



Pleistocene animal communities of a 1.5 million-year-old lake margin grassland and their relationship to *Homo erectus* paleoecology

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ABSTRACT

The ecological and selective forces that sparked the emergence of *Homo*'s adaptive strategy remain poorly understood. New fossil and archaeological finds call into question previous interpretations of the grade shift that drove our ancestors' evolutionary split from the australopithecids. Furthermore, issues of taphonomy and scale have limited reconstructions of the hominin habitats and faunal communities that define the environmental context of these behavioral changes. The multiple ~1.5 Ma track surfaces from the Okote Member of the Koobi Fora Formation at East Turkana provide unique windows for examining hominin interactions with the paleoenvironment and associated faunas at high spatiotemporal resolution. These surfaces preserve the tracks of many animals, including cf. *Homo erectus*. Here, we examine the structure of the animal community that inhabited this landscape, considering effects of preservation bias by comparing the composition of the track assemblage to a skeletal assemblage from the same time and place. We find that the track and skeletal assemblages are similar in their representation of the vertebrate paleocommunity, with comparable levels of taxonomic richness and diversity. Evenness (equitability of the number of individuals per taxon) differs between the two assemblages due to the very different circumstances of body fossil versus track preservation. Both samples represent diverse groups of taxa including numerous water-dependent species, consistent with geological interpretations of the track site environments. Comparisons of these assemblages also show a pattern of non-random hominin association with a marginal lacustrine habitat relative to other vertebrates in the track assemblage. This evidence is consistent with behavior that included access to aquatic foods and possibly hunting by *H. erectus* in lake margins/edaphic grasslands. Such behaviors may signal the emergence of the adaptive strategies that define our genus.

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1. Introduction

Reconstructing the environments where hominins lived and evolved is critical to understanding what drove adaptive shifts in our evolutionary past and what effects our ancestors' presence had on the world around them (Hill, 1981). Human evolutionary theory

proposes links that hominin speciation/extinction events and important shifts in behavior were linked to global-scale patterns of climate change (e.g. Dart, 1925; Robinson, 1954; Jolly, 1970; Vrba, 1988; Coppens, 1994; de Menocal, 1995; Potts, 1998a; Trauth et al., 2005) and variability (Potts, 1998b; Kingston, 2007). Hominins themselves have been proposed as agents of ecological change as well, fundamentally altering faunal communities (e.g. Werdelin and Lewis, 2013; Faith, 2014; Lyons et al., 2016) and accelerating recent global warming (e.g. Vorosmarty et al., 2000; Hughes et al., 2003; Karl and Trenberth, 2003).

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What drove the evolutionary origin of our own genus, *Homo*, and what the impacts of this emergence were, remain central questions in paleoanthropology (e.g. Wood, 1992; Wood and Collard, 1999; Anton et al., 2014). Early definitions of *Homo* focused largely on increased brain size and the appearance of stone tools (Le Gros Clark, 1955; Leakey et al., 1964), suggesting that our ancestors were intensively processing resources within their environment and possibly relying on meat (DeVore and Lee, 1968). However, recent discoveries have shown that not all members of our genus were large-brained (Brown et al., 2004; Potts et al., 2004; Spoor et al., 2007; Lordkipanidze et al., 2013) and that tool use significantly predates the earliest fossils attributed to *Homo* (McPherron et al., 2010; Harmand et al., 2015). In the face of this eroding definition, newer theories have suggested that the adaptive suite that defines our genus includes other methods of more effectively extracting resources from the environment, including changes related to energy allocation (Aiello and Wheeler, 1995; Pontzer, 2012; Pontzer et al., 2016), cooking (Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Carmody and Wrangham, 2009) and hunting behavior (Bramble and Lieberman, 2004; Roach et al., 2013; Merritt, 2016), as well as shifts in social structure (Wrangham et al., 1999), cooperation (Anton et al., 2014) and land use (Roach et al., 2013, 2016). Each of these hypotheses concerns aspects of the paleobiology of *Homo* that are intricately tied to the environment, and evaluating these theories hinges upon improved understanding of the paleoecological context of early *Homo*.

Given the importance of paleoecology for addressing these competing evolutionary models, it is not surprising that the last two decades have been marked by the development and application of important new methods (e.g. isotopic geochemistry, dental microwear analyses and ecomorphology). However, these new techniques have often revealed additional variability and complexity in the data used to reconstruct paleoenvironments. Quantitative data generated by these methods frequently resist easy classification into archetypal habitat categories (e.g. grasslands, woodlands, bushlands). For example, many fossil hominin sites have evidence of multiple habitat categories and are frequently termed “mixed habitats” (e.g. Plummer and Bishop, 1994; Leakey et al., 2001; Bobe, 2006; Kingston, 2007). While this “mosaic” characterization of paleohabitats may represent true vegetation patchiness at a single time period, it can also represent a palimpsest of shifting environments at one site over time or differences in time and spatial scale between methodologies. Inter-site comparisons are also complicated by differing depositional regimes and post-depositional processes. Furthermore, regional responses to global climate trends can vary between contemporaneous sites within the same rift system (e.g. Kingston et al., 1994; Kingston, 2007; Cerling et al., 2011; Levin, 2015). These different signals recorded at different scales and using different methods result in continuing debates about how to reconstruct hominin habitats.

The ~1.5 Ma fossil track assemblage from near the town of Illet in northwestern Kenya preserves snapshots of hominin behavior and habitat use that are uniquely resolved in time and space (Bennett et al., 2009; Hatala et al., 2016, 2017; Roach et al., 2016). These trackways contain 97 hominin footprints, tentatively attributed to cf. *Homo erectus* based on their large size, modern foot morphology, gait parameters and putative group structure (attribution discussed at length in Bennett et al., [2009], Hatala et al., [2016]). In addition to the many hominin tracks recovered, these ancient land surfaces also record the presence and movement of many other animals near the Pleistocene lakeshore in successive stratigraphic units. Because these track surfaces are found within Okote Member deposits that also preserve geological information

about the paleoenvironment and skeletal and dental fossils spanning ~20 ka (Roach et al., 2016), we have the opportunity to compare different samples of the vertebrate paleocommunity and also to examine how differences in temporal scale affect paleoecological interpretations of the animal community.

It is unusual for paleocommunity reconstruction to be based on both tracks (ichnofossils) and skeletal fossils (Krapovickas et al., 2009), as these are rarely found in the same strata. Here, our primary objective is to combine community-based approaches (e.g. Fleming, 1973; Andrews et al., 1979; Van Couvering, 1980; Damuth, 1982; Reed, 1998; Andrews and Humphrey, 1999; Kovarovic et al., 2002) with neoecological metrics to reconstruct the faunal community that included the cf. *H. erectus* track makers. Using quantitative measures of diversity, richness and evenness for the trace and skeletal fossil assemblages from the same narrow time interval, we statistically test how this fossil community differs at different scales. We then assess the unique information provided at each scale against various taphonomic and spatiotemporal biases. Through this process, the examination of biasing factors in the two assemblages allows underlying real differences in community structure to emerge. All data and bias information are then incorporated into our reconstruction of the paleoenvironment at this important time.

A unique aspect of the two Okote Member faunal data sets presented here is that aspects of animal behavior can also differentially bias one data set over the other. This gives us the opportunity to assess some aspects of hominin land use in a way that was not possible previously. Further, the unusually short temporal scale of each trackway surface in the footprint assemblage also helps connect the fossil record to modern ecological studies and theory. This is especially valuable given that most theorized human behavioral adaptations occur within hominin individuals' life spans (e.g. hunting and tool-making) and not the thousands of years represented by most paleoecological proxies (e.g. isotopic analyses of dental remains). We conclude our study by combining our own data with the current literature to propose a model for early *H. erectus* paleobiology.

