Dietary ecology of mixed-feeding antelopes in the Omo-Turkana basin during the Plio-Pleistocene: a tool to investigate hominin palaeo-environments

Photo: L. Crété

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Abstract

Dietary ecology of mixed-feeding antelopes in the Omo-Turkana basin during the Plio-Pleistocene: a tool to investigate hominin palaeo-environments

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To assess whether detailed studies of the dietary ecology of mixed-feeding antelope species could be used to investigate hominin palaeo-environments in the Omo-Turkana basin during the Plio-Pleistocene (3.5-1.6 Ma), a detailed study of the dietary ecology of mixed-feeding antelopes was proposed. This research focused on the diets of the impala (genus *Aepyceros*) and the springbok (genus *Antidorcas*), whose extant relatives demonstrate a high dietary plasticity. The dietary ecology of these taxa was evaluated through stable carbon and oxygen isotope, mesowear and dental microwear textural analyses.

To provide more tools to interpret fossil evidence, predictive models were tested to study the relationship between land cover and dietary behaviours of modern populations. The high variability of stable carbon isotope values observed across modern impala specimens and the wide range of habitat types they were associated with showed that impalas tend to rely heavily on palatable grasses and forbs, suggesting a preference for herbaceous plants. The diet of modern impalas therefore does not always reflect the vegetation types prevailing in their environments, as availability of their preferred foods can be influenced by local year-round land cover patterns and by seasonal fluctuations in climate. However, the predictions generated for fossil *Aepyceros* samples for the Omo-Turkana basin were consistent with previous palaeo-environmental studies for this region, demonstrating the potential of this method and the relevance of using these taxa as palaeo-environmental indicators.

Significant differences in dietary ecology were observed for the studied taxa when comparing assemblages from different fossil localities, as well as when comparing assemblages between members. Results suggested the presence, across all three fossil localities of the Omo-Turkana basin, of long-lived mosaic habitats, which could have supported a high diversity of mammalian taxa with varying ecological requirements. Results confirmed previous studies which suggested patterns of grassland expansion and increased habitat fragmentation in the region from ~2.0 Ma, as well as an increase in seasonal and interannual rainfall variability between 2.27 and 1.9 Ma. Such conditions have been previously hypothesized to have influenced local faunal biodiversity in the region, adding selective pressures associated with seasonal changes in resources abundance and distribution, acting, in turn, as an additional driver of hominin evolution.

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Pour Papa,

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Glossary & Abbreviations

General terms

Faunal turnover: coordinated speciation and extinction event experienced by many faunal species within a geographical area.

Hominin: Even if it varies depending on classifications, "a hominin is a member of the sister clade of the lineage leading to *Pan*" (Foley and Lewin, 2013). The hominin tribe usually includes humans (*Homo*), and their extinct relatives based on their shared anatomical and molecular characteristics when known. Any human ancestor which appeared after the divergence between *Pan* and *Homo* clades is a hominin. Based on molecular evidence, this divergence must have happened between 5 to 8 Ma (Mayr, 2001).

Ma (abbreviation for the Latin "*megaannus*"): unit of time representing one million (years), commonly used in scientific fields such as geology or palaeontology. The abbreviation Myr (million years) is used for durations of millions of years.

Phytoliths: Siliceous microscopic remains originating from plant tissues, resulting from biological and physical processes by which certain plants deposit solid silica in an intracellular or extracellular location after absorbing soluble silica from groundwater. After the plant's decay, these pieces of silica are deposited in the soil as microscopic particles of varying sizes and shapes. They can be found in sediments, or imbedded in animal dental enamel or calculus as the result of plant consumption (Piperno, 2006).

Pleistocene: geologic epoch from ~2.58 Ma to 11,700 years BP (before present). It follows the Pliocene epoch, and is followed by the Holocene epoch (from 11,700 BP to today). It is part of the Cenozoic era, and of the Quaternary period (from ~2.58 Ma to today).

Pliocene: geologic epoch from ~5.3 Ma to ~2.58 Ma, following the Miocene epoch (from ~23 Ma to 5.3 Ma), and followed by the Pleistocene epoch. It is part of the Cenozoic era (from ~66 Ma to today), and of the Neogene period (from ~23 Ma to ~2.58 Ma).

Ecology

Biome: complex biotic community characterized by a combination of distinctive plant and animal species, and maintained under the climatic conditions of the region. Biomes are classified based on the prevailing vegetation and the adaptations of organisms to that particular environment (e.g. deserts, forests, grasslands, tundra).

Browser: herbivore that feeds primarily (>90%) on leaves, twigs, buds, flowers, and/or fruits (Green and Croft, 2018).

Grazer: herbivore that feeds primarily (>90%) on grasses (Green and Croft, 2018).

Habitat: ecological area inhabited by a given species or community, where it is natural for them to live and grow.

Mixed-feeder: herbivore that feeds on a mixture of leaves, twigs, buds, and grasses (Green and Croft, 2018).

Niche: In ecology, the definition of the "niche" concept is highly debated. It generally refers to the fit of a species living under specific environmental conditions, and its role within the community, based on the relationship between the organism and its environment (Whittaker, Levin and Root, 1973). Hutchinson (1957) defined the niche of a species as "the volume, in the space of environmental variables, where the species can survive indefinitely (the fundamental niche), or the volume, limited because of interaction with present competitors, where the species actually survives (the realized niche)" (Pocheville 2015, p.575).

Dental morphology

Brachydont: Molar teeth with low crowns, well-developed roots with narrow canals (e.g. humans) (Hillson 2005).

Bunodont: molar teeth with crowns in the form of rounded or conical cusps, ideal for crushing and grinding chewing patterns. Cups are low, rounded, separated by grooves and fissures, and distributed over broad occlusal surfaces (e.g. omnivorous species such as bears and suids). (Hillson 2005)

Distal: Direction of the tooth surface oriented towards the gingiva beyond the tooth, away from the anterior midline (Nelson 2014).

Hypsodont: High-crowned teeth with enamel extending below the gum line, typical of grazers with an abrasive diet (e.g. equids) (Hillson, 2005).

Labial/buccal: Side of a tooth adjacent to - or the direction towards- the inside of the cheek, as opposed to “lingual”. “Buccal” technically refers only to posterior teeth (where the cheeks are present), while “labial” refers to anterior teeth (where the lips are present). However, both terms are often used interchangeably to refer to posterior and/or anterior teeth, for surfaces facing the cheeks or the lips. The term “vestibular” can be used to describe both labial and buccal surfaces (Nelson 2014).

Lingual: Side of a tooth adjacent to -or the direction towards- the tongue (lingua, compare linguistics and language), as opposed to “buccal/ labial” (Nelson 2014).

Lophodont: molar teeth with crowns with transverse ridges on the grinding surface. Cusps have coalesced into folds, and the long axis of the folds is mainly bucco-lingual (Hillson 2005).

Mesial: Direction of the tooth surface oriented towards the anterior midline of the dental arch, as opposed to distal (Nelson, 2014).

Selenodont: Molar teeth with crowns formed in crescent-shaped cusps, with crescentic folds running mesio-distally with the long axis (Hillson 2005).

Use-wear analyses (all definitions from Green and Croft 2018).

Abrasion: tooth wear caused by interactions between a tooth and exogenous particles.

Attrition: tooth wear that is caused by tooth-on-tooth interactions.

Confocal microscope: microscope using point illumination and a spatial pinhole placed at the confocal plane of the lens to reduce out-of-focus light, creating a three-dimensional image.

Facet: a smooth, flat area of enamel on the occlusal surface of a tooth that is formed by wear.

Stable isotopes (all definitions from Higgins 2018)

Bulk-analysis: Analysis of a single sample per specimen, to obtain an average value for the sample that includes its entire span of formation.

Depletion: relative term to describe a trend in the relative abundance of one isotope over another in a sample, often referring to a loss in the heavier isotope.

Enrichment: relative term to describe a trend in the relative abundance of one isotope over another in a sample, often referring to an increase in the heavier isotope.

Fractionation factor (α): expression of the fractionation of isotopes during reactions or changes of phase, such as the fractionation of carbon isotopes from food (substance A) to carbon isotopes found in the tooth enamel of herbivores (substance B). It is shown as: $^{\alpha}A\text{-}B= R_A=R_B$

where $^{\alpha}$ A−B is the fractionation factor from substance A (food) to substance B (tooth enamel); R_A is the ratio of the heavier isotope of carbon (^{13}C) to the lighter isotope of carbon (^{12}C) in substance A (food); R_B is the ratio of the heavier isotope of carbon (^{13}C) to the lighter isotope of carbon (^{12}C) in substance B (enamel)

Isotopic Enrichment (ε*): expression of the fractionation of isotopes during reactions or changes of phase, such as the fractionation of carbon isotopes from food (substance A) to carbon isotopes found in the tooth enamel of herbivores (substance B). It is shown as: $^{\varepsilon}$A-B* = ($^{\varepsilon}$A-B* -1)

where $^{\varepsilon}$A-B is the fractionation factor from substance A (food) to substance B (tooth enamel).

Serial analysis: type of analysis in which fossil specimens that show incremental growth are sampled multiple times along the direction of growth to capture isotopic changes during the growth of the organism. For teeth, the term "intra-tooth" analysis if often used.

Stable isotope: Isotopes are atoms of elements of different masses, due to variations of the number of neutrons in the nucleus. For some isotopes, the different number of neutrons makes the nucleus unstable, resulting in radioactive decay and the conversion of that atom to a different element. For others, no decay occurs, and the isotope is called stable.

V-PDB: international scale used for measurement of carbon and oxygen isotopes, typically from carbonate. PDB refers to the Pee Dee Belemnite, which was collected from the Pee Dee Formation in South Carolina in the 1950s. The δ^{13}C and δ^{18}O values for the original PDB were assigned values of zero. The supply of the original Pee Dee Belemnite has since been exhausted. The more commonly available standards NBS-19 (a limestone - δ^{13}C = +1.95‰, δ^{18}O = −2.20‰) and L-SVEC (a lithium carbonate - for carbon only, δ^{13}C = −46.6‰) are now used instead to serve as reference points for calibrating laboratory analyses to the V-PDB scale.

V-SMOW: international scale used for measurement of hydrogen and oxygen isotopes, typically from water. SMOW refers to Standard Mean Ocean Water, a presumed average of the isotopic values of ocean water world-wide. The international community currently uses defined values SMOW (δ^{2}H=0‰, δ^{18}O =0‰) and SLAP (Standard Light Antarctic Precipitation - δ^{2}H = −427.5‰, δ^{18}O = −55.50‰) as the reference points for calibrating laboratory analyses to the V-SMOW scale.

Chapter 1: Introduction

1.1 Background: Human evolution and climate change

1.1.1 Plio-Pleistocene hominins

The fragmented remains of a few early hominin individuals, and sometimes their tools and footprints, are the only direct traces available today to study our ancestors, their life, behaviour, and evolution, to which environmental elements can be added by studying past geology, vegetation and fauna. These fragmentary remains have revealed over time the existence of various hominin species between 4.5 and 1 million years ago (Ma), mostly in eastern and southern Africa (Potts, 2007; Spoor *et al.*, 2007; Wood and Leakey, 2011; Leakey *et al.*, 2012; Foley and Lewin, 2013; Mbua *et al.*, 2016). Although sharing morphological similarities that demonstrate their taxonomic relationships, each species developed special traits, partly in relation to their ecology (Table 1).

The oldest potential hominins - dated between 7.0 to 4.5 Ma - were found in Chad, Kenya and Ethiopia and belong to the genera *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (White *et al.* 1994, Senut *et al.* 2001, Brunet *et al.* 2002, Potts 2007). *Orrorin* and *Ardipithecus* appear to have been associated with wooded habitats, while *Sahelanthropus tchadensis* was associated to relatively open habitats (Vignaud *et al.*, 2002). According to various studies, these species might be the earliest specimens demonstrating a shift from quadrupedal to bipedal locomotion, as well as changes in dental morphology, two of the key differences between *Homo* and *Pan* (Richmond and Jungers, 2008; White *et al.*, 2009; Wood and Harrison, 2011; Machnicki *et al.*, 2016). The fossil record is more substantial from 4 Ma ago onwards in East and South Africa, with the appearance of relatively well-represented lineages, such as *Australopithecus* sp., *Paranthropus sp.*, and *Homo* sp. The Omo-Turkana basin is particularly rich in hominin remains dated between 4.3 and 0.5 Ma, showing a wide range of morphological variation, with the three genera mentioned above being represented in this area (Table 1). If precise relationships between taxa are difficult to assess (Wood and Harrison 2011), as well as hominin diversity per se (Maxwell *et al.*, 2018), some aspects of hominin evolution can be studied in detail, such as the relative taxonomic diversity that existed in the past between and within genus and species, and adaptive behavioural shifts (e.g. first stone tool technology, 3.3 Ma – Harmand *et al.* 2015).

1.1.2 Plio-Pleistocene climate change and evolutionary theories

Human evolution is characterised by speciation, extinction, and dispersal events, with numerous studies suggesting that changing landscapes and climates had an impact on species' evolutionary paths (e.g. deMenocal 2004, Behrensmeyer 2006, Faith and Behrensmeyer 2013), although biological evolution cannot be explained solely by environmentally-induced processes, with other factors such as genetic drift and neutral mutation influencing evolutionary processes (Lande, 1976; Hartl, Dykhuizen and Dean, 1985). Major Pliocene and Pleistocene climate transitions have been suggested to have led to cooling, drying trends that resulted in the spread of grasslands and the shrinking of forests (e.g. Demenocal 1995, Spencer 1995, Lee-Thorp *et al.* 2007), which were hypothesized, in turn, to have led to major changes in the structure and composition of local floral and faunal communities (e.g. Pulse Turnover Hypothesis, Vrba 1985). Such changes would then have triggered the major biological and behavioural changes observed within the hominin lineage (e.g. tool use, increase in brain size, dispersal events… etc), particularly in relation to the emergence of genus *Homo* (R A. Dart, 1925; Hopley *et al.*, 2007).

Table 1: Hominin species identified in East African localities between 4.3 and 1.0 million years ago, with basic traits, main localities, dates, and ecology. In bold **are the formations under study where remains of *Aepyceros* sp. and/or *Antidorcas* sp. were excavated.**

Species	Dating	Provenance	Body proportions	Cranial capacity	Locomotion	Dietary preferences	References
Australopithecus afarensis	4.3 - 2.7 Ma	**East Turkana**; Lothagam; Kantis (Kenya)	Size: 105 - 151 cm Weight: 30 - 45 kg	400 - 550 cm3	Bipedal with retained arboreal morphologies	C_4 foods (grass, sedge) + fruits, meat	Wood and Leakey, 2011; Behrensmeyer and Reed, 2013; Foley and Lewin, 2013; Klein, 2013; Mbua *et al*,. 2016
Kenyanthropus platyops	3.5 Ma	**West Turkana** (Kenya)	Unknown	450 - 530 cm3	Unknown	C_4 foods (grass, sedge)	Potts, 2007; Behrensmeyer and Reed, 2013
Paranthropus aethiopithecus	2.6 - 2.3 Ma	**West Turkana** (Kenya)	Unknown	420 cm3	Bipedal with retained arboreal morphologies	C_4 foods (grass, sedge)	Wood and Leakey, 2011; Klein, 2013
Homo habilis	1.9 - 1.7 Ma	**Koobi Fora** (Kenya) Olduvai (Tanzania) Hadar; **Shungura G**, H (Ethiopia)	Size: 115 - 130 cm Weight: 30 - 40 kg	550 - 680 cm3	Bipedal with retained arboreal morphologies	C_4 foods (grass, sedge)	Ungar *et al.,* 2006; Spoor *et al.,* 2007; Klein, 2013
Paranthropus boisei	2.3 - 1.4 Ma	**Koobi Fora; West Turkana** (Kenya) Olduvai (Tanzania) Konso; **Shungura G** (Ethiopia)	Size: 124 - 137 cm Weight: 34 - 49 kg	500 - 600 cm3	Bipedal with retained arboreal morphologies	C_4 foods (grass, sedge - 75 to 80% of its diet)	Wood and Leakey, 2011; Klein, 2013
Homo ergaster	1.9 - 1 Ma	**Koobi Fora;** Ologersailie? (Kenya)	Size: 155 - 170 cm Weight: 50 - 65 kg	850 cm3	Bipedal	C_4 foods (grass, sedge)	Spoor *et al.* 2007; Wood and Leakey, 2011; Klein, 2013

The palaeo-vegetation of a given region is shaped by a combination of factors, such as climatic and environmental conditions, hydrological factors, geology, topography, altitude, and soil matrix. Evidence of past changing environments have been investigated mainly through sedimentary, palynological, and palaeontological studies (e.g. Vrba, 1993; Behrensmeyer *et al.,* 1997; Bobe *et al.,* 2002; Bonnefille *et al.,* 2004; Bobe, 2006; Potts, 2013; Cerling *et al.,* 2015), with global and/or regional palaeo-climatic records linking major climatic events to important changes in ecosystems and in mammal lineages (Demenocal, 1995; Trauth *et al.*, 2005; Carto *et al.*, 2009; Castañeda *et al.*, 2009; Donges *et al.*, 2011) (Figure 1). Most particularly, two major climatic events have been suggested to have had a significant impact on palaeo-environments and on mammal evolution across the Plio-Pleistocene transition: the intensification of the Northern Hemisphere Glaciation (iNHG) and African aridification at ~2.8-2.4 Ma (Vrba, 1995; deMenocal, 2011); and the onset of the Walker Circulation at ~2.0-1.7 Ma (Demenocal, 1995) (table 2). These major changes have been hypothesized to have played a predominant part in human evolution and innovations (e.g. emergence of genus *Homo*, first tools…etc), leading to several theories and studies aiming at untangling the complex relationships between palaeo-environmental conditions and the biological processes that shaped the hominin lineage (table 3).

Table 2: Major Plio-Pleistocene global climatic events

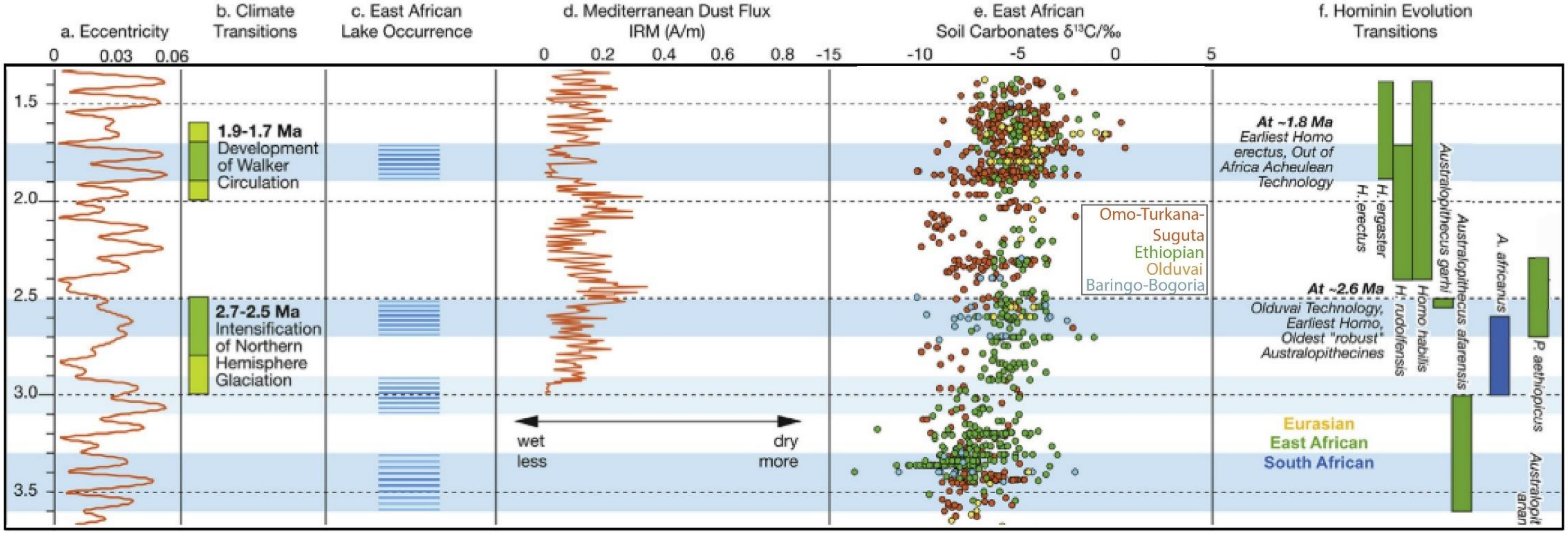
Climatic event	Date	Description	Environmental impact
Intensification of Northern Hemisphere Glaciation (iNHG)	3.2 - 2.5 Ma	• Culmination of long-term high latitude cooling, which began with the Late Miocene glaciation of Greenland and the Arctic, and continued through to the major increases in global ice volume at ~2.55 Ma (Maslin *et al.*, 1998). • The extent of glaciation became then characterised by cyclic advances and retreats of ice sheets on a hemispherical scale (i.e. 'glacial-interglacial cycles').	• Growth and decline of large lakes between 2.7 and 2.5 Ma in the Baringo-Bogoria Basin (Deino *et al.*, 2006; Kingston *et al.*, 2007) • Significant increase in the amount of dust coming off the Sahara and Arabia, potentially indicating aridity in the region in response to the iNHG (Demenocal, 1995; deMenocal, 2004). • For East African sites, it was suggested that the iNHG had less of an impact on faunal and hominin evolution (e.g., Behrensmeyer *et al.* 1997; Faith and Behrensmeyer 2013) than the subsequent development of Walker Circulation.
Onset of the Walker Circulation (oWC)	2.0 - 1.7 Ma	• A shift in long-term records of sea surface temperature in the Pacific Ocean was observed at ~2.0 Ma, with a strong east-west temperature gradient developing across the tropical Pacific Ocean (Ravelo *et al.*, 2004; McClymont and Rosell-Melé, 2005; Brierley *et al.*, 2009). • This shift was interpreted as evidence for the development of a stronger Walker circulation as part of the gradual global cooling, with the tropics and sub-tropics switching to the modern mode of circulation with cool sub-tropical temperatures from ~2 Ma (Ravelo *et al.*, 2004; Maslin and Christensen, 2007). • This strong east-west temperature gradient in the Pacific Ocean is thought to impact upon the properties of the El Nino-South Oscillation (ENSO) and, in turn, to be the main cause of interannual variability in rainfall in the region today (Saji *et al.*, 1999).	• The intensified Walker Circulation has been suggested to have triggered mammalian evolution (deMenocal 1995; Vrba 1985). • Stable carbon isotope data suggests that trend towards open-environments after 3 Ma, with a marked change towards open grass-dominated landscapes after 2 Ma (Lee-Thorp, Sponheimer and Luyt, 2007). • Re-analysis of terrestrial dust records from the Arabian Sea (deMenocal, 1995, 2004), the eastern Mediterranean Sea (Larrasoana *et al.*, 2003) and of subtropical West Africa (Tiedemann, Sarnthein and Shackleton, 1994) suggests an increase in aridity and variability after ~1.9-1.5 Ma (Trauth, Larrasoañ and Mudelsee, 2009). • Evidence for large, deep, fluctuating lakes in East Africa (Trauth *et al.*, 2005, 2007).

Table 3: Main theories discussing the relationship between environmental change and mammal evolutionary processes.

Theory	Description	Evidence from previous studies
Savannah hypothesis (Dart, 1925) [developed further by several researchers such as Johanson *et al.,* 1982; Vrba *et al.,* 1988; Berger and Loutre, 1991; Demenocal, 1995, 2004; Reed, 1997]	• **Increase in aridity and grassland-dominated landscapes** in Pliocene and Pleistocene Africa (especially east of the African rift), which forced early hominin species to adapt from dense wooded habitats to more open environments. • **Periods of enhanced aridification** are hypothesized to have likely triggered speciation events in the hominin lineage (Demenocal, 1995; deMenocal, 2004).	• Evidence of a progressive vegetation shift from C_3 plants to C_4 plants during the Pliocene and Pleistocene, based on soil carbonates (Levin *et al.*, 2004; Wynn, 2004; Segalen, Lee-Thorp and Cerling, 2007) and fossilised mammal teeth (Harris *et al.*, 2008; Brachert *et al.*, 2010).
Turnover Pulse Hypothesis (Vrba, 1985)	• **Major biotic turnover** (speciation, extinction, and dispersion of mammal species) **occurring in pulses, in line with global climatic changes** [such as the Intensification of Northern Hemisphere Glaciation], which triggered changes in habitats/vegetation (Vrba, 1985, 1993). • These changes are thought to occur when environmental changes create fragmentation of habitats, leading to vicariance (Potts and Behrensmeyer, 1992).	• In the South African mammal fossil record, a transition from wooded environment at ~3 Ma, to more open grasslands at ~1.4 Ma was observed (Vrba, 1975). • Radiations in bovid species at ~2.5 Ma, as observed by Vrba (1985), which seems to coincide with the iNHG. • Limited evidence in East Africa, where mammalian evolution does not seem to correspond so closely with major reported ecological changes (Bibi and Kiessling, 2015). • Some studies suggested that apparent 'pulses' in the fossil record might actually be a reflection of preservations biases and time averaging, rather than a reflection of the living community (Maxwell *et al.*, 2018).

Variability Selection Hypothesis (Potts, 1998) & Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009)	• Changes within lineages and increased intraspecific variation were not caused by any specific environmental condition or trend, but rather by **heightened environmental instability and habitat heterogeneity**, which encouraged species behavioural and ecological plasticity to ensure survival in variable environments (Potts, 1998, 2013; Potts and Faith, 2015). • the 'Pulsed Climate Variability Hypothesis', highlights, in addition to environmental instability, the role of **short periods of extreme climate variability** (specific to East Africa) in driving hominin evolution (Maslin and Trauth, 2009). • Hominin speciation events, dispersals, and encephalisation, would have been driven by these punctuations within the long-term drying trend in East Africa.	• Precession cycles shown to have triggered punctuated episodes of short, alternating periods of extreme aridity and humidity, in 400 or 800kyr cycles driven by the eccentricity maxima (Deino *et al.*, 2006; Maslin and Trauth, 2009; Maslin, Shultz and Trauth, 2015). • Periods of extreme environmental variability have been documented for the eastern African Plio-Pleistocene (Campisano and Feibel, 2007; Hopley *et al.*, 2007; Kingston *et al.*, 2007; Lepre *et al.*, 2007; Trauth *et al.*, 2007). • Growing body of evidence for precessional forcing of East African lakes, such as in the Baringo Basin (Central Kenyan Rift): major lacustrine episode (between 2.7 and 2.55 Ma) consisting of five palaeo-lake phases separated by a precessional cyclicity of ~23 Kyrs (Deino *et al.*, 2006; Kingston *et al.*, 2007).
Mosaic Habitat Model (Domínguez-Rodrigo, 2014; Reynolds *et al.,* 2015; Du and Alemseged, 2018)	• 'Mosaic habitats' are areas comprised of multiple habitats scattered across the landscape, providing a diversity of resources that favours local biodiversity (Tews *et al.,* 2004). • The presence of mosaic habitats in east Africa during the Plio-Pleistocene is hypothesized to have been one of the environmental factors that favoured diversity in the hominin lineage (Domínguez-Rodrigo, 2014; Reynolds *et al.,* 2015; Du and Alemseged, 2018).	• Mosaic patterns of vegetation associated with grassland expansion suggested in later hominin-bearing localities, such as in the Koobi Fora and Nachukui formations, particularly between 2.4 – 1.4 Ma (e.g. Quinn *et al.,* 2013). • Yet, it is unclear whether these suggested mosaic habitats actually reflect alternating woodland-dominated phases and grassland-dominated phases or if this habitat heterogeneity was a real, long-lasting, feature of the fossil record (Hopley and Maslin, 2010; Domínguez-Rodrigo, 2014; Reynolds *et al.,* 2015; Du and Alemseged, 2018).

Figure 1: Comparison of eccentricity variations (Berger and Loutre, 1991), East African lake occurrence (Trauth *et al.*, 2005, 2007; Shultz and Maslin, 2013) with Mediterranean dust flux (Larrasoana *et al.*, 2003), soil carbonate carbon isotopes (Levin, 2013), with Hominin Evolution Transitions (see references in Shultz *et al.*, 2012) (modified from Maslin *et al.* 2014, figure 4, p.5), for the period ranging between 3.5 Ma and 1.5 Ma.



One of the main evolutionary theories is the "savannah hypothesis", which first arose from Raymond Dart's (1925) work on *Australopithecus africanus* and was later developed further by several researchers (e.g. Johanson *et al.* 1982, Vrba *et al.* 1988, Berger and Loutre 1991, Demenocal 1995, 2004, Reed 1997). This theory argued that an increase in aridity and grassland-dominated landscapes in Pliocene and Pleistocene Africa (especially east of the African rift) forced early hominin species to adapt from dense wooded habitats to more open environments by developing bipedal locomotor morphologies along with dentitions adapted to a more abrasive diet (more typical of open environments – Coppens 1985), with periods of enhanced aridification which likely triggered speciation events in the hominin lineage (deMenocal, 1995).

However, since the time of Raymond Dart (1925) the role of habitat change and grassland expansion on human evolution has been debated (e.g. Vrba, 1974, 1975; Bobe and Behrensmeyer, 2004), following the discovery of evidence for wooded environments associated with some of the earliest species of the hominin lineage: *Orrorin tugenensis* (Pickford and Senut, 2001; Senut, 2006) and *Ardipithecus ramidus* (White, Suwa and Asfaw, 1994). In addition, mosaic patterns of vegetation associated with grassland expansion have been suggested in later hominin-bearing localities, such as in the Koobi Fora and Nachukui formations, particularly between 2.4 – 1.4 Ma (e.g. Quinn *et al.,* 2013). "Mosaic habitats" are areas or sites comprised of multiple habitats scattered across the landscape, providing a diversity of resources that is important to create or maintain local biodiversity (Tews *et al.*, 2004). In the fossil record, mosaic habitats tend to be defined as areas with a mixture of grassland and woodland associated to a water source (Reynolds, Bailey and King, 2011; Reynolds *et al.*, 2015). It could be argued that the presence of mosaic habitats in east Africa during the Plio-Pleistocene might have been one of the environmental factors that favoured diversity in the hominin lineage, as mosaic habitats today enhance local biodiversity (Tews *et al.*, 2004). However, it is unclear whether these suggested mosaic habitats actually reflect alternating woodland-dominated phases and grassland-dominated phases or if this habitat heterogeneity was a real, long-lasting, feature of the fossil record (Hopley and Maslin, 2010; Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Du and Alemseged, 2018).

Yet, from the savannah hypothesis (Dart, 1925), to Vrba's Pulse Turnover Hypothesis (1985), Potts' Variability Selection Hypothesis (1998), and the Pulsed Climate Variability Hypothesis (Maslin *et al.,* 2015), the link between climate change and faunal evolution remains debated, as none of these hypotheses fully explain the timing or the causes of the main evolutionary events observed among mammals and hominins (Maslin and Christensen, 2007; Trauth, Larrasoañ and Mudelsee, 2009; Potts, 2013). This might be partly due to global/regional palaeo-climatic records not necessarily being representative of local climates in East Africa, where long-term climatic change is strongly influenced by tectonics (Shultz and Maslin, 2013; Maslin *et al.*, 2014).

As a result of these diverging evolutionary theories and diverging records, studying past environments in hominin-bearing key locations in eastern Africa has been central to palaeoanthropology, as a way to provide insights into the ecological context in which our ancestors evolved and assess how changes in these habitats may have impacted hominin adaptations and behaviour (e.g. Potts *et al.* 1988, Alemseged 2003, Bobe and Behrensmeyer 2004, Bobe *et al.* 2008, Cerling 2013, Negash *et al.* 2015, Plummer *et al.* 2015). The Omo-Turkana basin, more particularly, has been the focus of extensive research due to the discovery of several hominin species in relatively rich and well-dated fossil deposits.

1.2 The Omo-Turkana Basin

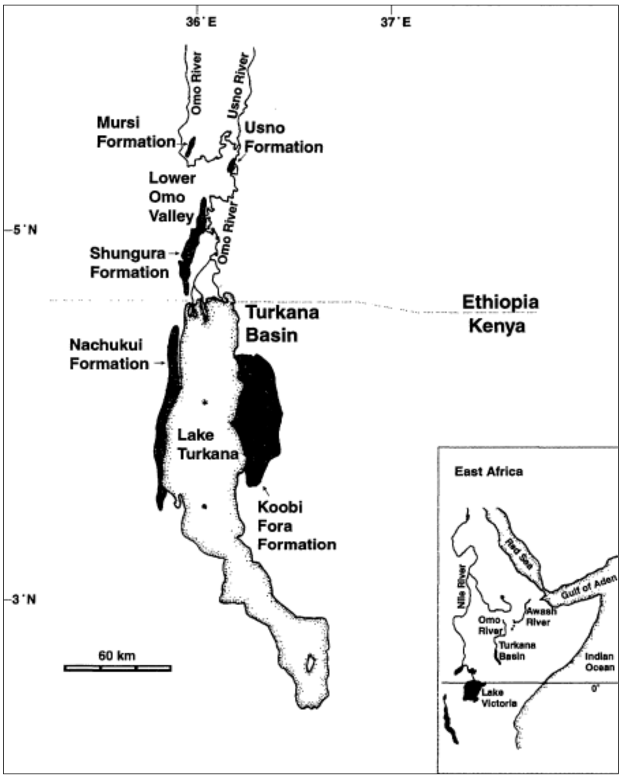


Figure 2: Map of the Omo-Turkana basin, with the Plio-Pleistocene formations under study (from Bobe & Eck 2001 p.3).

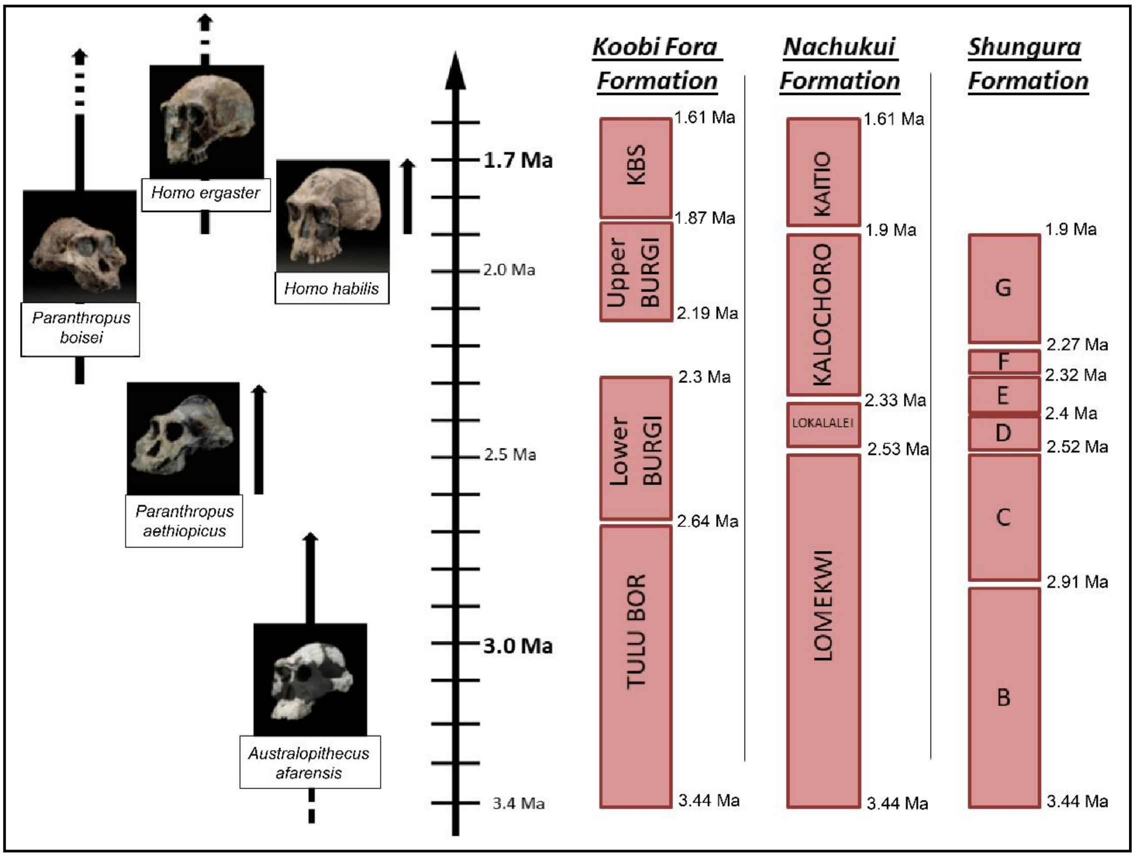


Figure 3: Stratigraphic sequences of the studied sites and members (stratigraphic unit) and associated hominins.

The Plio-Pleistocene fossil deposits of the Omo-Turkana basin are represented by the Shungura, Mursi, Nkalabong, and Usno Formations in the lower Omo Valley, by the Koobi Fora Formation on the northeast side of the lake, and by the Nachukui Formation on the northwest side of the lake (Brown and Feibel, 1991; Harris *et al.,* 2006) (Figure 1). The presence of volcanic tuffs in these formations allows cross-dating and correlations between the various localities of the basin to study the depositional history of the region and its associated evolutionary history (see chapter 2 for more detail). The present study focuses on the Shungura, Koobi Fora and Nachukui Formations, in members (i.e. stratigraphic units) that were associated with hominin remains (Figure 2).

Previous studies have suggested that if the Omo-Turkana region was relatively humid prior to ~4.0 Ma, a tectonic reorganisation of the basin due to large-scale uplift events in the early Pliocene triggered a gradual change towards more arid conditions in the region between ~4.0 and ~2.0 Ma (e.g. Sepulchre *et al.,* 2006; Feibel and Smith, 2011; Fortelius *et al.,* 2016). An increase in relative abundance of phylogenetic tribes of grazing herbivores such as *Alcelaphini*, *Antilopini* and *Hippotragini* near the end of the Pliocene also pointed to a general environmental trend towards seasonally arid grasslands or bushland, and therefore towards an expansion of arid environments (Bobe *et al.*, 2007). During this interval, the region appears to have been drier than the rest of eastern Africa (Fortelius *et al.,* 2016). After ~2.0 Ma, the Turkana basin ceased being more arid than the general east African background (Fortelius *et al.,* 2016), and studies have shown that climatic conditions became increasingly warmer and drier after 2.2 Ma (Cerling and Hay, 1986). For instance, carbon isotope studies from plant wax biomarkers from the Nachukui formation (West Turkana) highlighted the highly dynamic vegetation structure of the area (ranging from 5 to 100% of C_4-vegetation; i.e. grassland-type habitats) between 2.3 and 1.7 Ma, with an overall shift towards more open grasslands after ~2.1 Ma (Uno *et al.,* 2016).

1.3 State of knowledge for the Omo-Turkana Basin environmental sequence: contradictions between palaeo-vegetation proxies

If most studies agree on the general palaeo-environmental trends presented above, more detailed reconstructions of habitats within each of the Omo-Turkana basin fossil localities have proven more complex, with individual palaeo-environmental proxies sometimes disagreeing for some localities during specific time-intervals. For example, while pedogenic carbonate data from the Burgi member in Koobi Fora suggested a predominance of C_3 -vegetation (i.e. woodland-type habitats) in the locality between 2.64 and 1.87 Ma (Cerling, Bowman and O'Neil, 1988), results from faunal analysis suggested grassland habitats in this locality during that time period (Bobe, 2011). Similar discrepancies between results from palaeontological data and pedogenic carbonates can be found in the literature for the Kalochoro member in Nachukui (2.3-1.9 Ma) and for member F in Shungura (2.32-2.27 Ma) (Bobe and Eck, 2001; Alemseged, 2003; Brugal, Roche and Kibunjia, 2003; Bobe, 2011; Cerling, Levin and Passey, 2011; Levin *et al.*, 2011; Quinn *et al.*, 2013). Likewise, while some studies have argued for relatively varied and heterogeneous local habitats in the region (i.e. 'mosaic habitats') during the Plio-Pleistocene, as opposed to the more homogeneous grassland-dominated habitats suggested by other studies for part of the sequence, it remains difficult to find additional environmental proxies to assess whether such habitat heterogeneity was a true long-term environmental feature in the region, or a by-product of time-averaging or of methodological limitations (Hopley and Maslin, 2010; Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Du and Alemseged, 2018).

Diverging conclusions between studies could relate to the limitations of each method and of the fossil record, but could also highlight the complexity of palaeo-habitats, each method and palaeo-environmental proxy contributing to refining the picture drawn of the landscapes inhabited by hominins. Indeed, the various proxies used in previous studies all record palaeo-environmental information at different spatial and temporal scales, either as direct or indirect evidence of palaeo-vegetation conditions, and are influenced by different biases inherent to the fossil record or to the approach (Table 4).

