ma indicate significantly more woody cover than those at 2.0–1.8 Ma (Table 6). All other lithic site paleosol $\delta^{13}C_{VPDB}$ value comparisons yielded no significant differences. Below we place all $\delta^{13}C_{VPDB}$ values within each paleogeographic setting and reconstruct vegetation for basin environments relative to lithic sites (Fig. 6; Table 7).

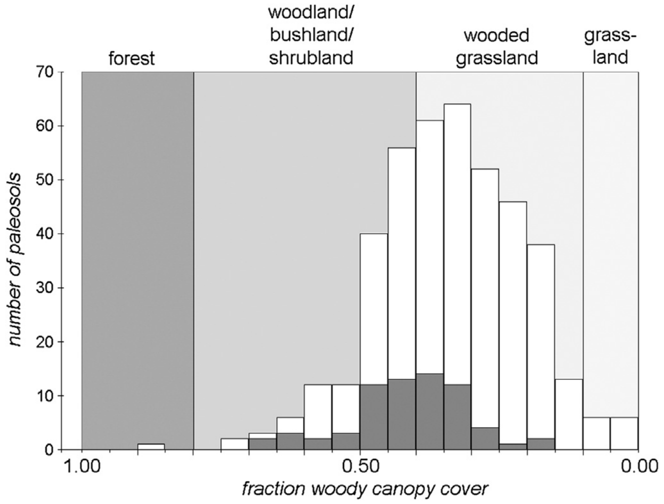

Figure 4. Histograms of estimated f_{wc} against UNESCO structural categories for African vegetation (after methods of Cerling et al., 2011b) for all Turkana Basin environments (white bars; data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study) compared to those of all lithic sites (gray bars; data from Quinn et al., 2007; Levin et al., 2011; this study) from the Nachukui and Koobi Fora Formations (2.4–1.4 Ma). UNESCO structural categories: 1) forest, 2) woodland/bushland/shrubland, 3) wooded grassland, 4) grassland.

Table 3

Turkana Basin $\delta^{13}C_{VPDB}$ values (‰) from Nachukui and Koobi Fora Formations and estimated f_{wc} (methods after Cerling et al., 2011b) through time (data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study).

Age	Members	N	Mean $\delta^{13}C_{VPDB}$	$\delta^{13}C_{VPDB}$ St dev	Mean f_{wc}	f_{wc} St dev
2.4–1.4 Ma	Okote/Kaitio – L. Burgi/ L. Kalochoro (all)	444	−5.6	1.7	0.34	0.13
2.4–2.2 Ma	L. Burgi/L. Kalochoro	38	−6.7	1.3	0.42	0.11
2.2–2.0 Ma	U. Burgi/U. Kalochoro	41	−6.4	2.0	0.40	0.15
2.0–1.8 Ma	L. KBS – U. Burgi/ L. Kaitio-U. Kalochoro	122	−5.9	1.7	0.35	0.13
1.8–1.6 Ma	U. KBS/U. Kaitio	111	−5.3	1.7	0.31	0.13
1.6–1.4 Ma	Okote/Natoo	132	−5.2	1.6	0.30	0.11

Groups are separated based on paleogeographic reconstructions.

At 2.4–2.2 Ma, mean and median basin f_{wc} of 42% and 43%, respectively, indicate woodland/bushland/shrubland as the dominant structural category, but the wooded grassland category was also present. Paleosols sampled adjacent to lithic archaeological sites Lokalalei 1A and 2C yielded f_{wc} that average 8% (median: 5%) more woody cover than coeval basin environs. At 2.2–2.0 Ma, the basin shows evidence for both woodland/bushland/shrubland and wooded grassland structural categories; notably this interval is the only one that preserves a forest category. No archaeological sites from the west side are known in this interval, and there is a depositional hiatus on the east side. At 2.0–1.8 Ma, the basin shows evidence for three structural categories: woodland/bushland/shrubland, wooded grassland, and grassland. The mean and median basin f_{wc} values, 35%, indicate wooded grassland was the most abundant structural category. Paleosols sampled adjacent to lithic archaeological sites FxJj 1, FxJj 3, FxJj 10, and FwJj 20 (Koobi Fora Formation) yielded mean and median f_{wc} values of 42% and 39%, respectively, which are 7% and 4% more woody than the overall basin environs. The difference in median values, however, is statistically insignificant (Table 7). Basin paleosol f_{wc} values at 1.8–1.6 Ma suggest that three structural categories were present: woodland/bushland/shrubland, wooded grassland, and grassland, but mean and median values of 31% indicate that the wooded grassland category was most abundant at this time. Paleosols sampled adjacent to the Kokiselei archaeological site complex (KS1-6) (Nachukui Formation) and archaeological sites FxJj 38 and FxJj 83 (Koobi Fora Formation) gave f_{wc} mean and median values 6% and 7% higher than basin environments, respectively. Basin paleosols from 1.6 to 1.4 Ma have mean and median f_{wc} values of 30% and 29%, respectively, indicating the wooded grassland category was dominant at this time. Similar to the previous temporal interval, f_{wc} values indicate the presence of three structural categories. Paleosols were sampled adjacent to archaeological sites FxJj 11, FxJj 16–20 (Koobi Fora Formation). Basin paleosol f_{wc} values are the lowest of the study interval, yet the archaeological lithic site f_{wc}

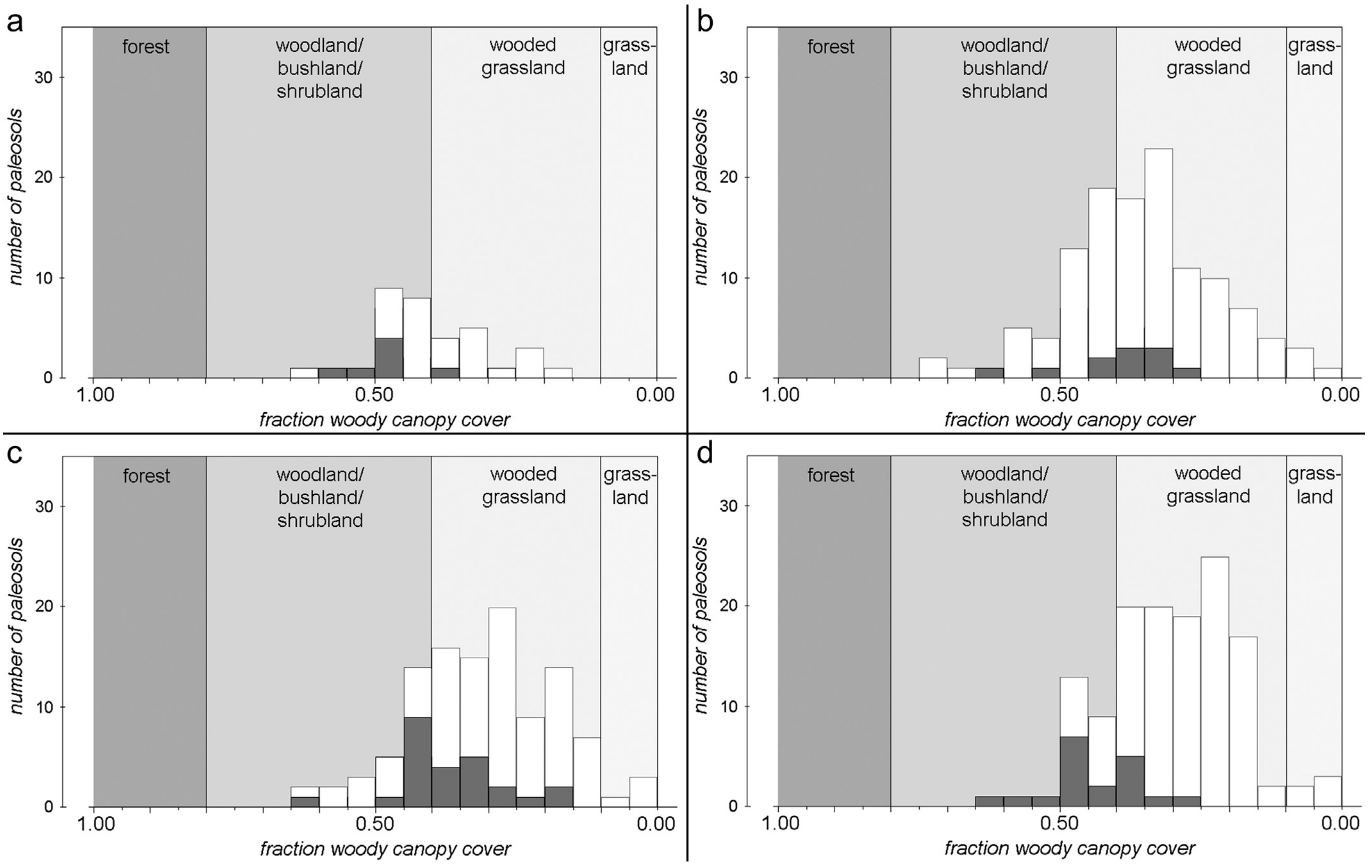

Figure 5. Histograms of estimated f_{wc} against UNESCO structural categories for African vegetation (after methods of Cerling et al., 2011b) for Turkana Basin environments (white bars; data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study) compared to those of lithic sites (gray bars; data from Quinn et al., 2007; Levin et al., 2011; this study) from the Nachukui and Koobi Fora Formations separated into paleogeographic/temporal intervals (a: 2.4–2.2 Ma; b: 2.0–1.8 Ma; c: 1.8–1.6 Ma; d: 1.6–1.4 Ma). UNESCO structural categories: 1) forest, 2) woodland/bushland/shrubland, 3) wooded grassland, 4) grasslands.

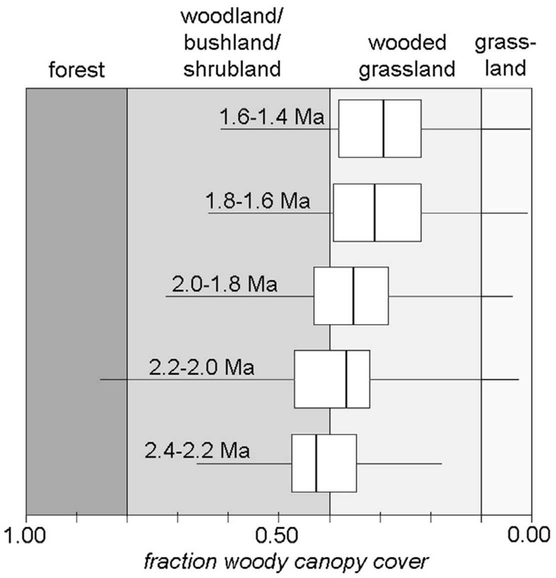

Figure 6. Box plots of estimated f_{wc} against UNESCO structural categories for African vegetation (after methods of Cerling et al., 2011b) for all Turkana Basin environments (data from Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007; Passey et al., 2010; Levin et al., 2011; this study) by paleogeographic interval (a: 2.4–2.2 Ma; c: 2.2–2.0 Ma; d: 2.0–1.8 Ma; e: 1.8–1.6 Ma; f: 1.6–1.4 Ma). UNESCO structural categories: 1) forest, 2) woodland/bushland/shrubland, 3) wooded grassland, 4) grassland.

mean and median values fall within the woodland/bushland/shrubland category and are, respectively, 13% and 12% higher than coeval basin environs.

Discussion

Habitat preference of early Pleistocene tool makers in the Turkana Basin

We do not suggest that our isotopically measured paleosols necessarily represent the exact land surface on which tool-making hominins lived, made and used tools. However, we assert that given statistical treatment in large temporal bins within paleogeographic regimes and proximity of paleosols to lithic sites, that we are statistically evaluating if lithic site paleosol $\delta^{13}C_{VPDB}$ values and estimated f_{wc} were significantly different from those in the basin. Our results demonstrate that lithic archaeological sites had significantly more wooded vegetation compared with what was present throughout the basin from 2.4 to 1.4 Ma. Even as environments became increasingly more grassy, lithic sites continued to be located in a more wooded landscape. Moreover, as the basin transformed from fluvial to lacustrine and back to fluvial hydrological regimes encompassing numerous microenvironments and highly variable geomorphic settings, hominin lithic sites maintained a consistent pattern of f_{wc} circa 40%. We suggest that our results demonstrate that tool-making hominins utilized behavioral strategies to maintain a relatively more wooded habitat through

Table 4
One-way ANOVA and post hoc Tukey of Turkana Basin estimated f_{wc} from Nachukui and Koobi Fora Formations through time by paleogeography group.

One-way ANOVA

Source	Type III SS	Df	Mean Sq.	*F*	*p*
Model	0.699	4	0.175	11.436	**0.000**
Error	6.704	439	0.015		
Total	7.402	443			

Post Hoc Tukey

Group 1	Group 2	Mean Diff.	SE	*q*	*p*
1.6–1.4 Ma	1.8–1.6 Ma	−0.010	0.011	0.914	0.967
	2.0–1.8 Ma	−0.054	0.011	4.885	**0.005**
	2.2–2.0 Ma	−0.097	0.016	6.228	**0.000**
	2.4–2.2 Ma	−0.119	0.016	7.403	**0.000**
1.8–1.6 Ma	2.0–1.8 Ma	−0.043	0.011	3.780	0.058
	2.2–2.0 Ma	−0.087	0.016	5.448	**0.001**
	2.4–2.2 Ma	−0.109	0.016	6.625	**0.000**
2.0–1.8 Ma	2.2–2.0 Ma	−0.044	0.016	2.769	0.287
	2.4–2.2 Ma	−0.065	0.016	4.033	**0.035**
2.2–2.0 Ma	2.4–2.2 Ma	−0.022	0.020	1.107	0.936

Bold indicates statistical significance.

time potentially to mitigate the effects of environmental perturbations in the basin.

We cannot gauge how much time early Pleistocene hominins spent making and utilizing tools in daily life, and therefore, only suggest that a portion of time was spent making, using, and discarding tools. We interpret our results to indicate that during tool-related activities, hominins demonstrated a preference for more wooded environments in the basin than what was generally available at the time. Moreover, we do not know who the tool maker(s)/user(s) was/were. Although the genus *Homo* has traditionally been linked to lithic technology (Leakey et al., 1964), we cannot discount other sympatric species (*Paranthropus*) as candidates (Susman, 1991). As such, we review potential ecological behaviors and potential selective pressures of early Pleistocene toolmaking hominins in the Turkana Basin in accordance with our results.

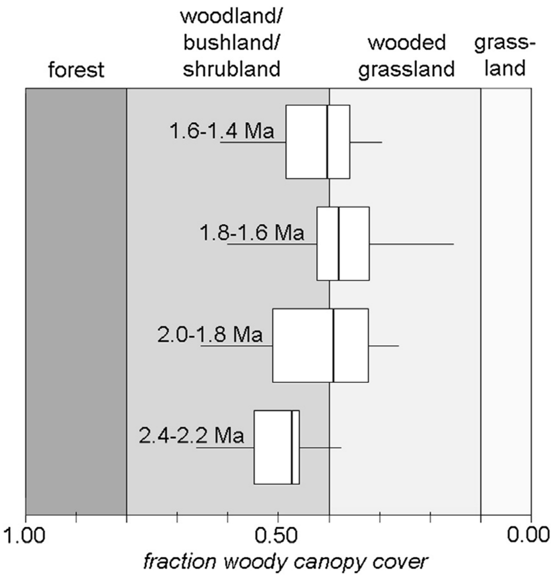

Figure 7. Box plots of estimated f_{wc} against UNESCO structural categories for African vegetation (after methods of Cerling et al., 2011b) for all Turkana Basin lithic sites (data from Quinn et al., 2007; Levin et al., 2011; this study) by paleogeographic/temporal interval (a: 2.4–2.2 Ma; b: 2.0–1.8 Ma; c: 1.8–1.6 Ma; d: 1.6–1.4 Ma). UNESCO structural categories: 1) forest, 2) woodland/bushland/shrubland, 3) wooded grassland, 4) grassland.

Table 5
Lithic site $\delta^{13}C_{VPDB}$ values (‰) from Nachukui and Koobi Fora Formations and estimated f_{wc} (methods after Cerling et al., 2011b) through time (data from Quinn et al., 2007; Levin et al., 2011; this study).

Age	Members	*N*	Mean $\delta^{13}C_{VPDB}$	$\delta^{13}C_{VPDB}$ St dev	Mean f_{wc}	f_{wc} St dev
2.4–1.4 Ma	Okote/Kaitio – L. Burgi/ L. Kalochoro (all)	68	−6.6	1.3	0.41	0.10
2.4–2.2 Ma	L. Burgi/L. Kalochoro	8	−7.7	1.0	0.50	0.09
2.0–1.8 Ma	L. KBS – U. Burgi/ L. Kaitio-U. Kalochoro	12	−6.7	1.5	0.42	0.13
1.8–1.6 Ma	U. KBS/U. Kaitio	25	−6.1	1.2	0.37	0.10
1.6–1.4 Ma	Okote/Natoo	23	−6.8	1.0	0.43	0.09

Groups are separated based on paleogeographic reconstructions.

Thermoregulation

Passey et al. (2010) demonstrated that soil temperatures commonly in excess of 33 °C span 4–<1 Ma in the Nachukui and Shungura Formations. As such, hot and sunny environments were likely a strong selective pressure for thermophysiological adaptations in early Pleistocene hominins in the Turkana Basin and may have included large, linear postcranial morphology (Ruff, 1991, 1993; Wheeler, 1992b, 1993; Ruff and Walker, 1993; Aiello and Wells, 2002; Bramble and Lieberman, 2004), efficient bipedality (Wheeler, 1991), reduced hair cover and increased sweat glands (Wheeler, 1992a). Although physiological adaptations for evaporative water loss and heat storage are effective in maintaining the body at optimal temperatures in hot environments (Baker, 1958; Hanna and Brown, 1983; Frisancho, 1993), there are environmental settings where physiological heat stress resulting in heat stroke and potentially death can occur despite physiological adaptations (Ulijaszek, 2001). In savanna-living primates, high ambient temperatures have been shown to impact male stress hormone levels and reproductive physiology (Gesquiere et al., 2011) and female estrus cycling and conception (Beehner et al., 2006; Gesquiere et al., 2008). In the !Kung of South Africa, heat stress has been suggested as one of the contributors of high energetic expeditures that result in low reproductive rates in females (Bentley, 1985).

Behavioral strategies adopted by primates and humans living in hot, arid environments to reduce heat stress include cave-dwelling (Pruetz, 2001, 2007; McGrew et al., 2003; Barrett et al., 2004) and sand-bathing (Marshall, 1976; Brain and Mitchell, 1999). In African savanna ecosystems, tree cover significantly reduces direct solar radiation (by 45–65%) and reduces air and ground temperatures (by 5–20 °C) (Belsky et al., 1989). In these environments, humans and primates show a reduction in activity level during the hottest

Table 6
One-way ANOVA and post hoc Tukey test of lithic site estimated f_{wc} from Nachukui and Koobi Fora Formations by paleogeography group.

One-way ANOVA

Source	Type III SS	Df	Mean Sq.	*F*	*p*
Model	0.112	3	0.037	3.990	**0.011**
Error	0.598	64	0.009		
Total	0.710	67			

Post Hoc Tukey

Group 1	Group 2	Mean Diff.	SE	*q*	*p*
1.6–1.4 Ma	1.8–1.6 Ma	0.059	0.020	2.984	0.161
	2.0–1.8 Ma	0.008	0.024	0.314	0.996
	2.4–2.2 Ma	−0.070	0.028	2.495	0.300
1.8–1.6 Ma	2.0–1.8 Ma	−0.051	0.024	2.136	0.437
	2.4–2.2 Ma	−0.129	0.028	4.643	**0.009**
2.0–1.8 Ma	2.4–2.2 Ma	−0.078	0.031	2.488	0.302

Bold indicates statistical significance.

Table 7
Mann-Whitney *U* tests comparing Turkana Basin and lithic site estimated f_{wc} from Nachukui and Koobi Fora Formations by paleogeography group.

	2.4–1.4 Ma		2.4–2.2 Ma		2.0–1.8 Ma		1.8–1.6 Ma		1.6–1.4 Ma	
	Environ f_{wc}	Sites f_{wc}	Environ f_{wc}	Sites f_{wc}	Environ f_{wc}	Sites f_{wc}	Environ f_{wc}	Sites f_{wc}	Environ f_{wc}	Sites f_{wc}
Mean	0.34	0.41	0.42	0.50	0.35	0.42	0.31	0.37	0.30	0.43
Median	0.34	0.40	0.43	0.48	0.35	0.39	0.31	0.38	0.29	0.41
Std dev	0.13	0.10	0.11	0.09	0.13	0.13	0.13	0.10	0.11	0.09
N paleosols	444	68	38	8	122	12	111	25	132	23
Mann-Whitney *U*	*U* stat = 20520.0 *p* = **0.000**		*U* stat = 221.0 *p* = **0.046**		*U* stat = 906.0 *p* = 0.179		*U* stat = 1803.5 *p* = **0.019**		*U* stat = 2483.5 *p* = **0.000**	

Bold indicates statistical significance.

part of the day and out of direct solar radiation (McCarthy and McArthur, 1960; Stelzner, 1988; Ulijaszek, 2001; Hill, 2006). Hominins utilizing shady spots for lithic activities in the Turkana Basin has been suggested since the application of central place foraging models (Isaac, 1978). Moreover, Turkana hominins may have repeatedly occupied sites with tree cover, water and raw material resources, and protection from predation (Kroll, 1994; Brugal et al., 2003). Wheeler (1994) suggested that shade-seeking behavior for 4 h during thermally-stressing periods of the day could have reduced the water requirement for African savanna-dwelling Pleistocene hominids by 35–66% (range based on hair-covered or naked skin). Our results suggest that (some) hominin groups in the Turkana Basin may have engaged in behavioral strategies to perform tool-related activities in wooded environments potentially to reduce heat stress thereby decreasing energetic outputs, increasing reproductive health, and ultimately increasing fitness.

Access to drinking water

Drinking significantly reduces heat stress (de Garine and de Garine, 2001). Several studies have documented behavioral strategies of obligate-drinking primates and humans living in arid environments to maximize access to potable water resources during daily foraging activities (McCarthy and McArthur, 1960; Lee, 1965, 1979; Silberbauer, 1972; Tanaka, 1976; Mitchell et al., 2009). Notably, all $\delta^{18}O$ analyses of hominin enamel carbonate to date show low values as compared with other mammals (review in Grine et al., 2012), which is consistent (among other dietary inputs) with obligate drinking. Early Pleistocene hominins in savanna ecosystems have been suggested to require a minimum of 1.5–1.3 L of water per day, likely combining surface water with dietary water from meat and vegetation (Wheeler, 1991). African structural categories are strongly influenced by the distribution of perennial and ephemeral rivers; C_3 trees require relatively more water than C_4 grasses. In savanna ecosystems, C_3 dominated gallery forests are typically present along riverbanks and C_4 grasses are located on distal floodplains (Tieszen et al., 1979). If differential access to potable water sources for drinking was selecting hominins to focus lithic tool making and using activities in proximal locations to rivers, our interpretation of hominin habitat preference of wooded habitats may simply be a by-product of C_3 vegetation- and hominin-water needs.

Access to raw materials

Raw materials for early Pleistocene lithic tools in the Turkana Basin were primarily procured from local axial and margin river channels (Rogers et al., 1994; Lepre, 2001; Harmand, 2007, 2009a,b; Braun et al., 2008). In African savanna environments, perennial and to a lesser degree ephemeral waterways support a higher percentage of woody species relative to grasses on the distal floodplains (Tieszen et al., 1979). Based on sedimentological and paleogeographic correlations to $\delta^{13}C_{VPDB}$ values of paleosol carbonates, Quinn et al. (2007) demonstrated that C_3 vegetation was patterned along axial and marginal rivers within different subregions of the Koobi Fora Formation from 2.0 to 1.5 Ma. On a larger scale, Levin et al. (2011) showed a greater percentage of C_3 vegetation in the Shungura Formation relative to the Koobi Fora and Nachukui Formations as a result of proximity to the axial river system. Other East African paleosol isotope studies show a similar relationship (Levin et al., 2004). Bunn (1994) suggested that stone tools (but not cutmarked bone) were differentially discarded in proximity to the material source (Omo River in the Karari region) relative to areas of raw material scarcity (ephemeral streams and lake margin at Ileret). On a finer scale, Braun et al. (2008) demonstrated that the patterned distribution of Okote Member (Koobi Fora Formation) lithic sites via artifact discard is correlated to distance from paleochannels within the Karari region. We assert that this pattern of archaeological site accumulations (potentially via differential artifact discard) in proximity to paleochannels may have been more widespread across the Turkana Basin as shown by our results of lithic sites in relatively more wooded regions and thus near rivers. In this scenario, tool-using hominins were not necessarily selecting for more wooded regions per se, but were preferring river channels with abundant raw materials for tool making. Thus, the wooded environment-lithic site correlation is an artifact of the riverine landscape. Lithic accumulations in wooded portions of the landscape were a hominin raw material procurement and/or discard strategy, rather than a habitat preference.

Diet

Habitat selection for a more wooded portion of the landscape (albeit during tool making/use) may speak to the question of diet. Oldowan and Acheulean technologies may have been utilized by hominins for extraction of carcass meat and marrow (Bunn, 1981; Potts and Shipman, 1981; Bunn and Kroll, 1986; Blumenschine and Selvaggio, 1988; de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005; Braun et al., 2009). Some researchers suggest that members of the genus *Homo* preferred more open habitats relative to australopithecines (Reed, 1997) in association with tool-assisted carcass acquisition (Rogers et al., 1994; Sikes, 1994, 1999; Sikes et al., 1999). Our correlation for lithic sites in the vicinity of more wooded habitats could be interpreted as refuting the idea that hominins preferred grasslands. However, the number of cutmarked specimens of grazing herbivore species at early Pleistocene sites suggests that hominins were indeed exploiting open grasslands. As such, our data may be the result of carcass (and stone tool) transport to protected areas to avoid predation during processing and consumption (Potts, 1991). If so, tool makers were utilizing a broad spectrum of habitats within the savanna ecosystem, potentially preferring open landscapes for carcass acquisition and relatively more closed environs during lithic-related carcass processing.

Blumenschine's (1986, 1987) actualistic study of the Serengeti and Ngorongoro ecosystems demonstrated a patterned distribution of herbivore carcasses at ecotones. If that pattern holds true for the early Pleistocene, tool-making hominins may have preferred to exploit habitats between C_3 and C_4 environments. The maintained pattern of Turkana Basin lithic sites circa $f_{wc} = 40\%$ throughout our study interval even as basin environs were becoming increasingly open may indicate a hominin preference for an ecotonal boundary separating woodland/bushland/shrubland and wooded grassland structural categories. If lithic technologies were indeed used to procure meat and marrow as demonstrated by the presence of cutmarked bones at early Pleistocene hominin sites, the central place between C_3 and C_4 biomes may have afforded hominins access to a higher percentage of carcasses on the landscape.

Alternatively, the association of lithic sites to wooded areas could be the result of a preference for aquatic dietary resources (Stewart, 1994). Braun et al. (2010) have suggested that early *Homo* may have incorporated aquatic resources such as crocodiles and catfish into the diet based on taphonomic and faunal evidence in association with the lithic assemblage at FwJj 20 in the Il Dura region (Koobi Fora Formation). Shabel (2006, 2008) proposed that the dental morphology and carbon isotopic values of *Paranthropus robustus* could have been the result of freshwater shellfish procurement. Although our association is not with *Paranthropus* or *Homo*, but hominin lithic sites, it is possible that *Paranthropus* and/or *Homo* were utilizing tools for freshwater invertebrate faunal extraction and vertebrate carcass processing. Dietary utilization of aquatic resources by tool-making hominins is plausible. However, no taphonomic studies to date have found percussion or extraction marks on invertebrate shell, and Braun et al. (2010) found relatively low frequencies of percussion/cutmarks on aquatic vertebrate bone. At present, dietary stable isotopic studies do not offer the resolution necessary to discriminate aquatic dietary contributions from terrestrial animal resources.

Plants were important components to the diets of early Pleistocene omnivorous hominins (Sept, 1986, 1994) and likely contributed the majority of calories to the overall diet as compared with animal products (e.g., Zihlman and Tanner, 1978; van der Merwe et al., 2008). Dental microwear evidence suggests that *Homo* sp. maintained a wide diversity of dietary resources and did not specialize in meat (Ungar et al., 2006). If tool-related activities were directed at processing vegetal material (e.g., Keeley and Toth, 1981; Brain, 1985; Schick and Toth, 1993; Toth, 1997), our results may indicate that tool-making hominins preferred C_3 plant foods over the increasingly available C_4 plants in the Turkana Basin. After 2.2 Ma, wooded grasslands, which are dominated by C_4 plants, were relatively more abundant in the Turkana basin relative to other C_3 structural vegetation categories. Lithic sites, which may represent where hominins foraged plant resources, were located in relatively more wooded habitats.

South African and Tanzanian *Homo* sp. enamel carbonate $\delta^{13}C$ values indicate whole diets were composed of 20–35% and 23–49% C_4 resources, respectively (Lee-Thorp et al., 2000; van der Merwe et al., 2008). Although $\delta^{13}C$ values of Turkana Basin *Homo* sp. enamel carbonate have not yet been reported, current results indicate that *Homo* sp. consumed relatively more C_3 foods. In actualistic studies of analogous environments of the African Pleistocene, fleshy fruits and young leaves are identified as the highest ranking potential plant foods of early hominins (Peters and O'Brien, 1981; Stahl, 1984; Peters and Vogel, 2005), which are primarily derived from woody species (Sept, 1994; Copeland, 2007). However, Turkana Basin lithic sites were certainly not located in forested habitats, but primarily at the ecotone between wooded grassland and woodland/bushland/shrubland structural categories. Isotopic results of *Homo* sp. indicate that C_4 resources were sizable dietary contributions (especially for OH65 at 49% C_4; van der Merwe et al., 2008). Actualistic studies also demonstrate that edible C_4 plant species are abundant especially in wetland environments (Peters and Vogel, 2005). *Paranthropus boisei*, however, has been demonstrated to have consumed mostly C_4 resources (61–91%) based on enamel carbonate $\delta^{13}C$ values (van der Merwe et al., 2008; Cerling et al., 2011a). These dietary data introduce an interesting conundrum to our correlation of tools in relatively more woody environments: if paranthropines were tool makers, then tool-related activities occurred in different habitats than those exploited for plant food resources or paranthropines were selecting the C_4 plants within the woodland/bushland/shrubland habitats over potentially available C_3 plant resources. Again, this suggests that potential early tool makers may have utilized a broad spectrum of habitats in the savanna ecosystem for different purposes. If the traditional model of tool maker taxonomic identity is correct (i.e., *Homo* sp.), then tool-related activities were positioned in comparable habitats as the isotopic diet.

Conclusions

Our new pedogenic carbonate $\delta^{13}C_{VPDB}$ results from the Nachukui Formation corroborate previous sedimentological and faunal studies, interpreted to represent mosaic savanna environments, as well as previous paleosol isotopic studies from the Turkana Basin showing grassland expansion through time influenced by paleogeography. Pedogenic carbonate $\delta^{13}C_{VPDB}$ values of paleosols in the Nachukui and Koobi Fora Formations located adjacent to lithic archaeological sites were significantly lower and indicate that more wooded landscapes were present than those of coeval basin environments at 2.4–1.4 Ma. As basin environments demonstrate increased expansion of grassland communities due to climatic and tectonic factors and influenced by a dynamic paleogeographic setting, hominin lithic sites maintain f_{wc} circa 40%. Our results suggest that 'stone age visiting cards' (Isaac, 1981) were differentially left in relatively more wooded areas in the Turkana Basin. We interpret this to indicate that tool-making hominins preferred more wooded habitats during lithic-related activities potentially to reduce heat stress and in order to gain access to potable water, raw materials, and/or dietary resources at or near river channels and lake margins. We also suggest that the maintained lithic site f_{wc} circa 40% throughout our study interval may indicate a preference for ecotones between woody and grassy habitats for differential access to terrestrial ungulate carcasses. Finally, our results may be indicative of preference for C_3 plant resources to the omnivorous hominin diet.

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