1.1. Hypotheses

Reconstructing the faunal community that existed in East Turkana at the time of the putative *H. erectus* footprint makers requires an understanding of how the track and skeletal fossil assemblages sampled the original community. Here, we provide descriptive and statistical assessments of community structure and the taphonomic, behavioral and ecological biases that affect both data sets. With these comparisons we assume that the skeletal fossil assemblage generally represents the original presence and frequency of taxa within the Pleistocene faunal community (Western and Behrensmeyer, 2009 — their study compares surface bone in a modern ecosystem and does not include taphonomic processes post burial). The primary null hypothesis (H_0) of our comparisons is that the track and skeletal assemblages will not differ in community structure or be differentially affected by bias-inducing processes. These two data sources have been differently sampled, and it is clear that the fossil track assemblage has lower levels of temporal and spatial averaging than the bone assemblage (Roach et al., 2016). Each track surface represents a very short-term snapshot of the fauna in a small area, although the combined sample of all of these surfaces extends over ~20 ka and they are distributed over a total area of ~1 km². The skeletal samples are time-averaged over ~20 ka and were recorded over approximately the same area. Support for H_0 would imply that either the more finely resolved footprint assemblage or the time-averaged faunal sample is a random subset of the other assemblage. However, we anticipate

that taphonomic processes affected the two assemblages differently. For instance, there is a size bias against the preservation of smaller mammals in the skeletal record, and it also represents a wider range of depositional circumstances (such as deltaic plain, distributary channel and lake margin) than in the trackways. Accordingly, our secondary null (H_0) posits that differences between the track and skeletal assemblages will result from sampling or preservation bias and not differences in the underlying animal community. We propose that data that violate both null hypotheses represent true ecological differences particular to the lake margin habitat where the footprints were deposited.

2. Materials and methods

2.1. Data sources

The track assemblage analyzed here is composed of two different data sets: 1) four large targeted excavations, and 2) 20 1 m² random test squares (Fig. 1). The targeted excavations, conducted between 2006 and 2014, uncovered large track surfaces where hominin tracks (or other tracks of interest) had been discovered (Bennett et al., 2009; Hatala et al., 2016, 2017; Roach et al., 2016). These sites are tightly time bracketed within the

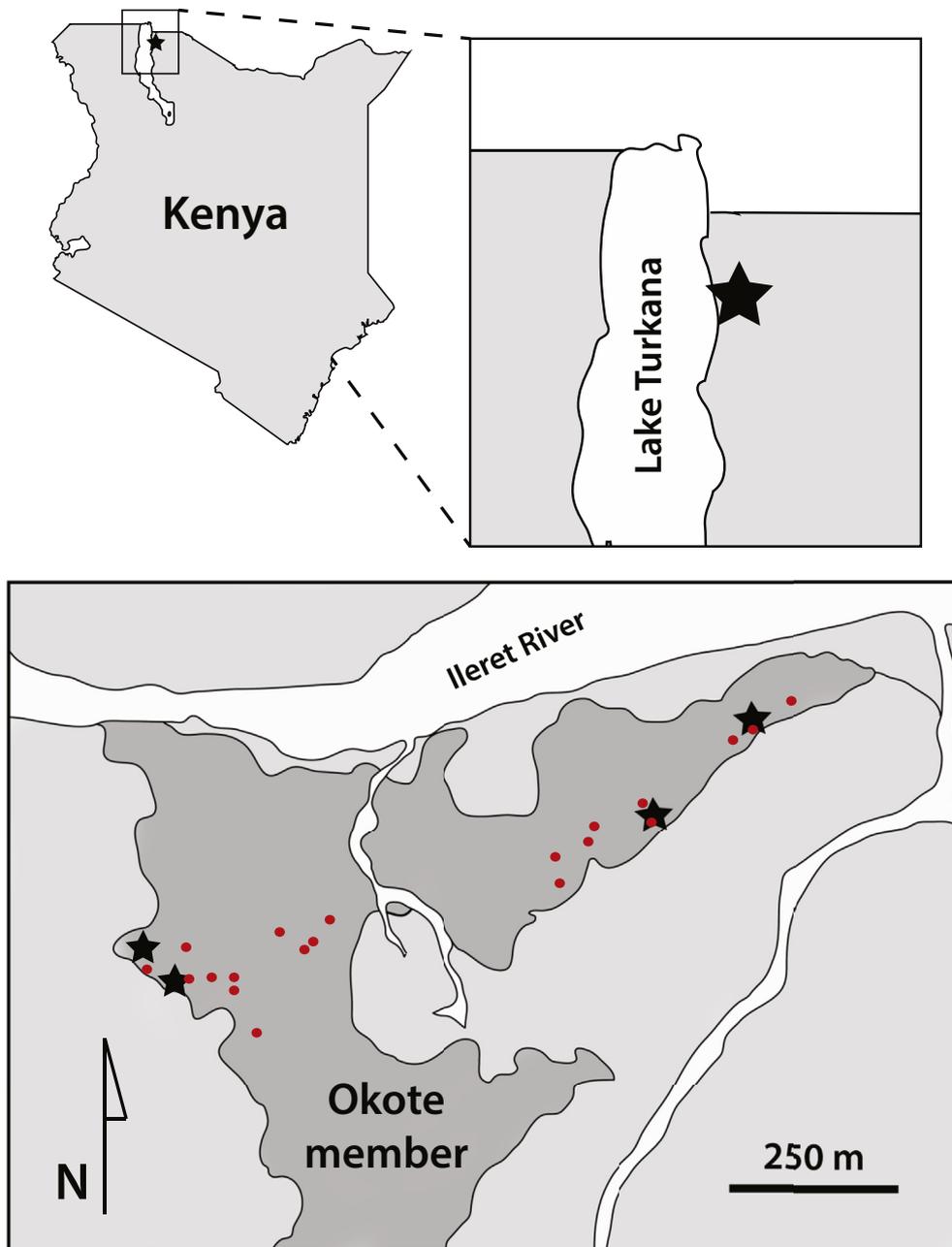


Figure 1. Location of the Ileret fossil trackway sites. The fossil tracks are located in northwestern Kenya, along the east side of Lake Turkana, approximately 5 km east of the town of Ileret. All track surfaces in this study occur within the Okote Member of the Koobi Fora Formation and are dated to between 1.51 and 1.53 million years ago (Brown et al., 2006; McDougall and Brown, 2006; Bennett et al., 2009). In the bottom panel, hominin track localities are shown with black stars and other track-bearing test excavations are shown with red dots. Skeletal fossils were collected from the same general area as the track sites. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Ileret Tuff complex (ITC) to 1.51–1.53 Ma. The largest of these sites, Fwjj14E (referred to throughout as 14E), contains a total of 54 m² of exposed track surface and accounts for nearly 75% of all hominin tracks recovered. The three other targeted excavations exposed a combined 40 m² of outcrop. Given the outsized importance of 14E in behavioral and habitat reconstructions, as well as the potential for this single site to significantly skew our animal community reconstructions simply due to its size, we also conducted all analyses in parallel with 14E removed. The random test surveys, conducted in 2014, were a series of twenty 1 m² excavations from the same survey areas (1A and 3) within the ITC (Roach et al., 2016). The locations of these test squares were randomly chosen and surveyed for any identifiable animal tracks. If a track was found within 50 m of the randomly selected GPS locale, a test square was gridded and excavated and all tracks were recorded.

Tracks were included in the data set analyzed here if they were deemed identifiable to a broad taxonomic category. Some classifications are more precise than others. For example, while artiodactyl tracks are easy to identify as such, separating bovid from suid was often not possible in deep or distorted tracks, so we conservatively chose to use a combined bovid/suid category for classification. It should be noted that this mixing of different hierarchical classification levels will up-weight the contributions of some taxa in our analyses (e.g. Reptilia lumps lower taxonomic categories) while down-weighting others (e.g. Artiodactyla is split into Families). While the use of low taxonomic resolution limits our ability to detect within-family differences between the data sets, it does give us confidence that those detected differences between the track and skeletal assemblages are meaningful.

2.2. Overview of analysis

To address how representative the track assemblage is of the overall faunal community, we compare the track data to a skeletal fossil assemblage collected from the same square kilometer of Area 1A within the ITC, making both data sets of comparable spatial scale. This bone assemblage was recorded in 1979 by AKB using standardized surface surveys (“bone walks”), where subsections of Area 1A ITC outcrop were visually surveyed and all identifiable surface fossils were recorded (Behrensmeyer, 1985; Roach et al., 2016). For quantitative analyses, all skeletal data were collapsed into the same broader taxonomic categories used for the track assemblage. This effectively removes issues of taxonomic scale between the data sets. Only fish in the skeletal sample were

excluded, as they do not leave trace fossils in the same manner as the tetrapods that comprise the rest of the data set.

All descriptive and statistical analyses use the estimated minimum number of individuals (MNI) present in the skeletal assemblage and on each track surface. Skeletal assemblage MNIs were estimated by aggregating elements (by taxa and age) from the same exposed stratigraphic interval and across several meters laterally. All bones conceivably belonging to a single individual were then lumped into one record in the data set. Given the limited extent of the bone walks, this method was employed to account for both the lateral dispersal of bones as well as recent movement due to erosion. Typical element counts used to estimate MNI obviously are not possible for fossil tracks. Accordingly, we tested various methods for discounting multiple track records from single individuals (e.g. parsimoniously attributing tracks reflecting the same body mass to the same individual, and discounting “extra” tracks based on the number of print-making limbs). However, we were not satisfied that these corrections were adequately accounting for the structure of the trackways without introducing additional sources of bias. We settled on a method of assigning tracks as repeated records of single individuals when size and directionality were consistent with an individual walking (Fig. 2). This allowed for the inclusion of multiple tracks per individual and also provided an estimate of gait structure. However, this method cannot account for the possibility of an individual crossing a track surface more than once. While we view this possibility as unlikely due to the limited spatial extent and short amount of time represented by the trackways (Roach et al., 2016), it remains a potential source of error. Furthermore, the possibility of crossing a track surface more than once would not be limited to any particular taxon. It should also be noted that each track excavation occurs in localized sedimentary layers, most of which are at different stratigraphic levels within the ITC, and thus each is assumed to represent a different period of time with unique individuals moving across discrete land surfaces.

All statistical analyses were conducted using R software, v. 2.15.2 (R Core Team, 2013).

2.3. Community structure (alpha diversity metrics)

Our goal is to compare the faunal composition in two very different samples of the ITC vertebrate paleocommunity. At the most basic level, a faunal community can be described in terms of taxonomic richness and evenness. Richness is the number of taxa present, while evenness compares the number of individuals per taxonomic category in the assemblage (Faith and Du, 2017). A

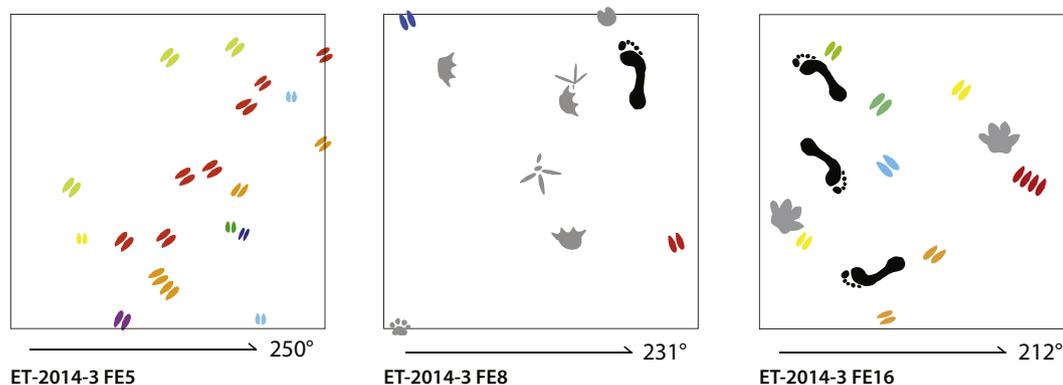


Figure 2. Estimating minimum number of individuals (MNI) for trackways. Color-coding of potential single bovid/suid individuals is shown for representative 1 m² test excavations. Tracks are estimated to represent a single individual if their size and orientation could be consistent with the path of a single animal across the land surface at a single point in time. Site name and backwall orientation are shown below the figures. Note: MNI information is only shown for bovid/suid tracks and not for other taxa. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

perfectly even community will have its individuals distributed uniformly across all taxa (i.e. all taxa have the same number of individuals). One problem with richness measures is that they are known to be highly correlated with sample size (Hurlbert, 1971; Gotelli and Colwell, 2001). Diversity estimates, which incorporate information from both richness and evenness, are similarly affected by the number of individuals in the sample (Magurran, 2004). Comparing measures of evenness or estimates of diversity between sites or data sources that differ in sampling effort or sample size can be especially problematic.

This problem has been resolved for evenness measures by calculating the probability of interspecific encounter or PIE (Hurlbert, 1971). The PIE (Appendix 1, Equation [Eq.] A.1) avoids sample size effects because it is an unbiased measure that calculates the likelihood that any two individuals extracted from a sample represent different taxa (1 is the highest evenness attainable, while 0 is the lowest). We bootstrap the calculation of this measure 1000 times to establish 95% confidence intervals.

Sampling intensity bias, which may affect comparison of richness and diversity, is often addressed by “rarefying” the community with the larger sample down to the number of individuals present in the smaller community (Sanders, 1968; Hurlbert, 1971; Simberloff, 1972; Gotelli and Colwell, 2001). However, the ratio of richness between rarefied communities will depend on the arbitrary number of individuals to which it is down-sampled. This means that one can conclude, at most, that one community is larger than the other, and this method does not measure the magnitude of the differences (Alroy, 2010; Jost, 2010; Chao and Jost, 2012). To avoid this, we have chosen to use a rarefaction method based on sample coverage and not on the number of individuals. To do this, we first estimate coverage (Good, 1953; Chao and Jost, 2012), which is a measure of sample completeness (Appendix 1, Eq. (A.2)). This is calculated as the proportion of individuals in the total, unseen sample that are represented by the taxa within the observed sample (1 representing complete coverage, 0 being no coverage). We then rarefied all samples to the lowest coverage estimate in the three candidate communities (All tracks, Tracks without 14E, and Body fossils).

To calculate richness and diversity, we used a method that leverages the effective number of taxa (Hill number) in each rarefied data set, which is the number of equally abundant taxa needed to recover the same value of diversity (MacArthur, 1965; Hill, 1973; Jost, 2006). Higher order Hill numbers (q) yield an increased focus on more dominant species in a community. Furthermore, higher order Hill numbers will be less affected by sampling bias because rare species (or rare higher taxa), which are less likely to be recovered in small samples, are down-weighted. Diversity estimates with a Hill number $q = 0$ do not include abundance information, considering common and rare taxa equally. This measure is simply rarefied taxonomic richness. Hill number $q = 1$ is Shannon diversity, which weights species in accordance with their abundance. Hill number $q = 2$ is Simpson diversity, which up-weights common species. Using a bootstrap method with 1000 iterations (Chao et al., 2014), we calculate rarefied diversity estimates and 95% confidence intervals for Hill number orders $q = 0, 1, 2$ (Appendix 1, Eq. (A.3)).

2.4. Community similarity (beta diversity metrics)

Beyond comparisons of community structure, we also directly measure how different the skeletal and track communities are in their composition. The Dice pairwise dissimilarity index is the simplest statistic for comparing the similarity of these two assemblages and is interpreted as the average proportion of a sample that is not shared with another (Dice, 1945; Sorensen, 1948). This

ratio is calculated using the presence/absence of taxa within each community (Appendix 2, Eq. (B.1)). A β_{dice} value of 1 represents two communities that share no taxa in common, whereas 0 indicates identical communities. The Dice index can be additively partitioned into turnover and nestedness components (Baselga, 2010). Turnover is defined as the replacement of taxa when comparing one community to another. It is calculated as ratio of unique to total taxa in the less-rich community and is defined using the same variables as the Dice index (Appendix 2, Eq. (B.2)). Nestedness represents differences between the assemblages resulting from the smaller assemblage being a subsample of the larger community (Appendix 2, Eq. (B.3)). We parsimoniously attribute to nestedness all differences that result from taphonomic and sampling processes. Therefore, if we have two identical communities and taphonomic and sampling processes remove taxa from one of these, the altered community should be a perfect subset of the unaltered one.

While these measures derived from the Dice index are useful for identifying differences between the skeletal and track assemblages, they rely solely on presence/absence data with no accounting for differences in abundance. To account for these differences, we also calculate the Horn measure of overlap and the Morisita-Horn index (Horn, 1966). Paralleling the weighting of abundance using Hill numbers, the Dice index weighs rare and common species equally, the Horn measure of overlap (Appendix 2, Eq. (B.4)) weighs species in accordance with their abundance and the Morisita-Horn index (Appendix 2, Eq. (B.5)) up-weights common species. These measures have been mathematically linked to richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$) respectively (Jost, 2006).

When used to compare communities, these metrics are known to be affected by difference in sample size and alpha diversity (Chase et al., 2011). Therefore, we calculated the ratio of the observed metric between the two assemblages to the expected value if both communities sampled the same taxonomic pool (as a standardization factor). The expected metric was calculated using Monte Carlo methods, where both assemblages were pooled and 1000 random draws were taken with replacement according to the sample size of each assemblage (thereby holding differences in sample size and richness constant). The relevant measure was calculated for each of the 1000 pairwise simulated communities, the median of which was taken as the expected value. This method only measures turnover, with nestedness disregarded and attributed to sampling or taphonomic bias. Here a dissimilarity value of 1 again represents two communities that share no taxa in common, whereas 0 indicates perfectly nested communities.

2.5. Spatial patterning in the trackway community

Spatial clustering of taxa and taxic diversity among the twenty discrete random track sites may represent patterns of taphonomic bias across sites or potentially real differences in habitat usage patterns on a small spatial scale. To assess any potential spatial patterning within the track assemblage, we calculate the locational quotient (LQ) for each taxon at each site (Haig, 1926; Kalkhan, 2011). This ratio essentially compares the relative concentration of individuals from a certain taxon on the local scale to the prevalence of individuals from that same taxon on the global scale of the whole sample (Appendix 3, Eq. (C.1)). An LQ value of 1 indicates comparable representation of a taxon on both the local and global scale. LQ values below 1 show an underrepresentation of a certain group on the local scale compared to their prevalence in the overall faunal community, while values above 1 indicate an overrepresentation. It is worth noting that this ratio is highly sensitive to the presence of rare taxa. Data were then grouped by locality,

GPS coordinates or specific taxon representation for statistical analysis.

3. Results

The skeletal assemblage of 105 elements found within the ITC in Area 1A is estimated to represent a total of 81 individuals, while the 480 fossil tracks recovered from the same locale are estimated to have been made by 262 individuals (Table 1). The large size of the track assemblages is reflected in both higher abundance and raw richness than the body fossil assemblage (Fig. 3). However, when examined independently of sampling effort, the skeletal assemblage is more even (Fig. 4). Statistical comparison of the skeletal and track assemblages shows a significant difference in community structure (Fisher's exact – Monte Carlo, $0.0005 > p > 0.0001$). The fact that excluding of the largest excavated site, FwJ14E, from the track sample does not significantly alter the skeletal/track comparisons (Fisher's exact – Monte Carlo, $0.0005 > p > 0.0001$) or the probability of interspecific encounter suggests a similar compositional structure for all track sites. Further, a comparison of the track assemblage MNIs with and without 14E shows no difference in community structure when this site is removed (Fisher's exact – Monte Carlo, $0.987 > p > 0.985$).

Although there are large differences between MNI estimates for the skeletal and track assemblages, coverage estimates show both datasets are comparable and near complete at the chosen taxonomic resolution (all tracks $\hat{C} = 0.985$, tracks without 14E $\hat{C} = 0.986$, body fossils $\hat{C} = 0.963$). To enable valid statistical comparison between data sets, all samples were rarefied down to the lowest coverage (0.96) resulting in reduced MNIs (all tracks $MNI_R = 62$, tracks without 14E $MNI_R = 66$, body fossils $MNI_R = 42$). Coverage-adjusted richness is slightly lower on average in the skeletal assemblage than for the track assemblage, but not significantly so when accounting for the bootstrapped confidence intervals (Fig. 5, Table 2). However, when abundance is taken into account, the bone sample shows significantly higher diversity (by 1.5 fold). This higher diversity in the skeletal assemblage is even more pronounced (by 1.7 fold) when common species are up-weighted (Fig. 5, Table 2). The skeletal assemblage's increased diversity is likely driven by its being more even, thus sampling more taxa per individual than the more skewed track data sets.

Direct comparisons between the skeletal and track assemblages show most taxa are shared between the two data sets (β_{dice} with approximately one third of the taxa being unique to one assemblage or the other (Table 3). Both turnover and nestedness contribute fairly equally to the overall dissimilarity of the assemblages, with a slightly larger contribution from nestedness. Given

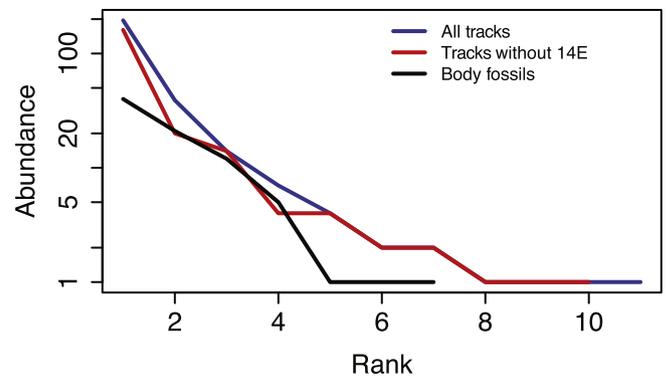


Figure 3. Rank-abundance for track and skeletal assemblages. Taxa are rank ordered in terms of abundance and plotted in descending order (Data from Table 1). Body fossils show overall lower richness (fewer taxa, resulting in a shorter curve along the x-axis). Evenness (based on the slope of each curve) is variable.

that nearly all taxa within the body fossil sample (except giraffids) are a subset of the taxa found in the track sample, it is not surprising that this data set is highly nested. Thus, while some of the dissimilarity can be accounted for by nestedness, sampling and taphonomic biases, there is still some degree of turnover present, possibly reflecting real compositional differences. Sample size-adjusted dissimilarity values are also quite low suggesting high nestedness or compositional similarity between the skeletal and track assemblages (All tracks versus Body fossils – Dice = 0.167, Horn = 0.239, Morisita-Horn = 0.167; Tracks without 14E versus Body fossils – Dice = 0.143, Horn = 0.229, Morisita-Horn = 0.169). Dissimilarity shows a small increase when directly accounting for abundance, although this dissimilarity decreases again when looking at only the most common taxa (i.e., using the Morisita-Horn dissimilarity; Fig. 6).

Spatial analyses show no East-West patterning of any taxon when track sites are grouped by GPS easting coordinates (Mann–Whitney; U range 41–55; p range 0.34–1). This lack of patterning for aquatic taxa is consistent with a deltaic, lake margin zone that fluctuated in position over the ~20 ka years of discontinuous track surface deposition. At the two largest sites (14E – 54 m² and FE3 – 18 m²) where hominin tracks and individuals are more abundant relative to the overall assemblage (hominin LQ > 1), the mean LQ of all non-hominin taxa is half that of sites where hominin tracks are underrepresented relative to those of other taxa (Friedman; $\chi^2_r = 4$ $p = 0.046$). This suggests that extending excavations generally increases the number of tracks found but will not significantly increase taxic diversity. This is consistent with the

Table 1

Number of identified specimens (NISP) and the minimum number of individuals (MNI) for the track and body fossil assemblages (percentages in parentheses).

	NISP				MNI			
	All tracks	Tracks without 14E	Random squares	Body fossils	All tracks	Tracks without 14E	Random squares	Body fossils
Aves	29 (6)	29 (8.6)	10 (4.9)	–	14 (5.3)	14 (6.7)	6 (4.4)	–
Bovidae/Suidae	325 (67.7)	264 (73.3)	176 (85.9)	42 (40)	195 (74.4)	161 (76.7)	115 (85.2)	40 (49.4)
Carnivora	1 (0.2)	1 (0.3)	1 (0.5)	–	1 (0.4)	1 (0.5)	1 (0.7)	–
Cercopithecidae	1 (0.2)	1 (0.3)	–	1 (1)	1 (0.4)	1 (0.5)	–	1 (1.2)
Equidae	2 (0.4)	2 (0.6)	2 (1)	–	2 (0.8)	2 (1)	2 (1.5)	–
Giraffidae	–	–	–	1 (1)	–	–	–	1 (1.2)
Hippopotamidae	13 (2.7)	4 (1.2)	4 (2)	15 (14.3)	7 (2.7)	4 (1.9)	4 (3)	12 (14.8)
Hominin	97 (20.2)	29 (8.6)	8 (3.9)	1 (1)	34 (13)	20 (9.5)	3 (2.2)	1 (1.2)
Proboscidea	1 (0.2)	1 (0.3)	–	7 (6.7)	1 (0.4)	1 (0.5)	–	5 (6.2)
Reptilia	4 (0.8)	4 (1.2)	4 (2)	38 (36.2)	4 (1.5)	4 (2)	4 (3)	21 (25.9)
Rhinocerotidae	2 (0.4)	2 (0.6)	–	–	2 (0.8)	2 (1)	–	–
Tubulidentata	5 (1)	–	–	–	1 (0.4)	–	–	–
Total	480	337	205	105	262	210	135	81

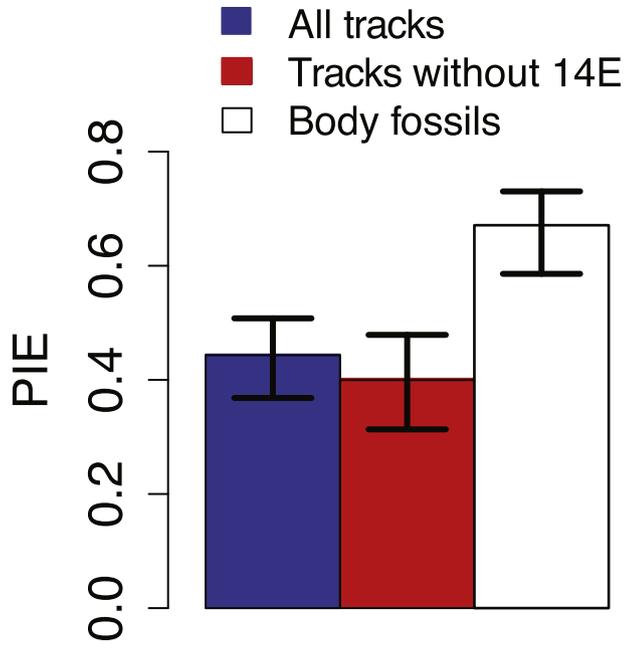


Figure 4. Probability of interspecific encounter (PIE). When sample size effects are accounted for, evenness, a measure of the number of individuals represented in each taxon, between the track assemblage and the body fossils is significantly different (95% confidence intervals show no overlap). The body fossil data are significantly more even (PIE = 0.671 (white)) than the track assemblage (all tracks PIE = 0.443 (blue); without 14E PIE = 0.4 (red)). Data are from Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

expectation that only a limited number of individuals and species will cross an active track surface during the short track emplacement time window (Roach et al., 2016). However, when all sites containing hominins are pooled versus non-hominin bearing sites, sites with hominins show a greater diversity of taxa with an average LQ 1.75 times higher than the non-hominin sites (Friedman; $\chi^2_r = 3.6$; $p = 0.05$). This may be driven by the fact that bovid/suid tracks are less common at sites where hominin prints are found (Mann Whitney; $U = 10$; $p = 0.015$) and that sites with proportionally fewer bovid/suid tracks are significantly more diverse (Friedman; $\chi^2_r = 7.4$; $p = 0.007$).

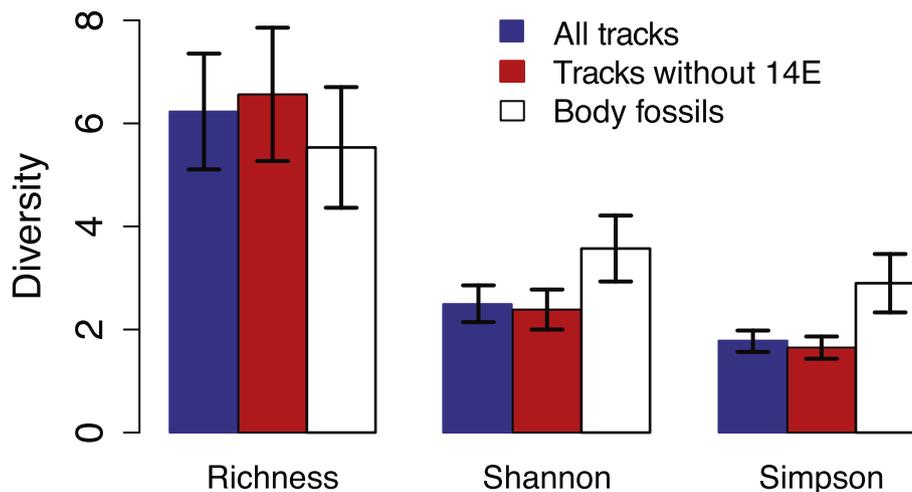


Figure 5. Alpha diversity estimates. When rarefied to comparable data set sizes, track and body fossil diversity do not differ in taxonomic richness. However, when taken in proportion to abundance, the body fossil data show greater diversity (Shannon diversity). This effect is further exaggerated when common taxa are up-weighted (Simpson diversity). Raw values for each Hill number order are reported in Table 2. Black bars indicate 95% confidence intervals. Data are from Table 1.

Table 2

Hill number diversity estimates (all diversity estimates are rarefied to 0.96 coverage and bootstrapped 1000 times to generate confidence intervals [CI]).

	Diversity estimate	0.025 CI	0.975 CI
Diversity of orders $q = 0$ (i.e. richness)			
All tracks	6.230283	5.106319	7.354246
Tracks without 14E	6.563702	5.269668	7.857736
Body fossils	5.533029	4.362409	6.703648
Diversity of orders $q = 1$ (i.e. Shannon diversity)			
All tracks	2.499902	2.142664	2.857141
Tracks without 14E	2.387735	1.999557	2.775914
Body fossils	3.571345	2.931753	4.210937
Diversity of orders $q = 2$ (i.e. Simpson diversity)			
All tracks	1.772909	1.565362	1.980456
Tracks without 14E	1.649023	1.433210	1.864836
Body fossils	2.898649	2.332067	3.465232

Table 3

Beta diversity estimates.