For instance, while studies focusing on palaeobotany or on the geochemical properties of paleosols and plant wax biomarkers can provide direct evidence for local flora, these proxies can suffer greatly from diagenesis, or from the discontinuity of the deposition processes (Bonnefille, 1976; Scott, 2002; Breecker, Sharp and McFadden, 2009; Nguyen Tu *et al.*, 2011). More particularly, studies have suggested that paleosol records might yield reconstructions biased towards a higher proportion of C_3-vegetation compared to other proxies, due to the preferential formation of pedogenic carbonates in woodland floodplains or riparian corridors (Breecker, Sharp and McFadden, 2009; Quade *et al.*, 2013; Du *et al.*, 2019).

While the palaeontological record often provides rich assemblages to help reconstruct faunal palaeo-communities, studies focusing on faunal composition and/or faunal diversity provide indirect evidence for palaeo-environments. These are based on the assumptions that palaeo-communities can be compared faithfully to modern ecological niches, and that associated palaeo-habitats can be inferred from faunal composition based on comparisons with modern data on biomes and associated faunal communities. However, such assumptions remain difficult to verify, with studies suggesting that Plio-Pleistocene biodiversity differed greatly from modern examples, with, for example, a significant reduction in species biodiversity of large mammals during the past two million years, likely resulting in differing niche competition and niche partitioning dynamics between taxa in the present compared to the past (McKee, 2001).

Table 4: Summary of the main proxies used for palaeo-environmental reconstructions for the Omo-Turkana basin, with their aims, advantages, and limitations.

Approach	Aims/Advantages	Limitations	Examples of studies
Palaeobotanical data	Direct floral evidence of local vegetation	- Records often short and discontinuous - Pollen assemblage reflects the essential character of the local flora, but not a detailed record of local vegetation - Scarcity of pollen sequences and poor diagnostic value of fossil grass pollen in light microscope analyses - Fossil stems and leaves are often difficult to identify below the family or subfamily level	Bonnefille and Dechamps 1983, Bonnefille 1984
Isotopic studies of plant wax biomarkers	Commonly preserved in sedimentary organic matter, with high resistance to diagenetic alteration and isotope exchange: can be used as a local vegetation proxy	Microbial processes can potentially lead to early diagenesis, which would alter the plant wax's isotopic composition	Uno *et al.* 2016; Lupien *et al.* 2018
Pedogenic carbonates in paleosols	Reflect the proportion of C_3 (trees, bushes and cool-season grasses and sedges) versus C_4 (warm-season grasses and sedges) vegetation on the local landscape	- Distribution limited primarily to floodplain deposits that remained stable long enough for carbonates to form - Formation of pedogenic carbonate favoured by high evaporation-to-precipitation ratio: humid episodes are therefore poorly recorded	Cerling *et al.,* 1988; Quinn *et al.,* 2007, 2013; Cerling, Wynn, *et al.,* 2011; Levin *et al.,* 2011

Approach	Aims/Advantages	Limitations	Examples of studies
Herbivore palaeodiet (i.e. stable carbon isotopes, dental usewear analyses)	- Inferred dietary ecology of fossil taxa likely related to palaeo-environmental conditions - Can be studied at the community, tribe, taxon, or species level - No assumption on fossil dietary ecology based on extant relative taxa - Relies on dental remains, which tend to be well-preserved and identifiable at least to tribe or taxa level	- For migrating species, dietary signal might not reflect local vegetation - Little variation in diet expected from specialist feeders (e.g. obligate browsing or obligate grazing taxa) - Biases might be introduced by grouping of taxa, or by focusing on specific taxa (i.e. not at the community level) - Palaeovegetation inferred from dietary information based on the assumption that a species' diet is linked to the physical and ecological characteristics of its habitats	Lee-Thorp, 1989; Merceron *et al.,* 2007; Cerling *et al.,* 2015; Ungar *et al.,* 2016; Bignon-lau *et al.,* 2017; Blondel *et al.,* 2018; Rivals *et al.,* 2018; Uno *et al.,* 2018; Sewell *et al.,* 2019
Faunal associations/Faunal abundance/ Ungulate mammal diversity / Micromammal studies	- Assesses the composition of faunal palaeo-communities represented in fossil deposits in their globality - Takes advantages of abundant fossil evidence	- Assumes similarity in ecology between fossil taxa and their extant relatives, and relies on comparisons with modern faunal communities and modern ecosystems - Often requires identification at the genus/species level, which introduces biases and reduces sample sizes - Potential biases related to species identification/preservation	Vrba, 1974; Behrensmeyer, 1975; Wesselman, 1984; Harris, 1991; Bobe and Eck, 2001; Alemseged, 2003; Brugal *et al.,* 2003; Reed, 2007, Bobe, 2011; O'Brien *et al.,* 2020

Approach	Aims/Advantages	Limitations	Examples of studies
Ecomorphology (particularly bovids)	- Functional morphology used to infer habitat preference based on the theory that an organism's locomotor anatomy should have adaptations to the particular substrate(s) and environment(s) it locomotes across - Approach relatively independent from taxonomy and phylogeny (i.e. does not require identification to the genus or species level)	- Difficulty of constructing a habitat grouping scheme that is both sufficiently precise and sufficiently accurate, especially when species use a range of habitat types. - Based on the assumption that characters found to be indicative of habitat in extant species are similarly indicative of habitat in fossil taxa - Variations in ecomorphological patterns through time will likely reflect changes over a longer time-scale than other direct proxies related to local vegetation conditions (i.e. slow evolutionary changes)	Kappelman *et al.,* 1997; Reed, 1997; DeGusta and Vrba, 2003; Kovarovic and Andrews, 2007; Barr, 2015; Plummer *et al.,* 2015
Palaeogeographic reconstructions	Evaluates changes in local physical landscapes, providing vital information regarding landscape dynamics and hydrological conditions (e.g. changes related to tectonic/volcanic activities; fluctuations in lake levels…etc)	Focuses on landforms, hence not providing evidence directly related to vegetation conditions	Brown and Feibel, 1991; McDougall and Brown, 2008

In addition, studies based on faunal composition (as well as on fossil pollen) rely strongly on species identification, which can be limited by the preservation of the assemblages, which greatly differs across localities and deposits due to deposition modes and taphonomical processes (Bonnefille, 1976; Scott, 2002; Matthews *et al.*, 2017). In contrast, while studies focusing on ecomorphological characteristics of specific ungulates do not necessarily require identification at the genus or species levels, they record information that relates to larger temporal scales, as they reflect gradual evolutionary processes partly influenced by environmental factors (DeGusta and Vrba, 2003; Kovarovic, 2004).

Studies of mammal palaeo-diets have been abundant over the last few decades. These studies benefit from the good preservation of fossil teeth, from the ability to identify dental remains to the tribe, genus, or species levels (in most cases), and from the multitude of techniques that have been developed to infer the dietary ecology of extant species (e.g. stable isotope analyses, dental use-wear analyses, studies of calculus phytoliths content, etc). Such studies have the advantage of not relying on prior assumptions regarding the studied taxa's ecology, allowing to check whether or not the dietary behaviours of extinct species resembled that of their extant relatives. While such studies do not necessarily require identifications to the genus or to the species level, results might greatly differ in scope whether the entire fossil community is studied as a whole, or whether specific taxa are targeted for analysis upon the assumption that such taxa might be better environmental proxies than others (e.g. bovids; e.g. Merceron *et al.* 2013, Negash *et al.* 2015, Ungar *et al.* 2016). However, while it is often assumed that the dietary behaviours of faunal communities or of specific taxa are influenced in part by their environment and hence reflect the vegetation-conditions of their habitats, such assumptions have seldom been verified (Robinson *et al.*, 2021).

The various advantages and pitfalls associated with each of the approaches previously used to reconstruct palaeo-environments in the Omo-Turkana basin highlight the relevance of studies combining several proxies, as a way to mitigate for the limitations of the methods and to improve the resolution of the proposed reconstructions. Identifying additional palaeo-environmental proxies based on available material from the Omo-Turkana basin might therefore prove useful to provide supplementary information about local vegetation heterogeneity and help reconstruct the habitats associated with the different hominins that inhabited this region.

The present study therefore proposes to take advantage of the abundance of bovid dental remains in the Omo-Turkana fossil deposits, and of the multiplicity of methods available for dietary ecology studies, to test the relevance of detailed palaeo-dietary analyses of mixed-feeding herbivores for palaeo-environmental reconstructions. Ecological data from modern populations and their associated habitats are explored as well, in order to evaluate the strength of the relationship between the dietary behaviours of mixed-feeding herbivores and the vegetation conditions of their habitats. This will allow to assess what type of indirect evidence such dietary analyses can and cannot provide to inform on past and present vegetation conditions in a given area, and test whether modern data on dietary behaviour and habitat vegetation conditions can be reliably used for comparisons with the fossil record.

1.4 Bovid teeth as a bio-proxy for vegetation change

Herbivores are often considered faithful reflectors of prevailing vegetation types in a habitat and are typically more abundantly preserved than hominin remains. Indeed, as primary consumers dependant on local forage availability, herbivores are expected to be more likely to reflect local vegetation conditions than taxa occupying higher trophic levels (Kingdon, 1997). Bovids, especially, are considered good indicators of past environments because they show dietary specialisations that are linked to their digestive anatomy (Janis and Fortelius, 1988; Gagnon and Chew, 2000; Hillson, 2005). They are usually well-represented in the fossil record and can be studied in detail, by looking, for instance, at shifts in species abundance (Vrba, 1974, 1980, 1995; Harris, 1991; Kappelman *et al.*, 1997; Bobe and Eck, 2001), or by studying their feeding ecology (Brink and Lee-Thorp, 1992; Sponheimer, Lee-Thorp, *et al.*, 2003; Daryl Codron *et al.*, 2007; Lüdecke *et al.*, 2016; Blondel *et al.*, 2018).

Figure 4 Examples of acacia savanna with woodland, the preferred habitat of *Aepyceros melampus* (Photographed at a) Masai Mara National Reserve, Kenya, b) Nairobi National Park, Kenya, April 2017).

Bobe and Eck (2001) and Greenacre and Vrba (1984) highlighted in their work the adaptability of the impala (genus *Aepyceros*), a highly successful antelope whose fossilized remains are found abundantly across East Africa. and that is still thriving today. Modern impala (*Aepyceros melampus*) is an abundant and widespread edge (ecotone)-species that is able to feed on both browse and graze according to the available vegetation and to seasonal variations in land cover and in niche competition (Wronski, 2002; Sponheimer, Grant, *et al.*, 2003; Cerling *et al.*, 2015). They are generally found in acacia savannas and light woodlands close to water, and primarily graze when grasses are green and growing in the wet season, switching to browse on bush, fruits, foliage, forbs, seedpods and shoots when necessary, often in the dry season (Jarman and Jarman, 1973; Estes, 1991). *Acacia tortilis* and *Acacia* *nilotica* pods seem to be particularly favoured due to their high protein content (Kingdon and Hoffman, 2013) (Figure 3). Because of the abundance of Aepycerotini remains in the fossil record of East Africa, and because of the reported dietary plasticity of modern *Aepyceros* populations, the impala was selected as the focal study taxon in this project.

Similarly, particular attention has been given in previous work to another mixed-feeding herbivore, the springbok (genus *Antidorcas*), especially for the South African Plio-Pleistocene record where remains from several *Antidorcas* species are abundant (Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018; Sewell, 2019; Sewell *et al.*, 2019). The springbok is an antelope species with a high dietary adaptability, the extant species *Antidorcas marsupialis* favouring open and semi-open habitats, and being described as a mixed-feeder with a preference for browse (Bigalke, 1972). Modern springbok tend to feed primarily on succulent shrub leaves (e.g. *Acacia mellifera*) and coarse/hard-stemmed grasses (e.g. *Aristida*, *Eragrostis*, *Cynodon*, *Panicum* and *Sporobolus*), but have also been observed feeding on karroid vegetation, tall shrubs, leaves from the ground, roots, succulents, and cucurbits (Eloff, 1959; Van Zyl, 1965; Bigalke, 1972; Davies, Botha and Skinner, 1986; Nagy and Knight, 1994b; Skinner and Louw, 1996; Kingdon, 1997; Cain, Krausman and Germaine, 2004). Extinct species *A. recki*, *A. australis*, and fossil *A. marsupialis* appear to have been mixed-feeders to varying degrees, while extinct *A. bondi* has been suggested to have been an obligate grazer, based on isotopic studies and tooth morphology (Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018). While modern springbok populations are now confined to southern Africa due to man-made barriers such as fences, remains of *A. recki* were identified in deposits from the Omo-Turkana basin (Harris, 1991). Data from these *A. recki* specimens were therefore collected for this research project, in order to test whether eastern African fossil springbok had a dietary flexibility similar to that of their extant relatives, as well as to allow future comparisons between Plio-Pleistocene eastern African and southern African *Antidorcas* assemblages.

Such flexible feeding behaviours are likely to have been a key factor in the evolutionary success of *Aepyceros* and *Antidorcas* species, and could provide interesting data regarding environmental changes in this region as the two species might have adapted their diet locally and/or seasonally according to the prevailing vegetation in the area. By studying mixed-feeding herbivore species, this study seeks additional evidence for general environmental trends directly related to the vegetation available to the overall faunal community, an approach which has proven effective in the past (Vrba, 1980, 1992; Demenocal, 1995; Reynolds, 2005). Plio-Pleistocene antelopes did not necessarily rely on the same resources in the past than their extant relatives (Sponheimer and Lee-Thorp, 1999) but because mixed-feeders can adapt to the vegetation around them, differences in their dietary behaviours are expected to be observed through time in relation to shifts in climate and changing vegetation conditions (Sewell *et al.*, 2019).

Even though East African hominin-bearing localities have been studied intensively, these formations have never been studied so far focusing specifically on ubiquitous mixed-feeding antelope taxa that must have witnessed and adapted to local climate changes through most of the stratigraphic sequence. Studying formations with well-dated continuous sequences from the perspective of animals that continuously inhabited the basin over time could help investigate local changes in vegetation cover, specifically regarding aspects of seasonality and spatial heterogeneity of vegetation in this area (Bobe and Eck, 2001; Patterson *et al.*, 2017). Because the present work also aims at evaluating if the fossil herbivore species studied shared identical levels of dietary flexibility with their modern counterparts, data from modern specimens were also collected to gauge the extent of dietary variation in extant impalas and springbok in various habitats.

Checking for potential variations in diet from obligate browsers and obligate grazers (which usually rely heavily on browse or on graze, respectively), can also contribute to a better understanding of vegetation structure and resource availability, as such specialised species only usually turn to other resources when preferred foods are lacking, due to environmental factors, or niche competition (Ramdarshan *et al.*, 2016). Therefore, this study also uses data from fossil and modern specimens of selected obligate browsing (giraffids – *Giraffa* sp.) and obligate grazing (equids – *Equus* sp.) herbivores, as a way to evaluate the limits of the dietary spectrum in each locality and time period under study. This is to help calibrate the overall dietary spectrum of ancient herbivores through time by looking at how vegetation change might be reflected on specialist feeders.

1.5 Aims and objectives of the project

The main goal of this research project is to assess whether detailed studies of the dietary ecology of mixed-feeding antelope species could be used to investigate hominin palaeo-environments in the Omo-Turkana basin during the Plio-Pleistocene. More particularly, this project aims to assess whether abundant and adaptable herbivores such as the impala or the springbok could prove to be accurate local vegetation proxies, checking upon the assumption that their dietary behaviours are mainly influenced by the vegetation conditions in their habitats. This is to work towards the following research aims and objectives:

Table 5: Research aims, and their associated objectives.

Aims	Objectives
1. Provide a new method to compare past and present habitats by testing the relationship between modern impala dietary variability and their habitats (i.e. predictive land cover models)	Explore the dietary variability of selected modern impala populations, based on stable carbon isotope evidence
	Evaluate the diversity of habitat types inhabited by modern impala populations, based on land cover data, and quantify the land cover composition and structure of these habitats
	Assess whether relationships can be observed between specific habitat types and modern impala dietary patterns
	Evaluate to which types of habitat fossil impala specimens from the Plio-Pleistocene deposits of the Omo-Turkana basin were likely associated, based on stable carbon isotope data

Aims	Objectives
2. Study the dietary ecology of mixed-feeding antelope species in the Omo-Turkana basin between 3.5-1.6 Ma	Assess the overall dietary signatures of each studied species (extant and extinct), and evaluate inter-specific variations in diet between species of the same taxa
	Evaluate the degree of variation in dietary patterns within each fossil taxon across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time
	Explore the impact of seasonal variation on the dietary patterns observed among Plio-Pleistocene impala populations
	Explore the complexity of the dietary behaviours of fossil impala/springbok populations through the use of a multiproxy/multi-scale approach
	Make palaeo-environmental inferences for the Plio-Pleistocene Omo-Turkana basin, based on the dietary patterns observed in the modern and fossil mixed-feeding antelope assemblages studied
3. Discuss the palaeo-environmental implications of the inferred dietary patterns, in relation to human evolutionary theories	Compare results from mixed-feeding antelope dietary analyses with other datasets for climate and vegetation from the area
	Evaluate the pace of the changes (if any) observed through time (e.g. gradual, pulsed) in the dietary behaviours of mixed-feeders, and discuss the timing of these variations
	Evaluate the range of evidence available, from the proposed dietary analyses, to account for habitat heterogeneity (i.e. mosaic habitats) and environmental variability in the Omo-Turkana basin
	Discuss how these palaeo-environmental inferences agree/disagree with the main evolutionary theories proposed to explain mammal/human evolution

1.6 Research questions and hypotheses

To reach the aims and objectives set out for this project, the dietary behaviours of selected extant and extinct mixed-feeding antelopes are examined. A combination of methods is used to produce a comprehensive picture of these taxa's feeding ecology and, potentially, of the environmental conditions they experienced throughout the Plio-Pleistocene in the Omo-Turkana basin. This study was designed to address the following research questions and hypotheses:

1) What type of evidence can dietary studies of mixed-feeding herbivores provide to help make inferences about the prevailing vegetation conditions of their local habitats?

a) What is the relationship between modern impala dietary variability and the composition/structure of their habitats (evaluated through land cover analysis of modern landscapes)?

b) How do the studied taxa's dietary patterns in the past compare to the dietary signals of their extant relatives?

c) Can data from modern impala populations' dietary behaviours and habitats be used to identify modern African environments that might be similar to those experienced by impala populations in the past, and if so, what are the main characteristics of these modern habitats?

If modern *Aepyceros melampus* is as adaptable as hypothesized, the variation in diet observed for different modern populations should mirror differences in vegetation cover between their habitats. For instance, if modern impala does adapt its diet to prevailing vegetation conditions, impala populations associated with closed-wooded environments should yield dietary signals indicative of a preference for browse/C_3-vegetation, as opposed to populations associated with open-grassland habitats, which should yield dietary signals indicative of diets dominated by graze/C_4-vegetation. The degree of habitat fragmentation might as well be expected to have an influence on the diet of modern impala populations, with potentially more varied diets observed where habitats are highly fragmented and diverse, compared to more homogeneous habitats with less vegetation diversity. If such clear relationships can be established between modern impala diet and habitat vegetation-conditions, it will suggest that dietary analyses of mixed-feeding species such as the impala can be used faithfully as vegetation-proxies in further studies.

Because Plio-Pleistocene environmental conditions likely differed greatly from modern African climatic conditions, differences in inferred dietary patterns are expected when comparing modern and fossil mixed-feeding populations, albeit within the range of dietary variation observed today across modern populations. If similar dietary patterns can be identified between specific fossil impala assemblages and specific modern impala populations, it might indicate that these populations were associated to analogue habitats.

2) What additional insights into palaeo-environmental conditions in the Omo-Turkana basin do the inferred dietary patterns of mixed-feeding species provide, and how do these help to resolve apparent contradictions between other environmental proxies?

a) How much variation in inferred dietary behaviours can be observed throughout the Omo-Turkana sequences, and what type of trends do these variations suggest (i.e. no variation through time, gradual/pulsed changes, increased variability in diet, browsing/grazing alternance…etc).

b) Do the inferred dietary patterns of mixed-feeding antelope differ from one locality to the other across the Omo-Turkana basin (e.g. Lower Omo river valley vs East/West Turkana), and what do these differences (if any) could imply in terms of local vegetation conditions?

c) What additional information on the taxa's dietary ecology does combining dietary-proxies provide, as opposed to using each dietary-proxy in isolation?

For the dietary results of this study to confirm the long-term trend of regional aridification suggested by previous studies (e.g. Sepulchre *et al.,* 2006; Feibel and Smith, 2011; Fortelius *et al.,* 2016), general dietary trends for the studied mixed-feeding taxa are expected to demonstrate an increase in grazing signals through time. In addition, if the results of the present study agree with previous studies, dietary behaviours of fossil impalas and springbok should display an increased dietary variability through time, which might relate to varying degrees of habitat heterogeneity and to a gradual increase in climatic variability through time, as suggested by other studies (e.g. Potts, 2007 – see Chapter 2.2.2 for more detail).

For the dietary results of this study to confirm differences in local vegetation conditions across the Omo-Turkana basin suggested by previous studies (e.g. Bobe, Behrensmeyer, *et al.* 2007, Cerling, Levin, *et al.* 2011, Levin *et al.* 2011), differences in inferred dietary behaviours are expected between the assemblages, with a higher variability in diet through time and a stronger browsing/C_3-dominated diet signal in individuals from the Shungura formation, when compared to individuals from the Koobi Fora and Nachukui Formations. The presence of mosaic habitats (Domínguez-Rodrigo, 2014; Reynolds *et al.,* 2015; Patterson *et al.,* 2017) in the Omo-Turkana basin could be reflected in the dietary results of this study if mixed-feeding signals dominate the assemblages in some localities/members, with no distinct preference for either graze or browse, suggesting that a wide range of food resources were available to these herbivores throughout the sequence and the region.

Finally, if results from the various methods used for dietary analysis display similar patterns across the fossil assemblages, it will suggest that all methods are equally informative on dietary behaviours, and might be used in isolation without losing information or accuracy. If results differ between methods, it will highlight how each of these methods can complement each other when used in combination, by informing on different aspects of the studied animals' feeding ecology (i.e. geochemical or structural food properties, seasonal variation in diet…etc).

3) How do palaeo-vegetation and palaeo-climate inferences made from mixed-feeding antelope palaeo-dietary studies compare with the main evolutionary theories proposed to explain mammal/human evolution?

a) What are the timings/rates of dietary variation observed for mixed-feeding species towards the sequence, and what type of vegetation/climate change do these suggest?

b) What types of local vegetation conditions do the inferred dietary behaviours suggest across the basin, and do they seem to have varied seasonally?

Table 6: Main evolutionary theories and hypothesized results of palaeo-dietary analysis of mixed-feeding antelopes.

Theory	Expected dietary behaviours for *Aepyceros/Antidorcas*
Savannah hypothesis (Dart 1925)	• Increasing abundance of grazing signals observed through dental use-wear analyses, and of C_4-vegetation ($\delta^{13}C$) in the diet of the studied taxa throughout over the temporal range. • Increased aridity through time might be observable from the oxygen isotope content of the studied taxa ($\delta^{18}O$).
Turnover Pulse Hypothesis (Vrba 1985)	• Habitat specialists are more likely to be affected by climate and habitat change (i.e. increased extinction rates) than generalists (Vrba 1988), although adaptable herbivores such as *Aepyceros* and *Antidorcas* might demonstrate variations in diet through time • Marked shifts in dietary behaviours at times of major climatic changes (i.e. iNHG at 3.2-2.5 Ma; and oWC at 2.0-1.7 Ma).
Variability Selection Hypothesis (Potts 1998) & Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009)	• Environmental instability might be observable via temporarily increased intra- and inter-specific dietary variation (dental use-wear and stable carbon isotope analyses) within specific members, in addition to a gradual increase in grazing signals/C_4-diets across the sequence. • Increased seasonal variability in diet in some members (observed through intra-tooth isotopic analyses, and potentially through multi-method dietary analysis)
Mosaic Habitat Model (Domínguez-Rodrigo 2014, Reynolds *et al.* 2015a, Du and Alemseged 2018)	• No clear directional change would be apparent in dietary signals (dental use-wear and stable carbon isotope analyses), with a relatively high but constant intra- and inter-specific dietary variability. • Mixed-feeding signals should dominate the assemblage, suggesting the availability of varied food resources

For the inferred dietary behaviours to agree with the Savannah Hypothesis (Dart, 1925), a gradual increase in grazing/C_4-dominated behaviours through time will be observed across the mixed-feeding assemblages (Table 6). According to the Turnover Pulse Hypothesis (Vrba, 1985), marked changes in dietary behaviours are likely to be observed at specific points in time in relation to major climatic events (e.g. iNHG at 3.2-2.5 Ma; and oWC at 2.0- 1.7 Ma). If in agreement with the Variability Selection Hypothesis (Potts, 1998) or the Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009), the observed mixed-feeders' dietary signals should display a gradual increase in grazing/C_4-dominated signals, combined with an increased intra- and inter-specific dietary variation as well as increased seasonal variation in diet, potentially indicative of increased environmental instability and increased seasonality. If mosaic habitats were a predominant feature of the Omo-Turkana basin during the Plio-Pleistocene, as suggested by the Mosaic Habitat theories (Domínguez-Rodrigo, 2014; Reynolds *et al.,* 2015; Du and Alemseged, 2018), no clear directional change would be apparent in the dietary signals of the studied mixed-feeders, with a relatively high but constant intra- and inter-specific dietary variability.

1.7 Outline of the project method

Several methods are applied to the fossil and modern datasets used in this study to provide information on different aspects of the dietary ecology of the studied species and produce a detailed record of their dietary variability (Figure 4). Use-wear analyses of molar surfaces are performed to provide information on the type of vegetation that the animals fed primarily on by looking at traces of tooth-on-tooth contacts (attrition) and tooth-on-food contacts (abrasion), which varies depending on the abrasiveness of the food items consumed (Fortelius and Solounias, 2000; Ramdarshan *et al.*, 2016). Mesowear analysis provides information on the global use-wear accumulated through the life of each individual based on general cusp shape (Fortelius and Solounias, 2000). Dental Microwear Textural Analysis (DMTA) provides information on the type of foods associated with the individual's last feeding events based on textural parameters (Merceron *et al.*, 2005; Merceron, Ramdarshan, *et al.*, 2016). Stable carbon isotope ratios are measured from enamel samples to investigate the relative proportion of C_3 -C_4 plants (respectively trees, bushes and cool- season grasses and sedges, vs. warm-season grasses and sedges) ingested during tooth enamel mineralisation (Sponheimer and Lee-Thorp, 1999; Balasse, 2002; Copeland *et al.*, 2009). Changes in stable oxygen isotope ratios are investigated as well to identify potential changes in drinking patterns and local aridity conditions through time, as recorded in the enamel of the studied specimens from their water consumption. In addition to bulk enamel samples that were collected to provide average stable isotope ratios for each sampled individual, intra-tooth samples were collected and studied for selected specimens to provide more detailed sequential stable isotope data and investigate seasonal variation in diet in fossil impala populations. The results obtained from these different methods are combined to evaluate the detailed dietary behaviours of the studied fossil species (i.e. early life, lifetime, last weeks prior to death), allowing to investigate the structural properties of the food items consumed (toughness, abrasiveness, grain size) as well as their chemical properties (isotopic content).

Each of the methods used to infer palaeo-diets from fossil teeth have their own advantages and limitations. For instance, dental use-wear analyses provide indirect evidence of dietary behaviours through the observation of dental features that partly relate to known differences in structural properties between various foods (i.e. toughness, abrasiveness, grain size…)(Lucas *et al.*, 2013; Ramdarshan *et al.*, 2016), reflecting either the average diet of an individual (i.e. mesowear analysis) or the last meal of these individuals (i.e. dental microwear analysis). While such information can help infer the likely composition of the animal's overall diet, such signal can be biased by external factors that partially over-write the dietary signal, such as dust or grit (Hummel *et al.*, 2011; Ackermans *et al.*, 2018; Ackermans, Winkler, *et al.*, 2020; Schulz-Kornas *et al.*, 2020). Likewise, while stable carbon isotope analyses are commonly used to evaluate the relative proportion of C_3-C_4 foods integrated in the specimens' body tissues through food consumption, indirectly allowing to make inferences about the consumption of browse vs. graze in extinct species, the diversity and complexity of vegetation types and of photosynthetic pathways (i.e. C_3-grasses, CAM plants…etc) and of biological fractionation processes limit the ability to make inferences on palaeo-diet composition beyond the C_3-C_4 dichotomy. Results are therefore expected to vary slightly between each of those methods, allowing to mitigate for some of their limitations, and to accumulate dietary ecology evidence in terms of both geochemical and structural properties of the food items consumed by the studied taxa.

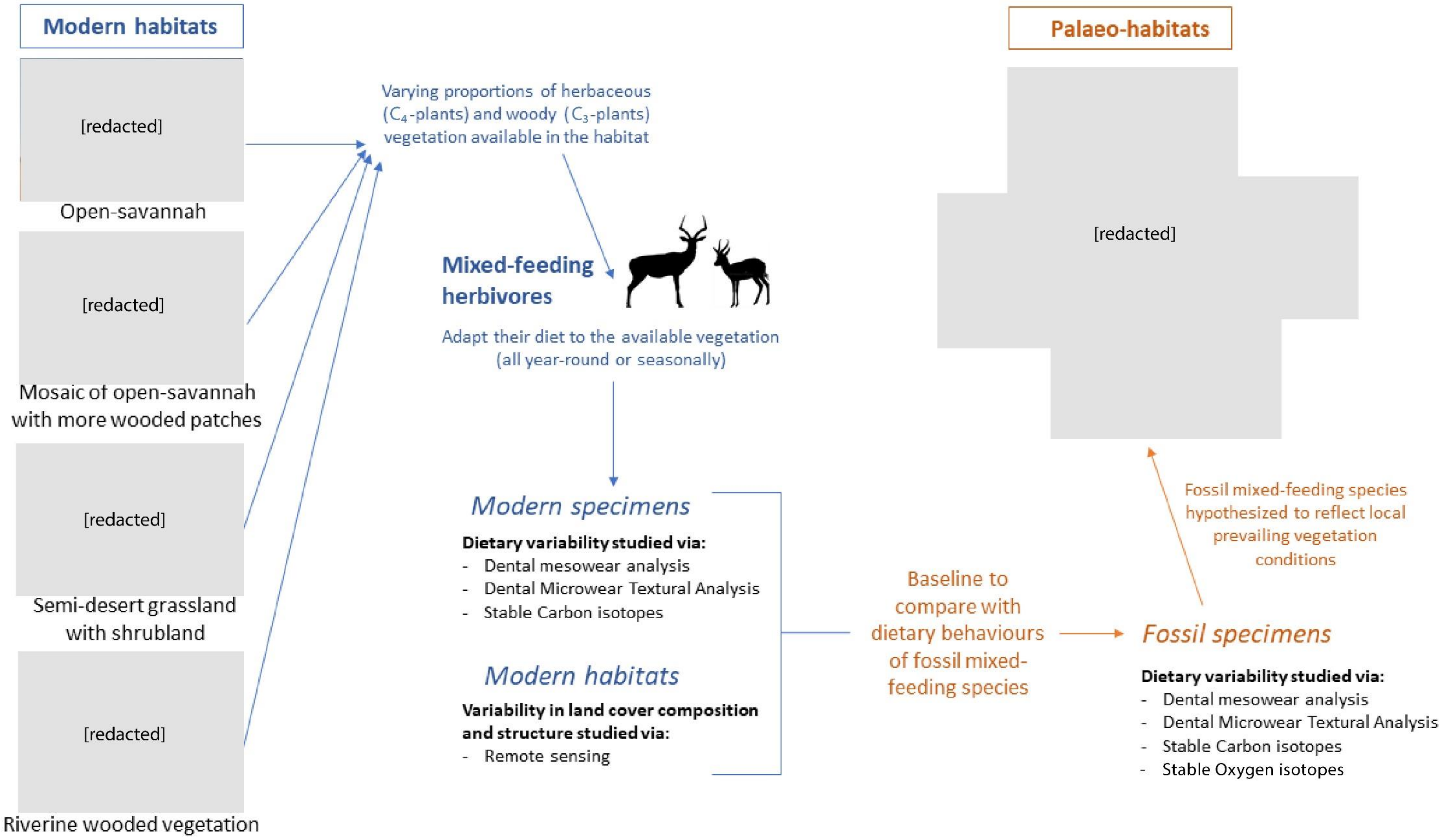


Figure 5: Summary of the rationale and methods used in this study. The list of modern habitat types depicted in this figure is non exhaustive and does not represent the full range of habitats associated with modern impala populations (Photographs from Kindt *et al.* 2014, Reynolds *et al.* 2015).

Dietary information from modern impala specimens and remote sensing of modern African landscapes inhabited by these populations are also used to compare with fossil data and evaluate in which types of landscape fossil impala species might have lived, alongside hominins, between 3.5 and 1.6 million years ago. To achieve this, the influence of local land cover patterns on the dietary behaviours of modern impalas is investigated using published stable carbon isotope data alongside land cover data from selected study areas in Africa. This data is then used to build predictive models designed to evaluate the degree to which some of the Omo-Turkana habitats (i.e. specific localities and members) might have resembled some of the studied modern-day African habitats, in terms of land cover composition and land cover structural heterogeneity. This is to test the feasibility of a new method to compare past and present habitats, by combining dietary analysis of modern impala populations with satellite imagery of their habitats.

While a variety of studies have focused on the Omo-Turkana region (see chapter 2 and references therein), the impala and the springbok have never been studied at such a high level of detail before in these deposits. Because the project compares results from different methods applied to a same dataset, it should provide critically needed data on the strengths and weaknesses behind the use of combined dietary proxies for palaeo-ecological and palaeo-environmental reconstructions. Likewise, this study should provide the scientific community with new avenues to explore to reconstruct hominins' palaeo-environmental contexts using modern land cover data alongside dietary data of modern herbivore populations.

1.8 Thesis structure

Following this introduction, a review of the Omo-Turkana basin study sites, studied taxa, as well as of the methods chosen for this research project is presented in chapter 2 to introduce the study design and rationale for this work.

Chapter 3 explores the dietary variability of modern impala populations, as inferred from published stable carbon isotope data, as well as the variability of modern impala habitats, as assessed through land cover analyses performed on selected modern study areas. This chapter evaluates the strength of the relationship between impala diet and prevailing vegetation conditions in their habitats, to discuss what type of information on local vegetation conditions can be deduced from stable carbon isotope analyses of modern impala populations. This modern data is then used to build models to predict the land cover composition and structure of palaeo-habitats from the Omo-Turkana basin and identify potential modern analogue habitats, using stable carbon isotope data obtained from fossil impala specimens.

The following chapters focus on the inferred dietary ecology of the studied taxa in the Omo-Turkana basin during the Plio-Pleistocene, through dental mesowear analysis (chapter 4), dental microwear textural analysis (chapter 5), and stable isotopes (chapter 6). The results from all three methods are then combined, compared, and discussed in chapter 7, to evaluate the differences and similarities between the dietary patterns suggested from each analysis, and discuss potential palaeo-environmental implications.

Chapter 8 presents the conclusion from this study, and discusses the main contributions of this work to the field of palaeo-environmental studies. Firstly, the potential of combining dietary analyses with land cover studies of modern mixed-feeding populations to provide an additional tool for palaeo-environmental reconstruction is discussed, as well as the differences between fossil taxa and their extant relatives. The dietary ecology of the studied mixed-feeding antelope species is then examined for the Omo-Turkana basin fossil record, summarising the trends observed for the inferred feeding behaviours, and discussing their potential palaeo-environmental implications. Finally, the palaeo-environmental conditions in the Omo-Turkana during the Plio-Pleistocene suggested from this study are discussed in relation to previous theories linking palaeo-environmental conditions/major shifts in climate to mammalian evolutionary events, to evaluate potential implications when considering hominin habitats and hominin evolution.

Chapter 2: Reconstructing palaeo-diets and palaeo-environments of the Plio-Pleistocene Omo-Turkana basin: literature review

2.1 Introduction

This chapter details the study design and rationale by presenting a review of the fossil localities, species and methods selected for this research project. Firstly, current knowledge on the palaeo-environments of the Omo-Turkana basin during the Plio-Pleistocene is reviewed. This allows to identify gaps and discrepancies in previously published palaeo-environmental reconstructions and the need for complementary studies to strengthen the current understanding of this important region of Africa. Secondly, the species selected for study are presented and the current knowledge of their past and present ecology is reviewed to highlight how detailed study of these species' dietary ecology might contribute to palaeo-environmental reconstructions, and which aspects of their ecology might require further exploration. Finally, the methods used to investigate dietary behaviours and land cover are introduced to highlight the strengths and weaknesses of each technique when used for palaeo-environmental studies, and discuss how the multi-methods approach chosen for this project might offer opportunities to enhance these strengths and mitigate for some of these weaknesses.

2.2 The Omo-Turkana basin

2.2.1 Lake Turkana

Lake Turkana (formerly called Lake Rudolf) is the third largest lake in Africa today. Although the presence of a large intermittent lake is attested to the area since about 4 Ma (Lonyumun Lake), modern lake Turkana only established within the last several hundred thousand years, with various changes in lake presence and size before that (Harris, Leakey and Brown, 2006). The lake takes its source from the Omo River, and seasonally from the Turkwel and Kerio Rivers in the south-western part of the basin. The main source of the Omo River is situated in the Ethiopian highlands, a region which is subjected to highly active tectonics. The geography of the Turkana basin therefore depends on the Ethiopian tectonism, in addition to local tectonic and volcanic activity within the basin (Rogers, Harris and Feibel, 1994).

Previous studies have shown that the Omo River used to flow through the Turkana basin towards the Indian Ocean during the Pliocene but that its outflow was occasionally disrupted by tectonic events, leading to the formation of temporary lakes in the basin with fluctuating water levels (Brown and Feibel, 1991). From ~2.5 Ma, major tectonic activity disrupted the basin stability, with a reported shift from a mainly fluviatile system with the palaeo-Omo river to a lacustrine system at ~2.0 Ma (Brown and Feibel, 1991). One of the major palaeo-lake phases that has been identified is the period of transgression and regression of Palaeolake Lorenyang, which occurred between 2.17 and ~1.76 Ma when the basin's outlet to the Indian Ocean closed due to volcanism and faulting (Harris, Leakey and Brown, 2006; Bruhn *et al.*, 2011; Boës *et al.*, 2019). Tectonic uplift and volcanic activity in the south-eastern Omo-Turkana Basin have been shown to have resulted in high lake levels from 2.2 to 1.7 Ma (Boës *et al.*, 2019), and the presence of molluscs in the lake sediments up to 0.7 Ma suggested that before this time the waters of the lake were not as alkaline as they are today (Harris *et al.* 2006). These various changes in the hydrologic dynamics of the Omo-

Turkana basin occurred at a time of gradual environmental change which has been reported to have triggered an increase in the abundance of tropical grasses in eastern African ecosystems between 4.0 and 1.0 Ma (Levin *et al.*, 2011; Cerling *et al.*, 2015; Levin, 2015).

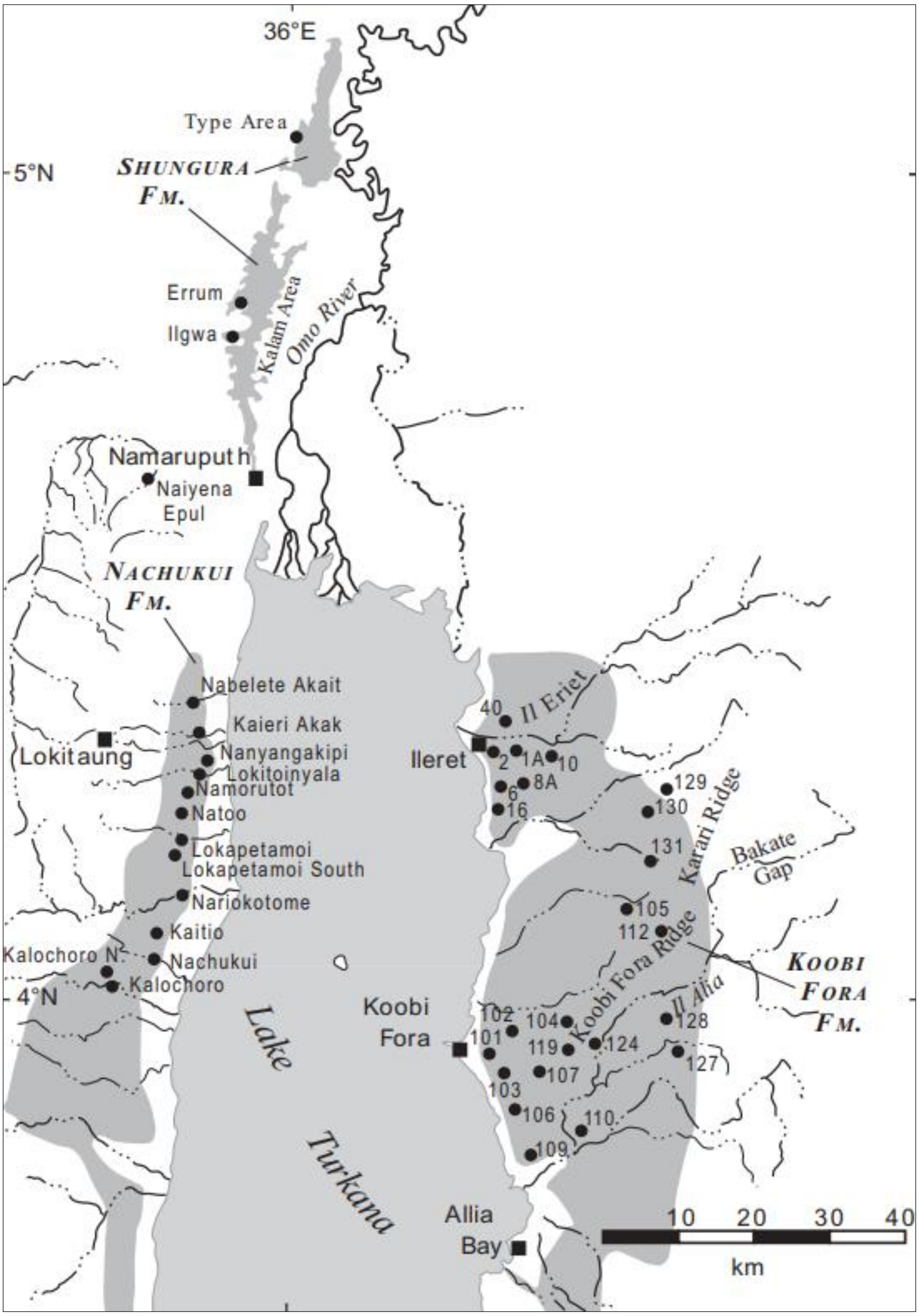


Figure 6: The lower Omo Valley, Ethiopia, and the northern part of Lake Turkana, Kenya, showing the Koobi Fora, Nachukui and Shungura Formations as shaded areas. Points indicate palaeontological collection areas. Localities and section names are given for the Nachukui and Shungura Formations (edited from McDougall and Brown, 2006, figure 1, p.186).

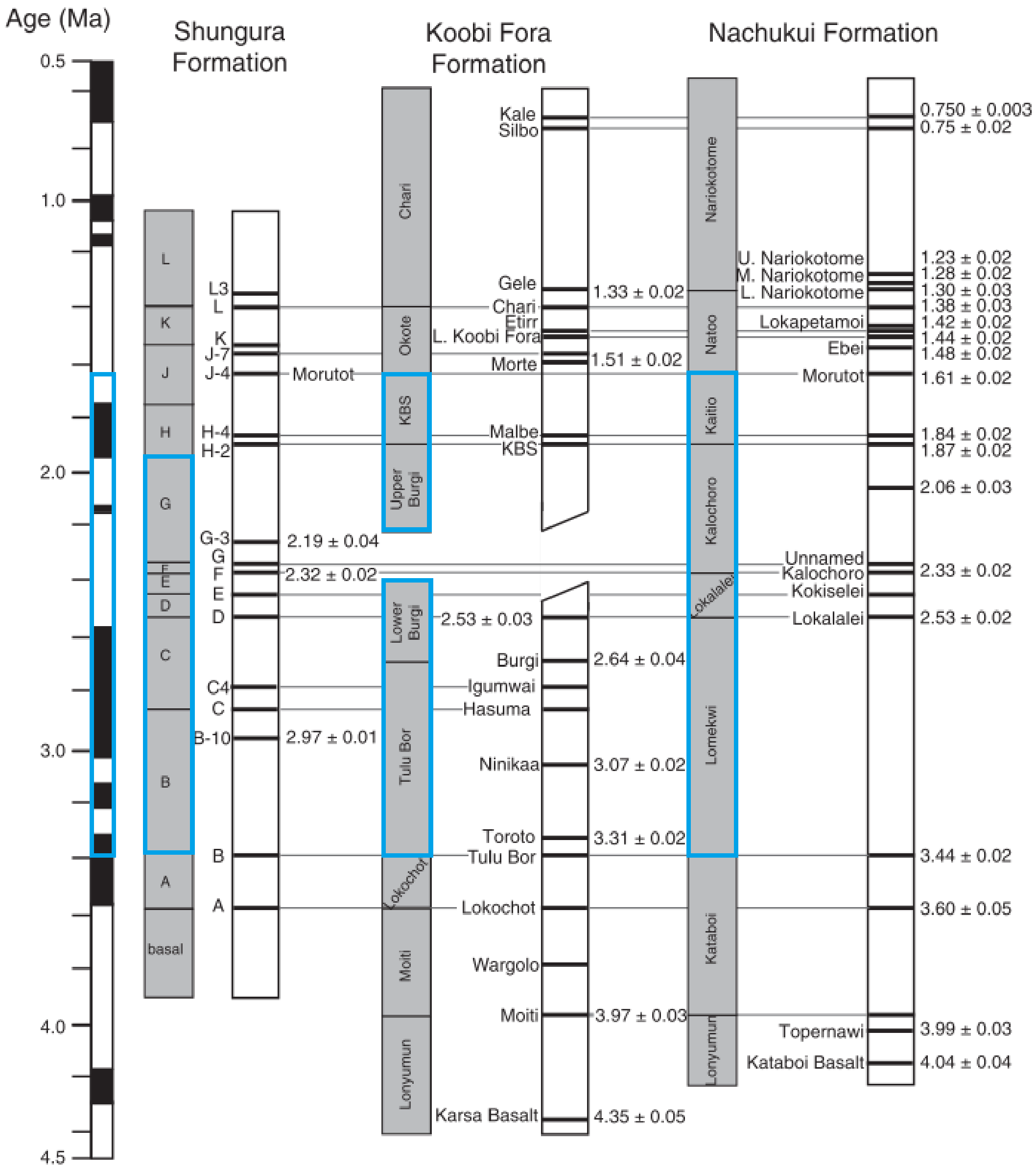


Figure 7: Formations, members and major tuffs from the Omo Group. Isotope chronology and tephra correlations are based on Brown *et al.* (1992), Katoh *et al.* (2000), WoldeGabriel *et al.* (2005), McDougall and Brown (2006, 2008). Tephra correlations are marked by solid lines within and between sections. Members of each formation are indicated in grey blocks, based on Feibel *et al.* (1989). The coloured squares represent the time interval studied and the members from which data were collected in this study (edited from Levin *et al.,* 2011, figure 2, p.77[1]).

The distribution of the Omo-Turkana Plio-Pleistocene fossil sites is closely related to the history of the basin, which inevitably impacted sedimentological processes in the area (Bruhn *et al.*, 2011). Geological deposits in this area are part of the "Omo group", which

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[1] Reprinted Levin, N. E., Brown, F. H., Behrensmeyer, A. K., Bobe, R., & Cerling, T. E. (2011). Paleosol carbonates from the Omo Group: Isotopic records of local and regional environmental change in East Africa. Palaeogeography, Palaeoclimatology, Palaeoecology, 307(1-4), 75-89, Copyright (2011), with permission from Elsevier.

comprises the Usno, Mursi and Shungura formations in the lower Omo river valley (Ethiopia), and the Koobi Fora and Nachukui formations, located East and West of Lake Turkana, respectively (Figure 5). This study focused on the Shungura, Koobi Fora and Nachukui formations, three of the richest fossil deposits of the Omo group.

Each of these formations is divided into members, which take their names from the volcanic tuff deposits that lie directly underneath the sediment deposit, which can be used for cross-dating and correlations across the basin (Figure 6) to study the depositional history of the region and the evolutionary history of associated habitats. Each geologic formation from the Omo group was dated using radiometric dating and tephra-chronology (Brown *et al.* 1985, McDougall 1985, Harris, Brown, and Leakey 1988, Feibel *et al.* 1989, McDougall and Brown 2006, McDougall *et al.* 2012).

2.2.2 Fossil study sites

2.2.2.1 Koobi Fora Formation

2.2.2.1.1 General description and chronology

The Koobi Fora formation, located east of Lake Turkana, is one of the richest fossil deposits in East Africa. Excavations were initiated by the International Omo Research Expedition (IORE) in 1968 under the leadership of Richard Leakey and led to the discovery of several hominin specimens such as the *Paranthropus boisei* cranium KNM-ER 406, the *Homo ergaster* skull KNM-ER 3733, or the *Homo rudolfensis* skull KNM-ER 1470 (Leakey, 1973; Leakey and Leakey, 1978; Wood and Lieberman, 2001; Harris, Leakey and Brown, 2006; Leakey *et al.*, 2012).

The formation is divided into eight members spanning between around 4.35 and 0.7 Ma, with the oldest being Lonyumum, followed by Moiti, Lokochot, Tulu Bor, Burgi, KBS, Okote and Chari. The Tulu Bor Member is the oldest member to contain hominin fossils, at ~3.44

Ma (Reed 1997). Because of an unconformity of 0.5 million years, the Burgi Member is divided into a lower and upper sections (Brown and Feibel, 1991; Brown and Mcdougall, 2011). Sediments derive mostly from fluvial deposits, but lacustrine deposits related to the presence of temporary lakes were found as well.

This study focused on the Tulu Bor (3.44–2.64 Ma), Burgi (2.64–1.87 Ma), and KBS (1.87–1.61 Ma) members (Figure 6).

2.2.2.1.2 Summary of previous palaeo-environmental reconstructions

Previous studies have reported a clear pattern of increasing open arid environments in the Koobi Fora formation (e.g. Bobe *et al.,* 2007; Levin *et al.,* 2011; Cerling *et al.,* 2015; Levin, 2015). Studies of the oxygen and carbon isotope composition of paleosol carbonates from this sequence suggested that a significant shift in vegetation conditions occurred more particularly at ~1.8-1.9 Ma, from C_3 - to C_4 - dominated landscapes (Cerling, Bowman and O'Neil, 1988; Quinn *et al.*, 2007; Levin *et al.*, 2011). Similarly, an increased abundance of grassland-indicative taxa and of mammal diversity in the Koobi Fora formation after ~2.2 Ma was described from palaeontological data (Harris, 1991; Reed, 1997; Bobe and Behrensmeyer, 2004; Bobe, Alemseged and Behrensmeyer, 2007; Bibi and Kiessling, 2015; Fortelius *et al.*, 2016). Analyses of East African aeolian deposits in ocean cores have suggested as well that an important climatic transition took place between 2.0 and 1.5 Ma (deMenocal, 2011).

Deposits from the Tulu Bor member (3.44 – 2.64 Ma) document, according to palaeogeographic reconstructions (Brown and Feibel, 1991), a riverine phase of the basin with flooding periods. This is in agreement with palaeontological observations and analyses of pedogenic carbonates which described flood plain environments dominated by C_3 -flora (Cerling, Bowman and O'Neil, 1988; Harris, 1991; Reed, 1997). While analyses of pedogenic carbonates suggested a dominance of C_3 -flora in the Burgi member (2.64 – 1.87 Ma), some analyses of faunal composition concluded that the region was likely dominated by grasslands during that time period (Bobe, 2011). Other faunal and pollen analyses proposed that this locality sustained a rather heterogeneous environment in that member, with more closed woodlands in the north and more open habitats in the south, providing a mixture of woodland and grassland areas (Harris, 1991; Reed, Fleagle and Leakey, 2007). The KBS member (1.87 – 1.61 Ma) appears to document a lacustrine phase of the basin (Brown and Feibel, 1991; McDougall and Brown, 2008), with environments dominated by C_4-plants, as reflected by faunal, pollen, palaeogeographic and pedogenic carbonate data, with the presence of more grazers possibly indicative of a grassland or shrubland environment (Bonnefille, 1984; Cerling, Bowman and O'Neil, 1988; Harris, 1991; Reed, 1997; Bobe, 2011; Levin *et al.*, 2011) (see table_A 1 in appendix 1 for more detail).

A recent faunal analysis of the Koobi Fora deposits between 1.98 and 1.38 Ma demonstrated that, when the assemblages are studied on a smaller geographic scale within the Koobi Fora area, shifts in faunal abundance varied across the different subregions, with an observed ecological shift in the Karari subregion between 1.98 and 1.38 Ma that was not reciprocated in the Ileret and Koobi Fora Ridge subregions (O'Brien *et al.*, 2020). It was hypothesized that the Ileret and Koobi Fora Ridge subregions likely retained edaphic grassland habitats due to their proximity to the basin margins, while the Karari subregion, further away from the lake, presented mesic habitats in the Upper Burgi member but shifted to xeric wooded grasslands after ~1.87 Ma. This hypothesis was consistent with previous observations made from pedogenic carbonates showing an increase in C_4 -vegetation and in habitat fragmentation from ~2.0 Ma, with closed savannah woodland/thicket and scrub in the Karari sub-region but a dominance of open low tree-shrub savannah in the Koobi Fora ridge subregion (Quinn *et al.*, 2007). Such results highlight the complexity of early Pleistocene landscapes in the Koobi Fora formation and show that the landscape of East Turkana was likely composed of different dynamic ecosystems which changed variably through time depending on their proximity with the lake margins and the hydrologic conditions in the basin.

Overall, while most palaeo-environmental reconstructions of the Koobi Fora formation agree on a general trend of increased C_4 -vegetation in the environment, some contradictions between studies can be found for the most recent members depending on the type of environmental proxy analysed and the geographic scale investigated. It seems therefore important to seek additional environmental proxies to complement previous studies and see if further detail on regional palaeo-vegetation heterogeneity can be gathered from fossil evidence.

2.2.2.2 Nachukui Formation

2.2.2.2.1 General description

Excavations in the Nachukui Formation, on the western side of Lake Turkana, were initiated in the 1980s by John Harris and Franck Brown, leading to the discovery over the years of several important hominin specimens, such as the Turkana boy (also called Nariokotome Boy – KNM-WT 1500 – attributed to *Homo ergaster*) and the "Black Skull" of *Australopithecus/Paranthropus aethiopicus* (KNM-WT 1700) (Brown *et al.*, 1985; Walker *et al.*, 1986; Harris *et al.*, 1988).

The Nachukui Formation covers 500 km^2 of discontinuous deposits which are separated into eight members ranging from ~4.0 to 0.6 Ma. The oldest member is the Lonuymum member, followed by the Kataboi, Lomekwi, Lokalalei, Kalochoro, Kaitio, Natoo and Nariokotome members. This sequence documents both lacustrine and fluvial environments, with fluvial deposits represented in most of the sequence, apart from a lacustrine phase observed in the middle of the Kalochoro member, associated to the transgression of Palaeolake Lorenyang at ~2.0 Ma (Brown and Feibel, 1991).

This study focused on four of these members: Lomekwi (3.44 - 2.53 Ma), Lokalalei (2.53-2.33 Ma), Kalochoro (2.33- 1.9 Ma) and Kaitio (1.9- 1.61 Ma).

2.2.2.2.2 Summary of previous palaeo-environmental reconstructions

Several studies have described the likely environments associated with most of the studied members. According to Bobe *et al.* (2007), the high proportions of Alcelaphini, Antilopini and Hippotragini specimens relative to other bovid tribes in the Nachukui assemblage suggest relatively open and arid environments in western Turkana. Work on soil carbon isotopes from palaeosol carbonates pointed to rapid increases in $\delta^{13}C$ values at ~2.52 and ~1.8 Ma, indicative of increases in C_4 -plant biomass (Wynn, 2004; Levin *et al.*, 2011). Similarly, plant wax biomarkers isotopic analyses indicated a highly dynamic vegetation structure in the region between 2.3 and 1.7 Ma, with a shift towards more C_4 -vegetation in the landscape after ~2.1 Ma (Uno, Polissar, Kahle, *et al.*, 2016). Results from an analysis of pedogenic carbonates from Nachukui by Quinn *et al.* (2013) proposed a slightly different habitat reconstruction for the region, indicating the presence of diverse habitats with a mosaic pattern of vegetation cover across the area. Similarly to other studies, they noted an overall increase in grassland after 1.61 Ma but argued that C_3 -woodlands remained an important component of the vegetation.

The Lomekwi member (3.44-2.53 Ma) has been described by most studies as relatively wet with diverse habitats associated to a large perennial river system, dominated by wooded vegetation with patches of wooded grassland (Behrensmeyer, 1975; Walker *et al.*, 1986; Reed, 1997; Tiercelin *et al.*, 2010; Bobe, 2011; Cerling, Wynn, *et al.*, 2011; Quinn *et al.*, 2013; Sonia Harmand *et al.*, 2015). While some analyses of the faunal record pointed to a dominance of grassland in the landscape in the Kalochoro member (2.33-1.9 Ma) (Bobe, 2011), results from other studies have suggested the presence of floodplains associated to a large river system, with a dominance of woodland/bushland/shrubland vegetation with wooded grassland (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013). The predominance of woodland in the Nachukui formation has been suggested to have persisted in the Kaitio member as well (1.9-1.61 Ma) (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013) (see table_A 2 in appendix A.1 for more detail).

The West Turkana locality therefore seems to have provided rather heterogeneous habitats between 3.44 and 1.61 Ma, with varying proportions of grassland, bushland and woodland through time, but a dominance of woodland or bushland in several members. This habitat heterogeneity within the Nachukui members was particularly highlighted by the species diversity study proposed by Brugal *et al.* (2003), which demonstrated how faunal composition varied across the west Turkana sub-localities, suggesting the presence of different habitat types across the Nachukui formation, within the same time period (i.e. member). Different sites analysed for the Kaitio member, for instance, reflect differing environments, from large wooden biotopes close to water (in the Naiyena Engol sites) to more open environments (in the Kokiselei sites). These observations mirror the ones highlighted previously for the Koobi Fora formation, where regional landscapes were suggested to be highly fragmented after ~2.0 Ma.

The different pictures painted across studies for the Nachukui palaeo-environments between 3.44 and 1.61 Ma demonstrate the difficulty in reconstructing palaeo-habitats. It is especially complex when using faunal abundance data, which can suffer taphonomic and identification/collection biases (e.g Maxwell *et al.,* 2018), and are also often interpreted based on behavioural ecology of modern mammals, assuming that ancestral species shared similar behaviours with their extant relatives. These difficulties highlight the necessity to find environmental proxies that might suffer less from these biases, such as direct assessments of past dietary behaviours without a priori biases based on the dietary ecology of extant relatives.

2.2.2.3 Shungura Formation

2.2.2.3.1 General description

The Shungura Formation is located on the northern side of Lake Turkana, west of the lower Omo river valley. Over 50,000 fossil vertebrate remains were collected by the International Omo Research Expedition (IORE) between 1967 and 1976, and by the Omo Group Research Expedition (OGRE) since 2006, among which about 250 hominin specimens from at least four different species, and the earliest records of *Homo* and *Paranthropus* (Arambourg and Coppens, 1968; Coppens and Howell, 1976; Suwa, White and Howell, 1996; Wood and Constantino, 2007; Andrews and Bamford, 2008; Boisserie *et al.*, 2008, 2010; Wood and Leakey, 2011; Souron, 2012; Villmoare *et al.*, 2015). The hominin taxa from the Shungura Formation include *Australopithecus* sp., *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Homo* sp.

The Shungura formation contains deposits that extend over a distance of 60 km (oriented north-south), and a composite stratigraphic sequence of 766 m. This sequence is the most continuous of the Omo-Turkana basin, and is divided into twelve members: the oldest deposits are found in the basal member, followed by members A to L (with no member I). Each of these members are also sub-divided into smaller units, providing a detailed stratigraphy of 111 units, ranging from 3.9 to 1 Ma (Feibel and Brown, 1993; Reed, 1997). This sequence documents fluvial (between the basal member and G-13) and lacustrine (above member G13) environments, related to changes in the geography of the Turkana basin (Brown and Feibel, 1991). Most of the Shungura formation deposits are records of ancient fluvial deposition from a large meandering river, from Member A (3.6 Ma) through the middle of Member G (2.1 Ma), at a time when the Omo palaeo-river flowed from the Ethiopian Highlands south through the valley (Hakala, 2012). This was followed by a shift to lacustrine conditions in middle and upper Member G (2.1 to 1.9 Ma), before a return to fluvial conditions after 1.9 Ma (De Heinzelin, Haesaerts and Howell, 1976; De Heinzelin and Haesaerts, 1983).

The present study focused on six of these members: B (3.44- 2.91 Ma), C (2.91- 2.52 Ma), D (2.52- 2.4 Ma), E (2.4- 2.32 Ma), F (2.32- 2.27 Ma), and G (2.27- 1.9 Ma).

2.2.2.3.2 Summary of previous palaeo-environmental reconstructions

As for the other two Turkana basin formations described above, several studies have proposed palaeo-environmental reconstructions for the Shungura sequence. Overall, most studies suggest the presence of mosaic habitats ranging from forests to open woodlands between ~3.4 and 2.0 Ma, with a gradual increase in C_4-vegetation through time (Jaeger and Wesselman, 1976; Bonnefille and Dechamps, 1983; Wesselman, 1984; Bobe and Eck, 2001; Alemseged, 2003; Levin *et al.*, 2011; Bibi *et al.*, 2013; Barr, 2015; Negash *et al.*, 2020; Plummer *et al.*, 2015; Negash *et al.*, 2015; Blondel *et al.*, 2018; Martin *et al.*, 2018).

The wide range of habitats represented in the lower Omo river valley during the Plio-Pleistocene was particularly well-documented by ecomorphological studies of bovid astragali (Barr, 2015; Plummer *et al.*, 2015), which demonstrated an abundance of heavy cover ecomorphs in the sequence, along with an increase in open ecomorphs between 2.9 Ma and 2.3 Ma (members C to F). The predominance of closed-wooded environments was suggested by several studies, such as the work undertaken by Bobe and Eck (2001) on faunal assemblages, which highlighted the abundance of bovid tribes associated with closed and wet habitats. The integrated approach to taphonomy and faunal change developed by Alemseged (2003) also suggested the presence of wooded habitats in the Shungura formation, and demonstrated continuous faunal change throughout the sequence, pointing to a potentially major biotic change in the area at ~2.3 Ma (i.e. base of member G) characterised by a change to open and edaphic grassland environments. Similarly, studies on the dietary ecology of tragelaphins demonstrated that some species (such as *Tragelaphus rastafari*) fed predominantly on browse before 2.9 Ma, after which they started to include more C_4-plants in their diet, potentially reflecting a change in the environmental conditions around them (Negash *et al.*, 2015; Blondel *et al.*, 2018). A dietary ecology study by Martin *et* *al.* (2018) also showed temporal variation in the diet of terrestrial papionins (family Cercopithecidae, genera *Papio* and *Theropithecus*), with a suggested increase in the consumption of herbaceous monocots between ~2.9 Ma and ~2.53 Ma. Studies of pedogenic carbonate stable isotopes suggested as well environments dominated by C_3 -flora, with a gradual increase in C_4 -vegetation after 2.0 Ma (member G) (Cerling, Wynn, *et al.*, 2011; Levin *et al.*, 2011). All together, these various studies point towards palaeo-environments dominated by C_3 -vegetation and closed-wooded habitats for a long part of the Shungura sequence (up to ~2.0 Ma), but suggest also mosaic habitats and variations in land cover through time, with a gradual and fluctuating increase in C_4 -vegetation and more open environments throughout the sequence.

Deposits from member B (3.44-2.9 Ma) were formed by a perennial river system with occasional riverine flooding which created flood plains (De Heinzelin, Haesaerts and Howell, 1976). Various habitat reconstructions suggested environments dominated by wet and relatively closed habitats associated with little open grasslands in the region during that time period (Jaeger and Wesselman, 1976; Bonnefille, 1984; Reed, 1997; Alemseged, 2003). Deposits from member C (2.9-2.52 Ma) have been previously reported to document similar environments to what has been observed in member B, with a bushland–woodland regime with a riverine forest and edaphic grasslands dominating the area (Reed, 1997; Alemseged, 2003). Member D (2.52-2.4 Ma) was deposited on nutrient-rich flood plains (de Heinzelin *et al.* 1976), and similarly appears to have been associated with riverine forests within a woodland–bushland regime and with edaphic grasslands (Bonnefille, 1984; Reed, 1997; Alemseged, 2003). Habitats in member E (2.4-2.32 Ma) have been also described as well-watered woodland–bushland environments with a riparian woodland or forest (Reed, 1997; Alemseged, 2003). A change in local climatic conditions has been suggested from member F (2.32-2.27 Ma) onwards, with habitats dominated by areas of edaphic grasslands, bushlands, and more open woodlands than in older members (Jaeger and Wesselman, 1976; Bonnefille, 1984; Reed, 1997). Deposits from member G (2.27-1.9 Ma) were reported to indicate the presence in the region of a river surrounded by open woodland, while the flood plain was suggested to have expanded to include edaphic grasslands during that time period (Reed, 1997; Alemseged, Coppens and Geraads, 2002) (see table_A 3 in appendix A.1 for more detail).

The Plio-Pleistocene sequence of the Shungura formation has been widely studied and benefits from a rich and well-preserved fossil record associated with clearly identified and well-dated members that allow for detailed studies of palaeo-environmental conditions through time at a relatively precise temporal scale. The very rich corpus of research material that has been produced so far on this region provides an interesting set of studies to which results from the present work can be compared. More particularly, studies that have used similar methods (i.e. stable isotopes, dental use-wear analyses) on taxa that likely shared the same ecological niche as the studied fossil species (such as Tragelaphines) were of particular interest to compare with the results from this research and assess if temporal shifts in dietary patterns could be observed to the same degree in these taxa. Furthermore, the consistency with which palaeo-environments in the lower Omo-river valley have been described, regardless of the environmental proxy studied, as dominated by closed-wet habitats throughout most of the sequence provides an opportunity to assess the validity of using mixed-feeding antelopes species as palaeo-habitats indicators: if the diet of extinct mixed-feeding antelope species did mirror prevailing vegetation conditions, the dietary patterns observed for fossil impalas from the Shungura formation should indicate the consumption of a significant amount of C_3 -vegetation in their diet, in agreement with previous palaeo-environmental reconstructions for Plio-Pleistocene deposits of this region.

2.2.3 Rationale for this study

Various palaeo-environmental proxies have been previously used to reconstruct Plio-Pleistocene habitats in the Omo-Turkana basin and report, overall, a general trend of increasing open grasslands in the environment, with a significant shift from C_3- to C_4-dominated landscapes occurring more particularly at ~1.8-1.9 Ma at the time of the transgression/regression of Lake Lorenyang in the basin. While more arid open habitats have been suggested in Koobi Fora and Nachukui, more wet closed environments were described for the Shungura deposits. However, some contradictions between studies could be found depending on the type of environmental proxy analysed and the geographic scale investigated, with more recent studies highlighting the complexity and spatial heterogeneity that likely characterised palaeo-habitats in this region. For instance, high habitat heterogeneity in the Omo-Turkana basin was suggested by results from a diversity analysis of large mammal communities by Du and Alemseged (2018), supporting the hypothesis that habitat heterogeneity may have influenced hominin presence and evolution through complex biotic interactions that necessarily impacted human foraging strategies and selective pressures.

Seeking additional environmental proxies is therefore essential to gain further detail on regional palaeo-vegetation heterogeneity. As mentioned previously, while fossil mammals constitute a significant part of the fossil record and can provide valuable evidence to reconstruct palaeo-environments, palaeontological studies can suffer from various biases (e.g. taphonomy, identification, preservation, ecological assumptions based on modern-analogue taxa). Using palaeo-environmental proxies that have not yet been studied in detail combined with methods that suffer less from these biases might therefore provide valuable information to assess the composition and heterogeneity of palaeo-habitats in the Omo-Turkana basin between 3.5 and 1.6 Ma.

This study proposes to complement current knowledge on the Plio-Pleistocene environments of the Omo-Turkana basin through a detailed assessment of the dietary behaviours of selected extant and extinct mixed-feeding antelopes species, using a combination of methods to produce a comprehensive picture of the dietary ecology of these species.

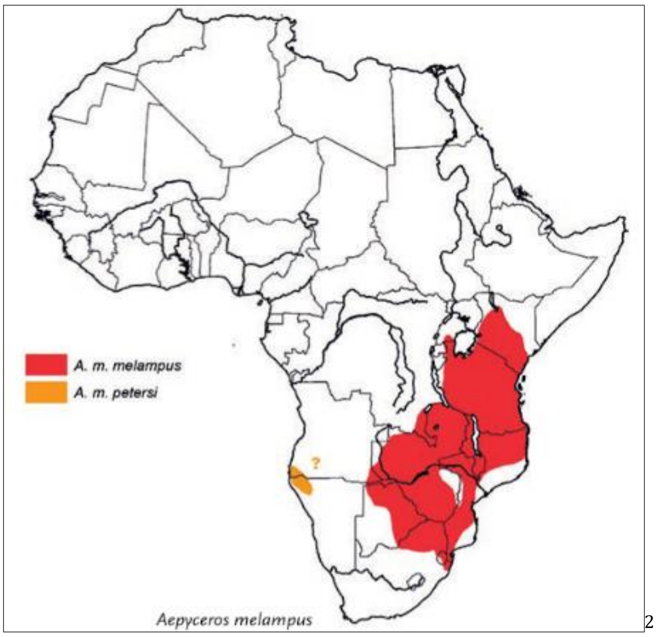
2.3 Studied species

2.3.1 Mixed-feeders as palaeo-environmental indicators: impala and springbok

2.3.1.1 Genus *Aepyceros* – Impala

2.3.1.1.1 General description

The impala (*Aepyceros melampus*, Lichtenstein 1812) is a large-bodied antelope (~60 kg for males, ~45 kg for females / Height: males 75-92 cm, females 70-85 cm) present today in Botswana, Kenya, Malawi, Mozambique, Rwanda, South Africa, Swaziland, Tanzania, Uganda, Zambia and Zimbabwe (Figure 7). Males have long lyre-shaped horns which curve backwards, often with transverse ridges (Estes, 1991) (Figure 8). Their pelage is reddish-brown on the back, with a lighter tan on the torso, white undersides, black at the tip of the ears, and white patches around the eyes, on the chin and on the muzzle. Both sexes have on the back of their hind legs patches of black hair covering metatarsal glands which are used for olfactory communication. They also have three distinctive black stripes on their rump: two on their flanks and one on the tail (Kingdon and Hoffmann, 2013; Castelló, 2016).



[2]

Figure 8: Geographic distribution of modern common impala (*A. melampus melampus*) and black-faced impala (*A. melampus petersi*) (from Kingdon and Hoffman, 2013 p.481 [2]).

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[2] ©Kingdon and Hoffman, 28 Feb 2013, 'Mammals of Africa Volume VI: Pigs, Hippopotamuses, Pigs, Deer, Giraffe and Bovids', A&C Black, an imprint of Bloomsbury Publishing Plc."

Most authors recognise three subspecies of impala: large-horned impala from East Africa (*A. m. suara*), common impala from the southern African regions (*A. m. melampus*) and a rare black-faced impala (*A. m. petersi,* Bocage, 1879) found only in northern Namibia and south-western Angola (Kingdon, 1997; Reynolds, 2005). Genetic studies have shown a decline in genetic diversity among modern impala populations towards the east of the African continent, suggesting that the southern impala populations might be older than those from eastern Africa, where extinctions might have occurred during the Pleistocene, to be re-populated later by populations migrating from southern Africa (Nersting and Arctander, 2001; Lorenzen, Arctander and Siegismund, 2006; Reynolds, 2007).

Figure 9: Modern impalas *Aepyceros melampus* a), b), c) males; d) female; e) females and calves (a), d), e) photographed at the Nairobi National Park, Kenya, April 2017; b), c) photographed at the Rhino and Lion Nature Reserve, Kromdraai, South Africa, October 2017).

The main differences between the long-horned impala (*A. m. suara*) from eastern Africa and the common impala (*A. m. melampus*) from southern Africa are horn and body size variations (Estes 1991). The black-faced impala (*A. petersi*) is smaller than *A. melampus*, and its natural habitat range does not overlap with that of the common impala. It has a well-defined black blaze on the middle of the face below the eyes, blacker on the tip of the ears and a longer tail. They live in small herds (3-15 individuals) and favour dense riverine vegetation, or moderately dense vegetation close to water (Castelló, 2016). They are considered very different genetically from other impala subspecies (Lorenzen and Siegismund, 2004).

This study focused on *Aepyceros melampus sensu lato*, as none of the modern subspecies have been identified in the East African fossil record.

2.3.1.1.2 Social organization and behaviour

Common impalas (*A. melampus*) have a life expectancy of about 15 years, with two birthing peaks a year in spring and autumn. Calves are usually weaned after 4-6 months, and they reach sexual maturity at around one year old for males, and one-and-a-half years old for females. Impalas are mostly sedentary, with a home-range of about 2-6 km^2. Females generally congregate in herds of about 15-20 individuals, which can go up to 50-100 individuals, while bachelor male herds can count up to 200 individuals. Both groups migrate through the territories held by dominant males or assemble in mixed-herds outside of the rut season (Estes, 1991).

Males are territorial, especially during the mating season, as they usually leave their natural clan by the age of 4 to move within a different herd range and avoid inbreeding (Estes, 1991). During these periods, males invest up to 75% of their time attending the females that enter their territory, hence spending less time feeding and ruminating, which tends to impact on their physical condition and body weight. For example, studies have shown that

East African territorial males are often in poorer condition than their counterparts in bachelor herds, even when resources are abundant (Estes, 1991).

Impalas are active throughout the day, alternating between feeding and resting, and usually drink at least once a day (Castelló 2016). They often rest and ruminate whilst standing in the shade of closed-canopy cover, due to poor thermoregulation against dry heat (Estes, 1991; Kingdon and Hoffman, 2013). However, their activity varies seasonally, requiring more movements within a larger home range during the dry season, which results in less ruminating time (up to 3km a day against at least 0.95 km in the wet season – Estes, 1991).

2.3.1.1.3 Dietary preferences and habitat

Modern impalas (*Aepyceros melampus*) are an ecotone species (i.e. they prefer transitional areas between two different biomes) inhabiting acacia savannas and open woodlands close to water (Skinner and Smithers, 1990). Male impalas seem to have a preference for dense habitats, which females avoid (Estes, 1991). Impalas prefer open woodland with little undergrowth and grassland of low to medium height, and require access to water sources during the dry season. In the wet season, they can survive without access to water due to the vegetation moisture content, where green grass and succulents are available (Estes, 1991; Kingdon and Hoffman, 2013). They also require an environment with firm footing and little relief (Estes, 1991).

Impalas are considered mixed-feeders with a varying seasonal diet: they primarily graze when grasses are green and growing in the wet season, but can browse on bush, fruits, foliage, forbs, seedpods and shoots when necessary, often in the dry season (Jarman and Jarman, 1973; Estes, 1991). *Acacia tortilis* and *Acacia nilotica* pods seem to be particularly favoured due to their high protein content (Kingdon and Hoffman, 2013). They can therefore adapt their diet depending on local food availability by shifting between grazing and browsing (Wronski, 2002; Sponheimer, Grant, *et al.*, 2003; Cerling *et al.*, 2015). Studies have also reported that impalas also tend to switch between grass and browse in response to changing resource conditions resulting from environmental factors, such as decreasing rainfall or fires (du Toit, 1988; Van Rooyen, 1992; Wronski, 2003; Skinner and Chimimba, 2005).

As a result, the dietary behaviours of impala populations tend to vary across the various niches they inhabit. For instance, impalas from Chobe National Park (Botswana) were sighted preferentially in Capparis and Combretum shrublands, where medium- to low-height vegetation and water is available, as well as browse of acceptable quality during the dry season (Omphile and Powell, 2002), which echoes observations made by Dunham (1980) in the Sengwa Wildlife Research Area (Zimbabwe), where *Capparis tomentosa* and *Combretum mossambicense* were among the plants with the highest use by impalas during the dry season. In the Moremi Wildlife Game Reserve in the Okavango delta (Botswana), where a wide range of habitats are available to herbivore communities, impalas were observed to avoid grasslands and floodplains during the rainy season (favouring mixed-open-woodlands), while favouring mixed-closed-woodlands and upper-floodplains during the dry season (Bonyongo, 2005). In the mixed-wooded-savannah environments of the Nylsvley Nature Reserve (South Africa), impala populations were observed to be evenly distributed through the different vegetation types during the wet season where they grazed primarily, while concentrating in areas of Acacia savanna during the dry season and shifting to a browse-dominated diet (Monro, 1980).

Impala diet is made up of 45% dicotyledons, 45% monocotyledons and 10% fruit (Gagnon and Chew, 2000), and according to Sponheimer *et al.* (2003a), males graze more than females. Seasonal variation in feeding strategies has also been recorded, with for example a diet composed of 75% grass around January in Sengwa, Zimbabwe after the major rains, against less than 10 % in the same area during the dry season in June/July (Dunham, 1980). Similarly, for impalas from Natal (South Africa), browse comprised 19% of their diet during the wet season, as opposed to 52% in the dry season (Van Rooyen, 1992). Likewise, studies observed that impalas respond to reduced food abundance during the dry season by selecting different plant parts and changing feeding heights, while selecting more for leaves than other browse parts, because of their high protein content (Dunham, 1980, 1982; Van Rooyen, 1992). Regional and sex-based variations in dietary content have also been observed by Sponheimer *et al.* (2003b) through carbon isotope data from Kruger Park, South Africa, depending mostly on forage quality and availability.

Further investigation in the same locality by Codron *et al.* (2006) supports the hypothesis that impalas select their food depending on protein content to maintain high levels of diet quality. Grass would be favoured during the wet season when its quality is higher, while browse is preferred during the dry season due to decreasing protein content in grasses (Dunham, 1980; Wronski, 2003). It has also been suggested that the digestibility of food items influences as well the type of plants selected by impalas, with populations from the Associated Private Nature Reserves (adjacent to Kruger National Park, South Africa) being shown, for example, to avoid browsing on mopane (*Colophospermum mopane*) despite its abundance during the dry season, likely due to its high condensed tannin concentration (Kos *et al.*, 2012).

2.3.1.1.4 Fossil Aepyceros species

2.3.1.1.4.1 Species descriptions

According to Kingdon and Hoffman (2013), the impala is considered to be the only member of its tribe (Aepycerotini), based on molecular analyses, with a proposed lineage ancestry of about 21.5 Ma. The earliest occurrence of genus *Aepyceros* in the fossil record is from Chad at ~7.0 Ma (Geraads *et al.* 2009), and their remains have been found in several East African formations. Three main *Aepyceros* species have been identified in the east African fossil record (see appendix A.2.1 for description of each fossil species).

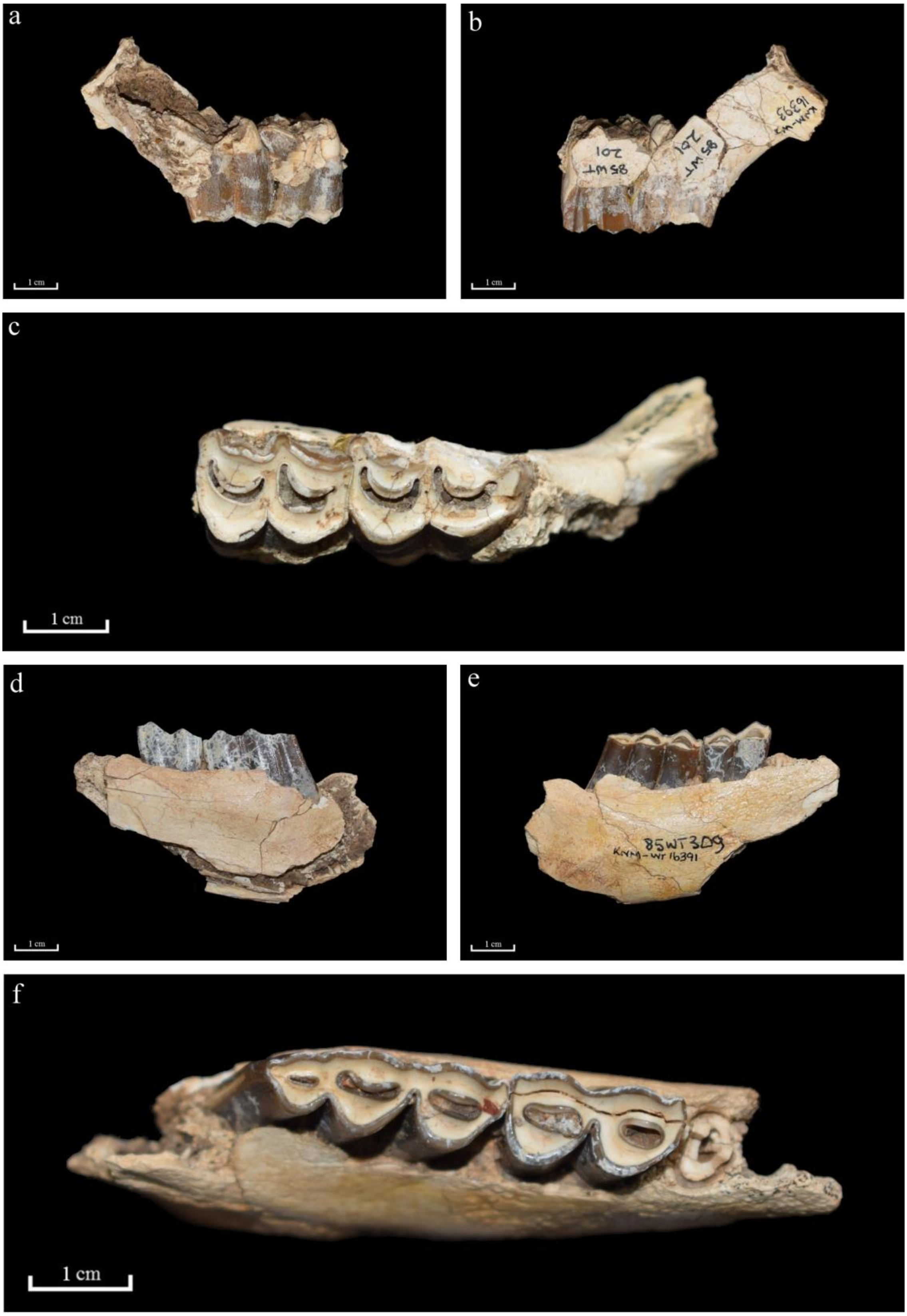

Figure 10: *Aepyceros shungurae* cranial remains. a) lingual view, b) buccal view and c) occlusal view of left maxilla (M2-M3) KNM-WT 16393(Nachukui, Lomekwi Member). d) lingual view, e) buccal view, and f) occlusal view of right mandible KNM-WT 16391 (Nachukui, Lomekwi Member).

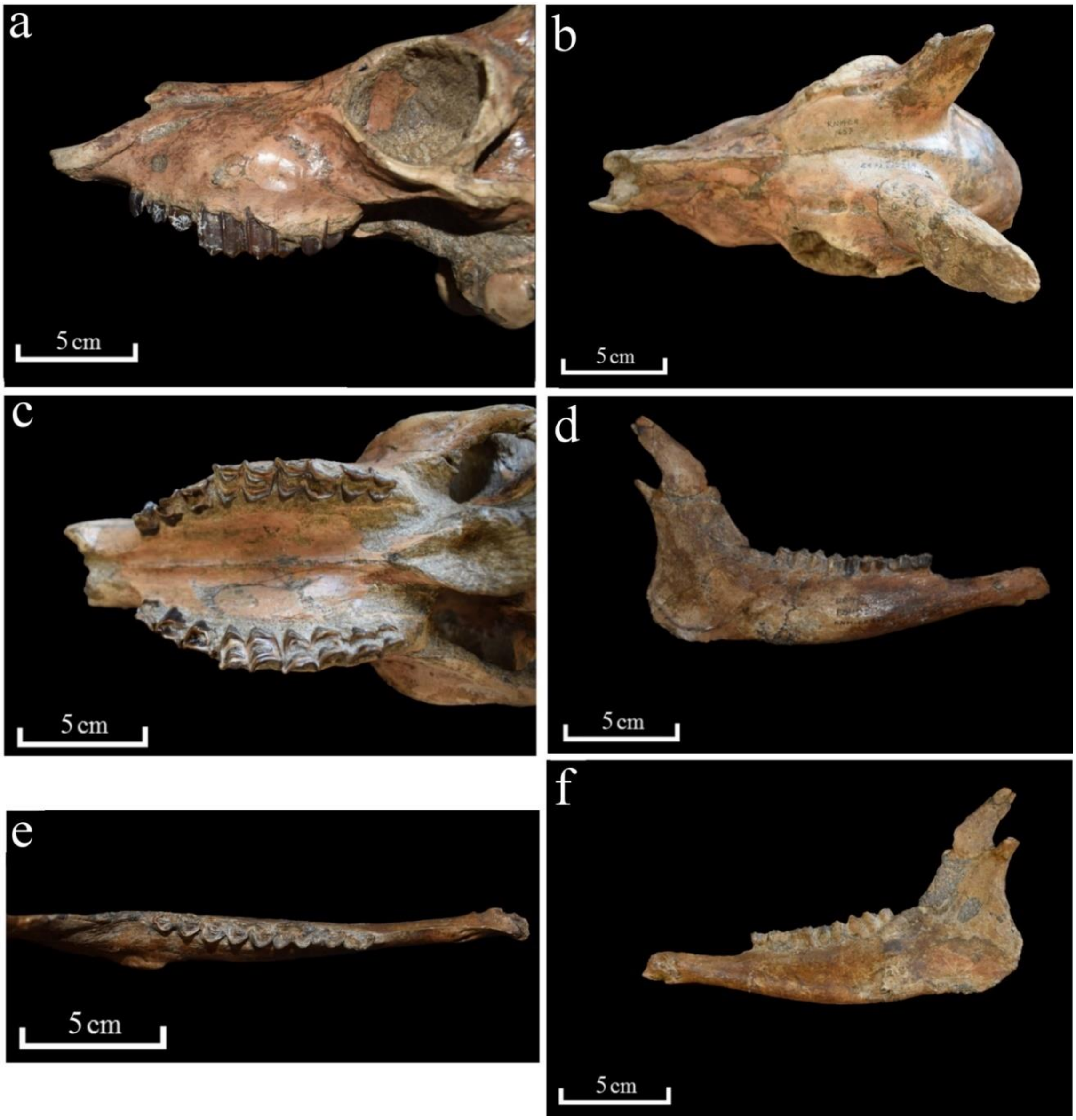

Figure 11: ***Aepyceros melampus*** **cranial remains. a) lateral view, b) superior view, c) occlusal view of cranium KNM-ER 1657 (Koobi Fora, Burgi Member). d) buccal view, e) occlusal view, and f) lingual view of right mandible KNM-ER 467 (Koobi Fora, KBS Member).**

Occurrences of *Aepyceros* prior to the late Pleistocene are rare and uncertain in South Africa, apart from some specimens found in Makapansgat Limeworks and identified by Vrba (1987) and Reed (1997b). The fossil impala species *Aepyceros premelampus* (Harris, 2003) has been identified in Lothagam, in the Nawata formation, as well as in the Nachukui formation (Apak and Kaiyumung members), with remains dated between the late Miocene and the middle Pliocene (i.e. 7 to 4 Ma – Reynolds, 2010). Fossil remains of *Aepyceros shungurae* (Gentry, 1985; Figure 9) have been identified in several fossil deposits of the

Omo-Turkana basin: Shungura formation (members B to G; 3.44 - 1.9 Ma), Usno formation (3-2 Ma), Koobi Fora formation (members Moiti to Tulu Bor; 3.97 - 2.64 Ma) and Nachukui formation (members Lomekwi to Kalochoro; 3.44 - 1.9 Ma) (Gentry, 1985, 2010; Harris *et al.*, 1988; Harris, Brown and Leakey, 1988; Harris, 1991). Remains of *Aepyceros melampus* specimens (Figure 10) were found in the Koobi Fora formation (members Burgi to Okote; 2.64 Ma - 1.38 Ma), and in the Nachukui formation (members Lokalalei to Nariokotome ; 2.53 Ma - 0.6 Ma) (Harris, Brown and Leakey, 1988; Feibel, Brown and Mcdougall, 1989; Harris, 1991).

Of these three species, only *Aepyceros melampus* and *Aepyceros shungurae* are represented in the fossil assemblages studied here.

2.3.1.1.4.2 Palaeo-ecology of fossil impalas

Plio-Pleistocene impalas may have relied more heavily on browse (Sponheimer *et al.,* 1999) and inhabited more closed woodlands than they currently do (Bobe and Eck, 2001). Isotopic studies on Plio-Pleistocene specimens suggest that impalas prior to ~4 Ma were predominantly mixed-feeders (i.e. 25% were grazers, 50% were mixed-feeders, and 25% were browsers), while geologically younger impala specimens had a stronger grazing component to their diet (i.e. 53% were grazers, 47% were mixed-feeders, and none were browsers) (Cerling *et al.,* 2015).

Aepyceros shungurae is very abundant across the sequence of the Shungura Formation (Ethiopia – Members B to G, from 3.44 to 1.9 Ma) where detailed studies of the formation have shown that habitats varied from closed woodlands to a more heterogeneous habitat with marshy forests and open and dry savannah (Gentry and Gentry, 1978; Bonnefille and Dechamps, 1983; Wesselman, 1984; Bobe and Eck, 2001). Based on their morphology (straighter, less lyrated and more gracile horn cores, shorter and thicker limb bones), *A. shungurae* may have inhabited preferentially more closed woodland habitats than *A. melampus* (Harris, 1991; Bobe and Eck, 2001).

2.3.1.1.5 Rationale for using Aepyceros as an environmental proxy

The rationale for choosing Aepycerotini as the main study-taxon in this project was two-fold: firstly, genus *Aepyceros* is very well-represented in the east African fossil record, often as one of the most-abundant bovid tribes. This provides appropriate sample sizes to investigate their dietary ecology in each fossil deposit, as well as through time. Indeed, as described previously, *Aepyceros* specimens have been discovered in every member of the Koobi Fora, Nachukui and Shungura formations between 3.44 and 1.6 Ma. Secondly, the dietary plasticity of modern impala, as well as their sedentary lifestyle, allow them to adapt to prevailing vegetation conditions without the need to migrate. If, as it appears likely, their fossil counterparts were equally adaptable, then their diets could provide data on the prevailing vegetation conditions in the fossil localities studied.

To ensure that fossil *Aepyceros* species can be used as reliable palaeo-environmental indicators, the relationship between the diet of modern impala populations and the land cover patterns of the habitats they inhabit, was investigated. Previous research has shown a high degree of dietary variability that could potentially relate to other ecological factors such as season, sex, or dietary niche partitioning. This part of the project explored modern impala dietary variability and to what extent their diet can inform on the land cover composition and structure of modern impala habitats.

2.3.1.2 Genus *Antidorcas* - Springbok

2.3.1.2.1 General description

The springbok (*Antidorcas marsupialis* –Zimmerman, 1780) is an antelope species present today in south-west and southern Africa (north-western South Africa, Namibia, Botswana) (Figure 11). It is particularly well-represented in dry areas, such as the Kalahari, Karoo and Namib deserts, but varies in size depending on the locality. This variation has led to the recognition of three subspecies of springbok (A*. marsupialis marsupialis, hofmeyri,* *angolensis*) (Skinner and Louw, 1996). Although generally considered sub-species, these are occasionally elevated to species level (Castelló, 2016).

Springbok are medium-sized antelopes (weight: 30-59 kg for males, 20-43 kg for females / shoulder height: 68-90 cm) with lyre-shaped horns present in both sexes, which curve backwards to form a hook at the tips (Figure 12). Their coat is generally light-brown, with a white head with a thin brown stripe from eye to muzzle. Along their dorsal crest are two folds of scent-secreting skin that can be erected, probably for visual or olfactory signal (Kingdon, 1997; Castelló, 2016). They are endemic to southern Africa.

The Angolan springbok (*A. angolensis*) is intermediate in body and horn size between South African and Kalahari springboks, with longer ears. It is native to Angola. The Kalahari springbok (*A. hofmeyri*) is a native species to Botswana, Namibia and South Africa. It is present in open, arid plains with grass or low scrub and is absent from mountains and rocky hills, also avoiding dense woodlands (Castelló, 2016).

This study considered *Antidorcas marsupialis sensu lato,* which includes these three suggested subspecies. Their ancestors were also considered, which are extinct today: *A. recki, A. australis,* and *A. bondi* (see 2.3.1.2.4).

[redacted]

Figure 12: Geographic distribution of modern springbok sub-species (*A. m. marsupialis, A. m. hofmeyri and A. m. angolensis***) (modified from** (Furstenburg, 2016)**, p.5).**

Figure 13: Modern springboks *Antidorcas marsupialis* (Photographed at the Rhino and Lion Nature Reserve, Kromdraii, South Africa, October 2017).

2.3.1.2.2 Social organization and behaviour

Springboks (*A. marsupialis*) have a life expectancy of about 7 to 10 years in the wild (Weigl, 2005) and can mate twice a year. Females give birth to one young per gestation (5-6 months), often just before the beginning of the wet season, and calves are weaned after 3-4 months, to reach sexual maturity at 11-12 months-old (Castelló, 2016; Kingdon and Hoffman, 2013).

Springboks live in family groups of 5 to 100 individuals during the dry winter period but tend to assemble into larger mixed herds during the rainy summer season. In the dry season, where the distribution of their preferred vegetation is less homogenous, populations are more widely dispersed in smaller herds (Bigalke, 1972). They are mobile, apart from the dominant males which become highly territorial when entering the rut, becoming sedentary until their resources are exhausted (Kingdon and Hoffman, 2013).

Springboks have a very thin pelage to allow for efficient body thermoregulation, which allows them to release excessive heat when necessary (e.g. after being pursued by predators), but which also makes them more vulnerable to changes in temperatures: they quickly shiver with moderately low temperatures, and gain heat rapidly when temperatures are high (Skinner and Louw, 1996). Although active throughout the day, they feed mainly around dawn and dusk, and usually lie down or stand up to ruminate during the hottest hours of the day (Castelló, 2016;, Kingdon and Hoffman, 2013).

The springbok was described as a highly mobile species up until the end of the nineteenth century, as it used to migrate over large distances during extended dry seasons, forced out of their home range only to return with the rains. However, this phenomenon called "trekbokken" has disappeared in modern populations due to anthropogenic influences such as fences and hunting practices, which prevent these animals from moving around freely (Bigalke, 1972; Estes, 1991; Skinner, 1993; Dewar *et al.*, 2006). Springbok populations have also been largely impacted by diseases such as rinderpest (Estes, 1991), or by parasites (Turner *et al.*, 2012). Most springboks in South Africa are now part of farmers' livestock, or within National Park lands, living and breeding within fenced areas (Kingdon, 1997).

2.3.1.2.3 Dietary preferences and habitat

The springbok has a high dietary adaptability, with the extant species *Antidorcas marsupialis* favouring open and semi-open habitat, inhabiting dry grasslands, bushlands or shrublands, where it can eat short grass, succulents, forbs and browse (Castelló, 2016). Springboks are however absent from woodland savannah, probably due to the presence of parasites to which they are very sensitive (Kingdon and Hoffmann, 2013).

The springbok has been described as a mixed-feeder with a preference for browse (Bigalke, 1972), and has been observed to be primarily a summer grazer and a winter browser, grazing on young grasses when available, and browsing on low shrubs and succulents when these are no longer available (Estes, 1991). Stable carbon isotope analyses agree with such classification (Sponheimer, Lee-Thorp, *et al.*, 2003). Springbok tend to feed primarily on succulent shrub leaves (e.g. *Acacia mellifera*) and coarse/hard-stemmed grasses (e.g. *Aristida*, *Eragrostis*, *Cynodon*, *Panicum* and *Sporobolus*) (Davies, Botha and Skinner, 1986; Nagy and Knight, 1994a; Skinner and Louw, 1996). They have also been observed feeding on karroid vegetation from riverbeds and dry lake beds, tall shrubs or leaves from the ground, as well as roots (Eloff, 1959; Van Zyl, 1965; Bigalke, 1972; Cain, Krausman and Germaine, 2004), succulents, and cucurbits in the absence of surface water (Kingdon, 1997). The anatomy of their digestive system is well adapted to a diet of mixed forage, but the ability to digest highly fibrous food is limited, which forces springboks to migrate to find other resources once the local vegetation becomes too lignified (Hofmann, Knight and Skinner, 1995; Skinner and Louw, 1996).

The springbok does not require the presence of groundwater and is therefore often present in very dry areas where it has less competition while foraging. It can satisfy its moisture requirements by feeding on succulents (e.g. leaflets of blackthorn *Acacia mellifera*), cucurbits or shallow roots (Kingdon and Hoffman, 2013; Kingdon, 1997), but will drink water when available (Estes, 1991; Skinner and Louw, 1996). In their study of springbok populations in the Kalahari, Nagy and Knight (1994) noted that springbok tend to consume a wider range of food resources with high water content (e.g. flowers) during the hot, dry season when in areas with no access to drinking water, whereas consuming less high-water-content resources in that season in areas with access to drinking water. It suggests that springbok tend to adapt their diet depending on the availability of drinking water.

The springbok dietary patterns therefore vary according to season, drinking-water availability, but also to sexes: in a study of the Karoo springbok, Davies *et al.* (1986) differences were observed in diet between adult males and females, with rams preferring more palatable shrubs. Nutritional intake is also affected by other factors, such as vigilance requirements, with individuals on the outskirts of a herd feeding less than those in the centre due to increased vigilance. Vigilance also increases when approaching trees, and decreases in open grassland (Bednekoff and Ritter, 1994). Such flexible feeding behaviours are likely to have been a key factor in the evolutionary success of these species.

2.3.1.2.4 Fossil Antidorcas species

2.3.1.2.4.1 Species descriptions

Fossil remains belonging to genus *Antidorcas* have been found within Pliocene and Pleistocene deposits in North, East and southern Africa (Skinner and Louw 1996). Alongside the extant *A. marsupialis*, the existence of two or three extinct species have been suggested from the fossil record: *Antidorcas recki, Antidorcas bondi* and *Antidorcas australis.* Based on cranio-dental morphology (i.e. especially horn cores), Vrba (1973) suggests that these species arose in East Africa 15 million-years ago from the ancestral *Gazella* lineage (Kingdon, 1997). It is possible that the modern springbok evolved from forms descended from Northern African populations, as some early *Antidorcas* fossils are known from the Atlas Mountains (Maghreb region, North Africa) and show that *Antidorcas* was already adapted to cool Eurasian-type habitats by 4 Ma (Kingdon, 1997). These populations could have migrated into South Africa through arid corridors which connected North and North-East Africa to South Africa during most glacial ages.

Fossil springbok specimens have been recovered in some members of the Koobi Fora and Nachukui formations (Harris 1991; Brugal *et al.* 2003), only represented by *A. recki* (Figure 13), between 3.4 and 1.6 Ma. This species seems to disappear from the eastern African fossil record after ~ 0.8 Ma (i.e. Olduvai Bed IV - Gentry and Gentry, 1978b), with a last recorded appearance of the *Antidorcas* genus in East Africa at the site of Lainyamok between ~392,000 - ~330,000 Ka (Potts and Deino, 1995). Despite its disappearance from East Africa, the *Antidorcas* genus remains in southern Africa, where *A. recki* is believed to have given rise to new species: *A. australis* and *A. bondi* (Brink and Lee-Thorp, 1992), and, eventually, to the modern springbok, *A. marsupialis* (Vrba, 1973). However, there is still debate regarding the origin of *A. marsupialis*, and the existence of *A. australis* as a separate species. Time at which migratory behaviour appears is still unknown. The chronology of the *Antidorcas* lineage and the debates around taxonomy are further described in appendix A.2.2.

It must noted, however, that while *A. recki* specimens have been reported for the Omo-Turkana fossil record, questions remain around the identification of this species, and about the similarity between the *A. recki* specimens identified in East Africa, compared to the *A. recki* specimens identified in the South African fossil record. While *A. recki* has been suggested to have been one of the most abundant antelope in eastern Africa (i.e. recorded from Olduvai Gorge, Kanjera, Peninj, Laetoli and Omo ; Gentry, 1978), it seems to have been less abundant in South Africa, where the classification of these specimens as *A. recki* (Vrba, 1976) has been questioned (De Ruiter, 2001). This could be due to issues in differential taxonomic classification, particularly with *A. marsupialis*, when working from isolated teeth only (see Table 1 in Sewell *et al.* 2019 for more detail on dental identification of *Antidorcas* species). This may be further complicated by sexual dimorphism of both species, as suggested by Adams *et al.* (2016). The difficulty in identifying fossil *Antidorcas* to the species level is therefore a caveat that must be taken into account when studying this taxon, especially for further comparisons between the eastern and southern fossil record.

Figure 14: *Antidorcas recki* left mandible from Koobi Fora formation (Tulu Bor Member - KNM-ER 2764). a) b) c) KNM-ER 1657 (Koobi Fora, Burgi Member. a) lingual view, b) buccal view, c) occlusal view.

2.3.1.2.4.2 Palaeo-ecology of fossil springbok

While the extant species *Antidorcas marsupialis* seems to be favouring open and semi-open habitat and is described as a mixed-feeder with a preference for browse (Bigalke, 1972), it is not necessarily the case of its extinct counterparts. For instance, carbon stable isotope analyses on south African fossil material have suggested that *A. bondi* probably used to be predominantly a grazer, while fossil *A. marsupialis* and *A. recki* appeared to have fed primarily on C_3-plants (Brink and Lee-Thorp, 1992; Luyt, 2001; Lee-Thorp, Sponheimer and Luyt, 2007; Ecker and Lee-Thorp, 2018; Sewell *et al.*, 2019). Seasonality of dietary behaviours has also been suggested among South African fossil *Antidorcas* species (Sewell *et al.,* 2018) and Olduvai *cf. A. recki* specimens (Rivals *et al.*, 2018), through combined isotopic and use-wear analyses. This could reflect similar seasonal dietary behaviours between extinct and modern springbok species.

Browsing diets in the South African *A. recki* has also been suggested through mesowear and microwear analyses (Sewell *et al.,* 2018), but several studies have stressed the inclusion of grass within a mixed-feeding diet and a preference for habitats dominated by woodland or bushland, for this extinct species (Plummer and Bishop, 1994; Spencer, 1997). A study on *cf. A. recki* specimens from Olduvai Gorge (Tanzania, ~1.7 Ma) highlighted the dietary plasticity of this fossil springbok species, with differences in dietary patterns observed through time (Rivals *et al.*, 2018). As springboks are represented only by *A. recki* in the Omo-Turkana fossil record, it will be interesting to see in this study if their dietary preferences in the Plio-Pleistocene Turkana basin mirrored the ones observed for that species in South African contemporary deposits.

2.3.1.2.4.3 Rationale for using genus *Antidorcas* as an environmental proxy

As for genus *Aepyceros*, genus *Antidorcas* was selected as a study taxon in this project for both its abundance in the fossil record and its dietary plasticity, which is attested in modern springbok and suggested as well from previous studies on extinct *Antidorcas* species (Sewell *et al.*, 2018). Although fossil springbok specimens are not as abundant in the Omo-Turkana fossil record as fossil impala specimens, representatives of the *Antidorcas* lineage are present in some members, and their dietary ecology can be compared to that of impalas, to see if similar patterns occur. Data from these *Antidorcas* specimens are therefore sought for this research project, to test whether eastern African fossil springbok had a dietary flexibility similar to that of their extant relatives.

The collection of data from the Omo-Turkana *A. recki* specimens was also undertaken to allow future comparisons between Plio-Pleistocene eastern African and southern African *Antidorcas* assemblages. Indeed, results from the present study are directly comparable to results produced by Sewell *et al.* (2019) on the South African fossil record, on which a similar approach was used, combining use-wear analyses and stable carbon isotopes to investigate potential variation in dietary behaviours within the *Antidorcas* lineage during the Pleistocene (see also Sewell, 2018). This allows comparisons to be made between the dietary signals of eastern and southern African *A. recki* specimens, which are represented in these two African regions during the Plio-Pleistocene, while keeping in mind that identification of *Antidorcas* dental remains to species can be problematic, raising the question whether *A. recki* truly occurred as one species in both eastern and southern Africa, especially if drastic differences in dietary behaviours are identified for this species when comparing both regions.

2.3.2 Obligate grazers and browsers to calibrate the overall dietary spectrum

Samples from one dedicated-browser and one dedicated-grazer taxa (i.e. genera *Giraffa* and *Equus*, respectively) were also analysed in this study to help calibrate the overall dietary spectrum of ancient herbivores through time, by investigating the diet composition of species that are expected to rely mainly on graze or on browse. These additional studied taxa are described briefly in this section.

2.3.2.1 Genus *Giraffa*

The modern giraffe (*Giraffa camelopardalis*) is a browsing species which usually inhabits dry savannahs dominated by acacia woodland and scrublands, or open woodland habitats (Hutchins *et al.*, 2003). It is native to Africa and can be found south of the Sahara to eastern Transvaal, Natal, and northern Botswana. Giraffes have disappeared from most of western Africa, except a residual population in Niger. Giraffes are ruminants with have a four-chambered stomach, feeding on leaves, flowers, seed pods, and fruits, favouring areas rich in *Acacia*, and occasionally eating soil or dried bones for their mineral content (Hutchins *et al.*, 2003). Their diet is usually constituted of 80% acacia browse, seeds, pods, fruits and shoots, and 10–20% herbaceous plants (Schulz, Calandra and Kaiser, 2013). Modern giraffes are not water-dependent and can therefore be found far from water sources as they can meet most of their water requirements from the water-content of their foliage. The consistency in the diet of modern giraffes, as well as their low dependence on drinking water, have been suggested to make giraffes ideal for studies on stable isotope aridity indices (Levin *et al.*, 2006).

Fossil giraffids are represented in the Omo-Turkana basin by several species, all of them extinct today. These species coexisted during the Plio-Pleistocene, and present variations in size, and in shape and orientation of their ossicones: *Giraffa jumae, Giraffa gracilis, Giraffa pygmaea* and *Giraffa stillei* (from the largest to the smallest species) (Harris, 1976; Mitchell and Skinner, 2003) (see appendix A.2.3 for more detail).

According to carbon isotope data (Cerling *et al.,* 2015), fossil *Giraffa sp*. from the Nachukui and Koobi Fora formations had a diet composition similar to that of extant giraffes, which can be described as obligate browsers. Their dental morphology, similarly to their modern counterparts', also suggests a predominance of non-abrasive foods, with a low crown height and sharp apices. However, it must be noted that an isotopic study of *Giraffa cf. G. gracilis* specimens from the Lower Awash valley (~2.8 – 2.6 Ma) has shown that some specimens consumed up to 40% of C_4-vegetation, which suggests perhaps a greater dietary variability in some extinct giraffids than is observed among modern giraffes (Rowan *et al.*, 2017), although a study by Cerling *et al.* (2015) reported that some of their sampled modern *G. camelopardalis* specimens exhibited isotopic values typical of mixed-feeders. Similarly, isotopic data from specimens of *G. jumae* and *G. stillei* from Laetoli suggested a diet with more grass, and a stronger reliance on drinking water among these specimens, compared with the Turkana basin giraffids (Harris *et al.,* 2010).

Considering the results from these previous studies, this study aims to test whether the fossil *Giraffa* specimens analysed actually reflect a dominance of browsing signals, as usually expected for representatives of this genus, or if, in fact, some degree of dietary variability could be observed within the Omo-Turkana Plio-Pleistocene fossil record. Because *Giraffa* individuals are usually observed to be primarily C_3 -biomass feeders, changes from this expected pattern might reflect unknown palaeo-dietary behaviours for this genus, or changes in local palaeo-environments which forced giraffids to rely on different food resources depending on what was available in their habitats. They should, therefore, help to evaluate the extent of the dietary spectrum, especially when it comes to the availability of browse, or to potential differences in canopy cover across regions/time periods (reflected in differences in stable carbon isotope content).

2.3.2.2 Genus *Equus*

Within the family Equidae, the genus *Equus* (Equini tribe) includes horses, asses, and zebras, and is the only Equidae genus comprising extant species today. Modern African equines are represented by four species of the genus *Equus*: the wild ass (*Equus africanus*), Grévy's zebra or imperial zebra (*Equus grevyi*), the plains or Burchell's zebra (*Equus quagga*, formerly *E. burchellii*), and the mountain zebra (*Equus zebra*) (Kingdon 1997). Zebra species are high-density, tropical grassland equines, while asses occur in low-density, desert areas. Species from genus *Equus* have a dentition adapted for grazing, with large incisors to grab grass blades, and highly crowned molars (hypsodont) for grinding (Estes, 1991). Their digestive systems can digest tough unpalatable grasses quickly.

African equines usually live in areas where their food and water supplies change drastically between seasons, which forces them to migrate where there is seasonal rainfall (Klingel, 1972). According to carbon isotopic analyses (Cerling *et al.,* 2015), modern *Equus* individuals are predominantly C_4 -grazers. *E. grevyi*, for example, feeds up to 70% on long and dry grasses, and at least on 30% browse during times of drought or in overgrazed areas, as fall-back resources (Schulz *et al.,* 2013). Although extant *Equus* is often described as an obligate grazer, some studies have indeed highlighted the ability of this genus to adapt to locally available plants, and include browse in some regions during droughts (Berger *et al.*, 1986; Roeder, 1999; Tütken *et al.*, 2013).

Equines are represented in the African fossil record by *E. burchellii, E. oldoywayensis* and *E. grevyi* in eastern Africa, and by *E. burchellii*, *E. zebra* and *E. capensis* in South Africa (Reynolds, 2007 and references therein). *E. burchellii* significantly differs from the other three fossil equid species by the smaller size of its teeth (Churcher, 1981; Eisenmann, 1983). In most fossil collections, isolated equid teeth are usually only assigned to genus (i.e. *Equus* sp.), due to the difficulty in differentiating species based solely on isolated dental remains (Reynolds, 2005). It was the case for all specimens analysed in this study.

Based on isotopic studies on the Omo-Turkana Basin fossil record, it appears that *Equus* has been a C_4-grazing genus since its first appearance in Africa during the late Pliocene (Cerling *et al.,* 2015). However, the proportions of grazing/mixed-feeding/browsing specimens differ slightly from the extant *Equus* specimens, with 82% grazers/18% mixed-feeders in the fossil record, against 91% grazers/8% mixed-feeders/1% browsers in extant *Equus* specimens. Overall, fossil African equids are usually classified as obligate grazers, which is consistent with their highly hypsodont dental morphology (see Figure A-2 in appendix A.2.4). For this reason, and because it is represented in most of the members of the Omo-Turkana study area, dental remains from genus *Equus* are used in this study as a way to evaluate the Plio-Pleistocene dietary behaviours of a predicted grazing taxon, which might vary more than expected, either due to more varied dietary behaviours, or due to differences in the type of graze consumed (e.g. differences in isotopic signature between arid and non-arid adapted grasses

2.4 Reconstructing palaeo-diets and palaeo-environments: review of the methods used in this study

To provide a detailed assessment of the dietary behaviours of the different taxa selected for this study, several methods are used in the present study: mesowear analysis, dental microwear textural analysis, stable carbon and oxygen isotopes, and land cover analysis. The main rationale for using these methods relies on the use of dental remains, which tend to be well-represented in the fossil record, and have the potential to yield precious information on dietary behaviours, at different scales and at a different level of detail depending on the method used. Combining several methods of dietary analysis on a same assemblage offers, in addition, the potential to draw a picture as detailed as possible of the studied taxa's dietary behaviours, allowing to collect indirect evidence on the structural and geochemical properties of the vegetation-types consumed by these animals. The rationale for using modern land cover data alongside dietary data is driven by the necessity to better understand the relationship between animal populations' dietary behaviours and their habitats, to facilitate interpretations of the paleo-dietary behaviours inferred from dental analyses.

This section introduces and discusses the strength and weaknesses of each of the methods used in this study, and how these can be used to make inferences about the dietary ecology of the studied taxa and, in turn, how these can be used to contribute to the current knowledge on Plio-Pleistocene habitats in the Omo-Turkana basin.

2.4.1 Mesowear analysis

2.4.1.1 General Principles

Mesowear refers to macroscopic wear on teeth, which is the result of accumulated attrition and abrasion on molar teeth acquired through life or during the last months/years of an individual's life (Fortelius and Solounias, 2000; Rivals *et al.*, 2007; Louys *et al.*, 2012;

Loffredo and DeSantis, 2014; Ackermans *et al.*, 2018; Ackermans, 2020; Ackermans, Martin, *et al.*, 2020). Attrition is the tooth wear caused by tooth-on-tooth contacts during mastication, and is the primary cause of wear in browsing herbivores that consume relatively soft food items such as leaves, twigs, flowers or fruits (Green and Croft, 2018). Attrition has been shown to result in enamel surfaces with sharp edges and well-developed facets. Abrasion is the type of tooth wear caused by interactions between teeth and exogeneous particles such as food or grit and is thought to be the primary cause of wear in grazing species that consume grasses or ground-level vegetation. Abrasion has been shown to result in enamel surfaces with round edges and obscured facets.

This phenomenon can be observed and/or measured from the buccal outlines of specific teeth according to a method defined by Fortelius and Solounias (2000). By evaluating the relative proportion of these two types of wear on molars, one can assess whether an animal was predominantly grazing or browsing throughout its life (Fortelius and Solounias, 2000; Mihlbachler and Solounias, 2006; Rivals and Semprebon, 2006; Semprebon and Rivals, 2007; Kaiser *et al.*, 2009; Ackermans, Martin, *et al.*, 2020). As highlighted by Fortelius and Solounias (2000), the fact that the original study was able to identify various degrees of mixed-feeding behaviours suggests that the method can help evaluate the relative degree of dental abrasion among mixed-feeding species, as well as among grazers and browsers. These levels of dental abrasion are likely related to the proportion of grass or abrasive matters present in the food resources of the animals. A controlled-feeding experiment on goats demonstrated that if diets rich in phytoliths (such as grass blades) are indeed responsible for more rounded cups and lower occlusal relief, the most change in mesowear can actually be observed with diets depleted of abrasives (such as browsing habits) in relation to dominating attrition-wear, leading to sharper cusps and higher relief (Ackermans *et al.*, 2018). This confirms that dental mesowear likely reflects the relative proportion of attrition-dominated and abrasion-dominated wear in an individual. A pilot study conducted on modern zebras by Kaiser and Schulz (2006) suggested that mesowear is likely to be related to humidity and seasonality, with high ratios of round cusps and high relief reflecting humid environments, while high ratios of blunt cusps and low relief being associated with drier habitats.

2.4.1.2 Mesowear Scoring

Mesowear is observed with the naked eye or at low magnification (e.g. hand lens). The method is implemented by observing the labial edges of the paracones and metacones of specific molars, using two variables: occlusal relief and cusp shape (Fortelius and Solounias, 2000). Occlusal relief (OR) is the relative difference in height between cusp tips and the valley between them, in lateral view. Cusp shape (CS) refers to the apex of the cusp (paracone or metacone) described as sharp, rounded, or blunt (see Figure 18 in chapter 3). This method of scoring is referred to as 'Mesowear I'.

A modified version of the mesowear method was proposed first by Rivals and Semprebon (2006) and used consequently in other studies (Rivals *et al.*, 2007; Semprebon and Rivals, 2007; Rivals, Schulz and Kaiser, 2009) where a single-variable is used to score mesowear, combining occlusal relief and cusp height into a single categorical score ranging from zero (high relief and sharp cusps) to three (blunt cusps and essentially no relief). Other researchers have adapted the method using various numeric scales, such as one ranging from zero to four (Kaiser *et al.*, 2009, 2013; Blondel *et al.*, 2018; Sewell *et al.*, 2019) or from zero to six (Mihlbachler *et al.*, 2011; Uno *et al.*, 2018). 0 always represents the most attrition-dominated mesowear signature (suggested to represent browsing habits), while the highest number on the scale represents the most abrasion-dominated signature (suggested to represent grazing habits). A mean score can then be calculated for each species and/or sample based on all available dental specimens (Kaiser *et al.*, 2013; Ozaki Kubo *et al.*, 2014). This method of scoring is referred to as 'Mesowear II'.

A recently published review of the method has highlighted the wide range of adaptations, simplifications and extensions of the original mesowear method that can be found today across the literature (Ackermans, 2020). While adaptations have been necessary to take into account specific dental morphologies and allow this method to be used beyond large-bodied herbivores, simplifications of the method can lead to a reduced capacity to identify more subtle variations in diet based on mesowear. Furthermore, the existence of so many different mesowear methods reduces considerably comparability between studies. To mitigate for this latter issue, both Mesowear I and Mesowear II scoring systems were used to facilitate comparisons with previous and future works.

2.4.1.3 Data acquisition

Fortelius and Solounias (2000) designed the mesowear method for the upper second molar (M^2) (see Figure 14 dental nomenclature). However, several papers have since attempted to extend the method to other tooth positions to allow for bigger sample size when applied to the fossil record as a minimum of ten dental specimens per sample has been advised for analysis. For instance, Louys *et al.* (2011) suggested to using the lingual side of the lower second molars (M_2), because the lingual cusps of lower molars are functionally similar to the buccal cusps of the upper molars. However, their results demonstrated that using other teeth alongside the M^2 would likely cloud the mesowear signal. The same had been observed by Franz-Odendaal and Kaiser (2003) when testing mesowear on the lower dentition, suggesting differential use-wear patterns for lower molars, which demonstrate an increased grazing signal. If the occlusal relief variables did not seem to differ between upper and lower dentition, there was however a difference regarding the cusp shape variables “sharp” and “rounded”, a pattern also observed by Kaiser and Solounias (2003) in plain zebras *Equus quagga*. Kaiser and Schulz (2006) and Kaiser and Solounias (2003) managed to extend the mesowear method successfully by including the upper tooth positions P^4, M^1 and M^3, for studies focusing on equids. However, when applied to other species, Franz-Oldendaal and Kaiser (2003) observed different results, suggesting that only upper third molars (M^3) should be used beside the M^2 for accurate dietary classification. Indeed, the combination M^2-M^3 provided consistent mesowear classifications for the species tested in that study.

While it has been suggested that analyses should take into account the effect of ontogenic-age on use-wear by examining (where possible) the age structure of fossil assemblages (Rivals, Mihlbachler and Solounias, 2007), Fortelius and Solounias (2000) demonstrated that mesowear is not sensitive to wear stages as long as very young (no wear) and very old individuals (enamel completed reduced by heavy wear) are excluded. Only the sharpest of the two cusps is scored, as sharpness is less likely to be influenced by factors other than diet, which is not true for roundness of the cusps.

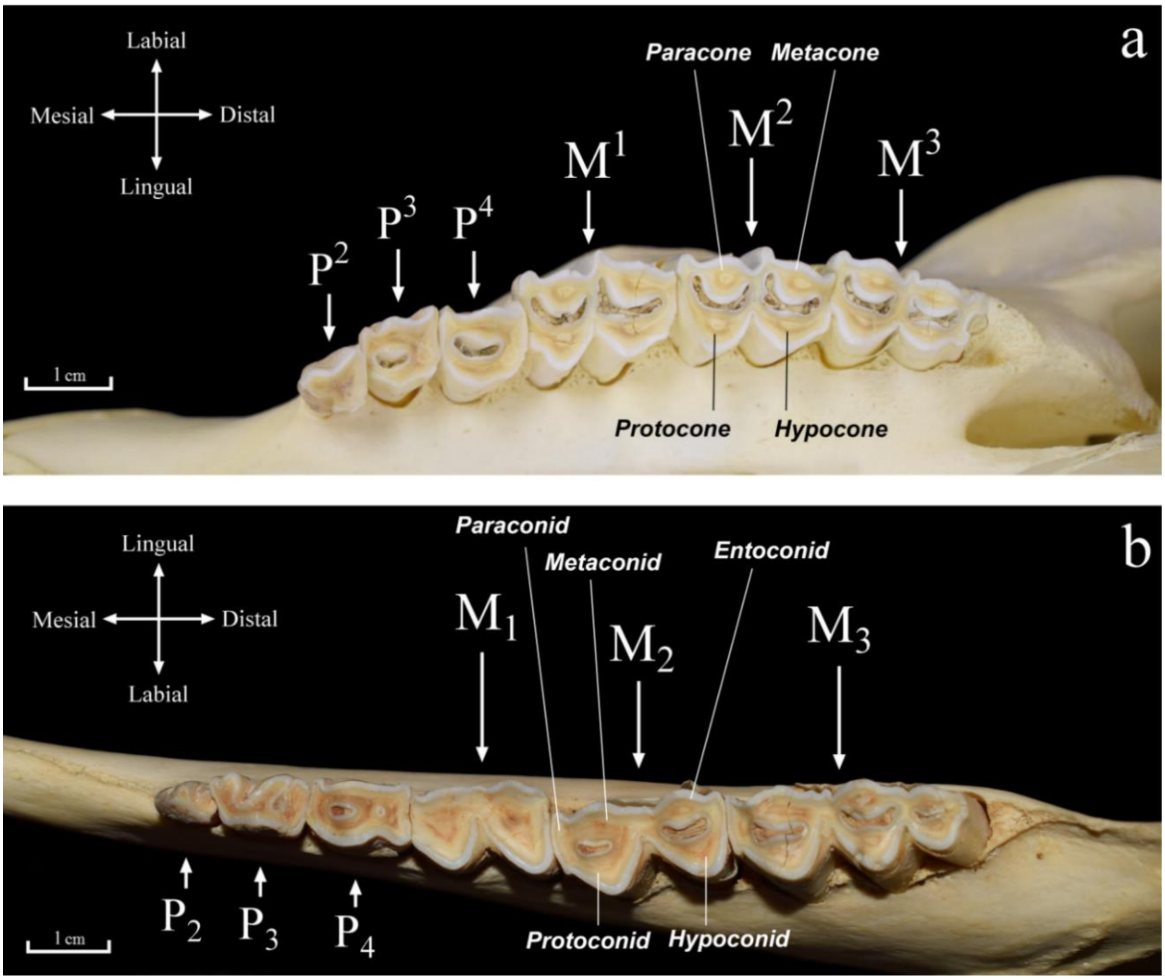

Figure 15: Example of dental nomenclature for (a) upper, and (b) lower dentitions, of *Aepyceros melampus* ((a) specimen AZ 532 and (b) specimen AZ 646, from the Ditsong Museums of South Africa, Pretoria).

2.4.1.4 Strengths and limitations of the mesowear method

The mesowear method presents the advantages of being relatively quick, inexpensive, non-destructive and easy to record directly on fossil material (Loffredo and DeSantis, 2014; Green and Croft, 2018). More importantly, one of the main strengths of this method is to be relatively taxon-independent because dental wear relates directly to the food items ingested, meaning than two individuals feeding on similar food items are likely to yield similar mesowear scores regardless of their taxa. This method was selected for the present studies because of these advantages.

However, the mesowear method presents several limitations. One of these is the fact that the method can only inform on the overall degree of toughness and abrasiveness of the consumed food items, which does not allow palaeo-environmental interpretations of greater detail than the open habitat vs closed habitat dichotomy based on the general grazing vs browsing dietary categories. Currently, very few feeding experiments have been conducted on this method (Kaiser *et al.*, 2013; Solounias *et al.*, 2014; Ackermans *et al.*, 2018; Ackermans, Martin, *et al.*, 2020), and it remains uncertain whether mesowear can be used to assess diets at a greater detail. Equally, because mesowear has been shown to be the result of dental use-wear accumulated over years (Ackermans, Martin, *et al.*, 2020), seasonal variation in diet cannot be assessed using this method.

To maximise the strengths of this method and mitigate for its limitations, mesowear analysis can be combined with other methods that assess dietary behaviours in greater detail and/or on a different temporal scale. Because dental microwear offers insights into the structural properties of the food items consumed on a shorter time scale than mesowear (i.e. last few days/weeks before death), microwear can be used beside mesowear analysis to detect seasonal changes in diet (Rivals, Solounias and Mihlbachler, 2007; Rivals *et al.*, 2015). Stable carbon isotopes can also be combined to dental use-wear analyses to provide information on the geochemical properties of the vegetation ingested during the time of enamel-mineralisation, and complement the data acquired from meso- or micro-wear studies (Sewell *et al.*, 2019).

2.4.2 Dental microwear textural analysis (DMTA)

2.4.2.1 General principles

Dental microwear is the study of microscopic tooth-wear resulting from dental use. Various food types have been shown to differ in resistance to structural breakdown during mastication, leading to differing use-wear patterns and differing marking patterns on the enamel surface (Walker and Teaford, 1989; Teaford, 1994). Unlike mesowear, microwear does not reflect a cumulative use-wear produced over months to years, but instead informs on the structural characteristics of the food items consumed up to two weeks before the animal's death, due to the rapid turnover rate of the traces imprinted on the enamel surface (Kaiser and Brinkmann, 2006; Ungar, 2015; Calandra and Merceron, 2016; Bignon-lau *et al.*, 2017; Green and Croft, 2018).

Many of the earliest methods focused on measuring and counting individual features on images of the tooth occlusal surface acquired through Light Microscopy or Scanning Electron Microscopy (see Ungar 2008 and Green and Croft 2018 for more detailed reviews of these methods). However, it was gradually recognised that these methods suffered from low repeatability and high inter-observer error (Grine, Ungar and Teaford, 2002; Scott, 2012). These concerns led to the development of an automated three-dimensional technique: dental microwear textural analysis (MTA) (Ungar, 2002; Ungar *et al.*, 2003; Scott *et al.*, 2005).

Dental microwear texture analysis (DMTA) is based on three-dimensional surface measurements taken using white-light confocal microscopy and scale-sensitive fractal analysis. A computer software is used to analyse the texture of a wear surface and its topography at various scales, as opposed to previous methods which quantified discrete microscopic features such as scratches and pits. The various surface parameters produced with this method (see 2.4.2.3 Textural parameters) allow quantitative characterizations of three-dimensional surfaces that are repeatable and free of observer measurement error (Ungar *et al.*, 2003; Scott *et al.*, 2006; Green and Croft, 2018). Several studies have demonstrated that DMTA can be particularly efficient for performing quantitative analyses of intra- and inter-specific variations in diet composition among ungulates (Ungar *et al.*, 2003; Merceron *et al.*, 2010; Scott, 2012; Merceron, Hofman-Kamińska and Kowalczyk, 2014; Calandra and Merceron, 2016; Bignon-lau *et al.*, 2017).

To understand the nature of the relationship between microwear and diet, several studies have focused on living animals such as primates (e.g. Scott *et al.,* 2005) or ungulates (e.g. Scott, 2012). These studies showed that use-wear is closely related to the properties of the consumed foods, especially its toughness and siliceous content, as it impacts the biomechanical chewing patterns of the animals as they adapt to access the nutrient content of the food items (Scott, 2012). Tooth morphology and microstructure have also been suggested to influence use-wear patterns and occlusal surface texture as it requires adapted chewing movements and biting force (Hua *et al.,* 2015; Calandra and Merceron, 2016).

Similarly, the differences in microwear patterns have been shown to relate to food particle size, with large hard particles being able to fracture enamel and cause more loss of dental tissue than smaller particles (Lucas *et al.*, 2008; Ramdarshan *et al.*, 2016). For instance, a controlled-food experiment on forty ewes fed on various types of food demonstrated that dental microwear textural analysis can provide a detailed account of the types of foods processed by browsers beyond the usual browser/fruit-browser dichotomy, such as observable variations in microwear textures according to the amount and type of seeds processed.

2.4.2.2 Data acquisition

Microwear data for textural analysis is frequently acquired from moulds (negative impressions) or casts (positive impressions) of the selected specimens to facilitate studies of museum collections and allow easier manipulation of the sample under the microscope (Green and Croft, 2018). Dental-grade moulding polyvinyl-siloxane products are often used to produce moulds from the original specimens, such as President Jet Light Body (low viscosity) and President Jet Regular Body (medium viscosity), which have been shown to produce high quality moulds (Goodall, Darras and Purnell, 2015). It has been shown that data from studies using different moulding materials should not be compared directly (Goodall *et al.* 2015).

While some researchers analyse microwear textures directly from the moulds rather than from casts (e.g. Schulz *et al.,* 2010; Ramdarshan *et al.,* 2016), casts are required (using the moulds made from the specimens) when using techniques that rely on light refraction or electron beam interaction. Scanning the original moulds rather than casts can reduce the risks of information loss that can arise from adding a step to the specimen replication process, although the degree of information lost between the original specimen and the mould itself has not yet been investigated in as much detail as the information loss between specimen and cast (Goodall, Darras and Purnell, 2015; Mihlbachler, Foy and Beatty, 2019).

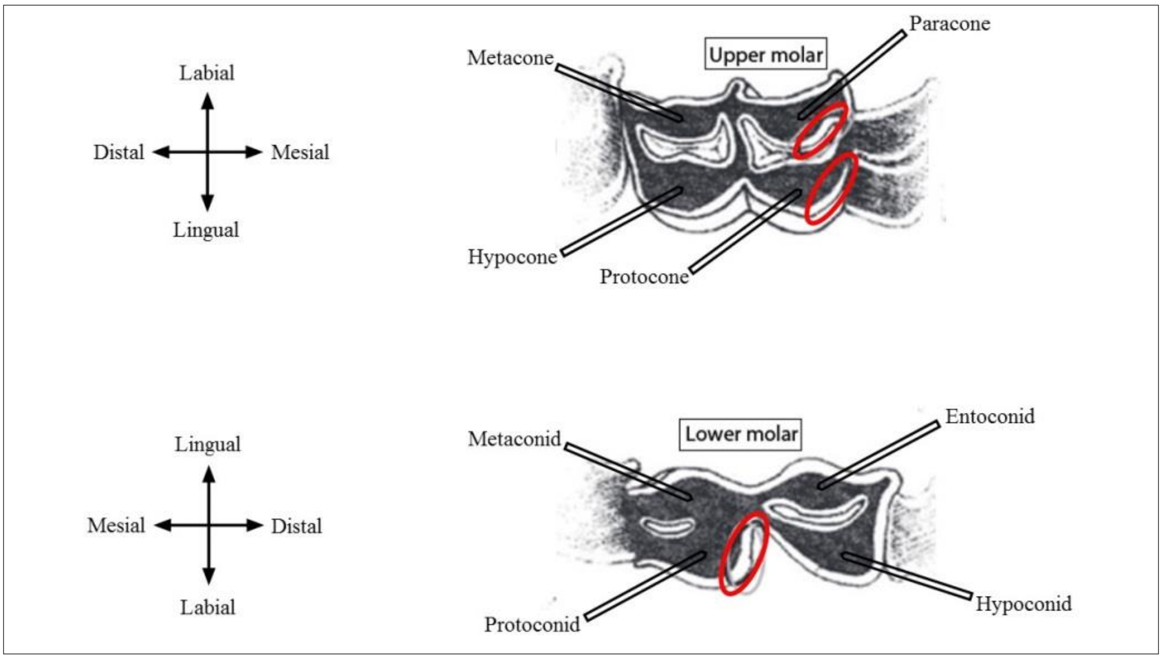

Figure 16: Occlusal view of bovid upper (right) and lower (left) second molars, highlighting the facets where dental microwear will be studied (modified from Scott 2012[3], based on illustration by G. Merceron).

Upper and lower molars are often used in dental microwear studies, especially when using fossil specimens, to ensure sufficient sample sizes. Recent experiments (Ramdarshan *et al.*, 2017; Ackermans, Winkler, *et al.*, 2020) have shown that values from all permanent molars (M1 to M3) of the same dentition (upper or lower) are statistically similar, suggesting that they can be combined together in statistical analysis. However, Ramdarshan *et al.* (2017) suggested that the combination of values from upper and lower dentitions should only be used for specific facets. The mesio-lingual facet of the paracone, and the disto-labial facet of the protoconid are traditionally used in dental microwear studies (Semprebon *et al.*, 2004; Merceron *et al.*, 2012; Scott, 2012; Rivals *et al.*, 2015) as these were thought to share similar microwear patterns because they occlude during shearing mechanisms (also called "phase I" shearing processes by Janis, 1979, 1990 - as opposed to "phase II" grinding mechanisms). However, Ramdarshan *et al.* (2017) observed significant differences in microwear textures between these two facets, suggesting that these facets should not be combined in statistical

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[3] Republished with permission of Walter de Gruyter and Company, Scott, J. R. (2012). Dental microwear texture analysis of extant African Bovidae. Mammalia 76 (2012): 157–174 © 2012 by Walter de Gruyter • Berlin • Boston; permission conveyed through Copyright Clearance Center, Inc.

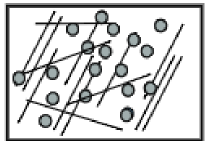
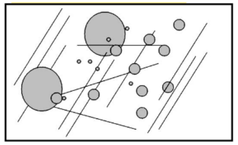
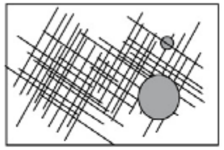
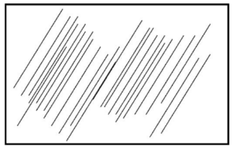
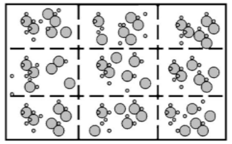
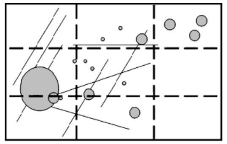
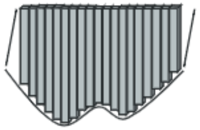
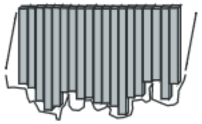
analyses. Nevertheless, they also demonstrated that the disto-labial facet of the protoconid and the mesio-lingual facet of the protocone share similar microwear patterns, which allow statistical analyses to be performed on these facets altogether (Figure 15). The mesio-lingual facet of the paracone can also be used in analyses but must be plotted separately from the protocone and protoconid facets, due to the microwear texture differences mentioned above.

While various equipment have been used to acquire dental microwear data from moulds or casts, confocal microscopy has been used predominantly in the most recent studies (Calandra and Merceron, 2016), and was used as well in the present project. Four adjacent scans are produced per facet, to be subsequently digitally levelled and cleaned of artefacts such as dust or glue residues (Scott *et al.*, 2006; Calandra and Merceron, 2016). A data point cloud is then generated and analysed with the Toothfrax (Surfact) and SFrax software programs designed for scale-sensitive fractal analysis (SSFA). These analyses allow to characterize changes in surface texture at differing scales through different textural parameters (Scott *et al.* 2006).

2.4.2.3 Textural parameters

Several ecologically significant textural parameters have been identified in previous studies and were shown to be reflective of animals' feeding patterns (e.g. Merceron *et al.,* 2012; Scott, 2012; Rivals *et al.,* 2015): complexity (area scale of fractal complexity - Asfc), heterogeneity of complexity (heterogeneity of the area scale of fractal complexity - HAsfc), and textural fill volume (Tfv). These parameters and their ecological significance are described in Table 3 (see appendix A.3 for more detail).

Table 7: Value-ranges and interpretations for each variable, and associated dietary categories, based on published literature.

Variable	Description	Values			Additional information	Sources
		Low	Mid-range	High		
Asfc	**Surface roughness at a given scale**. Complex wear fabrics appear to be consistent with high bite forces used to fracture hard objects (hard vs tough foods).	 **Consumption of tough and abrasive foods** (e.g. monocots, grass blades) (e.g. obligate grazers, variable grazers)	Browser-grazer intermediates, generalists	 **Consumption of hard items like seeds** (e.g. fruit-browsers, browsers)	Grazers foraging tough and abrasive monocots display high anisotropy coupled with low complexity and less dispersion in dental microwear textural parameters.	Scott 2012, Scott 2006, Ramdarshan et al. 2016, Berlioz et al. 2017, Teaford and Runestad 1992
epLsar	**Directionality of microwear**: As striations have a greater coincidence of orientation, epLsar increases: related to the **directionality of jaw movements** during mastication. These are **related to food properties (hard vs tough foods)**.	 **Scratches in opposite directions, potentially coupled with pits of varying size** (e.g. browsers and fruit-browsers, browser-grazer intermediates, generalists) = **hard/brittle food items** require more chewing force and a crushing mechanism	Variable grazers	 **Surfaces that feature parallel scratches** (e.g. obligate grazers) = **tough and abrasive foods** (e.g. monocots, grass blades)	Among the mixed feeding taxa, browser-grazer intermediates had higher values than generalists and variable grazers.	
Hasfc	**Degree of within-facet variation in microwear across different scales:** potentially related to factors such as the size and variability in wear-causing particles. **Likely related to the degree of variation in diet.**	 **Monotypic diet - low diet diversity** (e.g. obligate grazers, variable grazers)	Fruit-browsers, browser-grazer intermediates, generalists	 **Polytypic diet - high diet diversity** (e.g. browsers)	Among mixed feeders, browser-grazer intermediates and frugivores have higher values than variable grazers and generalists.	
Tfv	**Volume of square cuboids at a given scale that can fill a surface.** Greater for surfaces with larger, deeper, and more symmetrical areas of wear (i.e., heavily pitted surfaces) as more filling elements are likely to fit in such areas. Smaller seed size can also results in higher Tfv values.	 **Diet involving smaller particles or relatively soft foods, causing relatively shallow scratches and/or pit**s (e.g. obligate grazers)	Variable grazers, browser-grazer intermediates	 **Surfaces dominated by large pits or deep scratches** (e.g. fruit-browsers, then browsers, generalists) = **browse create deeper pits (hard items)**	Among the mixed feeding taxa, generalists had higher values for fi ll volume than browser-grazer intermediates.	

2.4.2.4 Strengths and limitations of the DMTA method

Similarly to the mesowear method, one of the main strengths of dental microwear analysis is to be relatively taxon-independent because dental wear relates directly to the food items ingested. Furthermore, the use of an automated three-dimensional technique allows to reduce inter-observer error and improve both accuracy and comparability of microwear studies when similar equipment and variables are used (Arman *et al.*, 2016), which is why this method was selected for the present study, in complement to mesowear analysis.

Dental microwear textural analysis can provide information on individual feeding behaviour based on the physical properties of the food items (abrasiveness, toughness, grain size) in greater detail and on a different temporal scale than mesowear analysis, and therefore can be used to evaluate variation in dietary behaviours within and between populations of a species, as well as seasonal and temporal changes in feeding ecology at the species, taxa or palaeo-community-level (e.g. Rivals and Solounias, 2007; Merceron *et al.,* 2010, 2014; Rivals *et al.,* 2015; Bignon-lau *et al.,* 2017; Berlioz *et al.,* 2018). However, because microwear reflects diet on short time scale, typical diets can be misrepresented if the populations sampled are not sufficiently representative, and if the species studied tends to change their diet seasonally or regionally (Kay and Covert, 1983; Rivals *et al.*, 2010). As suggested by Green and Croft (2018), this issue can be minimized by pooling individuals from limited spatial and temporal intervals (e.g. from the same geographic regions, geological formations, or members), but also by combining use-wear analyses with intra-tooth stable isotope studies to confirm seasonal variations in diet in the studied taxa

Other studies also investigated the potential biases related to DMTA, especially regarding the importance of exogenous particles (i.e. dust and grit) as a factor impacting enamel-loss and texture alteration during food processing. The impact of dust and grit on microwear patterns can be particularly relevant when studying species that feed at low-ground level and might therefore ingest a significant amount of exogeneous particles, more particularly in open-habitats with strong winds depositing a significant amount of aeolian dust on the vegetation (Schubert *et al.*, 2006; Sewell, 2019). While in vivo experiments conducted by Hoffman *et al.* (2015) suggested that increasing grain size of grit significantly increases the size of microscopic pits on the enamel surface, Ungar *et al.* (2016) and Merceron *et al.* (2016) demonstrated that dental microwear textures reflect predominantly dietary preferences and are only minimally impacted by grit load. A recent feeding experiment showed diets containing small external abrasives tend to generate a polishing effect on the enamel surface, while diets with external abrasives of increasing size tend to increase enamel surface roughness (Ackermans, Martin, *et al.*, 2020). *In vitro* experiments by Hua *et al.* (2020) highlighted the complexity of the relationship between microwear, food properties and exogenous particles by demonstrating that the effect of exogeneous grit on microwear texture is dependent of the material properties of the food items to which grit is adhering. More experiments are therefore still needed to fully understand the complex interactions between teeth, food, and grit. Overall, current knowledge suggests that dental microwear textural analysis can provide detailed information on feeding behaviours and that exogeneous particles only tend to significantly cloud the dietary signal by polishing dental facets when the dust particles ingested are particularly fine, which may be relevant to identify open, windswept habitats or potential aeolian dust fluctuations through time (Sewell, 2019; Ackermans, Winkler, *et al.*, 2020).

2.4.3 Stable isotope analyses

2.4.3.1 General principles

Tissues such as enamel or bone can provide valuable information on past environments through the study of stable isotopes. Through the air they breathe, the food they eat and the water they drink, living organisms integrate into their hard tissues the isotopic signature of their environment with known or predictable fractionations (Higgins, 2018). Because the isotopic composition of these elements of their environment are themselves influenced by climate and regional topography, studying the biochemistry of fossil animal remains can inform on palaeo-environmental conditions (Pollard and Heron, 2013). Isotopic ratios can be measured using mass spectrometry to separate the different isotopes based on their mass-to-charge ratio.

Stable carbon isotopes can be used to understand the composition of ancient animals' diets and, in turn, palaeo-habitats, as carbon is incorporated into biominerals through food consumption (Higgins, 2018). When studying herbivores, carbon isotopes can help distinguish between two major types of carbon fixation in plants (C_3- and C_4-pathways) and evaluate the relative proportion of plants of each type contained in the diet of the studied individual. Although the relationship between oxygen and the environments of the animals is complex, stable oxygen isotopes have been shown to relate to precipitation, humidity, and temperature, as oxygen is primarily integrated into bodily tissues through the meteoric water drunk by the studied specimens (Higgins, 2018). Carbon and oxygen isotopes are often studied together for dietary reconstructions as they are directly related to the type of plants and the water ingested by individuals. As demonstrated by, for instance, Hopley *et al.* (2006) and Louys *et al.* (2012), combining stable carbon and oxygen isotopic studies of tooth enamel with dental use-wear analyses can provide more details on past diets than when these two techniques are used separately. This approach was therefore chosen for this study.

2.4.3.1.1 Stable isotopes and dental enamel

Isotopic studies on bone collagen are often used in archaeology to study the average diet of an individual over the first years of its life. However, because collagen is generally not preserved in the Plio-Pleistocene palaeontogical record, isotopic studies are usually carried on dental remains when studying fossil deposits (Pollard and Heron, 2013).

Enamel is composed of densely packed and relatively large hydroxyapatite crystals ($Ca_{10}(PO_4)_6(OH)_2$), which results in a high mineral content (Hillson 1996). The oxygen isotopic composition of biological apatite can be measured by targeting the oxygen derived from the carbonate group (CO_2^{3-}), from the phosphates (PO_4^{3-}) or from all oxygen-containing groups of the sample (carbonate, phosphate and hydroxyl groups) via laser-ablation. Carbon isotopic composition can be measured from the carbonate apatite present in teeth (Lee-Thorp, Manning and Sponheimer, 1997; Pollard and Heron, 2013).

Permanent teeth start forming before and during early life and remain unaltered once erupted and fully-mineralised. This absence of remodelling ensures that the isotopic composition of the dental material represents dietary trends over the first months/years of life, before the tooth is fully-formed (Pollard and Heron, 2013; Green *et al.*, 2018). The isotopic signature is established in a tooth when it mineralizes (amelogenesis), and tooth enamel has been shown to be highly resistant to isotopic alteration compared to dentine and bone due to its inner structure (Lee-Thorp and van der Merwe, 1991).

2.4.3.1.2 Carbon stable isotopes

Because plants can be divided into three different isotopic groups based on their photosynthetic pathway, carbon isotopes can be used to study the relative composition of different types of vegetation in ancient environments (Smith and Epstein, 1971; Vogel, 1978; O'Leary, 1981; Higgins, 2018).

2.4.3.1.2.1 Plant photosynthetic pathways

Most plants follow the C_3 -pathway, where CO_2 is converted to 3-phosphogylycerate, an organic compound containing three carbon atoms. C_3 -plants thrive in areas with moderate sunlight intensity, moderate temperatures, and sufficient groundwater, and are found more abundantly at high latitudes and high elevation (Edwards *et al.*, 2010). Typical C_3-plants are, for example, cool-season grasses, trees, and shrubs.

The C_4 -photosynthetic pathway fixes carbon more efficiently during photosynthesis via the use of a solar-powered biochemical cycle, which allows C_4 -plants to tolerate higher temperatures, drier conditions and lower atmospheric CO_2 levels (Edwards *et al.*, 2010). The $\delta^{13}C$ value of these plants is therefore higher than that of C_3 -plants. As this system requires more energy, C_4 -plants tend to be outcompeted by C_3 -plants at lower temperatures and higher CO_2 levels (Ehleringer and Dawson, 1992; Ehleringer, Cerling and Helliker, 1997; Hopley, Latham and Marshall, 2006; Edwards *et al.*, 2010; Quirk *et al.*, 2019). Among C_4 -plants are typically found tropical grasses, rare shrubs, maize, cane sugar, certain millets, chenopods, sorghums and amaranths. Today, grasses using the C_4 -photosynthetic pathway dominate savanna ecosystems, following a reported period of C_4 -grassland expansion during the late Miocene and Early Pliocene (~8-4 Ma) (Osborne, 2008).

The third known metabolic pathway is the Crassulean Acid Metabolism (CAM), found in very arid environments only and unique to succulents. This pathway relies on collecting carbon dioxide at night and reducing evapo-transpiration during the day by keeping the pores of the plant closed. This improves the plants' photosynthetic performance in water and/or CO_2 deprived environments. Typical CAM-plants are cacti, many orchids and bromeliads in the tropical rainforest, as well as some aquatic angiosperms (Pollard and Heron, 2008).

2.4.3.1.2.1 Assessing diet composition from body tissues

Carbon stable isotopes in body tissues of herbivores reflect the relative proportion of leaves and grasses that were integrated in their diet, as the carbon isotopic compositions of the plans are assimilated through ingestion, with an additional fractionation process (Lee-Thorp and Van der Merwe, 1987; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Passey *et al.*, 2005) (Figure 16).

Previous studies have demonstrated that pure browsers (C_3 consumers) have $\delta^{13}C$ values which differ significantly from those of pure grazers (C_4 consumers), and that these values can vary depending on the canopy cover (e.g. Lee-Thorp *et al.,* 2007; Louys *et al.,* 2012). For instance, it has been reported that C_3 -plants have $\delta^{13}C$ values ranging from -32‰ in closed understorey canopy conditions to -21‰ in more open environments, while C_4 -plants can range from -21‰ to -9‰ (Cerling and Harris, 1999; Roberts *et al.*, 2017). $\delta^{13}C$ values of C_3 -plants in arid environments are usually slightly higher than those living under more humid conditions (Ehleringer and Dawson, 1992). Because atmospheric CO_2 levels directly influence the photosynthetic pathways of terrestrial vegetation, the $\delta^{13}C$ values of plants reflect the $\delta^{13}C$ values of atmospheric CO_2 at a given time. Past changes in the $\delta^{13}C$ values of atmospheric CO_2 in turn indicate past changes in global air temperatures and mean annual precipitation.

Similarly, previous studies have suggested that variation in $\delta^{13}C$ values can be observed among C_4 -plants depending on the enzyme (i.e. nicotinamide adenine dinucleotide phosphate-malic enzyme - NADP-ME; phosphoenolpyruvate carboxykinase – PEPCK/PCK; or nicotinamide adenine dinucleotide-malic enzyme - NAD-ME) used during photosynthesis for the decarboxylation of the C_4 acids (Hattersley, 1982; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Ehleringer, 2005; Codron *et al.*, 2005; Cerling *et al.*, 2015; Cacefo *et al.*, 2019). Plant taxa using the NADP-ME sub-pathway are mesic grasses (i.e. adapted to more humid environments), and have an average $\delta^{13}C$ value of −11.8 ± 0.2‰ (Hattersley, 1982; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Ehleringer, 2005; Segalen, Lee-

Thorp and Cerling, 2007; Levin *et al.*, 2008) (see Figure 16). Xeric savannas and bushlands (i.e. ecoregions where evaporation exceeds rainfall, with arid-adapted C_4 -grasses) are dominated by plants using the NAD-ME and PCK sub-pathways, with average $\delta^{13}C$ values of -12.4 to -13.4‰ for NAD-ME grasses. PCK plants have average $\delta^{13}C$ values that are intermediate between values for NAD-ME and NADP-ME plants and are most abundant in areas with intermediate rainfall. It therefore appears that C_4 grasses using the NADP-me sub-pathway are systematically enriched in ^{13}C by ~ 1-2 ‰ compared to those using the NAD-ME or the PCK sub-pathways (Hattersley, 1982). While such small differences might be difficult to statistically identify in most datasets, it is important to consider that slight variations in $\delta^{13}C$ values observed between enamel samples might, when dealing with values typical of C_4 -vegetation, reflect the consumption of C_4 -plants using differing photosynthetic sub-pathways.

However, because the vegetation structure of a given region is shaped by a combination of factors, such as climatic and environmental conditions, hydrological factors, geology, topography, altitude, and soil matrix, and because of the complexity of the C_3/C_4 photosynthetic pathways highlighted above, caution must be applied when comparing modern datasets from different regions of Africa. More particularly, while modern datasets are often from eastern or southern Africa, these two regions are characterised by very different landscapes, mainly due to different latitude and tectonic activity, resulting in differing climates, annual rainfall, landscape dynamics, soils properties, and seasonal patterns of climate and vegetation. All of these differences have an impact on regional vegetation composition and structure, and on the geochemical properties of regional plants. For instance, C_3-plants, have been reported to yield significant variation in $\delta^{13}C$, especially in hyper-arid areas or in closed-canopy forests (Ehleringer and Cooper, 1988; Van der Merwe, 1989; Cerling *et al.*, 2003). Such environmentally-driven variations in the isotopic composition of C_4-and C_3-plants can introduce errors when interpreting isotopic data from herbivore species from these two regions, since observed differences in $\delta^{13}C$ might not only be due to differing diets, but also to differing vegetation types under very different environmental conditions (Sponheimer, Lee-Thorp, *et al.*, 2003).

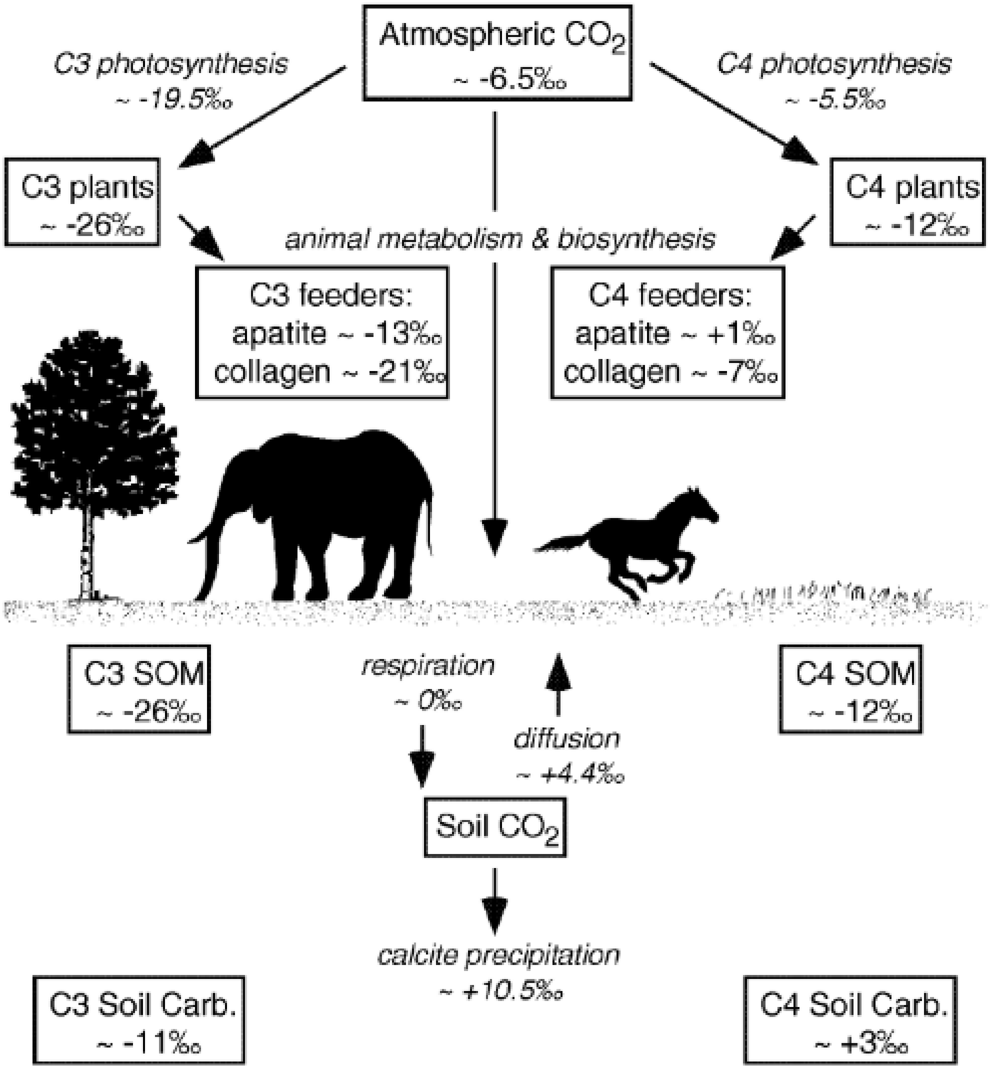


Figure 17: Carbon isotope cycle for carbon-bearing materials in continental ecosystems, from atmospheric CO_2 values (pre-industrial values) to soil carbonate values. The fractionation processes are indicated in italics (from Koch (2002), p.583).[4]

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[4] Republished with permission of Annual Reviews, Inc., from Koch, P. L., 2002. Isotopic Reconstruction of Past Continental Environments. Annual Review of Earth and Planetary Sciences, 26 (1), 573–613; permission conveyed through Copyright Clearance Center, Inc.

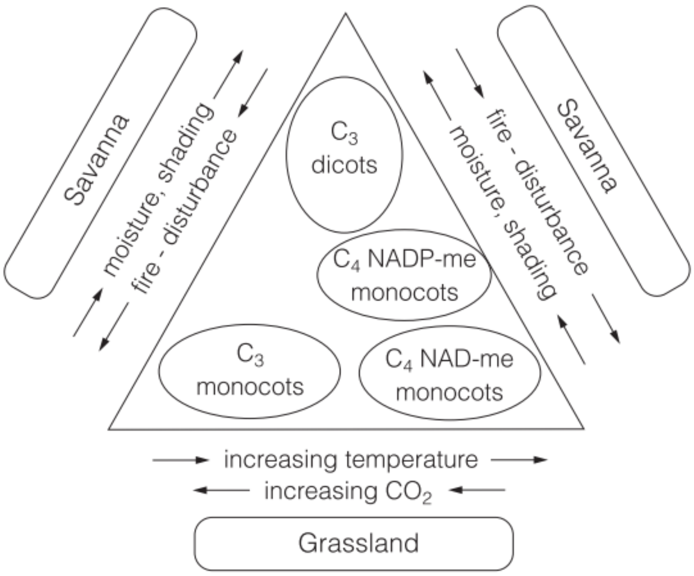

Figure 18: Climatic and non-climatic drivers of change in C_3 - C_4 ecosystems, with environmental and ecological factors that influence shifts in the abundances of the main plant types found within grassland and savanna ecosystems (from Ehleringer 2005, p.228 [5]).

2.4.3.1.2 Oxygen stable isotopes

Oxygen stable isotope ratios ($\delta^{18}O$) can serve as palaeo-climate indicators by quantifying the relative amount of oxygen isotope ^{18}O and oxygen isotope ^{16}O present in a sample. This calculation is based on the difference in weight between ^{18}O and ^{16}O: as ^{18}O has two more neutrons, it is heavier than ^{16}O which will induce a different reaction during physico-chemical processes. For example, ^{18}O will evaporate less easily, as it requires more energy than for ^{16}O. For that reason, clouds tend to be richer in $H_2{}^{16}O$ as isotopic fractionation will tend to favour the lighter isotope. On the contrary, condensation (hence rain) will be richer in $H_2{}^{18}O$, as well as oceans. If a sample is rich in ^{18}O, the $\delta^{18}O$ will be high relative to SMOW (Standard Mean Ocean Water).

The oxygen isotope composition ($\delta^{18}O$ values) of mammalian body tissue is directly related to the composition of ingested water. Enamel bioapatite contains two ionic forms of oxygen

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that can be used for isotopic analyses: structural carbonate (CO_3^{2-}) and phosphate (PO_4^{3-}), the latter being the most abundant in these tissues. Their oxygen isotope composition (respectively $\delta^{18}Oc$ and $\delta^{18}Op$ values) can be related to body water oxygen, which is itself related to the composition of ingested water at a constant body temperature (Longinelli, 1984; Luz, Kolodny and Horowitz, 1984; Iacumin *et al.*, 1996; Koch, 2002; Chenery *et al.*, 2012). The composition of ingested water can reflect, in turn, the oxygen composition of local meteoric water (Daniel Bryant and Froelich, 1995; Chenery *et al.*, 2012) or can be modified by evaporative processes (Kohn, 1996). The $\delta^{18}O$ values of meteoric water are believed to vary due to changes in air temperature, humidity and precipitation/evaporation balance within an ecosystem (McCrea, 1950; Dansgaard, 1964; Schmidt, LeGrande and Hoffmann, 2007).

As $\delta^{18}O$ reflects local evaporation and meteoric water composition through precipitation, it can be used to analyse climate changes as experienced by local species during a specific time period. Water-dependent animals usually have $\delta^{18}O$ values closely correlated with that of local precipitation (Bernard *et al.*, 2009). Oxygen isotope analysis of herbivore tooth enamel can therefore help reconstruct past air temperatures based on interdependent relationships between the $\delta^{18}O$ of apatite phosphate, body fluids, meteoric water and air temperatures (Bernard *et al.,* 2009).

However, temperature can be difficult to interpret from oxygen isotopes. As local temperature varies with season, latitude, and altitude, more positive oxygen values can represent either warmer or colder temperatures (Higgins, 2018). For large water-dependant terrestrial mammals, more positive values generally indicate warmer temperatures due to evaporation (Kohn, Schoeninger and Valley, 1998; Higgins and MacFadden, 2004). However, additional processes can complicate the interpretation of oxygen data in mammal teeth, such as the 'Amount Effect' highlighted by Higgins and MacFadden (2004) which is characterised by episodes of heavy rain occurring at high temperatures (>20°C) that can cause a depression in the oxygen isotopic curves mimicking winter-time cool temperatures.

Aridity (i.e. lack of precipitation in an area) can also be studied from stable oxygen isotopes by evaluating the difference (in mm/year) between water lost to the environment (through evaporation or transpiration) and the water gained through precipitation in a specific area (Higgins, 2018). In arid environments where more water evaporates compared to the amount of rainfall deceived, the δ^{18}O values of the remaining water tend to decrease relative to the original source water (i.e. rain). This process allows to estimate aridity in a studied area by comparing the δ^{18}O value of precipitations with that of local waters that have experienced evaporation (Blumenthal *et al.*, 2017). However, as the isotopic composition of rainwater and meteoric water cannot be studied directly from the fossil record, methods were developed to estimate aridity based on the oxygen composition of past living organisms depending on their sensitivity to evaporation.

According to Levin *et al.* (2006), the δ^{18}O enamel values of evaporation-sensitive (ES) animals reflect evaporative isotope enrichment with respect to source water (which increases with aridity, as food-water is sensitive to evaporation), whereas the enamel δ^{18}O values of evaporation-insensitive (EI) animals track local meteoric water δ^{18}O values. Because evaporation enriches the remaining water in the heavy isotope ^{18}O relative to source water, aridity can be evaluated by comparing one isotopic record that tracks meteoric water (EI taxa) with another that tracks evaporative enrichment (ES taxa). The relative enrichment between δ^{18}Oenamel values from ES and EI animals (εES–EI) is therefore believed to represent the degree of ^{18}O enrichment between leaf or body water and meteoric water, which increases with aridity. However, the use of this 'aridity index' remains limited to fossil species whose extant relatives are known to be either evaporation-sensitive (e.g. giraffids, tragelaphines, and hippotragines) or evaporation-insensitive (e.g. hippopotamids, elephantids, and rhinocerotids) (Blumenthal *et al.*, 2017). As it remains difficult to assess whether modern impala and modern springbok could be safely considered as either evaporation-insensitive or evaporation-sensitive taxa, this approach is not used in the present study.

2.4.3.2 Data acquisition

2.4.3.2.1 Sampling methods

To perform stable isotope analysis from fossil enamel, samples of powdered enamel are collected (at least 10 mg) using a slow-speed drill with dental burrs, after cleaning the specimen from dirt or other residues that could contaminate the sample (Higgins, 2018).

Bulk samples can be collected to obtain average isotopic values for the specimens by drilling a line perpendicular to the growth lines (if visible) along the length of the teeth. Serial samples (also called intra-tooth) can be collected by drilling multiple lines parallel to the dental growth lines to study the isotopic signals in more details and reconstruct part of the life history of the specimens and investigate, for instance, seasonal variations in isotopic composition.

2.4.3.2.2 Tooth selected

The choice of teeth used for isotopic sampling must be adapted to the purpose of the measurements and must be uniform for the ensemble of the dataset where possible. Since the isotopic signature of enamel is established once amelogenesis is over and does not change due to very little turnover in tooth composition, the stable isotope rates measured only reflect the individual's diet during the duration of crown formation. The main factor to take into account is the chronology of dental development in the taxon under study to ensure that the samples represent post-weaning diet, and that they span the longest time period possible if seasonal trends are to be measured through serial sampling.

For instance, the exact chronology of dental development for modern impala (*Aepyceros melampus*), which is relevant to the present study, has not been described specifically for this species, but the dental development of cattle and sheep have been studied in detail and can be used as proxies to guide the choice of teeth to sample (Brown *et al.*, 1960) (see table_A 4 in appendix A.4). More detail on the dental development of modern springbok (*Antidorcas* *marsupialis*) has been published and show a similar crown-development pattern, although spread over a shorter time period (i.e. crown formation taking place before birth and until ~ 1-year-old) (see table_A 5 in appendix A.4).

According to Copeland *et al.* (2009), fourth premolar (P4) and third molars (M3) should be chosen primarily for sampling as these teeth form after weaning, but their study on modern impalas showed that there is little statistical difference between the isotopic signals yielded by these teeth when compared to first molars (M1) which form before weaning. However, as previous studies (Lee-Thorp, Manning and Sponheimer, 1997; Hobson and Sease, 1998; Wright and Schwarcz, 1998; Balasse, 2002) have suggested that teeth formed prior to weaning may yield biased isotopic results due to the suckling-signal (more negative $\delta^{13}C$ values), it might be more cautious to avoid sampling first molars when the dataset allows. Since second and third molars (M2 and M3) require about one year each for the crown to develop, these teeth are more likely to provide a representative isotopic sample of the individual's diet over different seasons than P4 (whose crown develops over 6 months only) or M1 (which develops mainly *in utero* and before weaning). M2 and M3 should therefore be targeted primarily for bulk sampling, as impalas are weaned by age 4.5 months (Copeland *et al.,* 2009).

As the crown formation time of the posterior teeth overlaps, serial sampling should be conducted primarily on M2 combined with either M3 or P4 in order to reconstruct a sequence spreading from minimum 1 month up to 2 years.

2.4.3.2.3 Mass spectrometry

Pre-treatment procedures can be used prior to analysis to remove all traces of organic matter still present in the teeth and to avoid potential contamination of the samples (Wiedemann-Bidlack, Colman and Fogel, 2008). Mass spectrometers are then used to measure the abundance of specific isotopes in the samples by using atomic mass (Higgins, 2018).

Mass spectrometry is based on ionization and fragmentation of sample molecules in the gas phase. Because molecules fragment in a unique manner, the resulting ion fragmentation pattern can be used to obtain structural information on a given molecule. To analyse enamel samples and determine their isotopic composition, the enamel molecules must therefore be converted to a gas (carbon dioxide) by reacting the powdered sample with pure phosphoric acid (Higgins, 2018). The carbon dioxide produced can then be analysed for heavy carbon and heavy oxygen using electric and magnetic fields to measure the mass of the charged particles (see Higgins, 2018 for more detail). This generates raw data that can then be normalized to international reference scales by using standards (i.e. samples of known delta value analysed alongside samples of unknown delta value) calibrated to scales commonly used in research for carbonates: V-PDB (for carbon and oxygen) and V-SMOW (for oxygen only) (Higgins, 2018).

2.4.3.3 Strengths and limitations of isotopic studies on dental enamel

2.4.3.3.1 Discontinuous enamel mineralisation

While some studies have shown that enamel mineralization tend to occur from the tip of the tooth toward the root (Passey *et al.*, 2002), other authors (Balasse, 2002; Zazzo, Balasse and Patterson, 2006; Reade *et al.*, 2015; Green *et al.*, 2018) have demonstrated that enamel mineralisation is progressive and discontinuous, as it takes place in two stages. The first stage involves the completion of a protein-rich matrix which gradually mineralizes. The second stage is maturation, where mineralisation occurs through the enamel in different directions and through different thicknesses along the matrix. Because of this discontinuous pattern of enamel mineralisation, results from isotopic analysis can be biased due to time-averaged samples where small changes in dietary behaviour or associated environment might not be detected. One way to reduce the influence of this caveat on the results from isotopic analysis is to sample the entire depth of the enamel and the entire length of the tooth (Reade *et al.* 2015).

2.4.3.3.2 Contamination

Risks of contamination from organic matter and sediment carbonate must be considered when working on isotopic signatures from ancient material. Work done by Schoeninger *et al.* (2003) has demonstrated that fossil enamel can be chemically altered depending on the archaeological layer in which it was found, potentially altered by surrounding sediments. This is what that study observed for instance at the site of Allia Bay, Kenya (~ 3.9 Ma), where the original apatite had been contaminated by silica-bearing minerals. One way to take into account possible contamination from surrounding environments is to sample sediments that might be still present on the remains and test their isotopic signature (e.g. Lee-Thorp and Sponheimer, 2003).

Another way to reduce the risks of isotopic contamination of archaeological samples is through the use of enamel phosphates, rather than structural carbonates. Structural carbonates are often used predominantly to measure $\delta^{18}O$ in enamel bioapatite, due to easier and cheaper analytic processes required than when analysing enamel oxygen phosphates ($\delta^{18}Op$) (see methods described in Chenery *et al.,* 2012 for more detail). However, it has been suggested that the structural carbonate ion is more susceptible to diagenetic alteration due to weak C-O bonds (Lee-Thorp, 2002). Furthermore, the relationship between $\delta^{18}O$ of structural carbonate ($\delta^{18}Oc$) and $\delta^{18}O$ of drinking water ($\delta^{18}Odw$) is poorly understood, because $\delta^{18}Oc$ values need first to be converted into $\delta^{18}Op$ values to be interpreted. On the contrary, phosphate is abundant in tooth enamel, has a strong P-O bond which is able to resist chemical alteration (Sharp, Atudorei and Furrer, 2000), and the relationship between $\delta^{18}Op$ values in bioapatite and $\delta^{18}Odw$ is well established for some animal species, such *as Equus quagga* or *Bos Taurus* (Bryant and Froelich, 1995; Chenery *et al.,* 2012). Although analysing enamel phosphates could present a potential solution to check for sample diagenetic contamination of oxygen isotope ratios, it remains, as mentioned above, more expensive and time-consuming, and uses more enamel than when analysing enamel structural carbonates, which are substantial limitations when large numbers of samples are involved in a study.

Other studies have explored in detail contamination in carbon isotopes. Lee-Thorp (2002) explored the effect of diagenesis on the preservation of biogenic carbon isotopic signals using bone and tooth materials from series of fauna with predictable diets, from sites with isotopically different depositional contexts and ages. Observations from South African sites ranging between about 3 Ma and 1.5 Ka BP suggest evidence for isotopic alteration in older deposits, increasing with age, more pronounced in bone apatite samples. This study concluded that using carbon isotope analysis of enamel was feasible, but advised to determine the isotopic values of the end-members of the dietary spectrum, using obligate browsers and grazers to estimate how much their carbon values deviate from their modern counterparts (while taking into account of the "fossil-fuel effect" on modern values). This approach has been used for example by Bocherens *et al.* (2011) in their study of late Pleistocene fauna from Malawi, where they observed a clear difference in carbon and oxygen isotopic values in the enamel carbonate signatures of obligate browsers and grazers, but did not observe such clear patterns in their bone and dentine samples, which appeared to have been affected by diagenetic alteration. This approach is also used in the present study to evaluate the degree of potential diagenetic alteration in carbon stable isotopes.

2.4.3.3.3 Strengths of isotopic studies

Regardless of the various caveats highlighted previously, stable isotopes of carbon and oxygen in fossil teeth have been widely used for palaeo-environmental reconstructions because they can offer an excellent record of past habitats and past climatic conditions, granted that the inferred dietary behaviours of the studied assemblages can be trusted as faithful reflectors of prevailing vegetation conditions.

Since tooth enamel is heavily mineralized with little porosity, it is more likely to survive fossilization with minimal alteration of the original isotopic signal than other fossil materials such as bone (Higgins, 2018). Because the relationships between the isotopic composition of animals' body tissues and their direct environment have been studied in modern populations, strong scientific knowledge has been acquired over the years on these relationships as well as on the influence of diagenesis on the integrity of isotopic signals measured from fossil remains. This strong knowledge provides tools to extrapolate these known relationships into the past and help reconstruct palaeo-ecological conditions from faunal remains.

One of the greatest asset of stable carbon and oxygen isotope analyses is to be able to provide information that cannot be obtained using dental use-wear analyses, such as information on drinking behaviours, palaeo-temperatures, and the relative proportions of C_3 - C_4 vegetation included in the diet of extinct animals. This is why this approach was selected in the present study, alongside dental use-wear analyses.

Furthermore, serial sampling can provide a record of isotopic variation over time (Fricke and O'Neil, 1996; Sharp and Cerling, 1998; Reade *et al.*, 2015) that can be studied to investigate ancient seasonality. Studying seasonal changes in temperature and available foods is crucial to the understanding of past biodiversity (Bernard *et al.*, 2009). It has been hypothesised in previous studies that seasonal and interannual rainfall variability in eastern Africa increased at ~2.0 Ma in response to the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.*, 2004; Blumenthal *et al.*, 2017; Hopley *et al.*, 2018), but climate proxy records of seasonal resolution are rare. To investigate this hypothesis further, one part of this project focuses on intra-tooth carbon and oxygen isotope evidence from fossil impala specimens in the Shungura Formation (*Aepyceros shungurae*). Bulk carbon isotope measurements of *A. shungurae* from Shungura have been reported by Negash *et al.* (2015) and range from -8.0 ‰ to +2.5 ‰ (indicating a highly flexible dietary intake), with distinct differences in median and range between each of the six Shungura members. The drinking habits of *Aepyceros shungurae* are currently unknown, but comparison of the intra-tooth $\delta^{18}O$ data with modern and fossil relatives should aid interpretation of $\delta^{18}O$ as a proxy for standing water $\delta^{18}O$ and/or leaf-water $\delta^{18}O$ (Souron, Balasse and Boisserie, 2012; Blumenthal, 2015) and should be directly comparable to climate model simulations of $\delta^{18}O$ in Pliocene rainfall (e.g. Tindall and Haywood, 2015). This project expands the *A. shungurae* dataset by analysing the intra-tooth (seasonal) variation in $\delta^{18}O$ and $\delta^{13}C$ of this species to investigate dietary and ecological change during the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.,* 2004).

2.4.4 Land cover analysis: from habitats to the diet

2.4.4.1 General principles

Remote sensing is the science of detecting the physical characteristics of an area or an object by measuring its reflected and/or emitted electromagnetic radiation at a distance, using sensor technologies typically based on satellites or aircrafts. Because most objects in nature emit electromagnetic radiation as well as reflect radiation from other objects, emitted or reflected radiation can be studied via sensors to understand its behaviours as it passes through the atmosphere and interacts with objects (Campbell and Wynne, 2011). These behaviours will differ depending on the characteristics of the material emitting and reflecting radiation (e.g. vegetation, soils, rocks, water), and will be detected in different ways along the electromagnetic spectrum. Similarly, different types of vegetation will have different spectral signatures, allowing to differentiate certain classes of vegetation from one another, and to identify areas of healthy or stressed vegetation (Campbell and Wynne, 2011). Remote sensing techniques can allow scientists to explore different aspects of modern habitats on different scales, including shelter, shade and forage characteristics (van Bommel *et al.*, 2006). For instance, forage quality can be studied using indices such as the Normalised Difference Vegetation Index (NDVI), based on chlorophyll levels and vertical thickness of the vegetation, which can be detected through the radiation reflected by the biome, observable in optical spectral bands detected by Earth observation sensors.

Remote sensing data have been previously used in many disciplines, including ecology (e.g. Cohen and Goward 2004, van Bommel *et al.* 2005, Estes *et al.* 2008, Winnie Jr. *et al.* 2008, Nagendra *et al.* 2013) and archaeology (Wiseman and El-Baz, 2007; Parcak, 2009; Bailey, Reynolds and King, 2011; Lasaponara and Masini, 2012; Comer and Harrower, 2013). For instance, remote sensing proved to be useful to map with greater detail the geological units over the east side of Lake Turkana, and better understand its relation to the Omo River (Bruhn *et al.*, 2011). It has also been widely utilised in landscape ecology to help with spatial pattern description and land-cover mapping, and can provide useful insight into landscape structure and function if combined with ecological field data (Newton *et al.*, 2009). It has been used for example by van Bommel *et al.* (2006) to study the spatial and temporal habitat use of impalas in Botswana, by relating remotely sensed vegetation patterns to impala habitat preferences.

2.4.4.2 Data acquisition

2.4.4.2.1 Sensors and resolution

Depending on the purpose of the study, different types of remote sensing sensors can be used. The first type of sensors records the solar radiation reflected from the Earth's surface, using mostly energy in the visible and the near infrared parts of the spectrum (i.e. optical data; Campbell and Wynne, 2011). The second type records radiation emitted from the Earth's surface after solar radiation was partially absorbed by the objects and then reradiated as thermal infrared radiation. The last type of remote sensing sensors generates its own energy, which is then recorded when reflected back (back scattered) by objects from the Earth's surface. These are "active" sensors (such as radars and lidars) that are therefore independent of solar and thermal radiation, and are, as a result, effective even at night or despite cloudy cover. The first two types of remote sensing use "passive" sensors which do not generate energy themselves. For this study, land cover products using optical data were used, where different land cover types could be differentiated by their spectral reflectance signatures in the remotely sensed images.

The different types of remote sensing instruments that can be used vary in resolution (spatial, temporal, spectral and radiometric resolutions). It is essential to take this into account when working with remote sensing data, to ensure the right level of detail and the right type of information is provided by the instrument for the purpose of the study. Spectral resolution refers to the ability of a sensor to define fine wavelength intervals: satellite sensors able to detect more narrowly defined spectral regions will be able to differentiate surface materials more easily and in finer detail (Campbell and Wynne, 2011). Radiometric resolution refers to the ability of a sensor to record many levels of brightness and discriminate slight differences in reflected or emitted energy. Spatial resolution refers to the pixel size, and the level of spatial detail that can be perceived on the image (i.e. small objects can be identified on images with high spatial resolution). Finally, temporal resolution refers to the time it takes for the satellite to come back to one position (minutes to days). High temporal resolution is achieved by systems able to repeatedly record the same image sequence at relatively close time-intervals, which is particularly useful for studies of time-series, to explore, for instance, short-term changes in the landscape. High temporal resolution is also ideal for studies on seasonal change, as multiple images are available within each month. Because there is a trade-off between the different types of resolution, one type of sensor cannot provide data with the highest resolution for all resolution types (Campbell and Wynne, 2011). For instance, high spatial resolution (i.e. small pixel size) will require a longer journey of the satellite from pole to pole for global coverage, hence reducing temporal resolution. Similarly, high radiometric resolution implies lower spatial resolution: the bigger the area sampled per pixel, the more energy can be sensed, and fine divisions can be made. For this study, moderate spatial resolution was sought primarily, to be able to perceive enough spatial detail regarding vegetation to be able to discuss vegetation cover heterogeneity at a relatively small scale (i.e. spatial resolution <500 m).

2.4.4.2.2 Image classification

To produce land cover maps, digital image classification must be performed by assigning pixels to classes to form a mosaic of uniform parcels (Campbell and Wynne, 2011). One image classification method is to use “point classifiers”, where each pixel is considered individually and assigned to a spectral class based on its brightness values measured across spectral bands. An alternative method is to use “neighbourhood classifiers”, where groups of pixels are considered together by taking into account neighbouring pixels and using both spectral and textural information to classify the image. Spectral classes can then be assigned to informational classes (by grouping several spectral classes if necessary) that can be used for further analyses, such as land cover mapping.

Supervised classification procedures can be used where areas of known class are defined by the user to guide the classification of the rest of the image by the image processing software (i.e. machine learning) (Campbell and Wynne, 2011). This approach provides the analyst with control over the classification process but can introduce human error and requires prior knowledge of the region studied (such as field observations). Unsupervised classification can also be used where the image processor automatically classifies the image based on natural groups of pixels sharing similar spectral characteristics. While this method reduces the risk of human error and does not require prior knowledge of the studied area, it might generate classes that will be difficult to assign *a posteriori* to informational classes that can be used by the user for further analyses.

Because the various steps required to create land cover maps (i.e. images selection, pre-processing, and classification) are time consuming and necessitate a high level of expertise, land cover products already available for African landscapes were used in this project.

2.4.4.3 Strengths and limitations of land cover analysis applied to herbivore dietary ecology studies

Animal populations are distributed across the landscape in relation to their biological requirements, such as food resources, drinking water, shade and shelter. These features vary spatially and temporally, especially regarding vegetation availability and quality, in turn impacting the distribution of populations (Hutchinson, 1957). To better understand the ecology of animal species, it is therefore essential to explore their habitats, and how changes in these habitats might result in changes in their behaviours, including changes in their dietary patterns. Land cover data can be used to quantify habitat composition, heterogeneity, and structure, and subsequently compare different regions to one another to identify differences and similarities between habitats. However, for land cover data to be relevant to studies aiming to characterise animal dietary behaviours in relation to their environment, several challenges must be overcome.

Firstly, the data acquired to study the dietary behaviours of the studied species must include sufficient sample sizes, as well as sufficient information regarding the populations sampled. While information on population size, age-ranges, sex, and, most importantly, geographic location of the populations' home-range, can be obtained when sampling directly live or recently culled animals for a specific project, it remains a challenge when working from museum collections, as is often the case in palaeontological studies. While museum collections can offer large sample sizes, they often lack specific information on the specimen's origin (Kay and Covert, 1983). Targeting published dietary data with detailed information, or museum specimens associated with detailed collection information (geographic location, sex, age, year – and ideally season – of death) can help overcome this limitation, although it can result in small sample sizes as such detailed collections are usually rather limited (Green and Croft, 2018).

Secondly, the land cover data used to characterise the habitats of the studied populations must provide sufficient spatial resolution to evaluate dominating land cover patterns, even for small localities such as small, fenced wildlife research areas. The remote sensing images used to build these land cover products should also, ideally, have been collected within a reasonably similar time-range than the samples used for dietary analysis (i.e. no more than 5-10 years) to avoid misinterpretations of the relationships between diet and habitat composition due to temporal changes in landscape. Indeed, several studies have highlighted, using remote sensing, that significant changes in land cover patterns could be observed over time on the African continent, whether between 1975 and 2000 (Brink and Eva, 2009) or between 2000 and 2015 (Midekisa *et al.*, 2017). Similarly, if the samples collected for dietary analysis allow exploration of seasonal variation in diet, time-series of land cover data for the dry and wet seasons could be used to permit detailed interannual analyses of the relationships between herbivore diets and their habitats.

2.5 Conclusion

This study proposes to examine the dietary behaviours of selected extant and extinct mixed-feeding antelopes, using a combination of methods to produce a comprehensive picture of the environments experienced by these species during the Omo-Turkana basin fossil deposition. Mesowear, dental microwear texture, and stable isotope analyses are used to study spatial and chronological heterogeneity of the Omo-Turkana basin vegetation cover between 3.5 and 1.6 million years ago, by examining the dietary preferences of the studied antelope species across the basin (i.e. Koobi Fora, Nachukui and Shungura formations) and through time (i.e. members).

Combined, these dietary proxies can provide a thorough assessment of the dietary ecology of the studied species and mitigate for some of the limitations of each method, maximising the strengths of each proxy. Because dental microwear reflects diets at a shorter time scale than mesowear (i.e. last few days/weeks before death vs life-time accumulated wear), microwear is used beside mesowear analysis to detect seasonal changes in diet, as well as to provide greater detail on the structural properties of the food items consumed (Rivals, Solounias and Mihlbachler, 2007; Rivals *et al.*, 2015). Stable isotopes are used alongside dental use-wear analyses to provide information on the geochemical properties of the food items consumed during the time of enamel-mineralisation, and complement the data acquired from dental use-wear studies by investigating drinking patterns and seasonal dietary variability. To further explore the relationship between land cover distribution and modern impala dietary behaviours in different African regions, land cover maps of selected modern African landscapes are used to discuss habitat heterogeneity of extant *Aepyceros melampus* populations from targeted regions for which data for dietary study was available from published datasets.

It is hypothesized that if, across all dietary proxies, a predominance of diets dominated by a main vegetation-type (browse/ C_3 or graze/ C_4) was observed across taxa, this could indicate a rather homogeneous vegetation cover in that area during the time span examined, forcing a majority of the studied specimens to feed primarily on the type of resources that was available to them in larger proportion. A wider range of isotopic ratios and dental microwear textures, indicative of a large range of resources, would likely indicate the presence of more heterogeneous environments and more variable aridity levels, with habitats able to support a greater range of species, all year round or with marked seasonal variation. However, it must be remembered that a wide range of values might also indicate more time/climate averaging for some parts of the sequence (Hopley and Maslin, 2010; Davis and Pineda Munoz, 2016). Little changes in dietary patterns from one locality to the other across the Omo-Turkana basin (East, West and North of Lake Turkana) or between members might reflect little spatial and temporal variation in the dietary patterns of the studied taxa, which, in turn, might reflect only minor degrees of change in vegetation cover/availability in the region. Each of these alternatives are important for understanding the evolutionary implications for the species inhabiting this region.

This multiproxy approach is novel and provides valuable information to assess the composition and heterogeneity of palaeo-habitats in the Omo-Turkana basin between 3.5 and 1.6 Ma, and better understand the relationship between mixed-feeding herbivores such as the impala, and the land cover composition and structure of their habitats.

Chapter 3: Testing the relationship between modern impala dietary variability and their habitats: what can the dietary proxies tell us about vegetation cover?

3.1 Introduction

One of the challenges in palaeo-environmental reconstructions is a lack of quantifiable knowledge about the existence of analogue (modern comparative) habitats in Africa today. The aim of this part of the project was to provide a new method to compare past and present habitats by testing the relationship between modern impala dietary variability and their habitats (i.e. predictive land cover models). To achieve this, this project combined stable carbon isotope analysis with land cover data to explore modern African vegetation structure and investigate the relationship between land cover and dietary patterns in mixed-feeding herbivore species such as the impala.

Extant impalas (*Aepyceros melampus*) are known to be mixed-feeding animals with varied diets, eating both browse (C_3 -vegetation) or graze (C_4 -vegetation) in proportions that can vary with seasons and local habitat (Sponheimer, Grant, *et al.*, 2003; Codron *et al.*, 2005; Codron *et al.*, 2005; Copeland *et al.*, 2009). Such variation in diet could relate to the prevailing vegetation and potential niche competition within their home range, but could also result from a foraging behaviour that prioritizes vegetation-types with high protein and low fibre contents (Meissner, Pieterse and Potgieter, 1996; Sponheimer, Grant, *et al.*, 2003; Codron *et al.*, 2006; Copeland *et al.*, 2009). Impalas can be found in various environments, and are represented today in Botswana, Kenya, Malawi, Mozambique, Rwanda, South Africa, Swaziland, Tanzania, Uganda, Zambia and Zimbabwe. These countries offer a wide range of different habitats, and because impalas are mixed-feeders, it can be expected that their overall diet will differ depending on which country, region or locality the individuals live.

This chapter assesses the dietary variability of the modern impala as well as the variability of the land cover composition and structure of their habitats, to explore the relationship between diet and land cover in an extant mixed-feeding antelope species. Stable carbon isotopes are used to evaluate the degree of dietary variability that can be observed between and within selected samples of modern impala specimens of known provenance. Land cover maps derived from remote sensing for selected modern African landscapes are used to discuss habitat heterogeneity of modern impalas for targeted regions for which data for dietary study were available in published literature. By comparing case study areas using both land cover metrics and isotopic data, and by exploring the relationships between all of these variables, this project tests whether it can be possible to evaluate the types of land cover patterns that are associated with specific dietary patterns observed from dental samples. If the diet of modern *Aepyceros melampus* is primarily influenced by the prevailing vegetation conditions in their habitat, it can be hypothesized that impala individuals with high $\delta^{13}C$ values would be more likely to be associated with C_4 habitats, while individuals with low $\delta^{13}C$ values would be more likely to be associated with C_3-vegetation.

The material and methods (3.2) used for this analysis are presented in this chapter, followed by the results (3.3) obtained for each part of the analyses. Results are divided around the following objectives:

1) Explore the dietary variability of selected modern impala populations, based on stable carbon isotope evidence (3.3.1).

2) Evaluate the diversity of habitat types inhabited by the studied modern impala populations, based on land cover data, and quantify the land cover composition and structure of these habitats (3.3.2).

3) Assess whether relationships can be observed between specific habitat types and the modern impala dietary patterns observed through stable carbon isotope analysis, and build logistic models that can be used to predict associated habitats based on impala dietary data (3.3.3).

4) Evaluate to which types of habitat fossil impala specimens from the Plio-Pleistocene deposits of the Omo-Turkana basin were likely associated, based on stable carbon isotope data. This is done using the models produced from modern impala diet and land cover data (3.3.4).

Results are then discussed (3.4) to assess whether some of the modern specimens' diet and associated landscapes could reflect that of ancient impala populations in the Omo-Turkana basin between 3.5 and 1.6 million years ago, and bring new insights into Plio-Pleistocene land cover in this region.

3.2 Material and methods

3.2.1 Case study areas

Seven study areas were selected across eastern and southern Africa, based on the availability of land cover data and of stable carbon isotope data for impala populations from these areas. These case study regions are presented in Figure 19 and Table 8.

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Figure 19: Location of case study areas in Africa.

Table 8: Description of the case study areas and their main ecological characteristics.

Country	Locality	Study area	Elevation (m)	Area (km2)	Climate	Average annual rainfall (mm)	Biome	Dominant vegetation	Lithology/Soils/ Forage quality	Type of water sources
South Africa	Kruger National Park	North	300	19,633	Hot semi-arid climate	300-500	Semi-arid savanna, with arid bushveld in the north	Homogeneous woody plant component	Eastern-half dominated by fertile basalt lithology; western-half dominated by less fertile granite gneiss and arenite bedrocks	Sabie, Olifants, Crocodile, Letaba, Luvuvhu and Limpopo Rivers
		South				~500-700		Heterogeneous woodland savanna		
	Waterberg plateau (Limpopo province)	Welgevonden Private Game Reserve	1200-1500	330	Warm and temperate	>600	Mountainous savanna bushveld	Sour bushveld	Acidic and nutrient-poor soils: forage of poor nutritional quality	Two perennial rivers and several man-made dams
Kenya	Athi plains	Swara Plains Conservancy (formerly Hopcraft Game Ranch)	~1500	~280	Dry	800	Open wooded savanna, from shrubland to open grassland	Woody cover dominated by *Acacia drepanolobium*; grassland dominated by red oat grass (*Themeda triandra*).	/	Small rivers
	Laikipia plateau	Mpala Research Centre	1700	202	Semi-arid	550	Bush grassland	Herbaceous layer dominated by perennial tussock grasses; *Acacia*-dominated woody vegetation	High clay content ("black cotton soils"): poor drainage	Permanent rivers
		El Karama ranch	1800	57		500-700			/	Rivers
	Great Rift Valley	Nakuru National Park	1760	~188	Temperate	876	Grassland, scrub woodland, acacia woodland, and vegetation characteristic of saline water ecosystems	Very heterogeneous, with alkaline flats (i.e. seasonally flooded areas of high alkalinity), marshes, grassland, grass-shrub, Arucici woodland	Mostly alluvial soils	Lake Nakuru (shallow, alkaline, 40km2); fresh water from the Njoro and Nderit rivers

References: **Kruger National Park** (Young, 1972; Gertenbach, 1983; Redfern *et al.*, 2003; Sponheimer, Grant, *et al.*, 2003; Venter and Scholes, 2003; J. Codron *et al.*, 2005; Bucini *et al.*, 2009); **Welgevonden Private Game Reserve** (Daryl Codron *et al.*, 2005; Kilian, 2006; Mucina and Rutherford, 2006; Ramsay *et al.*, 2013; Codron *et al.*, 2016); **Swara Plains Conservancy** (Wesonga *et al.*, 2006; Shema, 2019); **Mpala Research Centre** (Young *et al.*, 1998; Gadd, Young and Palmer, 2001; Shorrocks, Cristescu and Magane, 2008; Riginos, 2009; Augustine, 2010; Sankaran, Augustine and Ratnam, 2013; Kartzinel *et al.*, 2015); **El Karama Conservancy** (Trial and Gregory, 1981; Georgiadis, Hack and Turpin, 2003; Sundaresan *et al.*, 2008);**Nakuru National Park** (Kutilek, 1974; Wirtz and Lörscher, 1983; Mwangi and Western, 1997; Dharani *et al.*, 2009; Thuo *et al.*, 2015).

3.2.2 Modern impala dietary ecology analysis

3.2.2.1 Material

Published stable carbon isotope data ($\delta^{13}C$ values) were studied to evaluate the early-years dietary signatures of *Aepyceros melampus* specimens from different populations. Differences in $\delta^{13}C$ values are likely to reflect local differences in vegetation composition since the body composition of animals feeding on vegetation varies depending on the isotopic composition of the plant ingested, as these isotopes are integrated in different body tissues in proportions which vary according to metabolically induced fractionation of the food during digestion (Pollard and Heron, 2013).

Stable carbon isotope data on modern specimens of the studied species were gathered from previously published research. Seven modern African localities were well-represented and well-documented among the *Aepyceros melampus* carbon isotope samples (from studies by Sponheimer, Grant, *et al.* 2003, Codron *et al.* 2006, Copeland *et al.* 2009, Cerling *et al.* 2015), and were therefore chosen as case studies: the El Karama ranch (Kenya), the Swara Plains Conservancy (Kenya; formerly Hopcraft Game Range), the Mpala Research Centre (Laikipia county, Kenya), Nakuru National Park (Kenya), Kruger National Park (divided into North and South; South Africa), and Welgevonden (South Africa) (Table 9). These case studies allowed to test whether differences in dietary patterns could be observed between impalas from different localities through carbon stable isotopes, and whether differences in vegetation cover could be observed between these areas when using remotely sensed land cover data.

Where only descriptive statistics were available for stable carbon isotopes for some of the studied samples (i.e. for the Kruger National Park and Welgevonden samples, in Sponheimer *et al.* 2003, Codron, Codron, Lee-Thorp, Sponheimer, and de Ruiter 2005), Gaussian random variables were generated for these samples prior to statistical analyses that required individual values. To do so, the Box-Mueller transform method (Box and Muller, 1958) was used based on the information provided for each sample in the relevant papers (i.e. number of individuals, mean, standard deviation), using the 'norminv()' function in Excel.

Table 9: Summary of modern *Aepyceros melampus* specimens with published carbon stable isotopes data from the selected case study areas. See appendix A.5 for detailed dataset.

Country	Locality	Year of collection	N	Material	Source
Kenya	Swara plains Conservancy	1999	9	Enamel	Cerling *et al.* (2015)
	Mpala research centre	2001	19		
	Nakuru National Park (shoreline)	2000	3		
South Africa	Kruger National Park - North	2001-2002	18	Hair	Sponheimer *et al.,* 2003
	Kruger National Park - South	2001-2002	18	Hair	Sponheimer *et al.,* 2003
	Welgevonden	2002-2003	14	Faeces	Codron *et al.,* 2005

3.2.2.2 Fractionation factors and δ^{13}C values-conversion

Because the *Aepyceros melampus* carbon isotope data selected from previously published research (from studies by Sponheimer, Grant, *et al.* 2003, Codron *et al.* 2006, Copeland *et al.* 2009, Cerling *et al.* 2015) came from studies that used different materials, the dataset was normalized to allow comparisons between studies. The measured δ^{13}C values were converted where necessary to δ^{13}C-enamel values using different fractionation factors depending on the material analysed. For faeces and hair, isotopic enrichments of −15.0 ‰ and + 11.1‰ were assumed, respectively, following previous studies (Cerling and Harris, 1999; Sponheimer, Grant, *et al.*, 2003; Sponheimer, Robinson, *et al.*, 2003). Values were converted to δ^{13}C-enamel (rather than to δ^{13}C-vegetation/δ^{13}C-diet) to facilitate comparisons with fossil δ^{13}C-enamel data without requiring further conversion of the fossil data, since the aim of the models was to compare directly modern and fossil data to predict the habitats most likely associated with the fossil samples studied.

3.2.2.3 Estimating the minimum percent C_4-vegetation

To estimate the minimum percent C_4 vegetation indicated by enamel, hair, or faeces $\delta^{13}C$ values, the parameters for linear equations published by Passey *et al.* (2009) were used, where

Equation 3. 1 $\% C_4 = 8.45998 * \delta^{13}C_{sample}(\text{enamel}) + 87.48$

This equation represents a linear mixed model between the 'max C_3' and C_4 endmembers for modern samples (i.e. where max $C_3 = -24.3$, and $C_4 = -12.6$). For this equation, individual enamel-$\delta^{13}C$ values were used.

A different dual-source linear mixed model was used at the sample level (i.e. for each locality) to estimate the relative proportion of C_4-plant material included in the diet of the selected samples and provide estimated mean and confidence intervals for each sample based specifically on isotopic data from modern African C_3 and C_4 plants. For this, the measured $\delta^{13}C$ values were converted to $\delta^{13}C$-diet values (i.e. estimated $\delta^{13}C$ value of the plant material ingested by the individuals) using different fractionation factors depending on the material analysed. For faeces, hair and enamel, isotopic enrichments of −0.9 ‰, +3.0 ‰ and + 13.5‰ were assumed, respectively, following previous studies (Cerling, Harris and Leakey, 1999; Balasse, 2002; Sponheimer, Grant, *et al.*, 2003; Passey *et al.*, 2005). The formulae developed by Phillips and Gregg (2001) were then used for calculating variances, standard errors (SE), and confidence intervals for source proportion estimates that account for the observed variability in the isotopic signatures for the sources (i.e. C_3 and C_4 plant materials) as well as the mixture (i.e. $\delta^{13}C$-diet). Mean proportion estimates of C_4-plant material in the diet of the studied impala samples were calculated for each sample using the spreadsheet IsoError (version 1.04) made available online by the authors (Phillips and Gregg 2001). First, the mean isotopic signatures and standard deviations for the sources were evaluated using published isotope data on

African C_3 - and C_4 -vegetation (Table 35). For each impala sample studied, the mean $\delta^{13}C$-diet value was then added to the model, along with the standard deviation and number of samples analysed. Estimates for the source proportions, their associated variances, standard errors, and 95% confidence interval limits were then automatically calculated, and the means, standard errors, and confidence interval limits for source proportions summarized.

Table 10: Mean isotopic signature and standard deviation (s.d.) of C_3 - and C_4 - plant materials, based on published isotope data on African C_3 - and C_4 -vegetation (for sample details see appendix A.15 table-A 33, and references therein).

Plant group	N	Mean	s.d.
C3	1047	-26.7544	1.9767
C4	1085	-12.3535	1.1785

3.2.2.4 Statistical analyses

To check for significant differences within the dataset between the studied impala samples, statistical analyses were performed using the software R Studio (see appendix A.6 for more detail). $\delta^{13}C$-enamel values were tested for normality (Shapiro-Wilk test) and for homogeneity of variance (Levene Test), but because these assumptions were not upheld, the non-parametric Kruskal-Wallis test was used, followed by Dunn's test to identify the significant differences between groups.

3.2.3 Land cover analysis

3.2.3.1 Land cover data used in this study

To study the selected localities with the best resolution possible, part of the remote sensing data used in this study was based on the products generated by the Africover project. Although Africover land cover maps of high spatial resolution were available to use in this project for Kenya, no product was available for South Africa due to the project being interrupted before the whole African continent could be covered. To mitigate for this, another source of land cover data (i.e. Globcover products) was used in addition to the Africover products to study land cover composition and structure in the selected South African localities.

3.2.3.1 The Africover products

Africover was a project administered by the United Nations Food and Agricultural Organization (UN FAO) that was approved in 1994 and focused first on the East-African region (Burundi, Egypt, Eritrea, Ethiopia, Kenya, Rwanda, Somalia, Uganda, Tanzania, Uganda and Zaire) (FAO, 1997). The main aim of the project was to establish a GIS-based land cover database compatible with the mapping scale 1 :200,000 based on systematic land cover classification and uniform mapping specifications for the whole continent of Africa (FAO, 1997; Latham *et al.*, 2002). For smaller countries and specific areas the mapping scale 1:100,000 was used (Torbick *et al.*, 2005).

Africover generated land cover maps using mainly Landsat-5 TM (Thematic Mapper) and Landsat-7 ETM (Enhanced Thematic Mapper) data that provide multispectral images with a 30m spatial resolution (Kalensky, 1998) (Table 11). The RADARSAT-1 standard or wide-mode Synthetic Aperture Radar (SAR) image products (30 m pixel size) were used in areas with persistent cloud cover (Latham *et al.*, 2002). Most of the satellite images used were acquired between 1995 and 1999 (Fritz, See and Rembold, 2010). The land cover maps generated were classified using the Land Cover Classification System (LCCS), which was developed by the UN FAO in this project, and became a standard for land cover products (Gregorio, Jansen and Resources, 1998; Fritz, See and Rembold, 2010)

Electromagnetic spectrum		**Satellite platform**	
Division	**Wavelenght**		
Gamma rays	< 0.03 nm		
X-rays	0.03–300 nm		
Ultraviolet	0.30–0.38 µm		
Visible light	0.38–0.72 µm	MERIS (Envisat) *Globcover*	Lansdat 5 (TM) & 7 (ETM) *Africover*
Near infrared	0.72–1.30 µm	MERIS (Envisat) *Globcover*	Lansdat 5 (TM) & 7 (ETM) *Africover*
Mid infrared	1.30–3.00 µm		Lansdat 5 (TM) & 7 (ETM) *Africover*
Far infrared	7.0–1,000 µm		Lansdat 5 (TM) & 7 (ETM) *Africover*
Microwave	1 mm–30 cm		
Radio	≥ 30 cm		

Table 11: Main divisions of the electromagnetic spectrum (based on Campbell and Wynne 2011), and the satellite platforms used to produce the land cover products used in this study.

To compile the AFRICOVER land cover map, a multi-phase image interpretation approach was used by the UN FAO. First, the preliminary delineation of interpretation units of similar appearance by visual interpretation of Landsat TM-ETM false-colour images was performed. It was then followed by field validation of 0.5% to 5% of the samples of interpretation units which resulted in a set of diagnostic attributes, the LCCS classifiers, which uniquely define the land cover class in each interpretation unit. Final interpretation of mapping units (land cover polygons) based on LCCS was then implemented, followed by an accuracy assessment of land cover classification based on a field control data set. The land cover layer was then finalized through editing, digitization, coding and geographic referencing of land cover polygons (Kalensky, 1998; Latham *et al.*, 2002).

3.2.3.2 The Globcover products

The Globcover products (© ESA 2010 and UCLouvain) (Leroy *et al.*, 2007; Bontemps *et al.*, 2008) were used to study the land cover patterns of the South African study localities, providing classified land cover data of 300 m spatial resolution for the years 2005-2006. A more detailed spatial analysis could have been achieved by using the ESA CCI land cover map of Africa 2016 based on one year of Sentinel-2A observations (ESA Climate Change Initiative Land Cover project; spatial resolution: 20 m), but because this map is currently only a prototype that has not yet been validated, there remains some uncertainties regarding overall accuracy and potential errors in land cover classes (Ramoino, Pera and Arino, 2018). Furthermore, the period covered by the earliest Globcover product (i.e. 2005-2006) provides land cover data more likely to reflect the environmental conditions experienced in the study areas by the specimens studied for dietary analysis (which were shot, at the latest, in 2003) than products providing more recent data.

The Globcover project developed a processing chain (Figure 20) meant to automatically deliver a land cover map based on the MERIS 300m Full resolution Full Swath (FRS) products, using data acquired between December 2004 and June 2006 and processed at level 1B (i.e. calibrated top of atmosphere gridded radiance) (Leroy *et al.*, 2007; Bontemps *et al.*, 2008). MERIS is a wide field-of-view push-broom imaging spectrometer that measures reflected solar radiation in 15 spectral bands (between ~412.5nm and ~900nm) (Rast, Bézy and Bruzzi, 1999). It was one of the main instruments on board the Envisat platform of the European Space Agency (ESA) between 2002 and 2012. A first data processing module processed the MERIS FRS level 1B data to produce mosaics of land surface reflectance through a series of pre-processing steps (Figure 59). A second data processing module then transformed the multispectral mosaics produced by the pre-processing modules into a land cover map, using the UN Land Cover Classification System (LCCS) as a typology (Figure 21).

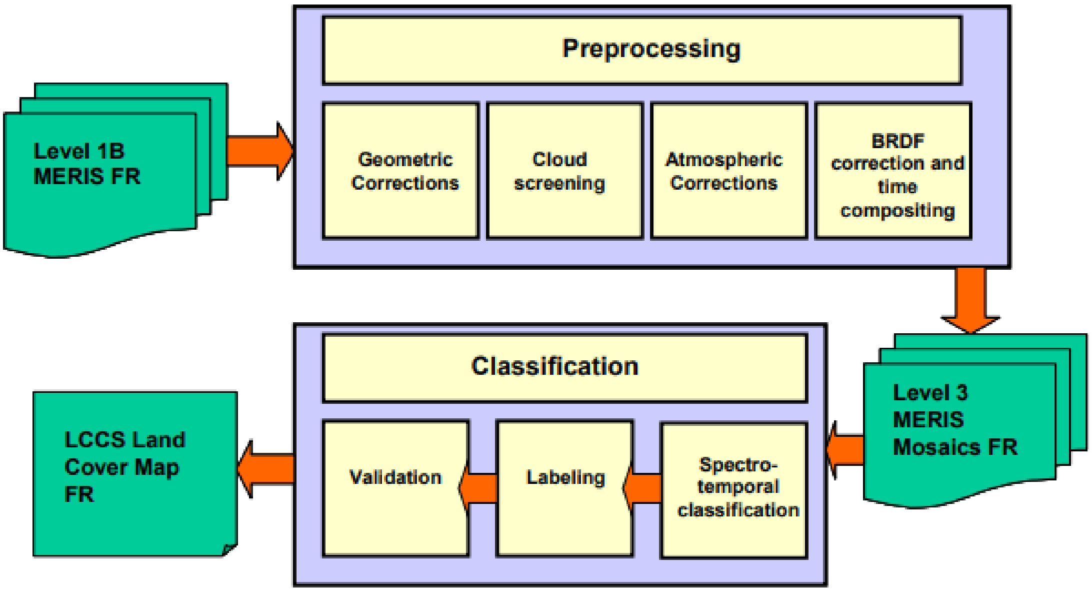

Figure 20: Algorithmic principle of the Globcover chain (from Bontemps *et al.,* 2008, p.8; © ESA 2010 and UCLouvain) .

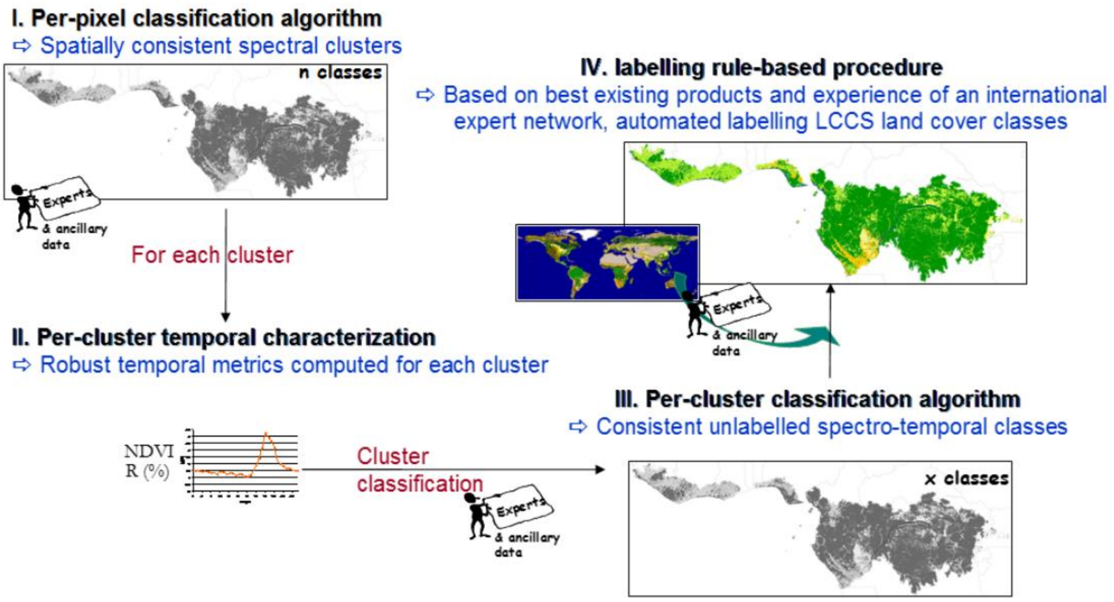

Figure 21: Principle of the classification algorithm starting by bi-weekly mosaics (from Bontemps *et al.,* 2008, p.11; © ESA 2010 and UCLouvain)

The Globcover products offer two levels of classification (Bontemps *et al.*, 2008). First, a global legend was defined (level 1, with 22 classes), which was designed to be a global, consistent land cover map at a worldwide scale. A second more detailed regional legend was also defined (level 2, with 46 classes), using more accurate regional information to define more land cover classifiers. Regional products were used for the South African study areas (i.e. for Kruger National Park and Welgevonden, South Africa) as they provide more detailed information on the vegetation types presents in each locality.

3.2.3.2 Land cover types and classification

To analyse and compare land cover patterns within and between case studies, a general land cover classification was defined based on the land cover classes used in the Globcover global and regional products (hereafter referred to as "general land cover classification"). From the 46 land cover classes represented in the Globcover products, 33 new classes were created by grouping some classes together to simplify the classification and focus on the level of detail required for this project (Table 12). For instance, all Globcover classes relating to various types of croplands were aggregated into one class because cultivated and managed areas are seldom used as food resources for impalas in the areas studied and are therefore not the primary focus of this study.

To provide a tool to assess the composition of the land cover in terms of C_3 - C_4 vegetation and be more closely comparable with data from carbon isotope studies, a second land cover classification was built containing 12 classes that aggregate Globcover classes depending on the nature of the vegetation described by each class (hereafter referred to as "C_3 - C_4 classification") (Table 12). For instance, all Globcover classes relating to forests or shrublands were aggregated into new categories indicating the occurrence of C_3 -vegetation. Where the Globcover class labels indicated areas dominated by forest or shrubs only, such classes were assigned to the "C_3 -vegetation (70-100%)" class, indicative of areas dominated by C_3 -vegetation. Where the Globcover class labels indicated mosaic areas dominated by forest or shrubs but where other vegetation types were present (e.g. grasslands), such classes were assigned to the "Mixed-vegetation - Predominance C_3 -vegetation (50-70%)" class, indicative of areas of mosaic vegetation dominated by C_3 -vegetation. The same process was also applied to Globcover classes indicative of areas dominated by C_4-vegetation (i.e. grasslands) at varying degrees. Land cover classes that could not be assigned to either C_3 or C_4 vegetation categories were kept as distinct classes (e.g. water bodies, bare areas, artificial surfaces, or cultivated and managed areas).

These two new land cover classifications were also used for the land cover maps created using the Africover products, based on the land cover labels and descriptions provided in these products for each of the 156 classes identified in the studied areas (Table 13).

The new classifications were then added to the Globcover legend import files to allow for the new classifications to be used in ArcGIS for land cover visualisation and analysis.

Table 12: New land cover classifications (C_3 - C_4 classes; New LC classes: General landcover classes) in relation to the original Globcover classes.

C3-C4 class	C3-C4 label	New LC class	New LC Label	Glob-cover class	Globcover label (regional)
Cplant-1	C3-vegetation (70-100%)	GC-4	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	40	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)
		GC-5	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest (>5m)	41	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest (>5m)
		GC-6	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)	42	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)
		GC-7	Closed (>40%) broadleaved deciduous forest (>5m)	50	Closed (>40%) broadleaved deciduous forest (>5m)
		GC-8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)
		GC-9	Closed (>40%) needleleaved evergreen forest (>5m)	70	Closed (>40%) needleleaved evergreen forest (>5m)
		GC-10	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)	90	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)
		GC-11	Open (15-40%) needleleaved deciduous forest (>5m)	91	Open (15-40%) needleleaved deciduous forest (>5m)
		GC-12	Open (15-40%) needleleaved evergreen forest (>5m)	92	Open (15-40%) needleleaved evergreen forest (>5m)
		GC-13	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)	100	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)
		GC-14	Closed (>40%) mixed broadleaved and needleleaved forest (>5m)	101	Closed (>40%) mixed broadleaved and needleleaved forest (>5m)
		GC-17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	130	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
		GC-18	Closed to open (>15%) broadleaved or needle-leaved evergreen shrubland (<5m)	131	Closed to open (>15%) broadleaved or needle-leaved evergreen shrubland (<5m)
		GC-19	Closed to open (>15%) broadleaved deciduous shrubland (<5m)	134	Closed to open (>15%) broadleaved deciduous shrubland (<5m)
		GC-22	Sparse (<15%) vegetation	152	Sparse (<15%) shrubland
		GC-23	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water	160	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water
				161	Closed to open broadleaved forest on (semi-)permanently flooded land - Fresh water
				162	Closed to open broadleaved forest on temporarily flooded land - Fresh water
		GC-24	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water	170	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water
		GC-26	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water	181	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	GC-3	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	32	Mosaic forest (50-70%) / cropland (20-50%)
		GC-15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	110	Mosaic forest or shrubland (50-70%) / grassland (20-50%)
Cplant-3	Mixed-vegetation (C3/C4 vegetation; 50/50%)	GC-3	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	30	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)
				31	Mosaic grassland or shrubland (50-70%) / cropland (20-50%)
		GC-22	Sparse (<15%) vegetation	150	Sparse (<15%) vegetation
		GC-25	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water	180	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	GC-16	Mosaic grassland (50-70%) / forest or shrubland (20-50%)	120	Mosaic grassland (50-70%) / forest or shrubland (20-50%)

Table 12 (continued)

C3-C4 class	C3-C4 label	New LC class	New LC Label	Glob-cover class	Globcover label (regional)
Cplant-5	C4-vegetation (70-100%)	GC-20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
		GC-21	Closed (>40%) grassland	141	Closed (>40%) grassland
		GC-22	Sparse (<15%) vegetation	151	Sparse (<15%) grassland
		GC-27	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water	185	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water
Cplant-6	Cultivated and managed areas / Rainfed cropland	GC-1	Cultivated and managed areas / Rainfed cropland	11	Post-flooding or irrigated croplands (or aquatic)
				12	Post-flooding or irrigated shrub or tree crops
				13	Post-flooding or irrigated herbaceous crops
				14	Rainfed croplands
				15	Rainfed herbaceous crops
				16	Rainfed shrub or tree crops (cash crops, vineyards, olive tree, orchards…)
Cplant-7	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/ forest) (20-50%)	GC-2	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	20	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)
				21	Mosaic cropland (50-70%) / grassland or shrubland (20-50%)
Cplant-8	Artificial surfaces and associated areas (Urban areas >50%)	GC-28	Artificial surfaces and associated areas (Urban areas >50%)	190	Artificial surfaces and associated areas (Urban areas >50%)
Cplant-9	Bare areas	GC-29	Bare areas	200	Bare areas
				201	Consolidated bare areas (hardpans, gravels, bare rock, stones, boulders)
				202	Non-consolidated bare areas (sandy desert)
		GC-32	Sand	203	Salt hardpans
Cplant-10	Water	GC-30	Water bodies	210	Water bodies
Cplant-11	Snow/Ice	GC-31	Permanent snow and ice	220	Permanent snow and ice
Cplant-12	No data	GC-33	No data (burnt areas, clouds,…)	230	No data (burnt areas, clouds,…)

Table 13: New land cover classifications (C3 - C4 classes; New LC classes: General landcover classes) in relation to the original Africover classes.

C3-C4 class	C3-C4 label	New LC class	New LC Label	MapCode	Africover - LCCOwnDescr	Africover - LCCLabel
Cplant-1	C3-vegetation (70-100%)	GC-17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	2SCJ	Closed shrubs	Continuous Closed Medium To High Shrubland (Thicket)
				2SCJ7	Closed shrubs with sparse trees	Medium To High Thicket With Emergents
				2WC7	Closed woody with sparse trees	Closed Woody Vegetation With Emergents
		GC-19	Closed to open (>15%) broadleaved deciduous shrubland (<5m)	2SCM2-FE	Closed medium shrubs (broadleaved deciduous) - Fern	Broadleaved Deciduous Medium High Thicket / Floristic Aspect: Fern
		GC-23	Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water	4TCF	Closed trees on temporarily flooded land - fresh water	Forest On Temporarily Flooded Land Water Quality: Fresh
				4TCFF1Y	Closed trees (broadleaved evergreen) on permanently flooded land - brackish water	Broadleaved Evergreen Forest On Permanently Flooded Land Water Quality: Brackish
		GC-24	Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water	4SCF	Closed shrubs on temporarily flooded land - fresh water	Closed Medium To High Shrubs On Temporarily Flooded Land Water Quality: Fresh
				4SCJFF1Y	Closed shrubs (broadleaved evergreen) on permanently flooded land - brackish water	Broadleaved Evergreen Closed Medium To High Shrubs On Permanently Flooded Land Water Quality: Brackish
		GC-5	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest (>5m)	2TC8	Closed trees with shrubs	Forest With Shrubs
				2TC	Closed Trees - Bamboo	Continuous Closed Trees Floristic Aspect: Bamboo
				2TCI177	Closed multilayered trees (broadleaved evergreen)	Multi-Layered Broadleaved Evergreen High Forest (With Second Layer Of Medium High Trees) With Emergents
				2TCI8	Closed high trees with closed to open shrubs	High Forest With High Shrubs
				2TCL8	Closed low trees with closed to open shrubs	Low Forest With High Shrubs
		GC-6	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)	2TPM18	Open general medium trees with open shrubs	Broadleaved Evergreen Woodland With Open Shrubs
				2TV8	Very open trees with closed to open shrubs	(40 - (20-10)%) Woodland With Shrubs
				2TVI	Very open high trees	Continuous Open (40 - (20-10)%) High Forest (Woodland)
		GC-7	Closed (>40%) broadleaved deciduous forest (>5m)	2WC27Y	Closed woody (broadleaved deciduous) with sparse trees	Broadleaved Deciduous Closed Woody Vegetation With Medium High Emergents
		GC-8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	2TO28	Open trees (broadleaved deciduous) with closed to open shrubs	Broadleaved Deciduous ((70-60) - 40%) Woodland With Shrubs
				2TP8	Open general trees with shrubs	Woodland With Shrubs
				2TPM8	Open general trees with open shrubs	Woodland With Open Shrubs
				2TV28	Very open trees (broadleaved deciduous) with closed to open shrubs	Broadleaved Deciduous (40 - (20-10)%) Woodland With Shrubs
		GC-9	Closed (>40%) needleleaved evergreen forest (>5m)	2TC3	Closed trees (needlelaved evergreen)	Needleleaved Evergreen Forest

Table 13 (continued)

C3-C4 class	C3-C4 label	New LC class	New LC Label	MapCode	Africover - LCCOwnDescr	Africover - LCCLabel
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	GC-15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	2SOJ67	Open shrubs with closed to open herbaceous and sparse trees	((70-60) - 40%) Medium To High Shrubland With Open Medium to Tall Herbaceous And Emergents
				2SPJ67	Open general shrubs with closed to open herbaceous and sparse trees	Medium To High Shrubland With Short Herbaceous And Emergents
				2SV6	Very open shrubs with closed to open herbaceous	(40 - (20-10)%) Shrubland with Herbaceous
				2SVJ67	Very open shrubs with closed to open herbaceous and sparse trees	(40 - (20-10)%) Medium To High Shrubland With Medium to Tall Herbaceous And Emergents
		GC-15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	2WP6	Open general woody with herbaceous	Open Woody Vegetation With Herbaceous Layer
		GC-17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	2SP6	Open general shrubs with closed to open herbaceous	Shrubland with Herbaceous
		GC-22	Sparse (<15%) vegetation	2SR6	Sparse shrubs with sparse herbaceous	Sparse Shrubs and Sparse Herbaceous
		GC-25	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water	4SOF6	Open shrubs with closed to open herbaceous on temporarily flooded land - fresh water	Open ((70-60) - 40%) Medium To High Shrubs With Herbaceous Vegetation On Temporarily Flooded Land Water Quality: Fresh
				4SPF6	Open general shrubs with closed to open herbaceous on temporarily flooded land	Open Shrubs With Herbaceous Vegetation On Temporarily Flooded Land
				4SVF6	Very open shrubs with closed to open herbaceous on temporarily flooded land - fresh water	Open (40 - (20-10)%) Medium To High Shrubs With Herbaceous Vegetation On Temporarily Flooded Land Water Quality: Fresh
		GC-26	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water	4TPF6	Open general trees with closed to open herbaceous on temporarily flooded land - fresh water	Woodland With Closed Herbaceous Vegetation On Temporarily Flooded Land Water Quality: Fresh
				4WPF6	Open general woody with closed to open herbaceous on temporarily flooded land	Open Woody Vegetation With Herbaceous Vegetation On Temporarily Flooded Land Water Quality: Fresh
		GC-8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	2TO268	Open trees (broadleaved deciduous) with closed to open herbaceous and sparse shrubs	Broadleaved Deciduous ((70-60) - 40%) Woodland With Open Herbaceous Layer And Sparse Shrubs
				2TOL268	Open low trees (broadleaved deciduous) with open herbaceous and sparse shrubs	Broadleaved Deciduous ((70-60) - 40%) Woodland With Open Medium to Tall Herbaceous Layer And Sparse Shrubs
				2TV268	Very open trees (broadleaved deciduous) with closed to open herbaceous and sparse shrubs	Broadleaved Deciduous (40 - (20-10)%) Woodland With Herbaceous Layer And Sparse Shrubs
				2TVL268	Very open low trees (broadleaved deciduous) with open herbaceous and sparse shrubs	Broadleaved Deciduous (40 - (20-10)%) Woodland With Open Medium to Tall Herbaceous Layer And Sparse Shrubs

Table 13 (continued)

C3-C4 class	C3-C4 label	New LC class	New LC Label	MapCode	Africover - LCCOwnDescr	Africover - LCCLabel
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	GC-20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	2H(CP)78	Closed to very open herbaceous with sparse trees and shrubs	Closed To Very Open Herbaceous Vegetation with Trees and Shrubs
				2H(CP)8	Closed to very open herbaceous with sparse shrubs	Closed To Very Open Herbaceous Vegetation with Shrubs
		GC-26	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water	4H(CP)F8	Closed to very open herbaceous with sparse shrubs on temporarily flooded land - fresh water	Closed to Very Open Herbaceous Vegetation With Sparse Shrubs On Temporarily Flooded Land . Fresh Water
Cplant-5	C4-vegetation (70-100%)	GC-20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	2H(CP)	Closed to very open herbaceous	Continuous Closed to Very Open Herbaceous Vegetation
		GC-22	Sparse (<15%) vegetation	2HR	Sparse herbaceous	Parklike Patches Of Sparse ((20-10) - 4%) Herbaceous Vegetation
		GC-27	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water	4H(CP)FF	Closed to Open Herbaceous On Permanently Flooded Land	Closed to Open Herbaceous Vegetation On Permanently Flooded Land.Fresh Water
				4HCF	Closed herbaceous on temporarily flooded land - fresh water	Closed Herbaceous Vegetation On Temporarily Flooded Land. Fresh water
				4HCJF7	Closed herbaceous with sparse trees on temporarily flooded land - fresh water	Closed Medium To Tall Herbaceous Vegetation With Low Emergents On Temporarily Flooded Land. Fresh water
Cplant-6	Cultivated and managed areas / Rainfed cropland	GC-1	Cultivated and managed areas / Rainfed cropland	G-	Cereals, Rice	Continuous Large To Medium Sized Field(s) Of Graminoid Crops Dominant Crop: Cereals - Rice (Oryza spp.)
				H-	Rainfed Herbaceous Crop(s)	Rainfed Herbaceous Crop(s)
				S-	Rainfed Shrub Crop	Permanently Cropped Area With Rainfed Shrub Crop(s)
				T-	Forest Plantation	Permanently Cropped Area With Rainfed Tree Crop(s) Crop Cover: (Plantation(s))
Cplant-8	Artificial surfaces and associated areas (Urban areas >50%)	GC-28	Artificial surfaces and associated areas (Urban areas >50%)	5A	Airport	Non-Linear Built Up Area(s) Built-up object: Airport
				5I	Industrial area - general	Industrial And/Or Other Area(s)
				5P	Port	Non-Linear Built Up Area(s) Built-up object: Port Area (including Docks, Shipyards, Locks)
				5Q	Quarry	Extraction Site(s)
				5U	Urban areas (general)	Urban Area(s)
				5UC	Refugee camp	Urban Area(s) Built-up object: Refugee Camp
				5UR	Rural settlements	Urban Area(s) Built-up object: Other - Rural Settlement
				5UV	Vegetated Urban Areas	Vegetated Urban Area(s)

Table 13 (continued)

C3-C4 class	C3-C4 label	New LC class	New LC Label	MapCode	Africover - LCCOwnDescr	Africover - LCCLabel
Cplant-9	Bare areas	GC-29	Bare areas	6R	Bare rock	Bare Rock(s)
				6S	Bare soil	Bare Soil And/Or Other Unconsolidated Material(s)
				6ST2	Bare soil very stony	Very Stony Bare Soil And/Or Other Unconsolidated Material(s)
				6SZ	Salt crusts	Bare Soil And/Or Other Unconsolidated Material(s)
		GC-32	Sand	6L	Sand	Loose And Shifting Sands
				8WT1	Sand beaches	Tidal Area (Surface Aspect: Sand)
Cplant-10	Water bodies	GC-30	Water bodies	7WP	Artificial Lakes or Reservoirs	Artificial Perennial Waterbodies (Standing)
				7WP-Y	Fish Pond	Artificial Perennial Waterbodies (Standing)
				8WFN1	River banks	Non-Perennial Natural Waterbodies (Flowing) (Surface Aspect: Sand)
				8WFP	River	Perennial Natural Waterbodies (Flowing) Salinity: Fresh, < 1000 ppm of TDS
				8WN2	Lake shore	Non-Perennial Natural Waterbodies (Standing) (Surface Aspect: Bare Soil)
				8WP	Natural lakes	Perennial Natural Waterbodies (Standing) Salinity: Fresh, < 1000 ppm of TDS
Cplant-11	Permanent snow and ice	GC-31	Permanent snow and ice	8SP	Snow	Perennial Snow

3.2.3.3 Land cover maps and study variables

To produce land cover maps of the eight study areas, their boundaries were first drawn as polygons in ArcGIS (version 10.1) and used to create isolated maps of each locality by clipping the polygons onto the Globcover or Africover country maps. Different maps were then created using the two new classifications schemes for symbology. To facilitate quantitative analysis, each map was transformed using the ArcTool "Polygon to raster" (cell size=300 for Globcover products; cell size=30 for Africover products), which allowed the land cover maps to be analysed using the software FragStats (version 4.2.1) which is designed to compute a wide variety of landscape metrics for categorical map patterns.

A series of variables were produced to help quantify and characterise landscape composition and configuration, in each studied locality. Class-level and landscape-level variables were computed (see Table 14). Class-level variables are metrics that are calculated for each land cover class observed in each studied locality (e.g. proportional abundance of each land cover class in the landscape, PLAND). These variables are therefore used as a way to assess the land cover composition of each study area. Landscape-level variables are metrics that help characterise the entire patch mosaic of each studied locality and evaluate their overall landscape structure when all land cover classes are considered together (e.g. for one locality, it is possible to evaluate the number of different patch types present, NP< or how divided/aggregated land cover patches are in the area, DIVISION).

Table 14: Class-level variables used in this study to describe landscape composition, and landscape-level variables used to describe land cover spatial configuration.

Variable		Units	Description	Range	Comments
Landscape composition (Class-level metrics)					
Percentage of Landscape	*PLAND*	Percent	Sum of the areas (m2) of all patches of the corresponding patch type, divided by total landscape area (m2), multiplied by 100.	PLAND approaches 0 when the corresponding patch type (class) becomes increasingly rare in the landscape. PLAND = 100 when the entire landscape consists of a single patch type.	Percentage of landscape quantifies the proportional abundance of each patch type in the landscape.
Number of Patches	*NP*	None	Number of patches of the corresponding patch type (class).	NP = 1 when the landscape contains only 1 patch of the corresponding patch type.	
Largest Patch Index	*LPI*	Percent	Area (m2) of the largest patch of the corresponding patch type divided by total landscape area (m2), multiplied by 100.	LPI approaches 0 when the largest patch of the corresponding patch type is increasingly small. LPI = 100 when the entire landscape consists of a single patch of the corresponding patch type.	Largest patch index at the class level quantifies the percentage of total landscape area comprised by the largest patch. As such, it is a simple measure of dominance.
Spatial configuration (Landscape-level metrics)					
Largest Patch Index	*LPI*	Percent	Area (m2) of the largest patch in the landscape divided by total landscape area (m2), multiplied by 100.	LPI approaches 0 when the largest patch in the landscape is increasingly small. LPI = 100 when the entire landscape consists of a single patch.	Largest patch index quantifies the percentage of total landscape area comprised by the largest patch. As such, it is a simple measure of dominance.
Landscape Division Index	*DIVISION*	Proportion	1 minus the sum of patch area (m2) divided by total landscape area (m2), quantity squared, summed across all patches of the corresponding patch type.	DIVISION = 0 when the landscape consists of single patch. DIVISION approaches 1 when the proportion of the landscape comprised of the focal patch type decreases and as those patches decrease in size.	Division is based on the cumulative patch area distribution and is interpreted as the probability that two randomly chosen pixels in the landscape are not situated in the same patch of the corresponding patch type.
Simpson's Diversity Index	*SIDI*	None	1 minus the sum, across all patch types, of the proportional abundance of each patch type squared.	SIDI = 0 when the landscape contains only 1 patch (i.e., no diversity). SIDI approaches 1 as the number of different patch types (i.e., patch richness, PR) increases and the proportional distribution of area among patch types becomes more equitable.	The value of Simpson's index represents the probability that any 2 pixels selected at random would be different patch types.

3.2.3.4 Evaluating the proportion of C_4-vegetation in the landscape – the C_4-Index

To facilitate comparisons between localities for land cover composition, an additional landscape-level variable was calculated based on the class-level metrics extracted from the land cover maps produced with the C_3 - C_4 classification, to build an index reflecting a gradient from C_3- to C_4-dominated landscapes. As a way to estimate the percentage of C_4-vegetation present in each studied locality, the new variable (C_4-Index) was calculated based on the PLAND values (i.e. Percentage of Landscape) of the main C_3 - C_4 land cover classes used in the maps (classes 1 to 5 - Table 15). Classes with no vegetation or with vegetation of unknown nature (classes 6 to 12) were excluded from the equation to focus only on the vegetation types identified in the landscape. As a result, the C_4-index reflects the relative proportion of C_4-vegetation present in the studied locality among the vegetation types identified. Values of PLAND for each class were converted into the variable rel.PLAND, to represent the proportional abundance of each patch type in the landscape when only classes 1 to 5 are considered (i.e. excluding all classes with no vegetation or with vegetation of unknown nature). A series of coefficients, from 0 to 1, where then applied to each rel.PLAND value to reflect the relative proportion of C_4-vegetation included in each of these classes (with 0 representing 0%, and 1 representing 100% of C_4-vegetation comprised in the land cover class). The sum of the output values for the five land cover classes was then calculated to form the C_4-Index, hence representing the proportional abundance of C_4-vegetation in the studied locality (in percent).

Table 15: C_3 - C_4 **land cover classes and** C_4 **-coefficients used to compute the** C_4 **-Index (where rel.PLAND is the proportional abundance of each patch type in the landscape when only classes 1 to 5 are considered).**

Code	C3-C4 land cover classes	C4-Coefficient
Cplant-1	C3-vegetation (70-100%)	0
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	0.25
Cplant-3	Mixed-vegetation (C3/C4 vegetation; 50/50%)	0.5
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	0.75
Cplant-5	C4-vegetation (70-100%)	1
C4-Index = (rel.PLAND_Cplant-1*0) + (rel.PLAND_Cplant-2*0.25) + (rel.PLAND_Cplant-3*0.5) + (rel.PLAND_Cplant-4*0.75)+(rel.PLAND_Cplant-5*1)		

3.2.3.5 Cluster analysis

Land cover data from the different study localities were used to identify clusters of similarity for land cover composition and/or structure, using K-means clustering analysis (using the software R Studio, version 1.1.453; see Appendix A.6 for details of the packages used). A first clustering analysis was performed using only the C_4-Index to identify clusters of localities with similar land cover composition, based on the maps built using the C_3-C4 classification. A second clustering analysis was then performed using the Division Index (DIVISION), the Simpson's Diversity Index (SIDI), the Largest Patch Index (LPI) and the C_4 -Index, to identify clusters of localities with similar land cover patterns when both land cover composition and land cover structure are considered. All variables were scaled and centred prior to analysis.

The optimal number of clusters (K) to be generated from the k-means analysis (i.e. minimum number of clusters where the total within-cluster sum of square is minimized) was determined with the Elbow method, which looks at the percentage of variance explained as a function of the number of clusters (Thorndike, 1953; Ng, 2012). When using the C_4-Index variable to identify clusters among the studied localities based on land cover composition, the results from the Elbow method suggest 2 or 3 to be the optimal number of clusters that could be generated by the K-means algorithm (see Appendix A.7 figure-A 3). When using the variables LPI, SIDI, DIVISION and C_4 -Index to identify clusters among the studied localities based on both land cover composition and structure, the results from the Elbow method suggested an optimal number of clusters of 3 (Appendix A.7 figure-A 4). The structural and/or compositional characteristics of each cluster were then assessed by observing the range of values attributed to the localities assigned to each cluster for the relevant variables.

3.2.3 Relationships between diet and land cover variables: multinomial logistic regression models

The purpose of this part of the analysis was to study the relationship between habitat type and the diet of modern impala, and consequently test the effect of *A. melampus* dietary signals on the identification of specific land cover patterns. To achieve this, the relationships between impala $\delta^{13}C$ values and land cover composition, and general land cover patterns (land cover composition and structure) were explored. Land cover composition and structure as a function of diet (evaluated with $\delta^{13}C$) was evaluated using simple multinomial logistic regression models to see if positive or negative relationships could be observed between selected land cover variables and the dietary patterns of *Aepyceros melampus* specimens as assessed through stable carbon isotope analysis.

Two models were tested: 1) Land cover composition as a function of diet; 2) Land cover composition and structure as a function of diet. The models were implemented using the clusters identified with the k-means algorithm to form the categorical dependant variables in each model.

The up-sampling method was used prior to each model building to correct for class unbalance in the dataset. This method adds more similar data points to the minority classes to make class distribution equal across the dataset. This was to mitigate for small sample sizes for some of the studied areas (hence for some land cover types) which relate more to inerrant data collection biases rather than to the actual rarity of occurrence of such land cover types in African landscapes. For both models, δ^{13}Cvalues were *z*-standardized prior to analysis via centering and scaling methods. The 95% confidence intervals (“Lower CI” and “Upper CI”) were calculated for the parameter estimates and odds ratios for the model.

3.2.3.1 Land cover composition as a function of diet (model 1)

The model took the form:

Equation 4. 2

$$\begin{aligned} \boldsymbol{y_i} \sim & \quad \mathbf{Multinom}(\boldsymbol{\mu_i}) \\ \boldsymbol{\mu_i} = \quad \boldsymbol{\alpha} + \boldsymbol{\beta} \mathbf{1} * & \quad \boldsymbol{\delta} \mathbf{13C}_{\boldsymbol{i}} \end{aligned}$$

where y_i is a categorical variable denoting whether the land cover structure i is 0: C_3-vegetation, 1: Mixed-vegetation, 2: C_4-vegetation, α is the intercept term, $\beta 1$ is the effect of diet on the land cover structure type, and X is the stable carbon isotope value (δ^{13}C).

3.2.3.2 Land cover composition AND structure as a function of diet (model 2)

The model took the form:

Equation 4. 3

$$\begin{aligned} \boldsymbol{y_i} \sim & \quad \mathbf{Multinom}(\boldsymbol{\mu_i}) \\ \boldsymbol{\mu_i} = \quad \boldsymbol{\alpha} + \boldsymbol{\beta} \mathbf{1} * & \quad \boldsymbol{\delta} \mathbf{13C}_{\boldsymbol{i}} \end{aligned}$$

where y_i is a categorical variable denoting whether the land cover structure i is 0: C_3-Heterogeneous/intermediate-mosaic, 1: Mixed/ C_4-Heterogeneous, 2: C_4-Homogeneous, α is the intercept term, $\beta 1$ is the effect of diet on the land cover structure type, and X is the stable carbon isotope value (δ^{13}C).

3.2.4 Model predictions: using modern data on impala habitats and diet to inform on land cover composition and structure in the past

For the last part of the analysis, the logistic regression models obtained after analysing the relationship between the diet of modern specimens and the remote sensing data from their region of origin were used on stable carbon isotope data on fossil impala specimens (genus *Aepyceros*) from Koobi Fora, Nachukui and Shungura. This was to evaluate to which land cover types these individuals were likely associated, based on stable carbon isotope data and predictions generated by the models produced in the study.

3.2.4.1 Fossil assemblage

3.2.4.1.1 Material

Fossil dental remains of *Aepyceros* specimens from the Koobi Fora and the Nachukui formations were sampled for isotopic studies at the National Museums of Kenya (Nairobi), as well as Aepyceros specimens from the Shungura Formation (Fm) curated at the National Museum of Ethiopia (Addis-Ababa) (see detail of the samples in the supplementary dataset).

3.2.4.1.2 Data collection

Prior to sampling, selected areas of the teeth were cleaned: adhering loose matrix was removed using a damp cotton swab, and acetone was used locally for glue residues if necessary. Bulk sampling was performed on the assemblage, and consisted in the extraction of 7-9 mg of enamel powder from the tooth surface using a 1mm diameter diamond-tipped drill bit. Slow-medium drilling speed was applied to prevent local heating (Lee-Thorp *et al.* 1997). This left a light scratch on the fossil tooth. The orientation of the samples varied depending on the museums' curatorial preferences (i.e. along broken edges at the National Museums of Kenya; following the mesio-distal width of the tooth at the National Museum of Ethiopia). A total of 259 bulk samples were collected on the fossil assemblage.

3.2.4.1.3 Additional data

To increase sample size, previously published data were also used in this study, from other *Aepyceros* specimens found in the Omo-Turkana basin (Cerling *et al.*, 2013, 2015; Negash *et al.*, 2015; Du *et al.*, 2019) (see appendix A.8).

3.2.4.1.4 Sample pre-treatment

The enamel powder collected on the studied specimens was cleaned using standard pre-treatment methods for the removal of organic and carbonate contaminants. In addition to the enamel samples collected for this study, enamel samples of known isotopic composition were also pre-treated (FBS and LES equid, provided by P. Hopley, Birkbeck), to be used as internal standards during isotopic analysis, and to check for the impact of pre-treatment on the expected values. Powdered enamel is typically pre-treated with dilute sodium hypochlorite (NaOCl) or hydrogen peroxide (H_2O_2) to remove organic matter, followed by leaching with a solution of acetic acid (0.1M) to dissolve secondary mineral contaminants (Koch, Tuross and Fogel, 1997; Rowland, 2006). This pre-treatment should only leave purified structural carbonate for analysis.

Each enamel sample therefore went through a first wash using 1ml dilute sodium hypochlorite (NaOCl - bleach 2%- rest for 45min), followed by 3 rinses using deionised water (ultra-pure), to remove organic matter. Each sample was then washed a second time using 0.5 ml dilute acetic acid (0.1M – rest for 15min), followed by 3 rinses using deionised water, to dissolve secondary mineral contaminants. The samples were centrifuged between each wash to facilitate the removal of the liquid elements and were dried overnight in a drying oven at low temperature (70°C).

To control for the effect of pre-treatment procedures on the samples, two internal enamel standards of known isotopic composition (LES and FBS standards, provided by Philip Hopley, UCL Birkbeck) were pre-treated and analysed alongside the studied samples. The LES standard controlled for the grazing end of the dietary spectrum (i.e. n = 12; $\delta^{13}C$ mean = 0.08‰, sd = 0.27; $\delta^{18}O$ mean = 2.00‰, sd = 0.5), while the FBS standard controlled for the browsing end of the spectrum (i.e. n = 15; $\delta^{13}C$ mean = -11.45‰, sd = 0.05; $\delta^{18}O$ mean = -4.55‰, sd = 0.12).

3.2.4.1.5 Mass-spectrometry data acquisition

The samples were analysed at the Stable Isotope Ratio Mass-Spectrometry (SIRMS) Laboratory (University of Southampton, National Oceanography Centre; procedure performed by Megan Spencer) using a Kiel Carbonate Device coupled to a MAT253 Isotope Ratio Mass Spectrometer (both Thermo Fisher Scientific, Bremen, Germany). 0.3-0.6 mg of each sample was weighed out into borosilicate glass vials according to their $CaCO_3$ concentration in order to match ~30-40 µg of pure $CaCO_3$. During subsequent analysis, they reacted with 106% phosphoric acid at 90°C for 800 seconds. After cryogenic removal of water vapour and other gases, the resulting CO_2 was measured multiple times against a reference gas. Following data reduction and corrections, data were normalised using a two-point calibration with NBS 18 and NBS 19 (IAEA, Vienna, Austria) and reported relative to VPDB (Vienna PeeDee Belemnite). The $\delta^{18}O$ and $\delta^{13}C$ values were obtained from these analyses using the following calculation:

Equation 3. 1: $\delta x = 1000[(R_{sample}/R_{standard}) - 1]$

(where δx is either $\delta^{13}C$ or $\delta^{18}O$, and R is either $^{13}C/^{12}C$ or $^{18}O/^{16}O$.)

In-house reference material (GS1) was used for quality assurance purposes and to report instrument precision (Coplen, 1994). Long-term instrument precision is 0.05‰ for $\delta^{13}C$ and 0.09‰ for $\delta^{18}O$ (Thermo Scientific, 2009).

3.2.4.2 Predicting land cover patterns – testing the models with fossil samples

The multinomial logistic regression models produced using modern data on land cover and impala dietary behaviours in the seven study areas were tested on the stable carbon isotope data collected from fossil *Aepyceros melampus* for this study. This was to assess what types of land cover patterns could potentially be 'predicted' from paleo-dietary data.

Prior to running the analyses, modern values were corrected (following Long *et al.*, 2005; Ferrio *et al.* 2005; Keeling *et al.* 2010; Bocherens *et al.* 2014) to take into account the "fossil fuel effect" (or Suess Effect) that led to a depletion of ambient atmospheric $\delta^{13}C$ values compared to values from the pre-industrial era (Keeling, Mook and Tans, 1979; Marino and McElroy, Michael, 1991; Kingston and Harrison, 2007).

3.3 Results

3.3.1 Dietary variation in modern impala specimens: Stable carbon isotope evidence

This section explores the dietary patterns that can be evaluated via stable carbon isotope studies from the extant impala (*Aepyceros melampus*) samples selected for each studied locality.

When the selected *Aepyceros melampus* samples from the seven studied localities (Table 16) were compared to stable carbon isotope data published for grazers (*Equus quagga*) and browsers (*Giraffa camelopardalis*) from some of the studied localities (Cerling *et al.*, 2015), the selected modern impala specimens were shown to yield a wide range of $\delta^{13}C$ values spreading across the dietary spectrum, indicative of a large dietary breadth for this species, as expected for mixed-feeding herbivores (Figure 22).

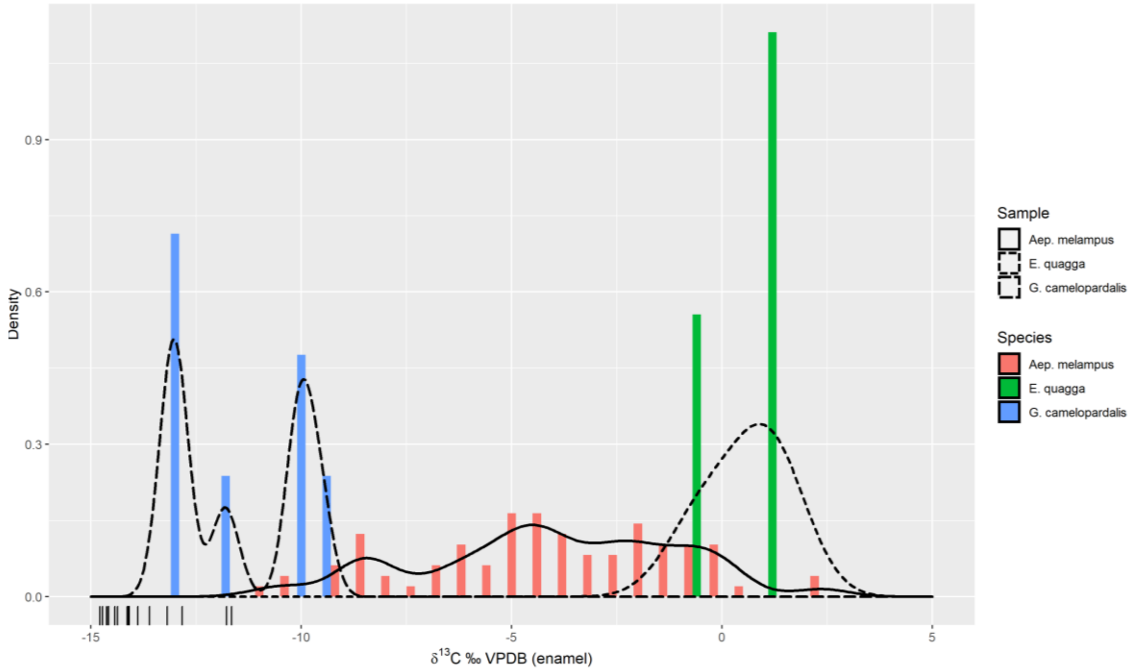

Figure 22: Kernel density estimates for δ^{13}C-enamel for the totality of the selected modern *Aepyceros melampus* specimens, along with values deriving from published data for *Giraffa camelopardalis* and *Equus quagga* specimens from some of the studied localities (Cerling *et al.* 2015; see Appendix A.8). These highlight, as expected for mixed-feeding herbivores, a large dietary breadth across all impala specimens.

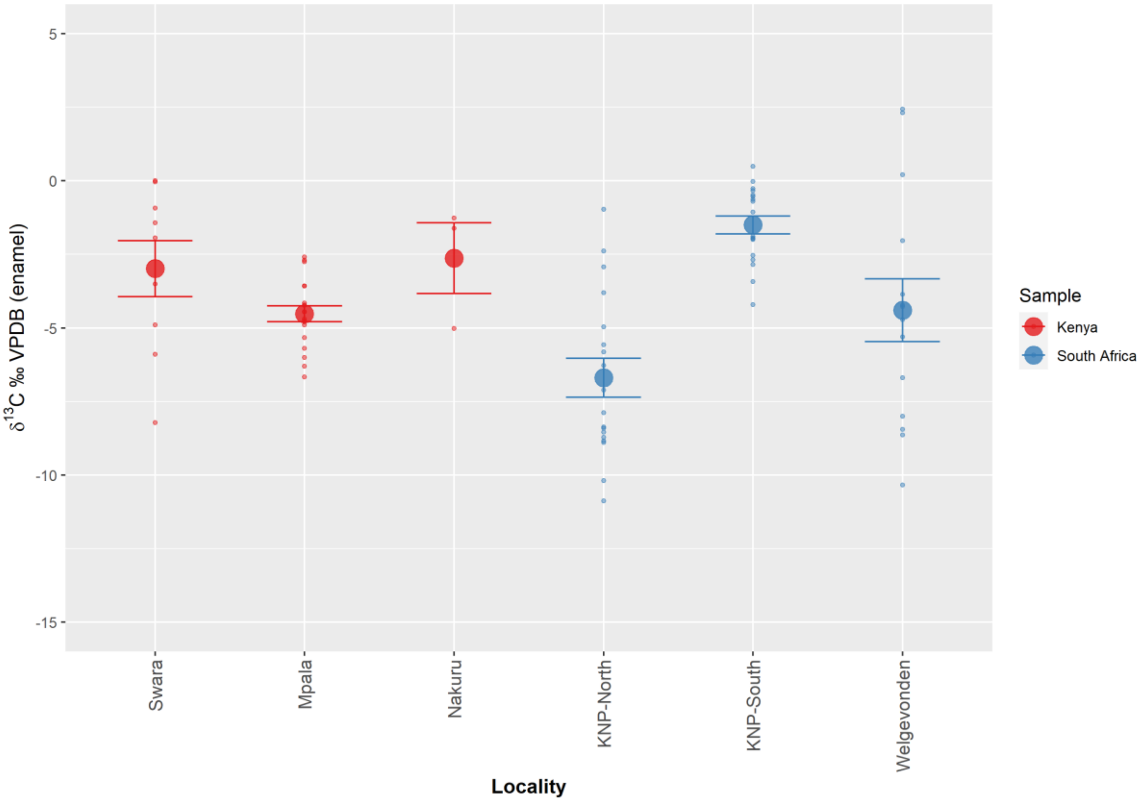

Figure 23: δ^{13}C-enamel values for each *Aepyceros melampus* sample studied, per locality.

Table 16: Descriptive statistics for stable carbon isotope samples of *Aepyceros melampus* specimens from each studied locality. δ^{13}C-raw values: carbon isotope values measured from the sampled materials (mean, standard deviation and standard error of the mean); δ^{13}C-enamel: measured or estimated enamel carbon isotope values (mean, minimum and maximum values).

Country	Locality - Year	N	δ^{13}C (‰) - raw values				δ^{13}C-enamel (‰)			Data
			Material	mean	s.d.	s.e.m.	mean	min	max	
Kenya	Hopcraft Game Ranch (Swara) - 1999	9	Enamel	-2.98	2.86	0.95	-2.98	-8.22	0.01	Levin *et al.*, 2006; Cerling *et al.*, 2015
	Mpala - 2001	19	Enamel	-4.52	1.17	0.27	-4.52	-6.67	-2.59	Levin *et al.*, 2006; Cerling *et al.*, 2015
	Nakuru NP shoreline - 2000	3	Enamel	-2.63	2.08	1.20	-2.63	-5.02	-1.26	Levin *et al.*, 2006; Cerling *et al.*, 2015
	El Karama - 1998	3	Enamel	-3.15	3.27	1.89	-3.15	-6.23	0.29	Levin *et al.*, 2006; Cerling *et al.*, 2015
South Africa	KNP-North - 2001-2002	18	Hair	-17.80	2.8	/	-6.70	/	/	Sponheimer *et al.*, 2003
	KNP-South - 2001-2002	18	Hair	-12.60	1.3	/	-1.50	/	/	Sponheimer *et al.*, 2003
	Welgevonden - 2002-2003	14	Faeces	-19.40	4.00	/	-4.40	/	/	Codron *et al.*, 2005

Table 17: Estimated percentage of C_4 -plant material contained in the diet based on stable carbon isotope samples of *Aepyceros melampus* specimens from each studied locality (mean, lower and upper confidence intervals – 95%). δ^{13}C-diet: estimated carbon isotope values of the plant material consumed (mean).

Country	Locality - Year	N	δ^{13}C-diet (‰)	% C_4-plant		
				LCI	mean	UCI
Kenya	Hopcraft Game Ranch (Swara) - 1999	9	-16.48	56.07	71.34	86.61
	Mpala - 2001	19	-18.02	56.71	60.65	64.59
	Nakuru NP shoreline - 2000	3	-16.13	37.88	73.77	100.00
	El Karama - 1998	3	-16.65	12.03	70.16	100.00
South Africa	KNP-North - 2001-2002	18	-20.80	31.66	41.35	51.03
	KNP-South - 2001-2002	18	-15.60	72.94	77.46	81.97
	Welgevonden - 2002-2003	14	-18.50	41.27	57.32	73.36

When evaluating the range of stable carbon isotopes values of the specimens (δ^{13}C-enamel) across the different modern impala samples, some degree of variation could be observed (Figure 23 and Table 16). The highest values were observed for the impala samples from KNP-South (mean δ^{13}C-enamel = -1.5 ‰), followed by samples from Nakuru (mean δ^{13}C-enamel = -2.63 ‰), Swara (mean δ^{13}C-enamel = -2.98 ‰), and El Karama (mean δ^{13}C-enamel = -3.15 ‰). The lowest δ^{13}C-diet values were observed at Mpala (mean δ^{13}C-enamel = -4.52 ‰), and for specimens from the South African localities Welgevonden (mean δ^{13}C-enamel = -4.4 ‰) and KNP-North (mean δ^{13}C-enamel = -6.70‰).

Table 18: Result from the Kruskal-Wallis test evaluating whether differences can be observed between localities based on the δ^{13}C-enamel values of the selected *A. melampus* specimens.

Kruskal-Wallis		
Chival	**DF**	**Pval**
31.9717465	5	**6.02E-06**

Table 19: Results from the Dunn-Test evaluating whether differences can be observed when comparing modern *A. melampus* samples per locality, based on δ^{13}C-enamel values.

Dunn Test			
Comparison	**ZVal**	**Pval**	**Pvaladjust**
KNP-North - KNP-South	-5.317	**0.000**	**0.000**
KNP-North - Mpala	-1.772	0.076	1
KNP-North - Nakuru	-2.060	0.039	0.433
KNP-North - Swara	**-3.019**	**0.003**	**0.000**
KNP-North - Welgevonden	-1.885	0.059	0.594
KNP-South - Mpala	3.616	**0.000**	**0.004**
KNP-South - Nakuru	0.782	0.434	1.000
KNP-South - Swara	1.322	0.186	1
KNP-South - Welgevonden	**3.088**	**0.002**	**0.026**
Mpala - Nakuru	-1.130	0.259	1.000
Mpala - Swara	-1.606	0.108	0.867
Mpala - Welgevonden	-0.252	0.801	1.000
Nakuru - Swara	0.078	0.938	1
Nakuru - Welgevonden	0.963	0.335	1
Swara - Welgevonden	1.313	0.189	1.000

Results from comparative statistics (Table 44 and Table 45) show that specimens from KNP-South significantly differ from KNP-North ($p<0.000$), from Mpala ($p=0.004$), and from Welgevonden ($p=0.026$) by having higher $\delta^{13}C$ values. On the other end of the spectrum, specimens from KNP-North significantly differ from specimens from Swara ($p<0.000$) by having lower $\delta^{13}C$ values. Significant differences are not found between other localities and either Nakuru or El Karama, potentially due to small sample size and high standard deviation/standard error within these samples.

These results suggest differing dietary patterns between the studied impala samples, more particularly with diets rich in C_4-vegetation in the Kenyan localities and in KNP-South, and mixed C_3 - C_4 diets in some of the South African localities (KNP-North and Welgevonden). These differences could potentially relate to differing environmental conditions, including differing land cover patterns.

3.3.2 Land cover data from modern impala habitats

This section explores the land cover composition and land cover structure of the studied localities as assessed from the data acquired and analysed from the Africover products from 1995-1999 (from Kenyan localities) and the Globcover land cover products from 2005-2006 (for the South African localities). Results from the land cover composition analysis are presented, followed by results from the clustering analyses.

3.3.2.1 Land cover composition - Class metrics

3.3.2.1.1 General land cover classes

When observing landcover patterns at the class level using the Africover and Globcover products using the general land cover classification, various patterns could be observed for each locality (Table 21-21 and Figure 24).

3.3.2.1.1.1 Kenyan localities – El Karama, Mpala, Nakuru and Swara

All localities in Kenya were shown to be dominated by closed to open (>15%) herbaceous vegetation (grassland, savannas, or lichens/mosses), followed by mosaic forest or shrubland (50-70%) / grassland (20-50%).

Mpala: land cover dominated by medium-size patches of closed to open (>15%) herbaceous vegetation (grassland, savannas, or lichens/mosses) (LPI=27.85%), and smaller patches of mosaic forest or shrubland (50-70%) with grassland (20-50%) (LPI=14.1%).

El Karama: land cover dominated by large patches of closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (LPI=91.23%), and small patches of mosaic forest or shrubland (50-70%) / grassland (20-50%) (LPI=6.57%).

Nakuru: land cover dominated by small-size patches of closed to open (>15%) herbaceous vegetation (grassland, savannas, or lichens/mosses) (LPI=7.7%), and slightly larger patches mosaic forest or shrubland (50-70%) / grassland (20-50%) (LPI= 12.73%).

Swara: land cover dominated by large patches of closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (LPI=80.96%), and small-size patches of mosaic forest or shrubland (50-70%) / grassland (20-50%) (LPI=9.97%).

3.3.2.1.1.2 South African localities – KNP-North, KNP-South, Welgevonden

All of the studied South African localities are dominated by large patches (KNP-South and Welgevonden with LPI>40%) or medium-size patches (KNP-North with LPI=29.92%) of closed to open shrubland. While this dominating shrubland is associated mainly with small patches (i.e. LPI<15%) of mosaic vegetation (50-70%) with cropland (20-50%) in Welgevonden and in KNP-North, it is associated mainly with small patches of open broadleaved deciduous forest/woodland in KNP-South.

Table 20: Class metrics summary for each studied locality (general land cover classification).

Country	Locality	Predominant land cover classes (PLAND)	Associated largest patch index (LPI)	Associated number of patches (NP)	Land cover class(es) with the largest number of patches (NP)
Kenya	El Karama	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (91.23 %)	91.23	1	Mosaic forest or shrubland (50-70%) / grassland (20-50%) (NP=5)
		Mosaic forest or shrubland (50-70%) / grassland (20-50%) (8.77 %)	6.57	5	
	Mpala	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (56.38 %)	27.85	11	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (NP=11) AND Open (15-40%) broadleaved deciduous forest/woodland (>5m) (NP=11)
		Mosaic forest or shrubland (50-70%) / grassland (20-50%) (28.39 %)	14.10	7	
	Nakuru	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (27.45 %)	7.70	9	Cultivated and managed areas / Rainfed cropland (NP=19)
		Mosaic forest or shrubland (50-70%) / grassland (20-50%) (27.29%)	12.73	3	
	Swara	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses) (84.02 %)	80.96	3	Mosaic forest or shrubland (50-70%) / grassland (20-50%) (NP=6)
		Mosaic forest or shrubland (50-70%) / grassland (20-50%) (15.39 %)	9.97	6	
South Africa	KNP-North	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m) (47.49%)	29.92	438	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%) (NP=1213)
		Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%) (22.71%)	1.9	1213	
	KNP-South	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m) (47.97%)	43.19	325	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%) (NP=724) AND Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m) (NP=719)
		Open (15-40%) broadleaved deciduous forest/woodland (>5m) (21.86%)	4.46	659	
	Welgevonden	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m) (58.12%)	52.66	17	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m) (NP=43)
		Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%) (24.09%)	13.94	36	

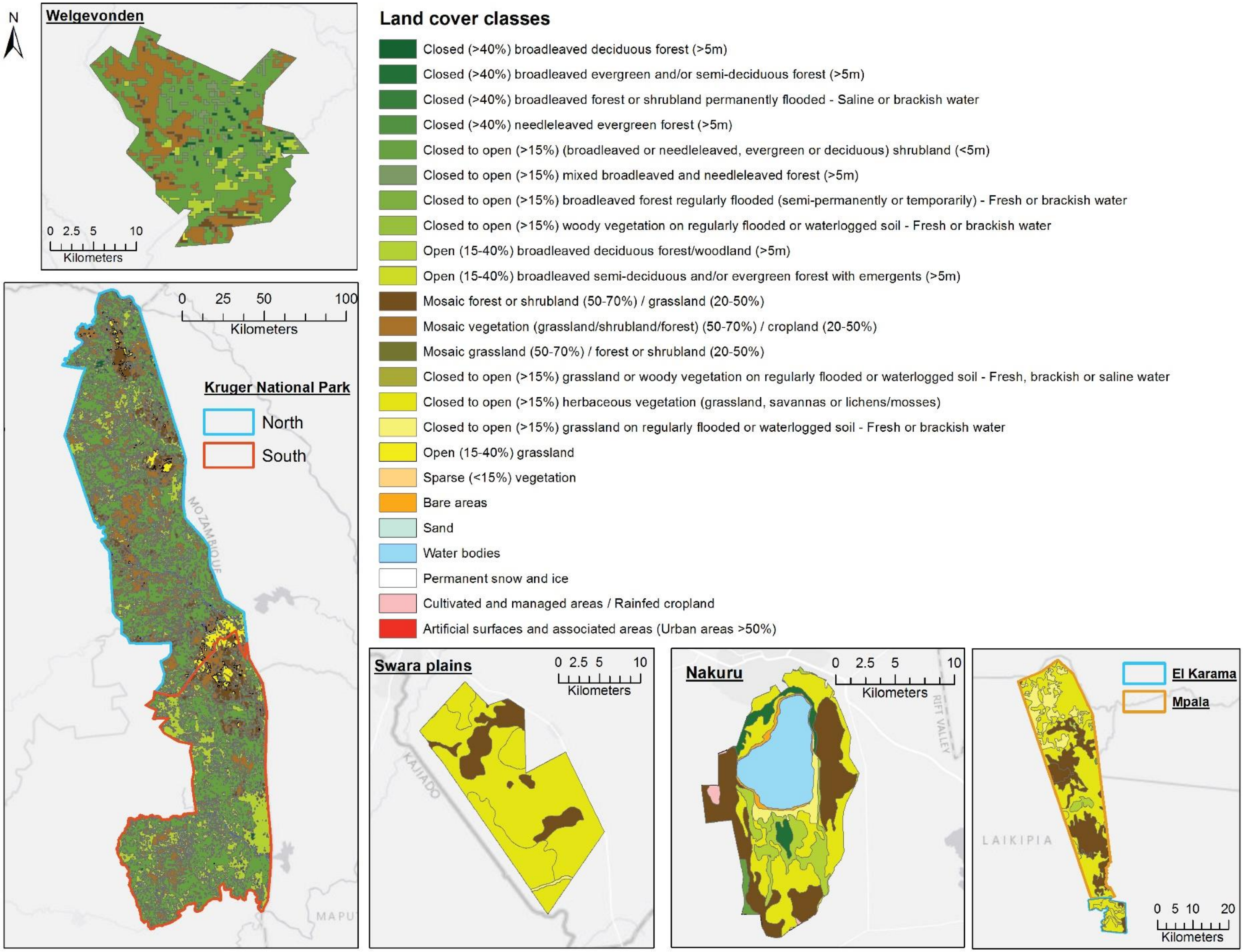

Figure 24: Land cover map (based on general land cover classes) for each studied locality.

Table 21: Percentage of Landscape (PLAND) values (based on general land cover classes) for each studied locality. ***(Note: land cover classes that were not identified in any of the studied localities were excluded from the table).***

LC	**Land cover class**	**Kenya**				**South Africa**		
		El Karama	**Mpala**	**Nakuru**	**Swara**	**KNP-North**	**KNP-South**	**Welgevonden**
1	Cultivated and managed areas / Rainfed cropland			0.98	0.00		0.03	
3	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)					22.71	11.30	24.09
5	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest (>5m)			4.79				
6	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)							
7	Closed (>40%) broadleaved deciduous forest (>5m)					0.92	0.54	2.70
8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)		2.46	11.02		9.21	21.86	7.41
10	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)					0.02		
13	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)					6.24	6.68	4.76
15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	8.77	**28.39**	**27.29**	**15.39**	8.62	7.76	2.77
16	Mosaic grassland (50-70%) / forest or shrubland (20-50%)					0.84	1.49	0.05
17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)		0.24	1.20		**47.49**	**47.97**	**58.12**
20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	**91.23**	**56.38**	**27.45**	**84.02**	0.78	0.41	0.12
21	Open (15-40%) grassland					2.72	1.74	
22	Sparse (<15%) vegetation					0.00		
25	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water							
26	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water		12.53					
27	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water			3.51	0.59			
28	Artificial surfaces and associated areas (Urban areas >50%)			0.03		0.02		
29	Bare areas			2.06				
30	Water bodies			21.66		0.41	0.22	
	Total area (ha)	**6291**	**84078**	**18567**	**28521**	**1290807**	**989442**	**38403**

Table 22: Largest Patch Index (LPI) values (based on general land cover classes) for each studied locality. (Note: land cover classes that were not identified in any of the studied localities were excluded from the table).

LC	Land cover class	Kenya				South Africa		
		El Karama	Mpala	Nakuru	Swara	KNP-North	KNP-South	Welgevonden
1	Cultivated and managed areas / Rainfed cropland			0.74	0.00		0.01	
3	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)					1.90	1.41	13.94
5	Closed (>40%) broadleaved evergreen and/or semi-deciduous forest (>5m)			3.27				
6	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)							
7	Closed (>40%) broadleaved deciduous forest (>5m)					0.16	0.08	0.23
8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)		1.82	9.26		0.56	4.46	1.24
10	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)					0.01		
13	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)					0.35	0.22	0.49
15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	6.57	14.10	**12.73**	9.97	0.95	2.34	0.49
16	Mosaic grassland (50-70%) / forest or shrubland (20-50%)					0.08	0.08	0.05
17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)		0.20	1.20		**29.92**	**43.19**	**52.66**
20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	**91.23**	**27.85**	7.70	**80.96**	0.05	0.06	0.09
21	Open (15-40%) grassland					1.42	0.39	
22	Sparse (<15%) vegetation					0.003		
25	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water							
26	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water		8.66					
27	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water			3.51	0.59			
28	Artificial surfaces and associated areas (Urban areas >50%)			0.02		0.02		
29	Bare areas			1.26				
30	Water bodies			21.65		0.03	0.02	

Table 23: Number of patches (NP) (based on general land cover classes) for each studied locality. (Note: land cover classes that were not identified in any of the studied localities were excluded from the table).

LC	Land cover class	Kenya				South Africa		
		El Karama	Mpala	Nakuru	Swara	KNP-North	KNP-South	Welgevonden
1	Cultivated and managed areas / Rainfed cropland			**19**	1		7	
3	Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)					**1213**	**724**	36
5	Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents (>5m)			2				
6	Closed (>40%) broadleaved deciduous forest (>5m)							
7	Closed (>40%) broadleaved deciduous forest (>5m)					111	73	28
8	Open (15-40%) broadleaved deciduous forest/woodland (>5m)		**11**	6		676	659	24
10	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)					3		
13	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)					776	**719**	**43**
15	Mosaic forest or shrubland (50-70%) / grassland (20-50%)	**5**	7	3	**6**	673	323	22
16	Mosaic grassland (50-70%) / forest or shrubland (20-50%)					188	198	1
17	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)		3	1		438	325	17
20	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	1	**11**	9	3	180	59	2
21	Open (15-40%) grassland					108	41	
22	Sparse (<15%) vegetation					3		
25	Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water							
26	Closed to open (>15%) woody vegetation on regularly flooded or waterlogged soil - Fresh or brackish water		**10**					
27	Closed to open (>15%) grassland on regularly flooded or waterlogged soil - Fresh or brackish water			1	1			
28	Artificial surfaces and associated areas (Urban areas >50%)			**11**		2		
29	Bare areas			2				
30	Water bodies			5		74	55	

3.3.2.1.2 C_3 - C_4 land cover classes

When observing landcover patterns at the class level using the Africover and Globcover products with the C_3 - C_4 classification, various patterns could be observed for each locality (Table 24-25 and Figure 25).

Among the studied localities, El Karama, Mpala and Swara (Kenya) appeared to be dominated by mixed-vegetation with a predominance of C_4 -vegetation (50-70%) (PLAND>40%), associated with a much smaller 'mixed-vegetation with a predominance of C_3 -vegetation (50-70%)' component (PLAND<15%).

The land cover in Nakuru (Kenya) was shown to be more heterogeneous, with a similar amount of 'mixed-vegetation with a predominance of C_3 -vegetation (50-70%)' (PLAND=27.48%) and 'mixed-vegetation with a predominance of C_4 -vegetation (50-70%)' (PLAND=27.45%) in the landscape.

The South African localities were all shown to be dominated by large patches of C_3 -vegetation associated with small patches of mixed C_3 - C_4 vegetation. The largest patches of C_3 -vegetation were observed in KNP-South, suggesting slightly less fragmented vegetation in this locality, especially when compared to KNP-North. The land cover patterns observed in Welgevonden seemed to differ slightly from those observed in the Kruger National Park when focusing on mixed C_3 - C_4 vegetation, which were represented by larger patches in Welgevonden than in the KNP localities.

These differences and similarities between the studied localities were also reflected in the C_4 -index values calculated for each locality based on the class-level metrics extracted from the land cover maps produced with the C_3 - C_4 classification (see 4.2.3.4 Evaluating the proportion of C_4 -vegetation in the landscape – the C_4 -Index).

Table 24: Class metrics summary for each studied locality (C_3 - C_4 classification).

Country	Locality	Predominant land cover classes (PLAND)	Associated largest patch index (LPI)	Associated number of patches (NP)	Land cover class(es) with the largest number of patches (NP)	C4-Index
Kenya	El Karama	Mixed-vegetation - Predominance C_4-vegetation (50-70%) (91.23 %)	91.23	1	Mixed-vegetation - Predominance C_3-vegetation (50-70%) (NP=5)	70.61
		Mixed-vegetation - Predominance C_3-vegetation (50-70%) (8.77 %)	6.57	5		
	Mpala	Mixed-vegetation - Predominance C_4-vegetation (50-70%) (67.94 %)	40.88	9	C_3-vegetation (70-100%) (NP=13)	59.08
		Mixed-vegetation - Predominance C_3-vegetation (50-70%) (28.6 %)	14.10	8		
	Nakuru	Mixed-vegetation - Predominance C_3-vegetation (50-70%) (27.48 %)	12.73	7	Cultivated and managed areas / Rainfed cropland (NP=19)	41.15
		Mixed-vegetation - Predominance C_4-vegetation (50-70%) (27.45 %)	7.70	9		
	Swara	Mixed-vegetation - Predominance C_4-vegetation (50-70%) (84.02%)	80.96	3	Mixed-vegetation - Predominance C_3-vegetation (50-70%) (NP=6)	67.45
		Mixed-vegetation - Predominance C_3-vegetation (50-70%) (15.39 %)	9.97	6		
South Africa	KNP-North	C_3-vegetation (70-100%) (63.88%)	55.41	252	Mixed-vegetation (C_3/ C_4 vegetation; 50/50%) (NP=1213)	17.73
		Mixed-vegetation (C_3/ C_4 vegetation; 50/50%) (22.71%)	1.90	1213		
	KNP-South	C_3-vegetation (70-100%) (77.04%)	76.24	104	Mixed-vegetation (C_3/ C_4 vegetation; 50/50%)(NP=724)	10.89
		Mixed-vegetation (C_3/ C_4 vegetation; 50/50%) (11.3%)	1.41	724		
	Welgevonden	C_3-vegetation (70-100%) (72.98%)	67.75	13	Mixed-vegetation (C_3/ C_4 vegetation; 50/50%)(NP=36)	12.89
		Mixed-vegetation (C_3/ C_4 vegetation; 50/50%) (24.09%)	13.94	36		

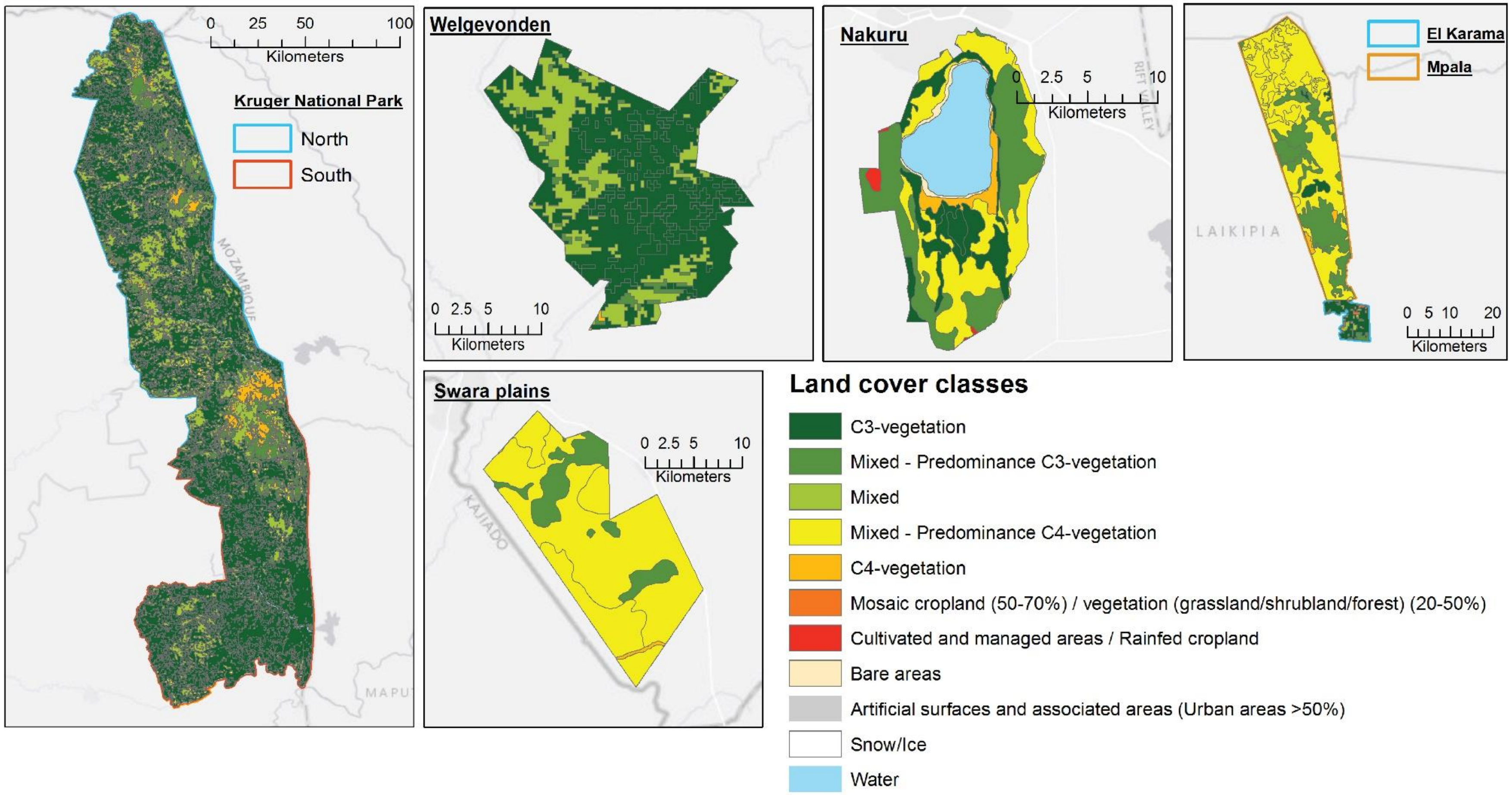

Figure 25: Landcover map (based on C_3 - C_4 land cover classes) for each studied locality.

Table 25: Percentage of Landscape (PLAND) values (based on C_3 - C_4 land cover classes) for each studied locality.

C3-C4 code	Land cover class	Kenya				South Africa		
		El Karama	Mpala	Nakuru	Swara	KNP-North	KNP-South	Welgevonden
Cplant-1	C3-vegetation (70-100%)		2.49	16.82		**63.88**	**77.04**	**72.98**
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	8.77	**28.60**	**27.48**	15.39	8.62	7.76	2.77
Cplant-3	Mixed-vegetation (C3/C4 vegetation; 50/50%)					22.71	11.30	24.09
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	**91.23**	**67.94**	**27.45**	**84.02**	0.84	1.49	0.05
Cplant-5	C4-vegetation (70-100%)		0.97	3.51	0.59	3.51	2.15	0.12
Cplant-6	Cultivated and managed areas / Rainfed cropland			0.98	0.00		0.03	
Cplant-7	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)							
Cplant-8	Artificial surfaces and associated areas (Urban areas >50%)			0.03		0.02		
Cplant-9	Bare areas			2.06				
Cplant-10	Water bodies			21.66		0.41	0.22	
Cplant-11	Permanent snow and ice							
	Total area (ha)	6286	84050	18571	28472	1290807	989442	38403
	C4-Index	70.61	59.08	41.15	67.45	17.73	10.89	12.89

Table 26: Largest Patch Index (LPI) values (based on C_3 - C_4 land cover classes) for each studied locality.

C3-C4 code	Land cover class	Kenya				South Africa		
		El Karama	Mpala	Nakuru	Swara	KNP-North	KNP-South	Welgevonden
Cplant-1	C3-vegetation (70-100%)		1.82	10.78		**55.41**	**76.24**	**67.75**
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	6.57	14.10	**12.73**	9.97	0.95	2.34	0.49
Cplant-3	Mixed-vegetation (C3/C4 vegetation; 50/50%)					1.90	1.41	13.94
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	**91.23**	**40.88**	7.70	**80.96**	0.08	0.08	0.05
Cplant-5	C4-vegetation (70-100%)		0.60	3.51	0.59	1.46	0.40	0.09
Cplant-6	Cultivated and managed areas / Rainfed cropland			0.74	0.00		0.01	
Cplant-7	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)							
Cplant-8	Artificial surfaces and associated areas (Urban areas >50%)			0.02		0.02		
Cplant-9	Bare areas			1.26				
Cplant-10	Water bodies			21.65		0.03	0.02	
Cplant-11	Permanent snow and ice							

Table 27: Number of patches (NP) (based on C3 - C4 land cover classes) for each studied locality.

C3-C4 code	Land cover class	Kenya				South Africa		
		El Karama	Mpala	Nakuru	Swara	KNP-North	KNP-South	Welgevonden
Cplant-1	C3-vegetation (70-100%)		**13**	4		252	104	13
Cplant-2	Mixed-vegetation - Predominance C3-vegetation (50-70%)	**5**	8	7	**6**	673	323	22
Cplant-3	Mixed-vegetation (C3/C4 vegetation; 50/50%)					**1213**	**724**	**36**
Cplant-4	Mixed-vegetation - Predominance C4-vegetation (50-70%)	1	9	9	3	188	198	1
Cplant-5	C4-vegetation (70-100%)		3	1	1	256	83	2
Cplant-6	Cultivated and managed areas / Rainfed cropland			**19**	1		7	
Cplant-7	Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)							
Cplant-8	Artificial surfaces and associated areas (Urban areas >50%)			11		2		
Cplant-9	Bare areas			2				
Cplant-10	Water bodies			5		74	55	
Cplant-11	Permanent snow and ice							

3.3.2.2 Land cover structure and composition - Landscape metrics

3.3.2.2.1 General observations

The various landscape metrics produced with the C_3 - C_4 classification allowed to compare more generally the composition (C_4 -Index) and structure (LPI, DIVISION, SIDI) of each studied locality to see how these might resemble or differ from each other (Table 28).

Table 28: Landscape metrics for each studied locality. Land cover structure variables (i.e. LPI, DIVISION and SIDI) are calculated from the general land cover classification maps. Land cover composition (i.e. C_4 -Index) is calculated from the C_3 - C_4 land cover classification maps.

Sample		Fragstats			
Country	**Locality**	**LPI**	**DIVISION**	**SIDI**	**C4-Index**
Kenya	El Karama	91.23	0.16	0.16	70.61
	Mpala	27.85	0.83	0.59	59.08
	Nakuru	21.65	0.90	0.79	41.15
	Swara	80.96	0.33	0.27	67.45
South Africa	KNP - North	29.92	0.90	0.70	17.73
	KNP - South	43.19	0.81	0.70	10.89
	Welgevonden	52.66	0.70	0.59	12.89

3.3.2.2.1.1 Largest Patch Index (LPI)

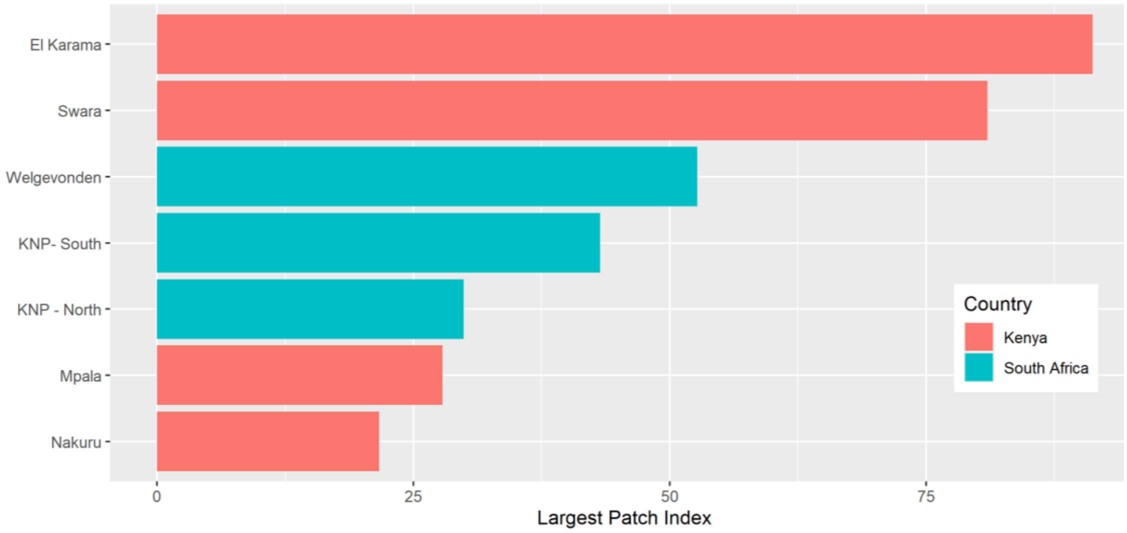

Figure 26: Largest Patch Index values per locality.

Values for the Largest Patch Index (LPI) (Figure 26) suggested landscapes mostly dominated by one patch type (i.e. high LPI values, LPI>70) at El Karama and Swara. On the contrary, the lowest LPI values (i.e. LPI<30) observed at Nakuru, Mpala, and KNP-North suggested landscapes composed of rather small patches, hence not dominated by large patches of one single vegetation type. The medium-range LPI values observed at KNP-South and Welgevonden indicated landscapes dominated by medium-size patches.

3.3.2.2.1.2 Landscape division index (DIVISION)

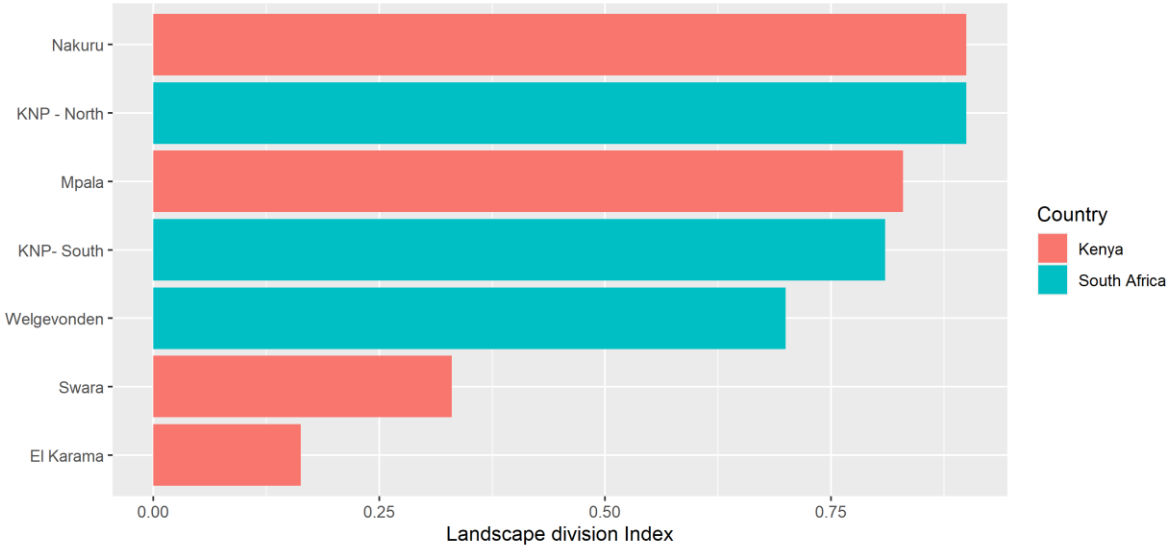

Figure 27: Landscape Division Index values per locality.

Similarly to the LPI, the Landscape Division Index (DIVISION) allowed to evaluate the degree of division within each locality's focal patches, with lower values observed when the landscape consists of a single patch, and higher values when vegetation patch types are highly divided across the landscape. The lower values (DIVISION <0.35) observed in El Karama and Swara confirmed that these localities consist mainly of one or few focal patches (Figure 27). The highest DIVISION values (DIVISION>0.7) observed for the other five localities suggested that in these localities the various patch types tend to be highly divided into single small patches.

3.3.2.2.1.3 Simpson's Diversity Index (SIDI)

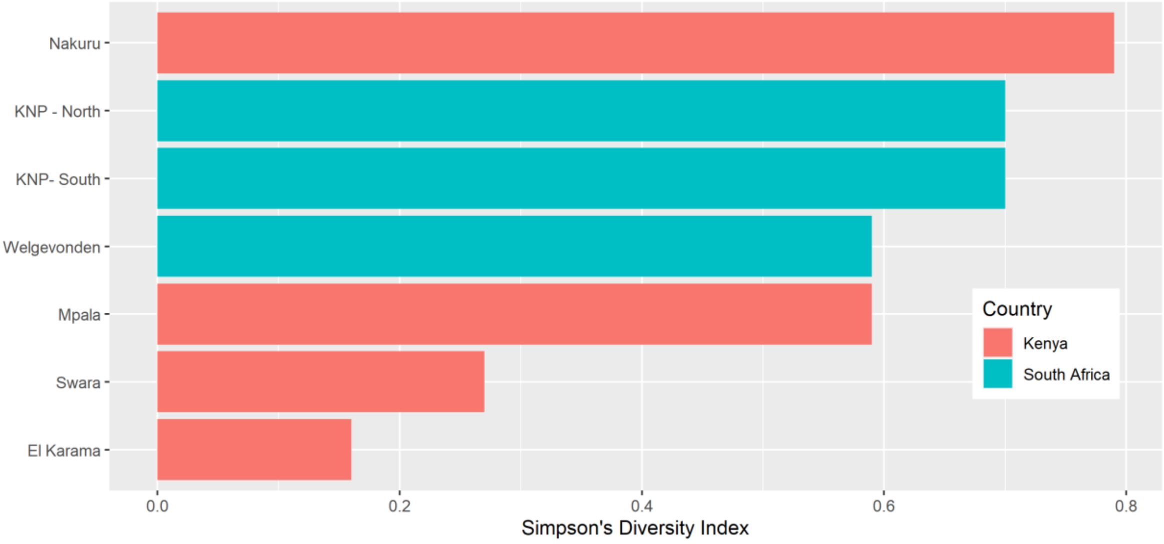

Figure 28: Simpson's Diversity Index values per locality.

The value of Simpson's Diversity Index (SIDI) represents the probability that any two land cover cells selected at random would be different patch types. