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The Pleistocene prehistory of the Lake Victoria basin



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ABSTRACT

Late Pleistocene sedimentary, biogeochemical, and fossil data from the Lake Victoria basin (the largest lake in Africa) suggest that its reduction or desiccation during periods of increased aridity repeatedly facilitated the dispersal of C₄ grassland ecosystems across the basin. Archaeological evidence from Middle Stone Age and Later Stone Age sites suggest that human groups diffused into the basin during intervals of declining lake levels, likely tracking the movement of the dense and predictable resources of shoreline environments, as well as the dense but less predictable C₄ grass grazing herbivores. Repeated cycles of lake expansion and contraction provide a push–pull mechanism for the isolation and combination of populations in Equatorial Africa that may contribute to the Late Pleistocene human biological variability suggested by the fossil and genetic records. Latitudinal differences in the timing of environmental change between the Lake Victoria basin and surrounding regions may have promoted movements across, within, and possibly out of Africa.

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1. Introduction

A suite of genetic, skeletal, and archaeological lines of evidence suggest multiple dispersals of populations of *Homo sapiens* across and out of Africa during the Late Pleistocene (~126–12 ka), but the mechanisms driving these dispersals remain poorly understood. Modern humans (*Homo sapiens*) first appeared in Africa, with the oldest fossil remains dating to ~195 ka (McDougall et al., 2005; Brown et al., 2012). Since their origins, dispersed populations accumulated substantial morphological, genetic, and cultural variability (Lahr and Foley, 1998; McBrearty and Brooks, 2000; Crevecoeur et al., 2009; Gunz et al., 2009; Harvati et al., 2011; Pearson, 2013; Campbell et al., 2014; Tryon et al., 2015). Subsequent Late Pleistocene dispersals out of Africa sampled only a small portion of that original variability (e.g., von Cramon-Taubadel and Lycett, 2008; Soares et al., 2012; Rito et al., 2013).

As *H. sapiens* replaced all other hominin taxa during their global expansion, investigating Late Pleistocene behavioral variability in Africa and how it formed is therefore essential to understanding the evolutionary success of our species. Our goal here is to examine the environmental basis for some of this variability in Equatorial Africa, specifically the impact of the contraction and expansion of Lake Victoria as a push–pull mechanism for the diffusion of populations into and out of the region (for similar investigations elsewhere in Africa, see Kingdon, 1989; Lahr and Foley, 1998; Cowling et al., 2008; Trauth et al., 2010; Blome et al., 2012; Mackay et al., 2014; Scerri et al., 2014; Faith et al., 2015).

To reconstruct Pleistocene environments, we synthesize the available geological, ecological, and fossil records for the Lake Victoria basin (Fig. 1), based in part on our own fieldwork in the region, which began in 2009. We develop a model for forager responses to lake level flux, and test aspects of the model against the archaeological record from two Late Pleistocene time intervals. We focus on two periods of increased aridity during which Lake

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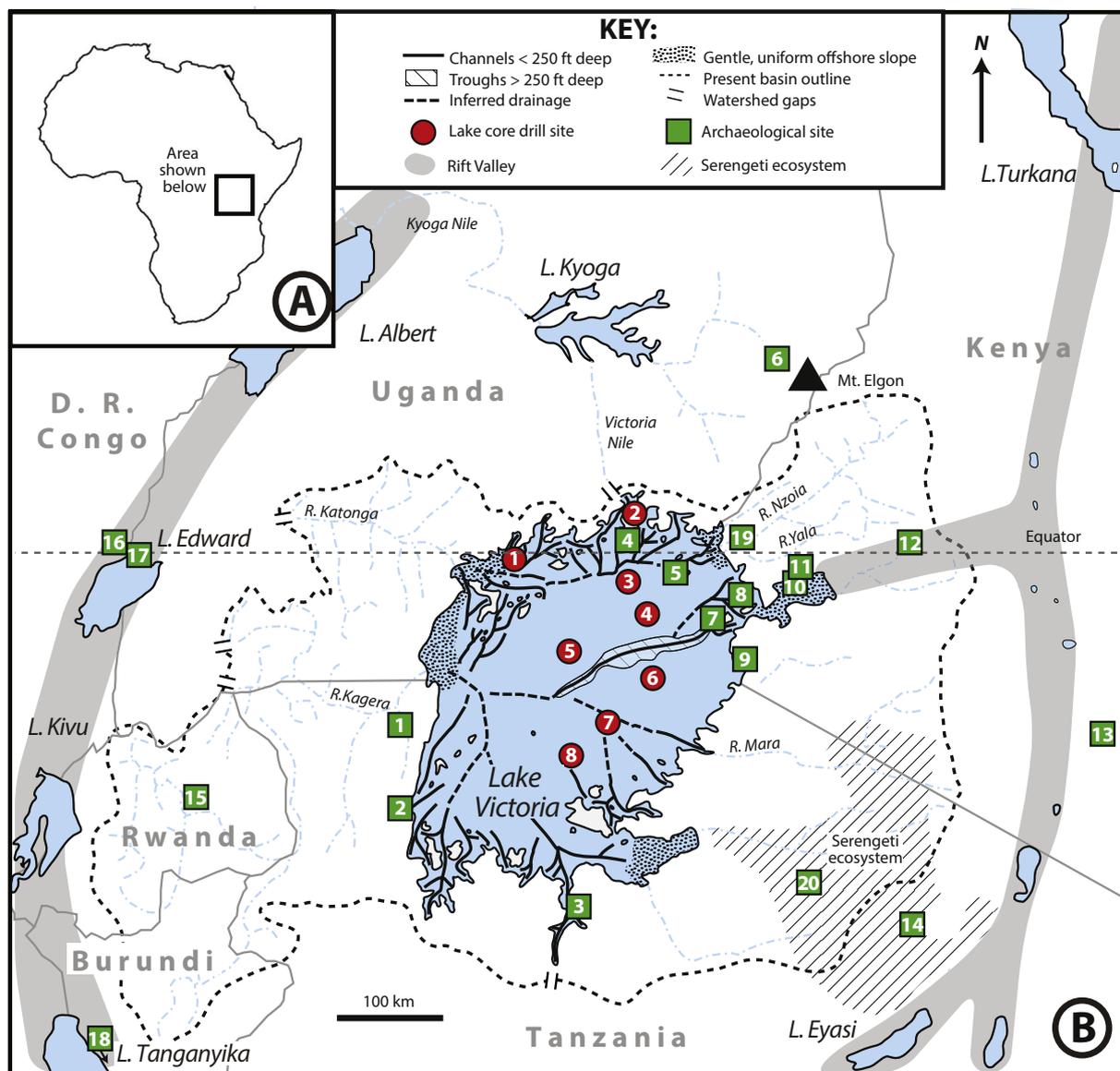


Fig. 1. Sketch map of Equatorial Africa and the Lake Victoria basin (after Temple, 1966; Sinclair, 1979; Stager et al., 1986; Johnson et al., 2000). Lake cores: (1) Ibis-1, (2) P-2, (3) Ibis-3, (4) V95-1P, (5) V95-6P, (6) V95-2P, (7) V96-7P, (8) V95-3P. Note that V96-7P is at the deepest point in the lake. Archaeological sites: (1) Kibwera, (2) Ruhanga rockshelter, (3) Chole rockshelter, (4) Munyama Cave (5) Lolui Island, (6) Walasi Hill, (7) Mfangano Island, (8) Rusinga Island, (9) Karungu, (10) Randhore, (11) Muguruk, (12) Songhor, (13) Lukenya Hill, (14) Naseru, (15) Rutonde, (16) Katanda, (17) Ishango, (18) Masango, (19) Siror, (20) Loiyangalani.

Victoria was desiccated or substantially reduced: (1) a younger period that follows the Last Glacial Maximum (LGM, ~19–26.5 ka; Clark et al., 2009) associated with a Later Stone Age (LSA) archaeological record; and (2) an older period that follows the end of the peak of the Last Interglacial (~125 ka), and spans from ~100 to ~35 ka, associated with a Middle Stone Age (MSA) archaeological record. The younger of these two intervals (informally referred to throughout as the Lateglacial interval) contains well-dated environmental and archaeological records spanning ~7.5 kyr that may sample a period characterized by substantial human biological variability no longer present in extant populations (Tryon et al., 2015). The older interval (referred to throughout as the ~100–35 ka interval) spans ~65 kyr and has comparatively reduced temporal resolution, but overlaps with the estimated timing of major movements of populations of modern humans across and subsequently out of Africa (e.g., Mellars, 2006; Rose et al., 2011; Soares et al., 2012; Rito et al., 2013).

2. Lake Victoria

Lake Victoria straddles the Equator from ~0.5°N to 3.0°S and lies in the trough between the eastern and western branches of the East African Rift Valley System (EARS) (Chorowicz, 2005) (Fig. 1). The lake formed during the last ≥400 ka, as continued but intermittent uplift of the western branch of the EARS caused the back-ponding and reversal of formerly westward-flowing streams that once crossed the basin (Temple, 1966; Bishop, 1969; Danley et al., 2012). A number of the buried channels of these streams can still be traced across the lake floor (Fig. 1). With a surface area of 68,800 km², Lake Victoria is the largest tropical lake in the world and the largest lake in Africa (Crul, 1995), and is thus today a defining geographic feature of Equatorial Africa. It is large enough to generate its own weather system (Thierry et al., 2015) and supports some of the most densely settled areas of human occupation in sub-Saharan Africa (Nelson, 2004). Vegetation around the lake today includes

predominantly C₃ bushland, thicket, and forest comprising a mosaic of taxa endemic to surrounding regions (White, 1983), a combination that may result from Pleistocene biome expansions (Kingdon, 1989; Cowling et al., 2008; Linder et al., 2012; Faith et al., 2015), with significant ecological restructuring occurring as recently as the last few millennia (Chritz et al., 2015). The lake also sits at the junction between central African forests to the west and savanna habitats to the east and forms an important boundary for large mammal populations, with forest species including red river hog (*Potamochoerus porcus*), okapi (*Okapia johnstoni*), and chimpanzee (*Pan troglodytes*) found to the west and savanna species, including wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and warthog (*Phacochoerus aethiopicus*) to the east.

Because average rainfall over the lake is almost equal to average evaporation, modern Lake Victoria is very sensitive to changes in precipitation (Piper et al., 1986; Sutcliffe and Petersen, 2007). Moisture is primarily delivered from the Indian Ocean via south-easterly winds (Nicholson, 1996). The mean annual precipitation varies spatially but is on average 1200–1600 mm/year over the catchment area (Piper et al., 1986; Crul, 1995; Yin and Nicholson, 1998). About 80% of the inflow to the lake is direct input from recycled lake water with ~20% contributed by tributaries (Yin and Nicholson, 1998; Sutcliffe and Petersen, 2007). The Kagera River (Fig. 1) is the largest tributary (~10% of total inflow) and drains the highlands of Rwanda and Burundi to the west (Shahin, 1985; Yin and Nicholson, 1998). Outflow is to the north at Jinja, where Lake Victoria serves as a primary source of the Nile (Fig. 1). Although large, the lake is shallow, with a current maximum depth of ~68 m (Johnson et al., 1996), leading E.J. Wayland (Wayland, 1928), the first scholar dedicated to the study of the history of Lake Victoria, to refer to it as “nothing but a titanic puddle.” As a result of this geometry, large changes in lake surface area can occur with modest changes in depth. Because local precipitation is derived primarily from the lake itself, Lake Victoria expands and contracts in response to changes in rainfall availability (Broecker et al., 1998; Yin and Nicholson, 1998; Milly, 1999; Bootsma and Hecky, 2003). Historical fluctuations of ~4 m have been documented during the 19th century (Nicholson, 1998) and can be linked to changes in precipitation (Kite, 1981, 1982; Sene and Plinston, 1994).

Several sedimentary features attest to the scale of these past fluctuations in lake level. Evidence for increases in lake level following formation of the modern lake basin includes wave-cut terraces and horizontally bedded beach deposits about the circumference of the lake at +3, +10–12, and +18 m above present water level (Doornkamp and Temple, 1966; Temple, 1966). The +3 m beach deposit is dated to ~4 ka (Bishop, 1969); the others are currently undated. Eight sediment cores from across Lake Victoria (Fig. 1), including ones from the deepest portion of the basin, preserve all or part of a >1-m-thick soil (interpreted as a paleo-Vertisol) that formed during complete desiccation of the lake ~17–16 ka, with a second, thinner paleo-Vertisol dated to ~15–14 ka visible in the Ibis-1 (“Damba Channel”) and V95-2P cores (Kendall, 1969; Talbot and Livingstone, 1989; Johnson et al., 1998; Talbot and Laerdal, 2000; Stager and Johnson, 2008; Stager et al., 2011). Seismic surveys across the lake show at least four basin-wide unconformities in the subsurface sedimentary record (Johnson et al., 1996). The uppermost is correlated with the ~17–16 ka desiccation event (the ~15–14 ka desiccation event is not readily distinguished in the seismic data). This suggests at least three additional major desiccation events in the history of Lake Victoria. These older desiccation events are undated and of unknown duration, although (Stager and Johnson, 2008) speculate an age of ~80 ka for the surface underlying the ~17–16 ka paleosol based on inferred sedimentation rates.

3. The environmental record

3.1. The Lateglacial history of Lake Victoria

Cores V95-1p, V95-2p, V95-3p, V95-6p, V96-7p, P-2, Ibis-1, Ibis-3 (Fig. 1) provide the most detailed record of the history of Lake Victoria since desiccation at ~17–16 ka, sample a large spatial extent of the lake, and include the deepest portions of the basin (Kendall, 1969; Stager, 1984; Talbot and Livingstone, 1989; Johnson et al., 1996, 1998; Beuning, 1999; Talbot and Laerdal, 2000; Stager and Johnson, 2008; Stager et al., 2011; Berke et al., 2012). These cores sample one or two soil horizons (paleosols) or other surfaces (e.g., shell lag deposits) that indicate multiple intervals of changes in the lake's shoreline position and water depth. Radiocarbon dates on sediments and plant remains from beneath, within, and above the paleosols, as well as on mollusk shells marking a former near-shore lag-deposit in the Ibis-1 core provide the ~17–16 ka age for that desiccation event. The overlying and less prominent ~15–14 ka desiccation surface is recorded in cores V95-2P and the Ibis-1 core (Stager et al., 2011). Both desiccation events have been linked to climatic changes that resulted in a reduction in moisture availability, with the ~17–16 ka surface tied to Heinrich Event 1 (Stager et al., 2011). Bonnefille and Chalie (2000) estimate a ~42–45% reduction in mean annual precipitation for the LGM and Lateglacial based on pollen data from cores in the Rwanda, Burundi, and Democratic Republic of the Congo highlands at the headwaters of streams that feed into Lake Victoria, broadly consistent with water balance models for Lake Victoria that suggest that a 50–75% reduction in precipitation could reduce the surface area of Lake Victoria to <10% of its present size (Broecker et al., 1998; Milly, 1999).

The ~17–16 ka soil in the basal sediments exposed in the V95-2P and Ibis-1 cores (the best described cores) consists of greenish-black crumbly muds with vertical cracks, sand grains, rootlet traces and small diffuse carbonate nodules that are interpreted as a paleo-Vertisol that formed on muddy lake flats sub-aerially exposed during lake desiccation (Talbot and Laerdal, 2000; Stager et al., 2011), typical of soils forming on exposed lake beds in eastern Africa today (Ahmad, 1996). Fragments of terrestrial plant debris are abundant, as are well-preserved grass cuticles showing typical C₄ cell morphology. The presence of grasses is consistent with soil $\delta^{13}\text{C}$ values of > -20‰ that indicate significant C₄ biomass (Talbot and Livingstone, 1989; Talbot and Laerdal, 2000), although ¹³C-enriched values in aquatic ecosystems can also reflect C₃ algal photosynthesis using bicarbonate to assimilate carbon (Farquhar et al., 1989). Pollen records from the V95-2P and P-2 cores show abundant (~40–50%) grass (Poaceae) pollen indicating extensive grasses in the area during lake lowstand (Kendall, 1969; Beuning, 1999), with moderate-to-large amounts (~15–40%) of sedge (Cyperaceae) such as papyrus (*Cyperus papyrus*), found in the Lake Victoria region today, and perhaps bulrush (*Typha*), common throughout East Africa (Lind and Morrison, 1974). These sedges suggest the presence of at least seasonally available bodies of standing water (e.g., as springs, seeps, swamps, small ponds or streams).

The V95-2P basal Vertisol is overlain by a thin layer (15-cm-thick) of diatomaceous muds that reflect a brief return to lacustrine conditions for perhaps 10²–10³ years prior to the second desiccation event ~15–14 ka; shell lag deposits in the Ibis-1 core similarly reflect a major shift in the lake shoreline position during this time (Stager, 1984; Talbot and Laerdal, 2000; Stager and Johnson, 2008; Stager et al., 2011). The second paleo-Vertisol is not recognized in most of the collected cores. This is likely a reflection of the 10-cm sampling interval used to study the cores as well as varied sedimentation rates, such that the thin mud layer that distinguishes the

upper and lower soils may either have been missed or may well be absent from some areas (Talbot and Laerdal, 2000). Isotopic and plant macrofossil data also suggest a C₄ grassland-dominated environment for the upper ~15–14 ka paleosol. The carbon isotopic composition of leaf wax biomarkers from core V95-1P suggests that C₄ plants comprised a major component of terrestrial vegetation within the lake catchment from ~15 to 1 ka (Berke et al., 2012). Sediments overlying the second paleosol indicate a rapid flooding of the basin and at the V95-2P core site, and pollen data from the core indicate the persistence of sedges (e.g., *C. papyrus*) such as those that now fringe much of the lake (Lind and Morrison, 1974). Lake Victoria subsequently filled to a depth near that of today, a level it has likely not fallen below since ~13 ka, with overflow via the Victoria Nile occurring by the onset of the Holocene (Kendall, 1969; Beuning, 1999; Johnson et al., 2000; Talbot and Laerdal, 2000; Talbot et al., 2000; Beuning et al., 2002). During the Holocene, the pollen record becomes increasingly dominated by the fig family (Moraceae), indicating the formation of fringing forests with the return to humid conditions (Kendall, 1969; Beuning, 1999), with increased humidity during the Holocene also reported from the Rwanda and Burundi highlands at the margins of the Lake Victoria basin (Bonnefille and Chalieu, 2000).

3.2. The history of Lake Victoria ~100–35 ka inferred from terrestrial deposits

No sediments have yet been recovered from cores beneath the ~17–16 ka unconformity. We infer the earlier history of Lake Victoria from sediments, soils, and fossils from terrestrial deposits that are exposed on Rusinga Island, Mfangano Island and near Karungu, Kenya (Fig. 1), using a variety of paleoecological, paleopedological, and biogeochemical analyses to reconstruct ancient habitats and rainfall regimes. It is important to stress that the ~100–35 ka terrestrial data are temporally less continuous than data from the Lateglacial lacustrine cores, and span a longer time interval but smaller geographic area. Furthermore, as the sediments from Rusinga, Mfangano, and Karungu are terrestrial rather than lacustrine, they do not provide direct evidence of the extent of the lake during their deposition. As sediment traps, they more likely reflect very local conditions characteristic of topographic lows rather than the region as a whole. This problem is partially offset by our analyses of fossil fauna, which include taxa with larger home ranges that sample larger portions of the landscape (Kingston, 2007). As detailed below, our combined observations from sediments, soils, fossil fauna, and isotopic analyses indicate a reduced or desiccated

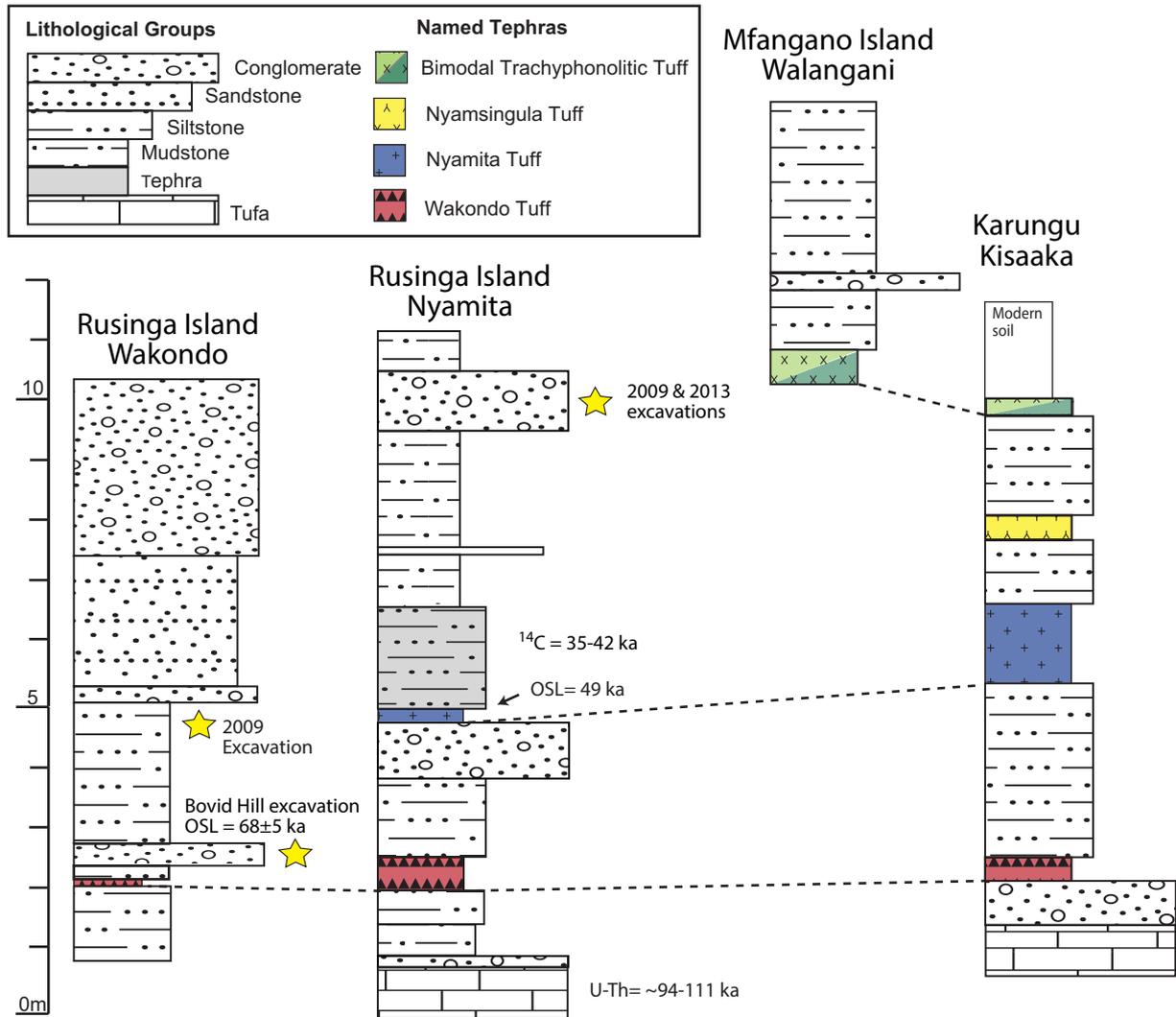


Fig. 2. Composite stratigraphic sections for Pleistocene deposits on Rusinga Island, Mfangano Island, and at Karungu, Kenya, including available radiometric dates and tephra correlations (dashed lines). Note that the Bimodal Trachyphonolitic Tuff is not definitively at Walangani, although it is found elsewhere on Mfangano Island. Stars denote archaeological excavations.

Lake Victoria with a C_4 -grass dominated landscape ~100–35 ka that was more open and drier than today, with locally abundant woody plants concentrated at moisture-rich topographic lows and more rugged slopes on present-day islands.

3.2.1. The sedimentary record

The Late Pleistocene sediments from Rusinga Island, Mfangano Island and near Karungu consist largely of alluvial silts and sands, variably developed paleosols, spring-deposited tufas, and primary fall-out and reworked volcanic ashes (tephra) (Tryon et al., 2010, 2012; Beverly et al., 2015a,b; Faith et al., 2015; Garrett et al., 2015). The tephra are correlative among the localities (Blegen

et al., 2015), indicating that they represent a single, coherent >10-m-thick sedimentary record dispersed among outcrops up to 60 km apart (Fig. 2).

The base of the sequence is best exposed at Nyamita on Rusinga Island, with U-series dates of 94.0 ± 3.3 ka and 111.4 ± 4.2 ka on tufa providing maximum ages for overlying sediments (Beverly et al., 2015b). The locally distinctive and widespread Nyamita Tuff defines the middle portion of the stratigraphic sequence (Fig. 2). The Nyamita Tuff has optically stimulated luminescence (OSL) dates of 46 ± 4 ka and 50 ± 4 ka that bracket a primary fall-out facies, indicating an age of ~49 ka for its deposition, with an additional three OSL dates producing an average of 68 ± 5 ka from the

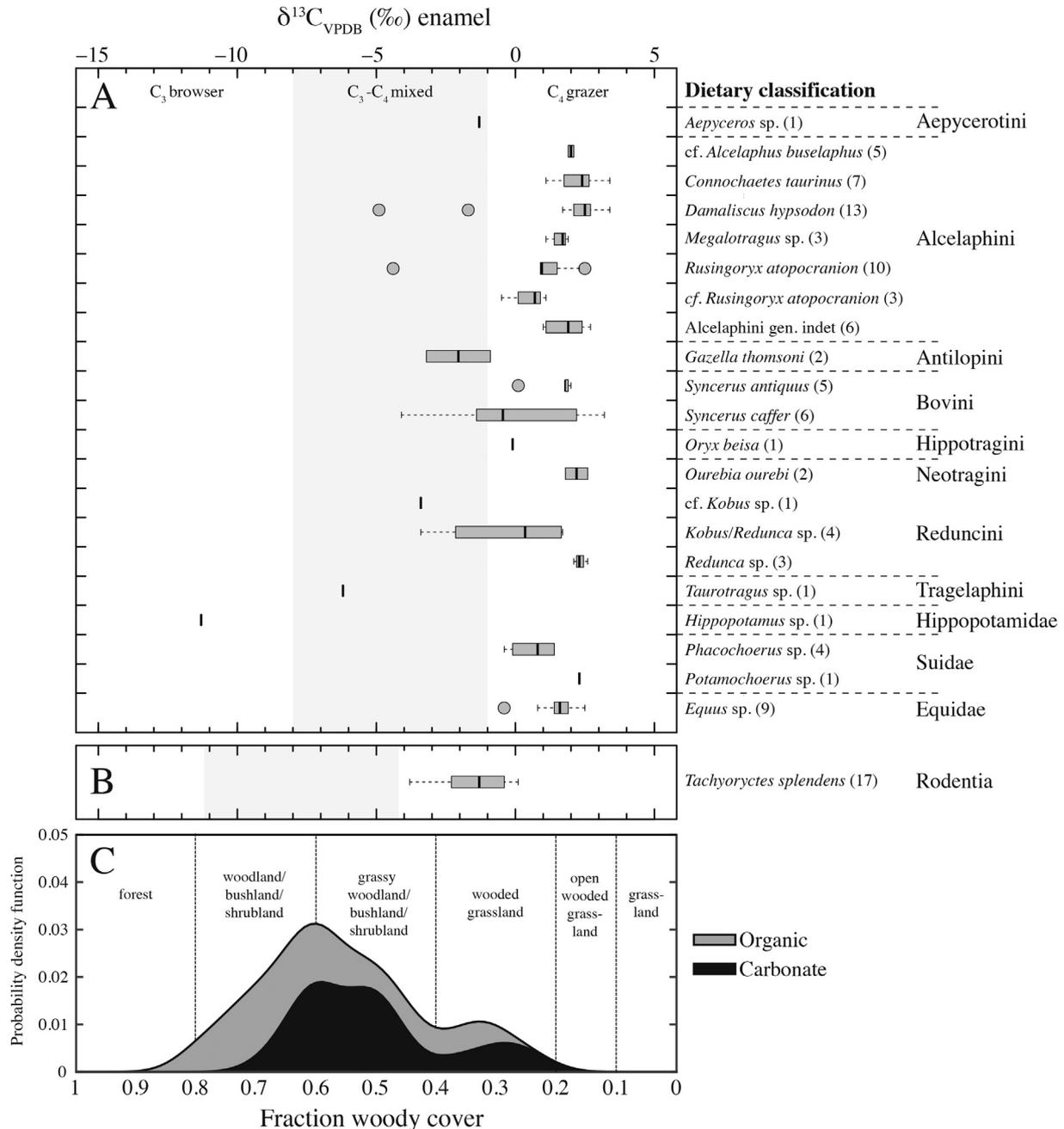


Fig. 3. Carbon isotopic composition of tooth enamel from (A) fossil large mammalian herbivores from Rusinga, Mfangano, and Karungu, (B) rodents from Karungu, and (C) paleosol carbonates and organic matter from Rusinga. $\delta^{13}C_{enamel}$ value of -8‰ as the boundary between C_3 -browsing (>ca. 75% C_3) and C_3/C_4 mixed feeding, and -1‰ as the boundary between mixed feeding and C_4 -grazing (>ca. 75% C_4), assuming diet-enamel enrichment (ϵ^*) of 14.1‰. For rodents we do not assign specific diet categories, although we identify the boundary between C_3/C_4 mixed feeding and C_4 -grazing using a diet-enamel enrichment (ϵ^*) of 11‰.

Wakondo locality, from strata between the Nyamita Tuff and the dated tufa at the base (Blegen et al., 2015). The age of the upper portions of the sedimentary sequence remain poorly constrained. Three radiocarbon dates on the shells of gastropods that burrowed into the Nyamita Tuff range from ~35 to 42 ka (Tryon et al., 2010), providing a reasonable minimum age for the sediments consistent with recovered MSA archaeological assemblages (Tryon and Faith, 2013).

The presence of alluvial sediments and particularly freshwater tufa deposits near the base of the sequence at Nyamita and multiple localities near Karungu (Beverly et al., 2015b) suggest that some of the deposits on Rusinga, Mfangano, and near Karungu, sample locally well-watered environments. Active springs at Nyamita and older (~455 ka) tufas at Karungu indicate that springs are recurrent landscape features. Three widespread paleosols (paleo-Vertisols and paleo-Inceptisols) occur throughout the stratigraphic sequence (Beverly et al., 2015a), and estimates of mean annual precipitation (MAP) using weathering indices derived from soil chemical composition (CIA-K and CALMAG) indicate MAP ranges of 813 ± 182 to 963 ± 182 mm yr⁻¹. These values are ~20–50% lower than present, and suggest drier conditions throughout much of the ~100–35 ka interval.

3.2.2. Isotopic reconstructions of vegetation

Following Cerling et al. (2011), the carbon isotopic composition of pedogenic carbonate and associated organic matter from the

Nyamita locality at Rusinga (Fig. 2) demonstrate that C₃ plants were locally abundant in that area during periods of pedogenesis. At Nyamita, woody cover abundance indicates that woodland/bushland/shrub (60–80%) and grassy woodland/bushland/shrub (40–60%) ecosystems were dominant with a minor contribution of woody cover associated with wooded grasslands (20–40%) (Fig. 3C) (Garrett et al., 2015). These data reflect a single site and may not be representative, but indicate the presence of dense vegetation at some well-watered localities.

3.2.3. Habitat reconstruction using faunal evidence

The ~100–35 ka fossil faunas from Rusinga Island, Mfangano Island, and Karungu are the most taxonomically diverse Late Pleistocene assemblage in East Africa (Tryon and Faith, 2013; Faith, 2014), and are summarized in Table 1. Individuals from extinct taxa account for >50% of the large mammals (>5 kg), and include the only reported Late Pleistocene East African occurrences of a suite of extinct taxa, including the bovids *Megalotragus* sp., *Rusingoryx atopocranion*, an unnamed impala (*Aepyceros* sp. nov.), the suid *Kolpochoerus* sp. and the aardvark *Orycteropus crassidens* (Lehmann, 2009; Faith, 2014; Faith et al., 2014). At present, much of our fossil sample consists of surface collected specimens. While much of the fauna can be reliably attributed to stratigraphic intervals bounded by characteristic tephra deposits, the total sample is time averaged across ~65 kyr.

Table 1

Specimen counts (NISP) for the mammalian fauna from Karungu, Mfangano Island, and Rusinga Island. † = extinct taxon.

		Karungu	Mfangano	Rusinga island
<i>Tachyoryctes splendens</i>	East African mole rat	11	0	10
<i>Otomys</i> sp.	Vlei rat	74	0	79
<i>Lepus</i> sp.	Cape hare	3	1	2
Leporidae indet.	Indet. leporid	2	0	2
<i>Homo</i> cf. <i>sapiens</i>	Human	0	0	1
<i>Papio</i> sp.	Baboon	0	0	1
<i>Canis</i> sp.	Jackal	0	0	1
<i>Crocuta crocuta</i>	Spotted hyena	1	0	3
Felidae cf. <i>Caracal/Leptailurus</i>	Caracal or Serval	1	0	0
<i>Panthera leo</i>	Lion	3	0	0
<i>Panthera pardus</i>	Leopard	1	0	0
<i>Orycteropus crassidens</i> †	Extinct aardvark	0	0	1
<i>Procavia</i> sp.	Hyrax	0	1	0
cf. <i>Loxodonta africana</i>	African Elephant	1	0	2
<i>Ceratotherium</i> cf. <i>simum</i>	White rhinoceros	7	0	3
<i>Diceros</i> cf. <i>bicornis</i>	Black rhinoceros	1	0	0
Rhinocerotidae indet.	Indeterminate rhino	0	1	0
<i>Equus quagga</i>	Plains zebra	54	1	20
<i>Equus grevyi</i>	Grevy's zebra	24	0	10
<i>Equus</i> sp.	Indeterminate zebra	52	3	22
<i>Phacochoerus</i> sp.	Warthog	24	1	15
<i>Potamochoerus</i> sp.	Bushpig	0	1	2
<i>Kolpochoerus</i> sp.†	Extinct bushpig	0	0	1
<i>Hippopotamus amphibius</i>	Hippo	9	1	6
<i>Taurotragus oryx</i>	Eland	4	0	2
<i>Tragelaphus scriptus</i>	Bushbuck	4	0	5
<i>Tragelaphus strepsiceros</i>	Greater kudu	0	0	1
<i>Tragelaphus</i> cf. <i>imberbis</i>	Lesser kudu?	0	0	1
Tragelaphini indet.	Eland or kudu	2	0	0
<i>Oryx</i> cf. <i>beisa</i>	Oryx	12	0	7
Hippotragini indet.	Oryx or roan/sable	1	0	2
<i>Redunca</i> cf. <i>arundinum</i>	Southern reedbuck	1	0	0
<i>Reduncini</i> sp. A	Kob or southern Reedbuck	4	2	35
<i>Redunca</i> cf. <i>redunca</i>	Bohor reedbuck	0	0	1
<i>Redunca</i> sp. B	Bohor reedbuck or Mountain reedbuck	1	3	15
Reduncini indet.	Reduncini	0	0	5
<i>Alcelaphus buselaphus</i>	Hartebeest	26	3	23
<i>Connochaetes taurinus</i>	Wildebeest	27	2	44
<i>Damaliscus hypsodon</i> †	Extinct blesbok	39	2	64
<i>Megalotragus</i> sp.†	Giant wildebeest	9	0	8
<i>Rusingoryx atopocranion</i> †	Extinct wildebeest	69	12	329

(continued on next page)

Table 1 (continued)

		Karungu	Mfangano	Rusinga island
Alcelaphini indet.	Indeterminate Alcelaphine	45	12	161
<i>Gazella granti</i>	Grant's gazelle	1	0	2
<i>Gazella thomsoni</i>	Thomson's gazelle	17	2	16
Antilopini indet.	Indeterminate Antelopine	2	0	0
<i>Aepyceros sp. nov</i> †	Extinct impala	1	0	11
<i>Syncerus antiquus</i> †	Long-horn buffalo	11	3	8
<i>Syncerus caffer</i>	African buffalo	26	2	10
<i>Syncerus sp.</i>	Indeterminate buffalo	1	1	7
<i>Ourebia ourebi</i>	Oribi	5	1	18
<i>Oreotragus oreotragus</i>	Klipspringer	0	1	0
<i>Madoqua sp.</i>	Dik-dik	0	1	0
<i>Sylvicapra grimmia</i>	Common duiker	0	1	9

The fossil fauna from Nyamita and elsewhere include water dependent taxa such as reedbucks (*Redunca* spp.), hippopotamus (*Hippopotamus amphibius*) and the vlei rat (*Otomys* sp.), the latter typically found in marshy habitats (Tryon et al., 2010, 2012; Faith et al., 2015). The presence of these taxa is consistent with the presence of tufas and the vegetation reconstructions from isotopic data. However, as discussed below, several lines of evidence indicate that the ~100–35 ka fossil faunas from Rusinga Island, Mfangano Island, and Karungu document a C₄ grass-dominated ecosystem drier than present that supported diverse populations of grazing herbivores throughout most of the stratigraphic sequence.

3.2.3.1. Bovid tribal abundance. Each of the fossil bovid assemblages is dominated by specimens belonging to the tribes Alcelaphini and Antilopini (Karungu: 76.3%; Rusinga: 82.5%; Mfangano: 68.8%), particularly the extinct taxa *Damaliscus hypsodon* and *R. atopocranium* (Table 1). Among modern ecosystems, the abundance of these tribes is indicative of dry grassland settings (Vrba, 1980). This impression is reinforced when the fossil assemblages are compared with the community analyses that demonstrate that the bovid abundances by tribe distinguish among wet edaphic grasslands, open/dry habitats, and woodlands (Alemseged, 2003); those from Rusinga Island and Mfangano Island suggest formation in an open/dry habitat similar to the modern Serengeti communities (Tryon et al., 2010, 2012), and a similar habitat at Karungu can be inferred based on the comparable dominance of Alcelaphini and Antilopini.

3.2.3.2. Hypsodonty. *Damaliscus hypsodon* – the most hypsodont of known African bovids (Faith et al., 2012) – is one of the most abundant bovids in the Lake Victoria basin. This reflects the widespread presence of a taxon well-suited to feeding on grass in open environments. To the extent that the occlusal relief of maxillary molars among grazing bovids is a reflection of abrasion related to consumption of dry versus wet grasses (see discussions in Fortelius and Solounias, 2000; Louys and Faith, 2015), the mesowear signature of *D. hypsodon* M1s and M2s from the Lake Victoria region, which includes mostly specimens with low occlusal relief (M2 only: n = 8, % low occlusal relief = 87.5, % round cusps = 100; M1, M2, and M1/2(?): n = 16, % low occlusal relief = 87.5, % round cusps = 93.8%, % blunt cusps = 6.3%), suggests a preference for dry grasses.

3.2.3.3. Isotopic reconstructions of diet and humidity. Environmental reconstruction is aided by isotopic analyses of tooth enamel from a large (n = 102) and diverse (at least 19 taxa) sample of Late Pleistocene fossils, including large mammalian herbivores (Fig. 3A), and rodents (Fig. 3B) from the Lake Victoria basin (Faith et al., 2015; Garrett et al., 2015). Based on the isotopic

composition of modern C₄ (tropical grasses) and C₃ (trees, shrubs, herbs) plants, diet-enamel enrichment (ϵ^*) of 14.1‰, and changes in the isotopic composition of atmospheric CO₂, we assign diet categories using a $\delta^{13}\text{C}_{\text{enamel}}$ value of –8‰ as the boundary between C₃-browsing (>ca. 75% C₃) and C₃/C₄ mixed feeding, and –1‰ as the boundary between mixed feeding and C₄-grazing (>ca. 75% C₄) (Cerling et al., 2015). The isotopic composition of tooth enamel in large mammals from Rusinga, Mfangano, and Karungu demonstrate the dominance of C₄ grazers (Fig. 3A). In some cases (e.g., *Taurotragus* sp., *Potamochoerus* sp.), fossil specimens indicate a more C₄-dominated diet than modern conspecifics (Garrett et al., 2015). A single analysis of *Hippopotamus* sp. indicates a more C₃-dominated diet than most modern specimens in eastern Africa, which consume a mixed C₃/C₄ diet (Cerling et al., 2008; Garrett et al., 2015). This suggests that the ground vegetation layer near aquatic habitats preferred by hippopotamus would have included substantial C₃ vegetation, likely including non-woody C₃ plants such as herbs. The presence of C₃/C₄ mixed feeding individuals in a variety of taxa, including Alcelaphini, Antilopini, Bovini, Reduncini, and Tragelaphini, indicates that C₃ browse was available, although most herbivores had a C₄-dominated diet, indicating either that C₃ plants were not abundant or not preferred (Fig. 3A). Following Cerling et al. (2015), the ratio of C₄-grazers, mixed C₃/C₄ feeders, and C₃-browsers (G:M:B) is 67:25:8 (dietary classifications made for bovids at the level of tribe and other taxa at the generic level). This ratio is similar to modern C₄-grazer dominated ecosystems, which includes both grassland and mosaic (mixed habitats including grasslands, woodlands, and forests) ecosystems (Cerling et al., 2015).

Oxygen isotopic analyses of these teeth and comparison of the aridity index of Levin et al. (2006) suggest at least a minimum 20% reduction in mean annual precipitation relative to the present (Garrett et al., 2015). This is consistent with estimates derived from the Karungu paleosols (Beverly et al., 2015a).

3.2.3.4. Biogeography. Fossils of extant taxa from Rusinga, Mfangano, and Karungu are found well beyond their current range. The most striking examples are the fossils of oryx (*Oryx beisa*) and Grevy's zebra (*Equus grevyi*) which indicate a substantial westward home range expansion of ~250–350 km into the eastern portions of the Lake Victoria basin (Tryon et al., 2010; Faith et al., 2013). Both animals are today restricted to the more arid regions of eastern and northeastern Africa. Fossil data from the Pleistocene and Holocene suggest that the ranges of these and other taxa, particularly the white rhino (*Ceratotherium simum*), underwent substantial contractions with the onset of more humid conditions during the Holocene (Faith et al., 2013).

3.2.3.5. Population ecology and bathymetry. Ecological observations suggest that small (~64 km²) islands such as Mfangano that are

dominated by steep volcanic uplands are unable to support viable herds of the gregarious and in some cases migratory ungulate species such as wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer* and *S. antiquus*), and plains zebra (*Equus quagga*), at odds with the recovered fossil assemblage (Tryon et al., 2012, 2014). Modeled changes in lake depth from integrated topographic and bathymetric data suggest that the fossil and archaeological deposits on Mfangano were deposited when the level of Lake Victoria was at least 25 m lower than present. This reduction in lake depth would have connected the island to the mainland, and provided a sufficiently large landmass to maintain viable populations of the taxa indicated by the fossils (Tryon et al., 2014).

3.2.3.6. 'Non-analog super-communities'. Within the limits of our temporal resolution, the fossil faunas represent 'non-analog super-communities' with combinations of taxa not found today due to separation by Lake Victoria, including *E. grevyi* as already noted (found east of Lake Victoria), as well as the white rhino (*C. simum*), today restricted to areas northwest of the lake, and the southern reedbeek (*Redunca arundinum*), today found only in Tanzania south of Lake Victoria (Faith et al., 2015, in press). The combination of these animals at multiple sites in the Lake Victoria basin may indicate diffusion into the basin from multiple directions, or their present distribution may represent remnant populations fragmented and isolated by lake expansion. The convergence of mesic-adapted species outside of their current ranges in the late Quaternary sediments deposited during humid conditions in the Kibish Formation of southern Ethiopia (Rowan et al., 2015) provides a complementary perspective, indicating that repeated wet/dry cycles contributed to major reorganization of faunal communities.

4. A model for human occupation of a dry Lake Victoria basin

The sedimentary and fossil records indicate that Lake Victoria was desiccated or substantially reduced one or more times during the Lateglacial period and from ~100 to ~35 ka. Intervals of lake recession coincided with the expansion of C₄ grasses across the basin, and at least during the ~100–35 ka period, this grassy ecosystem supported a grazer-dominated herbivore community with some taxa representing dry grass specialists and overall faunal similarities to the present-day Serengeti ecosystem. Dated sediments from the V95-2P and Ibis-1 cores indicates that drying, grass expansion and subsequent refilling of the Lake Victoria basin can happen on very brief timescales on the order of 10²–10³ yr (Talbot and Livingstone, 1989; Talbot and Laerdal, 2000; Stager et al., 2011). Rapid and repeated changes in shoreline position and cycling of habitats from shoreline to grassland serve as powerful push–pull mechanism for the concentration and subsequent dispersal of human populations across the Lake Victoria basin. These are conditions that over the long term can contribute to substantial biological and behavioral variability through processes of isolation, adaptation, drift, and exchange (Vrba, 1985; Faith and Behrensmeyer, 2013), as suggested for the extant and fossil faunal communities in the Lake Victoria basin (Faith et al., 2015, in press). Two factors would have contributed to this pattern of dispersal towards and away from the basin center: the persistent human occupation of lakeshore settings that offered an array of dense, predictable resources throughout the year, and continued hunting of large but mobile and therefore somewhat unpredictable herds of ungulates that populated the grasslands.

4.1. Human settlement along the shoreline

The lakeshore likely remained a focal point for human occupation during periods of lake stability, expansion, and contraction

because of its proximity to a range of environments and the presence of dense and predictable resources, particularly fish, shellfish, and a variety of different fruits, herbs, and other types vegetation, many of which were available year-round. A lakeshore focus is attested both by contemporary population density around the lake as well as by the Kansyore Holocene shell middens and other sites along Lake Victoria (e.g., Robertshaw et al., 1983; Robertshaw, 1991; Prendergast, 2010; Prendergast and Lane, 2010). Because of this preference, change in lake size and location was likely a primary mechanism for the diffusion of human populations across the Lake Victoria basin throughout the Pleistocene, and occupation likely tracked fluctuations in shoreline location. The shoreline provided accessible fresh water and a variety of fish that could be captured in near-shore settings, with or without boats (for detailed discussions of the historic and ethnographic range of fishing techniques used in Equatorial Africa, see Worthington and Worthington, 1933; Stewart, 1989; Peters, 1990, 1991). Shellfish in Lake Victoria known to have been used as food during the Holocene include bivalves *Aspatharia*, *Mutela*, and *Caelatura* (Robertshaw et al., 1983; Prendergast and Lane, 2010) that are most abundant in shallow, relatively calm waters (Muli and Mavuti, 2001; Muli, 2005). Aquatic and semi-aquatic plants such as the water lily (*Nymphaea* spp.), and sedges (Cyperaceae) such as papyrus (*Cyperus papyrus*) and the bulrush or cattail (*Typha* spp.) are found in similar water conditions, with water lily and papyrus common on the margins of Lake Victoria today (Lind and Morrison, 1974), and with sedges present during the Lateglacial as indicated by available pollen data (Kendall, 1969; Beuning, 1999). Water lilies and sedges produce carbohydrate-rich underground storage organs (USOs) that are available throughout the year in dense patches, are easily harvested, and are historically known to have supported large populations of foragers (reviewed in Wrangham et al., 2009). Thus, habitats in close proximity to the lake provided food and other resources found in near-shore tidal flats, swamps, forests, and more open savannas. Foragers based near the lake could also take advantage of seasonal abundances (e.g., flowering vegetation, honey production, game, inland fish spawns) in more distant areas as needed (for discussion, see Ichikawa, 1980; Marean, 1997; Dale et al., 2004; Prendergast, 2010).

Observations from human behavioral ecology and ethnography suggest that settings with a variety of dense, predictable resources, many of them available throughout the year and not just seasonally, are typified by (1) small defended territories, (2) low residential mobility, (3) informal lithic technologies that are heterogeneous at a regional scale due to low degrees of information exchange, (4) the use of multi-season occupations that lead to dense archaeological accumulations and include evidence for the use of aquatic resources (e.g., bone harpoons), and (5) have relatively little evidence for long distance movement or exchange detectable through the presence of non-local lithic raw materials (Ambrose and Lorenz, 1990; Wallace and Shea, 2006). Late Pleistocene Equatorial African archaeological examples that conform to these observations include ~60–70 ka deposits at Katanda and LGM deposits at Ishango, both near Lake Edward (Fig. 1) in the Democratic Republic of the Congo, with informal lithic technologies, bone harpoons, patchily dense artifact accumulations, and evidence consistent with multi-season occupation (Brooks and Smith, 1987; Peters, 1990; Brooks et al., 1995; Yellen et al., 1995; Yellen, 1996; Helgren, 1997; Feathers and Migliorini, 2001). We predict similar archaeological signatures for Late Pleistocene shoreline sites along Lake Victoria, particularly for shallow, relatively calm bays where shellfish and aquatic and semi-aquatic plants with USOs were most abundant, shown as areas with a gentle, uniform offshore slopes in Fig. 1.

4.2. Human settlement in grass-dominated ecosystems

Grasses likely expanded across the Lake Victoria basin more or less in lockstep with lake retreat. Grasses are among the earliest colonizers in a natural vegetation succession, with existing C₄ grasslands near the lake margin facilitating rapid colonization of the lake flats that likely kept pace with lakeshore retreat (cf. Belsky, 1986). Today, C₄ grasslands occur in the Serengeti near the south-eastern shoreline (Fig. 1) as well as along the western shoreline (Lind and Morrison, 1974; Cerling, 1992). Diffusion of populations of herbivorous taxa and associated carnivores would have coincided with the spread of these grasslands towards the center of the basin, as the herbivores tracked their preferred habitats. As human predation on gregarious herbivores is well established in Africa (and elsewhere) by the Late Pleistocene (Marean, 1997; Assefa, 2006; Faith, 2008), we expect that there was the diffusion of groups of human foragers into the basin as well during any Late Pleistocene period of lake reduction, either during the Lateglacial or ~100–35 ka.

The grassy ecosystems that characterized the Lake Victoria basin during intervals of lake reduction would have offered a different set of resources from those found at the shoreline. Tropical African savanna grasslands are environments where food resources are dense but unpredictable. This is largely due to temporal and spatial uncertainties about the locations of the large herds of mobile ungulates that provide one of the most important potential sources of food (Ambrose and Lorenz, 1990; Marean, 1997). Such settings are typified by large undefended territories, are characterized by high residential mobility and the use of highly portable, multi-functional lithic technologies that maximize utility while minimizing weight. In Late Pleistocene Africa these include Levallois approaches to flake production and the use of backed pieces or microliths (e.g., Ambrose and Lorenz, 1990; Wallace and Shea, 2006; Hiscock et al., 2011; Eren and Lycett, 2012). Lithic assemblages are relatively homogenous over large areas due to high levels of mobility and information exchange between groups, occupations are sparse and typically short, and show strong evidence for long distance movement through non-local lithic raw materials (Ambrose and Lorenz, 1990).

Although overall resource predictability is low, certain places on the landscape may see recurrent use because of the presence of predictable resources, and these areas likely accumulated a more dense archaeological record. Examples include sources of fresh water (both for drinking and the expected presence of game) and outcrops of stone suitable for tool manufacture. Topography also plays an important factor in determining which areas likely saw recurrent use. Topographic lows are sediment and moisture traps, topographically rough areas are typically avoided by grazing ungulates, and both areas are characterized by high vegetation diversity with non-grass species preferentially targeted by human foragers (see Ichikawa, 1980; Tryon et al., 2014). Plants with underground storage organs are typically abundant on well-drained, nutrient-poor soils formed on slopes (Vincent, 1985; Marean, 1997). In the case of Lake Victoria, many of the present day islands would have been transformed into inselbergs or hills that overlooked relatively smooth grassy areas during periods of lake recession. These topographic high points would also have provided excellent vantage points to observe migratory game as well as other human populations on the surrounding plains (see also Jochim, 1976; Clark, 2001) and would have been highly visible, prominent features on the landscape, serving as visual anchors for navigation, as territorial markers or places of aggregation, and perhaps as sacred places (Bernardini et al., 2013). The attractiveness of these locales would be increased if fresh water and lithic raw material sources were also nearby. MSA archaeological sites

with Levallois technology on inselbergs that were likely occupied to take advantage of seasonal game migrations include Nasera rockshelter in Tanzania (Mehlman, 1977, 1989) and GvJm-22 at Lukenya Hill in Kenya (Marean, 1997; Tryon et al., 2015), sites overlooking the dry grasslands of the Serengeti and Athi-Kapiti plains, respectively.

5. Lake Victoria's Lateglacial and ~100–35 ka archaeological record

We explore these models for human diffusion across the Lake Victoria basin during periods of lake level decline using archaeological data from the lateglacial and ~100–35 ka intervals. The nature of our data dictates complementary approaches. Our Lateglacial dataset is focused on diachronic change from a rich artifact record from a single LSA site from an island, useful for assessing the timing of the occupation of the basin relative to lake level fluctuations. In contrast, the evidence from ~100 to ~35 ka consists of a sparse record from multiple MSA sites within a broad temporal envelope. For the older period, we shift our focus from questions of temporal variation to geographic variation, emphasizing the extent to which the MSA archaeological record of the Lake Victoria basin defines regional similarities and discontinuities that provide evidence for diffusion from neighboring areas.

5.1. The Lateglacial archaeological record

The post-LGM and terminal Pleistocene archaeological record of the Lake Victoria basin (Fig. 1) is restricted to lithic data from Munyama Cave, Uganda (fossil flora and fauna are not preserved) and perhaps basal strata at Siror, Kenya (Dale and Ashley, 2010) although details from the Pleistocene strata at Siror are lacking. In contrast, the record from Munyama Cave is dense but obscure, restricted to two very brief published syntheses in English (Nenquin, 1971; Van Noten, 1971), as well as a brief synthesis (Van Noten, 1970) and an unpublished but data-rich thesis in Dutch (Valcke, 1974). The Munyama Cave record is well suited to explore the relationship between changes in human occupation of the Lake Victoria region with the drying of the lake and subsequent refilling of the basin, as it is <15 km from the P-2 core recovered from Pilkington Bay on the northern shore of Buvuma Island (Fig. 1), a well-dated core ($n = 28$ ¹⁴C dates over 17.66 m thickness) that contains a detailed palynological record spanning the last ~18 kyr (Kendall, 1969), permitting a detailed comparison of the archaeological record with a proximal paleoenvironmental archive.

Munyama Cave is a modest sized cave (220 m²) ~28.5 m above current lake level overlooking Gaya Bay on the southwestern side of Buvuma Island. The island is today opposite Lake Victoria's main outlet at Jinja and is separated from mainland Uganda by a <1 km wide and <9 m deep channel (MacIntyre et al., 2002). During lake level retreat, the site would have overlooked a major (now-buried) river channel to the west of the island (Fig. 1). Excavation of 18 m² in 1968 yielded a stratified (1.4-m-thick), rich ($n > 166,000$) quartz-dominated (>98%) LSA archaeological sequence (Fig. 4) with backed pieces (microliths) comprising an average of ~53% of the retouched tools (Valcke, 1974). Outcrops of quartz suitable for tool production occur locally on the island (Wayland, 1925). Four stratigraphically coherent radiocarbon dates from 50 to 90 cm below the surface range from $11,187 \pm 292$ cal BP to $18,218 \pm 245$ cal BP (Nenquin, 1971) when calibrated using OxCal 4.2 software and the IntCal13 calibration curve (Reimer et al., 2013). The assemblage shows no consistent changes in artifact typology over time, but does record substantial shifts in artifact density throughout the stratigraphic sequence (Valcke, 1974) that suggest changes in occupation intensity throughout the cave's history.

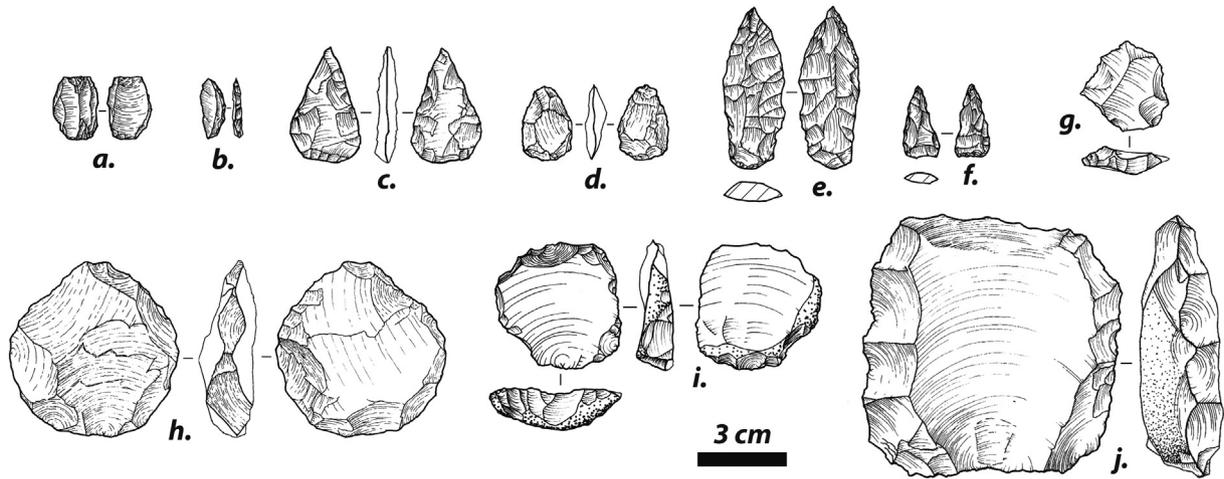


Fig. 4. Artifacts from the Lake Victoria basin and vicinity: (a) quartz bipolar core, Munyama Cave, (b) quartz backed microlith, Munyama Cave, (c) quartz bifacial point, Karungu, (d) quartz bifacial point, Walasi Hill, (e–f) quartz bifacial points from Chole rockshelter, (g) chert flake from a centripetally flaked core, Randhore (h) quartz Levallois core on flake, Walasi Hill, (i) chert Levallois core on flake, Randhore rockshelter, (j) lava Levallois core, Karungu. Artifacts from Munyama, Karungu, and Chole are redrawn from [Soper and Golden \(1969\)](#); [Van Noten \(1971\)](#); [Faith et al. \(2015\)](#). Those from Walasi Hill and Randhore are drawn from artifacts stored at the National Museums of Kenya and Boston University's Creighton Gabel Museum, respectively.

Fig. 5 plots artifact density by depth for Munyama Cave and the position of the radiocarbon dates, with an age–depth model of pollen spectra from the P-2 core plotted for comparison. The archaeological data show that peak occupation (as measured by artifact density) is broadly coincident with the timing of the ~17–16 ka desiccation event for Lake Victoria and the spread of *C4* grasses. The four radiocarbon-dated samples show a linear increase in age with depth ($r^2 = 0.958$, $p = 0.042$), using the midpoint of the 10-cm-thick stratum for each reported dated sample. This relationship allows us to interpolate an age–depth relationship for the 50–90 cm below surface (cmbs) levels. Extrapolation much beyond 50–90 cmbs makes unwarranted assumptions about regular sedimentation rates, but using the regression to calculate ages for adjacent bounding strata (40–50 cmbs and 90–100 cmbs) provides at least reasonable age estimates that allow us to better understand

the pattern of human occupation at the site. The results suggest that there is a marked increase in occupation intensity in the 90–100 cm level (extrapolated age = 21.4 ka) during the LGM. Although we lack direct evidence for the conditions of Lake Victoria during the LGM, pollen data from the Rwanda and Burundi highlands ([Bonnefille and Chalie, 2000](#)) suggest increased aridity near the headwaters of the western part of the basin that would have contributed to a reduction in the area and volume of Lake Victoria, consistent with reductions in other tropical African lakes at this time ([Gasse et al., 2008](#)). Given the narrow and shallow channel separating Buvuma Island from the mainland, it may well have been connected to the mainland during the LGM. There is a rapid drop in artifact abundances in the 60–70 cmbs stratum; the interpolated depth for the connection of Lake Victoria to the Nile at ~13 ka ([Beuning et al., 2002](#)) is ~62 cmbs, suggesting a connection

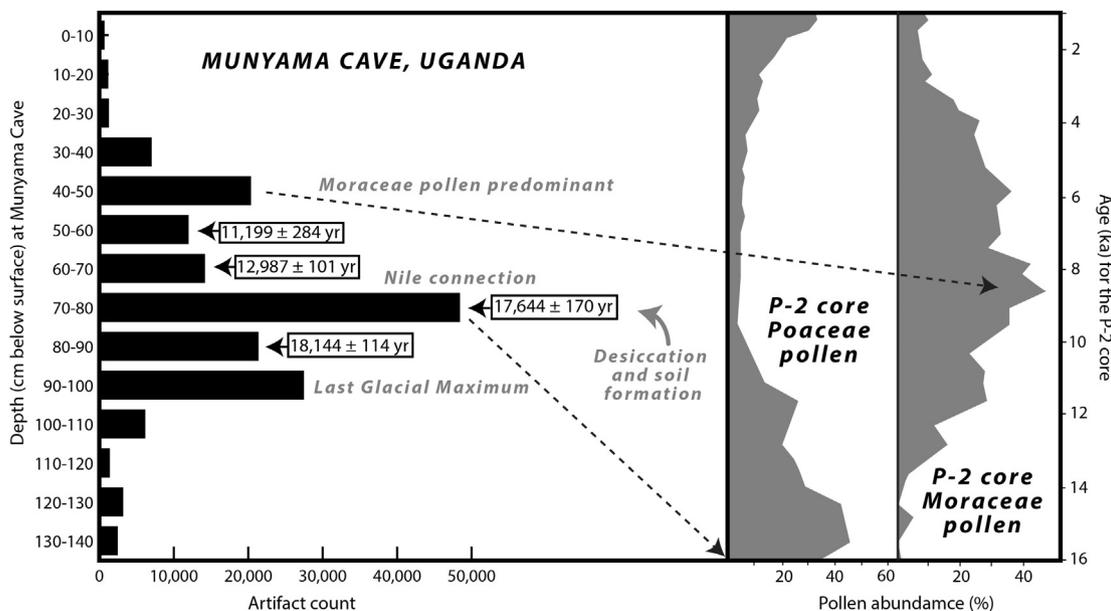


Fig. 5. Artifact density and calibrated radiocarbon dates plotted by depth for Munyama Cave, Buvuma Island, Uganda, with data from [Valcke \(1974\)](#). Shown in grey lettering are major events in the history of Lake Victoria, plotted against the pollen record (in grey) of the P-2 core from Pilkington Bay, Buvuma Island, after [Kendall \(1969\)](#) and [Berke et al. \(2012\)](#).

between reduced occupation intensity and high lake levels. Finally, artifact abundances fall substantially after the 40–50 cmbs level, with an extrapolated age of 8.6 ka, a date by which the pollen records from the proximal P-2 core and more distant V95-2P core (Kendall, 1969; Beuning, 1999) indicates that grass (Poaceae) pollen abundance is at a minimum and tree pollen (primarily Moraceae) is at its maximum abundance (Fig. 5).

In sum, the record from Munyama Cave suggests that occupation intensity is inversely related to lake level, indicating that human use of portions of the basin may have tracked lake contraction and expansion. That peak occupation density coincides with lake desiccation ~17–16 ka suggests that the site's utility to foragers may have been greater as a topographic high point overlooking a C₄ grass-dominated ecosystem rather than as an island, perhaps because offshore conditions were not conducive to dense shellfish or aquatic/semi-aquatic USO plant populations. The retouched tool component is dominated by backed microliths throughout the Pleistocene, consistent with use by groups living in areas characterized by dense but unpredictable resources (e.g., migratory game), although actual distance to the shoreline is unknown for most of the site's history. The lack of faunal or floral remains makes it difficult to infer if the site represents a residential area or a shelter repeatedly occupied on a seasonal basis, and the artifacts are made almost exclusively of quartz (no obsidian is reported), and thus assessing connections with more distant areas is not possible.

5.2. Archaeological evidence from ~105 to ~35 ka

All MSA sites from the Lake Victoria basin occur in terrestrial sediments with no clear evidence for proximity to a lake, as Holocene refilling of the basin eroded or buried shorelines formed during periods when the lake was smaller than present. Holocene archaeological sites are associated with the +3 m strandline around the lake (Brachi, 1960; Lane et al., 2006), but whether the +10–12 m or +18 m deposits date to the Holocene or Pleistocene is unknown, and as yet, no archaeological sites are known from either of them. The recovery of archaeological sites contemporary with the +10–12 m or +18 m strandlines remains a focus of ongoing research.

Of the MSA sites in the basin, the best described are those from Rusinga Island, Mfangano Island, and Karungu, and these consist of lithic artifacts (and rare cut-marked and percussed bones) collected during pedestrian survey, systematic surface collection, and excavation (Tryon et al., 2010; Jenkins et al., 2012; Tryon et al., 2012; Faith et al., 2015). Of these, Rusinga Island in particular offered a combination of topographic highpoints, fresh water springs, and locally available sources of high quality lava and chert raw materials (Tryon et al., 2014). The combined assemblage from Rusinga Island, Mfangano Island, and Karungu ($n > 750$), portions of which is derived from surface-collected material targeting only technologically diagnostic specimens, consists of flakes and blades removed from a variety of Levallois, discoidal, and single- and multi-platform cores (Fig. 4). Retouched pieces are rare, but include side scrapers and small (<5 cm) unifacial and bifacial points (Fig. 4). Artifacts are made primarily of a diverse array of locally available lavas, chert, quartz, and quartzite, as well as rare obsidian artifacts from sources in the Central Rift of Kenya, ~250 km to the east (Faith et al., 2015). Points and Levallois flakes are often made on unique raw material types, suggesting they entered the archaeological record far from the place of manufacture (Tryon et al., 2010), consistent with expected use by highly mobile groups as predicted for grassland settings with dense but unpredictable resources. Artifact density is low (Garrett et al., 2015), and the combined evidence is consistent with the interpretation that we are primarily sampling areas of hominin tool use and discard rather than areas of tool production or

prolonged occupation (cf. Roebroeks, 1988; Conard and Adler, 1997), many likely related to prey acquisition. Notably, the fossil assemblages are dominated by gregarious and probably migratory bovids *D. hypsodon* and *R. atopocranium* (Table 1; Faith et al., 2012), some of which were probably hunted using mass-capture techniques (Jenkins et al., 2012).

Other MSA sites with small points and evidence for Levallois technology occur around the margin of Lake Victoria (Figs. 1 and 4). These include collections from present-day islands that would have been connected to the mainland with the 25 m lake level drop suggested by evidence from Mfangano Island (Tryon et al., 2014), including Lolui and Bugaia Islands in Uganda (Nenquin, 1971; Posnansky et al., 2005). Other near-shore sites include Chole rockshelter, Ruhanga rockshelter, Kibwera and Loiyangalani in Tanzania (Soper and Golden, 1969; Bower and Grogan-Porter, 1981; Bower et al., 1985; Reid and Njau, 1994; Kwekason and Chami, 2003), and Muguruk, Songhor, and perhaps Randhore rockshelter in Kenya (Gabel, 1969; McBrearty, 1981, 1988). Walasi Hill in Uganda (O'Brien, 1939) lies just outside the basin margin at the foot of Mt. Elgon and near the headwaters of Lake Kyoga (Fig. 1), a region speculated to be an important source of water for the region during Lake Victoria's reduction (Livingstone, 1976: 24; Van Damme and Van Bocxlaer, 2009: 586). Unfortunately, none of these sites are well dated, and the artifact assemblages are in general only summarily described. Despite the coarseness of the available archaeological data, three general patterns emerge relevant to human occupation of the Lake Victoria basin.

5.2.1. A different archaeological record from sites west of Lake Victoria

Small point and Levallois based assemblages from the Lake Victoria basin are quite distinct from Late Pleistocene deposits in central Africa, further to the west. These are best represented at the ~60–70 ka Katanda sites, where an informal quartz-based industry occurs with shaped uni- and biserial bone harpoons (Brooks et al., 1995; Yellen et al., 1995; Yellen, 1998; Feathers and Migliorini, 2001), but also includes the undated site of Rutonde, Rwanda (Nenquin, 1967). The absence of Levallois technology and bifacial points at these sites is not explained by raw material properties, as quartz Levallois cores and bifacial points are found at Rusinga Island and Karungu in the Lake Victoria basin and Walasi Hill at the foot of Mt. Elgon (Fig. 4). Older (likely Middle Pleistocene) sites such as Masango in Burundi (Van Noten et al., 1972) further indicate the use of Levallois technology and the production of bifaces in regions west of Lake Victoria. These differences may be better explained by differences in resource predictability. Although environmental details are lacking for Rutonde, sites at Katanda suggest use of a range of terrestrial and seasonally available aquatic resources (Brooks et al., 1995; Helgren, 1997).

5.2.2. Archaeological similarities to areas east of Lake Victoria

Late Pleistocene small point and Levallois-based assemblages similar to those found around Lake Victoria are common throughout the eastern portion of the EARS and surrounding areas, which may indicate the westward expansion of technological traditions (and possibly populations) into the Lake Victoria basin (Tryon et al., 2012; Tryon and Faith, 2013; Faith et al., in press). The presence of eastern Rift Valley obsidian at MSA sites along Lake Victoria further demonstrates the connections between these areas during the Late Pleistocene (Faith et al., 2015).

Contemporaneous MSA archaeological sites with faunal assemblages similar to those from Rusinga Island, Mfangano Island, and Karungu include Nasera rockshelter in Tanzania (Mehlman, 1977, 1989) and GvJm-22 at Lukenya Hill in Kenya (Marean, 1997; Tryon et al., 2015), sites overlooking major migration pathways

on the dry grasslands of the Serengeti and Athi-Kapiti plains, respectively (Fig. 1). For sites on the eastern margin of Lake Victoria, the Serengeti and other dry grass plains east of the lake may have been a source area for the diffusion of plant, animal, and human populations.

5.2.3. Similarities to areas north of Lake Victoria

Faith et al. (2015) conducted a more formal analysis based on the geographic distribution of 14 different artifact types among a sample of 30 Late Pleistocene archaeological assemblages from across eastern Africa. The analysis indicates distinct differences in the artifact compositions of sites on either side of the Equator. Northern sites (>5°N) are distinguished from those at or below the Equator by less frequent use of bipolar cores and anvils, and more frequent use of Levallois points and cores and large bifaces (Faith et al., 2015). Significantly, exceptions to this geographic pattern include the samples from Rusinga Island and Karungu, Equatorial sites that show a 'northern' technological pattern unlike other southern sites. When combined with data indicating archaeological similarities to areas east of Lake Victoria, this observation suggests occupation of the basin from multiple directions about the periphery of the lake, parallel to observations about the formation of faunal non-analog super communities (Faith et al., 2015).

6. Conclusions

Seismic surveys and lake sediment cores demonstrate that Lake Victoria was desiccated or significantly reduced in size multiple times throughout the Pleistocene, most prominently at ~17–16 ka. One or more additional such events are inferred from discontinuous near-shore terrestrial deposits dating to ~100–35 ka. Periodic drying of the largest lake in Africa would have had a profound impact on the composition of local floral and faunal communities. Multiple lines of geochemical, ecological, and fossil evidence from both sediment cores and near-shore terrestrial deposits suggest that the spread of a C₄ grass-dominated ecosystem accompanied lakeshore retreat, at least in the eastern, northern, and central portions of the basin where data are available. The replacement of the lake with a grassland would have removed major dispersal barriers to a host of terrestrial animals, contributed to the range expansion of a number of dry grassland-adapted grazing herbivores, and led to the formation of non-analog super-communities (Tryon et al., 2010; Faith et al., 2013, in press).

Humans were apparently part of this process of range expansion and population diffusion, with groups likely tracking the movement of both the resource-rich shoreline and herbivores. The Later Stone Age evidence from Munyama Cave on Buvuma Island shows a clear and strong correspondence between lake level decline and increased occupation intensity, particularly during the ~17–16 ka desiccation event, indicating increased use of portions of the basin as lake level fell. Reliance on near-shore resources during the Late Pleistocene remains speculative, as much of the relevant evidence has been eroded or buried with subsequent lake level rise during the Holocene, but has the potential to be tested by targeted survey for raised shoreline deposits. A suite of technological and typological factors suggest strong similarities among the ~100–35 ka Middle Stone Age archaeological assemblages from Rusinga Island, Mfangano Island, and near Karungu with areas to the east and north of Lake Victoria. Although speculative, areas to the east and north may well have been the source regions for the C₄ grassland ecosystems that expanded into the basin; similarities between the fossil fauna and Serengeti ecosystem to the east are particularly strong.

Repeated Pleistocene contraction and expansion of Lake Victoria and C₄ grass ecosystems provides an explanation for much of the

legacy of environmental heterogeneity that characterizes the Lake Victoria basin today (Cowling et al., 2008; Linder et al., 2012; Lorenzen et al., 2012; Faith et al., 2015, in press). As a push–pull mechanism that repeatedly drew human populations towards the basin center with drying and caused their dispersal with lake expansion, the environmental flux of Lake Victoria may have led to the repeated isolation and combination of diverse populations of foragers that ultimately could have contributed to the diversity of Pleistocene human foragers across Equatorial Africa (e.g., Lahr and Foley, 1998; Harvati et al., 2011; Pearson, 2013; Tryon et al., 2015).

The environmental history of Lake Victoria has to be understood in a broader context. One distinctive feature of the Lake Victoria record is that the occupation of new landscapes, particularly those in the center of the basin, occurred during periods of increased aridity, as reduced moisture availability led to a reduction in lake volume and particularly surface area, and human populations tracked both the shrinking shoreline and herbivores moving into the area. In other areas in Africa such as the Sahara as well as the Arabian Peninsula, it was during intervals of reduced aridity that humans colonized new landscapes, particularly as deserts were transformed into grasslands (Drake et al., 2011; e.g., Rose et al., 2011; Groucutt and Petraglia, 2012; Scerri et al., 2014; but see Will et al., 2015). Latitudinal gradients in environmental change across Africa during the Pleistocene result in regions such as Equatorial Africa and the Sahara being out of phase, with drier periods near the Equator at times coinciding with more humid intervals in the Sahara (Blome et al., 2012). By removing potential dispersal barriers (e.g., large lakes and deserts), these differing environmental regimes may have both offered conditions conducive to human expansions beyond Equatorial Africa, and their coincidence ~105–80 ka has been linked to dispersals across and out of Africa (Cohen et al., 2007; Scholz et al., 2007; Blome et al., 2012). The Nile River has long been considered a corridor for migration and a connector to sub-Saharan Africa, particularly for the spread of Lupemban and Nubian MSA industrial complexes (for a recent review, see Scerri, 2013), but MSA sites on the White or main Nile are restricted to north of Khartoum at ~15°N (see Masojć, 2010; Rose et al., 2011), with the exception of a few surface-collected Levallois cores near Juba in South Sudan at ~4°50'N (Philipson, 1981). Given Lake Victoria's present position at the headwaters of the Nile, additional inter-regional comparisons between the Lake Victoria basin and regions to the north are certainly warranted.

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