	Bone versus ALL tracks	Bone versus Tracks (without 14E)
Dice	0.3333333	0.2941176
Turnover	0.1428571	0.1428571
Nestedness	0.1904762	0.1512605

4. Discussion

4.1. Community structure

Richness estimates for the track and skeletal assemblages show that both samples represent a faunal community with a comparable number of taxa. In both assemblages, richness values are driven by the representation of rare taxa with only a few common groups, a universal pattern found in all modern communities (McGill et al., 2007). However, when abundance is taken into consideration the skeletal fossil assemblage is always more diverse. This is due to the higher evenness in the skeletal fossil sample, in contrast to the notably large number of bovids/suids in the track assemblage. Bovids/suids are 5.7 times more abundant than the second ranking taxon within the track assemblage and less than two times more abundant than their closest neighbor in the skeletal assemblage (Table 4). Additionally, targeting bias in the track sample likely

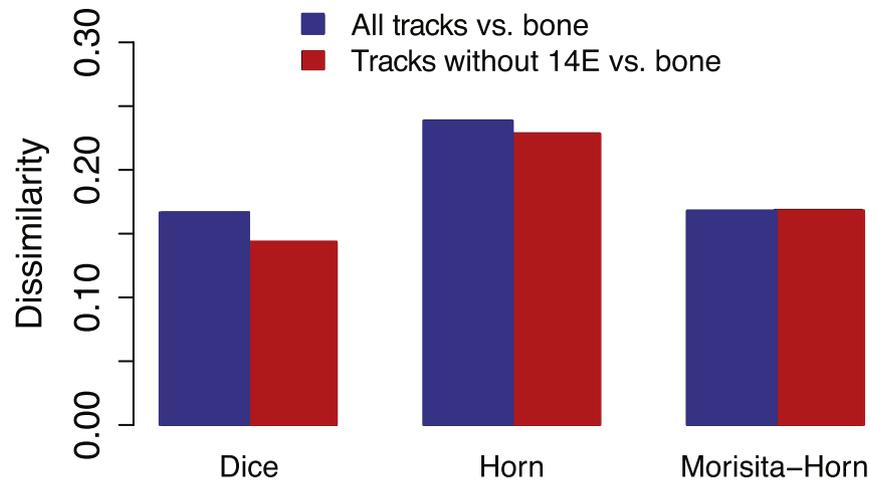


Figure 6. Beta diversity estimates accounting for abundance. These metrics are linked mathematically to Hill number diversity estimates (Dice— $q = 0$ or richness; Horn— $q = 1$ or Shannon; Morisita-Horn— $q = 2$ or Simpson) (Jost, 2006). Dissimilarity between the track and skeletal assemblages is low when up-weighting rare (Dice) and common taxa (Morisita-Horn). A slight spike occurs when directly accounting for abundance (Horn), however the values are still low, indicating that the comparisons with and without 14E are very similar. Data are from Table 1.

inflates the number of hominins, also reducing track evenness (Roach et al., 2016). Despite these confounding factors, subtle amounts of dissimilarity suggest that while these two assemblages are very similar to each other, there are minor, but real, compositional differences (invalidating our primary null hypothesis, H_0).

Although neither assemblage differs significantly in spatial or taxonomic scale, it is possible that some of the subtle differences between these data sets are the result of large differences in temporal scale. Experimentation has shown that individual track surfaces may represent a time window of a few hours to days (Roach et al., 2016), while the bone assemblage represents more continuous accumulation over ~20 ka. These differences in time-averaging should increase the proportion of rare taxa in the skeletal assemblage (Tomasovych and Kidwell, 2010b) as most species in a community will be rare and transient (Magurran and Henderson, 2003). This is because, while abundant taxa are already recorded (McGill, 2003), as more time is sampled more rare species will be captured, either due to more complete sampling or stochastic movement of taxa across the landscape (Grinnell, 1922). This agrees well with the higher evenness in the skeletal assemblage being driven by the addition of more rare taxa as well as the

more equal representation of common taxa. Given the higher return of rare taxa in time-averaged data sets, taxonomic richness should also increase in the body fossil assemblage (Preston, 1960; Rosenzweig, 1995; White et al., 2010), even when accounting for the larger number of individuals (Kidwell, 2002; Tomasovych and Kidwell, 2010a). That is clearly not the case here, suggesting that temporal scale alone does not explain all differences between the two assemblages.

Taphonomic processes and behavioral patterns may bias the composition of the two assemblages further. For example, the fact that large numbers of bovid/suid tracks at some sites are correlated with reduced diversity may reflect overprinting (i.e. making prints on a surface that damages or replaces existing prints or other features). The directional movement of a herd of medium sized bovinds over very short time intervals (Roach et al., 2016) could obliterate any tracks previously emplaced on an active trackway. This would inflate the relative abundance of bovinds/suids by reducing the number of non-artiodactyl tracks recovered. Furthermore, the short depositional history of the trackways, which was observed and tested on the modern lake margin (Roach et al., 2016), affects the likelihood of certain taxa being recorded. Obligate drinkers would be more likely to approach a lake margin during a period of a few hours to a day than would non-water dependent taxa. Short trackway duration could also interact with diurnal shifts in temperature to drive an unequal pattern of print deposition and infilling. High amounts of solar radiation during the day heat the land and lake differentially causing a convective pattern of wind blowing from the lake to the shore. In a hot, arid region like Pleistocene East Turkana (Passey et al., 2010; Blumenthal et al., 2017), this heat is differentially lost at night, reversing the wind direction. Such nocturnal inversion results in the appearance of a strong horizontal wind right at the ground surface (Blackadar, 1957; Zhang and Zheng, 2004), which is often the fastest wind experienced during a full day cycle, potentially causing higher seiche-driven, water level changes at night. Periods of higher pseudotide would cover track surfaces with water, and gentle wave action could infill the tracks with well-sorted, finely laminated sands. These sand layers, which coat the track surfaces but do not penetrate into the track bearing silts, help preserve tracks by creating a composite sediment surface that is less deformable than the silts alone. With the combination of short trackway duration, higher water level changes and night-skewed infilling, it is possible that

Table 4
The most common taxa by data type
(MNI = minimum number of individuals).

Taxon	MNI
<i>All tracks</i>	
Bovidae/Suidae	195
Hominin	34
Aves	14
Hippopotamidae	7
Reptilia	4
<i>Tracks without 14E</i>	
Bovidae/Suidae	161
Hominin	20
Aves	14
Hippopotamidae	4
Reptilia	4
<i>Body fossils</i>	
Bovidae/Suidae	40
Reptilia	21
Hippopotamidae	12
Proboscidea	5
Giraffidae	1

nocturnal and crepuscular species are forced away from these track surfaces by standing water or do not make prints in the sand covered sediments, potentially causing these taxa to be underrepresented in the footprint sample. This, combined with very low abundance in the overall community, could help explain the paucity of carnivore tracks in the fossil track assemblage, despite their documented preferential use of waterways for travel and foraging (Valeix et al., 2010; Haskell et al., 2013).

The skeletal assemblage is subject to different taphonomic biases. For example, size and bone durability bias work against the preservation of skeletal remains from birds and other small animals. This may explain why richness estimates are approximately equal between the skeletal and track assemblages, despite previous work showing that time-averaged assemblages should have higher richness even when accounting for sample size differences (Kidwell, 2002; Tomasovych and Kidwell, 2010b). While there is some degree of size bias in track preservation (Cohen et al., 1991; Falkingham et al., 2011), preservation bias against small prints likely acts on a longer time frame than these trackways represent. The abundance of bird tracks confirms that size bias does not limit the presence of small animals in the track assemblage. The inverse relationship between temporal scale and the likelihood of the preservation of delicate fossils predicted by the reciprocal taphonomic model (Kowalewski, 1997) explains why birds are present in the temporally narrow track assemblage and not the more time-averaged body fossil assemblage (Table 4). Assessing the effect of size bias on large animal tracks is more complicated. While large tracks are more likely to be preserved, larger animals typically have longer strides and leave fewer total tracks as they move across the landscape. However, large taxa also leave significantly larger tracks, potentially resulting in comparable levels of sediment disturbance and track recovery over a fixed linear distance. Similar issues affect estimates of large taxa representation in fossil assemblages. Positive preservation bias increases the likelihood that large taxa are sampled in any given assemblage. The true abundance of large bodied taxa in a faunal community is complicated by the fact that large animals live longer, reproduce more slowly and are less abundant on the landscape (eg. Calder III, 1984; Martin and Palumbi, 1993; Speakman, 2005; Western and Behrensmeyer, 2009), causing their bones to enter the death assemblage at slower rates and lower frequencies (Western, 1980). Further studies of how large animals living in extant communities are represented in track and bone assemblages are needed to address this possible source of bias more fully. Additionally, the bones of aquatic taxa are more likely to be preserved because they inhabit depositional environments with more constant sedimentation than the subaerial habitats of land taxa. Reptiles are among the most abundant taxa in the skeletal sample, which is in part driven by the continual shedding of crocodile teeth as well as their durability as sedimentary clasts. Ectothermic crocodiles and grazing hippopotamids leave the water frequently to bask and forage respectively, putting them in direct contact with lake margin sediment surfaces and potentially inflating their overall representation in the track assemblage.

While most differences in rank order such as these can be explained by taphonomic processes, the large number of hominins found in the track assemblage cannot be accounted for by such processes. Instead, we have argued that the large numbers of hominin tracks reflect a behavioral pattern, indicating repeated use of the lake margin habitat where the tracks were emplaced (Roach et al., 2016). This would therefore represent an ecologically driven difference between the two assemblages. Furthermore, if we expect that taphonomic processes explain most of the differences between the two assemblages, then β estimates of dissimilarity should largely be the result of nestedness (i.e. the assemblages are simply

different subsamples of the same larger community). Based on our analyses, turnover and nestedness contribute fairly equally to dissimilarity in these samples, and the turnover component indicates that there may be subtle but real ecological differences between the skeletal and track assemblages. Given that turnover is driven by a single individual of a rare taxon in our data sets (giraffids), distinguishing between ecological or behavioral differences and the stochastic effects of sampling is impossible at this time (requiring caution when evaluating our secondary null, H_0).

In sum, most of our quantitative tests indicate that the track and skeletal assemblages represent nested samples of the same animal community. Many differences between the two data sets are likely attributable to taphonomic bias or time-averaging relating mainly to depositional environment and different temporal scales of preservation. Other differences indicate spatial scale distinctions between the structure of the faunal community at large and the behavioral differences of particular taxa regarding their use of the deltaic, lake-margin habitat.

4.2. Community in context

The paleoenvironment of the 1.5 million-year-old Ileret track surfaces, based on the geology of the ITC and the tracks themselves, indicates the presence of edaphic grasslands bordered by a large, stable lake (Behrensmeyer et al., 2016; Roach et al., 2016; Hatala et al., 2017). This flat delta margin would have been inundated seasonally during periods of higher run-off of the associated fluvial system. Wind driven shifts in water level and gentle wave action also would have rapidly buried and protected these trackways. Delta margins are also areas with nutrient rich silts and oxygenated water, making them productive locales for plant growth and animal foraging.

The animal community represented within the combined track and skeletal assemblage is consistent with a deltaic lake margin grassland. Beyond the metrics reported here, these deposits show evidence in the skeletal fossil and track assemblages of large numbers of bovids and suids including herds of medium sized bovids (eg. alcelaphins and *Aepyceros*), isolated *Syncerus* (likely solitary males), large suids (including *Kolpochoerus* and *Metricochoerus*) as well as tragelaphins and reducins, which are commonly associated with mesic grasslands. Specific taxa known from skeletal fossils from this collection area include *Damaliscus*, *Kobus*, *Pelorovis* and *Megalotragus* (Harris, 1991). Bovid body fossils show higher numbers of grazers versus browsers/mixed feeders when compared to fauna from contemporaneous deposits five kilometers further from the paleo-lakeshore (Roach et al., 2016). Avian tracks include open water specialists such as *Pelecanus* and Anatidae, and lakeshore/grassland foragers such as Ciconiidae, Gruidae and *Leptoptilos*. Other aquatic taxa include Hippopotamidae (both *Hippopotamus* and pygmy aff. *Hippopotamus*) and Crocodylidae (*Crocodylus* and *Euthecodon*) that came ashore to feed or bask. Fish fossils are common. Individuals or small groups of Elephantidae, Rhinocerotidae and Giraffidae likely foraged or passed through this area on their way to water. Primates recovered by other teams working in this collection area include numerous *Theropithecus* fossils as well as occasional *Lophocebus* and *Colobus* (Jablonski and Leakey, 2008). Carnivorans known from other studies include *Dinofelis* and *Panthera* (Werdelin and Lewis, 2001). Hominins in our combined sample include an isolated *Paranthropus boisei* molar and 97 cf. *H. erectus* fossils (Hatala et al., 2016; Roach et al., 2016), although numerous fossils from both taxa have been recovered in this collection area (Wood, 1991).

With the exception of the 1.47 Ma hominin tracks from a similar lake margin setting 45 km to the south at Koobi Fora (Behrensmeyer and Laporte, 1981; Bennett et al., 2014), we

currently lack comparable data from other regions needed to address patterns of habitat use among hominins. The ITC evidence shows that *H. erectus* used a lake margin grassland repeatedly and extensively over a period of 20 ka (Roach et al., 2016). Previous studies of animal movement ecology show that prey species such as bovids frequently travel to water sources to drink and forage (Thrash et al., 1995; Redfern et al., 2003) and that carnivores leverage this spatial autocorrelation to improve their hunting efficiency by traveling extensively around and along water sources (Valeix et al., 2010). Lake margins have further been shown to provide corridors for carnivore movement (Haskell et al., 2013), enabling relatively unimpeded ranging with a higher probability of encountering prey. Our interpretations of the ITC trackways suggest that multiple hominin males traveled together in groups along the lakeshore in a manner consistent with this carnivore foraging strategy (Roach et al., 2016).

4.3. A model of *Homo erectus* paleobiology in the ITC

Assuming our taxonomic attributions are correct, the abundance of hominin traces associated with a lake margin grassland habitat suggests that behavioral patterns that characterized cf. *H. erectus* led them to spend time in immediate proximity to large bodies of water. There could be a number of possible explanations for this behavior, but the ITC track surface data, as well as other lines of archaeological and paleontological data, are consistent with the emergence of behavioral changes in *H. erectus* that could be linked to a changing diet.

Multiple lines of evidence suggest that hominin carnivory increased with the emergence of *H. erectus* (DeVore and Lee, 1968; Walker, 1984; Shipman and Walker, 1989; Milton, 1999; Stanford and Bunn, 1999, 2001; Zink and Lieberman, 2016). Sites bearing both stone tools and cut and percussion-marked bone, indicating early access to carcasses by hominins, increase dramatically in number at this time (Dominguez-Rodrigo, 1997; Pobiner et al., 2008; Ferraro et al., 2013). Trace element data suggest a possible trophic level shift in *Homo* consistent with more meat eating (Balter et al., 2012). Raw material movement indicates increased travel across the landscape by *H. erectus* relative to earlier hominins (Féblot-Augustins, 1997; Stout et al., 2005; Braun et al., 2008). This shift in land use is consistent with the larger home ranges occupied by carnivorans (Carbone et al., 2005). Furthermore, body size increases in *H. erectus* (Ruff et al., 1997; Grabowski et al., 2015) indicate a shift in diet quality, and a reduction in dentition suggests this new diet was less demanding to chew and ingest (Wood and Collard, 1999; Organ et al., 2011; Laird et al., 2016; Zink and Lieberman, 2016). Whether early *Homo* was cooking or intensively processing their food remains unclear (Zink and Lieberman, 2016), as evidence for the control of fire deep in time remains controversial (Bellomo, 1994; Wrangham and Carmody, 2010; Berna et al., 2012; Hlubik et al., 2017). *Homo erectus* does show adaptive changes in postcranial anatomy associated with increased athletic ability, such as endurance running and high-speed throwing, and these abilities would have aided hunting and predator avoidance (Bramble and Lieberman, 2004; Pontzer et al., 2010; Roach, 2012; Lieberman, 2013; Roach et al., 2013).

The lake margin grassland, which was occupied by the faunal community described in this paper, may have been an important habitat for early hunting behavior. Not only are water sources effective places to drink, find prey and scavenge carcasses, they are also rich with aquatic plants and prey species such as fish, shellfish and turtles. The earliest known use of such foods, from the 1.95 Ma site of Fwjj20 east of Ileret (Braun et al., 2010), slightly predates the known emergence of *H. erectus*. This use of aquatic resources represents a significant shift in prey recognition behavior from our

chimpanzee relatives (Watts, 2008). Furthermore, analyses of stone tool use within the Okote Member, which includes the ITC as well as other regions of East Turkana, indicate a spatial tie between aquatic taxa and the location of primary tool manufacture (Archer et al., 2014; Reeves et al., 2016). Aquatic plants may also have been an important source of fallback food (Wrangham et al., 2009), providing ready calories to hunters as they looked for prey and would have sustained them when they failed to capture game. Oxygen isotope data from *Homo* teeth support the inclusion of hydrophilic foods in the *H. erectus* diet (Cerling et al., 2013). Increased day ranging and protein metabolism probably also increased obligatory water drinking demands as metabolic water production from protein is very low (Mellanby, 1942) and water needs for efficient sweating can be quite high (Lieberman, 2015). Meeting this water demand by drinking may have allowed early hunters to be active in the heat of the day, avoiding competition with larger, crepuscular carnivorans.

Beyond the effects on hominin ecology, the entrance of *H. erectus* into the carnivore guild likely affected the structure of the Pleistocene faunal community. It is hypothesized that a major reduction in carnivoran diversity around 2 Ma in eastern Africa may have been driven in part by increased competition from the carnivorous genus *Homo* (Werdelin and Lewis, 2013). It is further possible that when increased predation pressure from hominins was combined with climatic shifts, extinctions and faunal turnover in prey taxa could have been accelerated. Such a period of high turnover is known to have occurred in eastern Africa between 1.8 and 2 Ma (Harris et al., 1988; Feibel et al., 1991; Bobe and Behrensmeyer, 2004; Werdelin and Lewis, 2005; Lewis and Werdelin, 2007). Future tests of this hypothesis could examine species last appearance data at sites in this time interval (i.e. ~1.5–2 Ma) that contain hominins and those that do not. Other avenues for future research include investigating shifts in preferred prey abundance and population demography, as well as modifications to faunal land use in response to shifting hominin movement patterns (e.g. Patterson et al., 2017). As *H. erectus* decoupled from the ecological constraints of earlier hominins, entered a more flexible carnivorous niche, migrated out of Africa (Gabunia et al., 2001; Lordkipanidze et al., 2007, 2013) and spread across the globe, they undoubtedly would have left their mark on many local animal communities. By investigating such ecological changes, we begin to address how and why the cognitive, technological and social changes that came to define our own genus emerged and evolved.

Author contributions

The research reported here resulted from professional scientific collaboration. Authorship acknowledges all significant contributions in accordance with accepted practices regarding intellectual property rights and NSF guidelines.

NTR, KGH and BGR conceived the research project. All authors contributed to data collection and compilation. NTR, AD and JSR analyzed the data. NTR wrote the manuscript with significant contributions from AD. All authors edited the paper.

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Gren Foundation, Leakey Foundation and the George Washington University Selective Excellence Initiative. We dedicate this paper to the memory of our friend and mentor Frank Brown.

Appendix 1. Alpha diversity equations

PIE is defined as,

$$PIE = \left(\frac{n}{n-1}\right) \left(1 - \sum_{i=1}^S p_i^2\right) \quad (A.1)$$

where n equals the total number of individuals in a community, S is the number of taxa in a community, and p_i is the relative abundance of the i th species.

Coverage is defined as,

$$\hat{C}_{ind}(n) = 1 - \frac{f_1}{n} \left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right], \text{ if } f_2 > 0$$

$$\hat{C}_{ind}(n) = 1 - \frac{f_1}{n} \left[\frac{(n-1)(f_1-1)}{(n-1)(f_1-1) + 2} \right], \text{ if } f_2 = 0 \quad (A.2)$$

where n equals sample size, f_1 is the number of taxa with one individual (singletons), and f_2 is the number of taxa with two individuals (doubletons).

Rarefied diversity estimates are defined as,

$$\hat{f}_k(m) = \sum_{X_i \geq k} \frac{\binom{X_i}{k} \binom{n-X_i}{m-k}}{\binom{n}{m}}$$

$${}^q\hat{D}(m) = \left[\sum_{k=1}^m \left(\frac{k}{m}\right)^q \times \hat{f}_k(m) \right]^{1-n}, \text{ if } q \neq 1$$

$${}^1\hat{D}(m) = \exp \left[\sum_{k=1}^m \left(-\frac{k}{m} \log \frac{k}{m} \times \hat{f}_k(m) \right) \right], \text{ if } q = 1 \quad (A.3)$$

where X_i is the abundance of the i th taxon, m represents the number of individuals to subsample down to (determined by the coverage level), and $\hat{f}_k(m)$ is the number of taxa related by abundance k in the sample size of m .

Appendix 2. Beta diversity equations

The Dice dissimilarity index is defined as,

$$\beta_{dice} = \frac{b+c}{2a+b+c} \quad (B.1)$$

where a is the number of taxa shared by both communities, b is the number of taxa unique to the first community, and c is the number of taxa unique to the second community.

Turnover is defined as,

$$\beta_{TO} = \frac{\min(b,c)}{a + \min(b,c)} \quad (B.2)$$

Nestedness is defined as,

$$\beta_{nest} = \frac{\max(b,c) - \min(b,c)}{2a + \min(b,c) + \max(b,c)} \times \frac{a}{a + \min(b,c)} \quad (B.3)$$

The Horn measure of overlap is defined as,

$$\beta_{Horn} = \frac{1}{\ln(2)} \left[\sum_{i=1}^S \left[\left(\frac{p_{xi} + p_{yi}}{2} \right) \times \ln \left(\frac{p_{xi} + p_{yi}}{2} \right) \right] \times \left[\frac{\sum_{i=1}^S p_{yi} \times \ln(p_{yi})}{2} - \frac{\sum_{i=1}^S p_{xi} \times \ln(p_{xi})}{2} + \ln(2) \right] \right] \quad (B.4)$$

where p_{xi} is the relative abundance of the i th taxon in the first community, p_{yi} is the relative abundance of the i th taxon in the second community, and S is the total number of taxa.

The Morisita-Horn index is defined using the same variables as,

$$\beta_{MH} = 1 - \frac{2 \sum_{i=1}^S p_{xi} p_{yi}}{\sum_{i=1}^S p_{xi}^2 + \sum_{i=1}^S p_{yi}^2} \quad (B.5)$$

Appendix 3. Spatial patterning equations

Locational Quotient is defined as,

$$LQ_{ij} = \frac{e_{ij} / \sum_i e_{ij}}{\sum_j e_{ij} / \sum_i \sum_j e_{ij}} \quad (C.1)$$

where e equals the number of track-making individuals, i is taxon and j is the excavated unit.

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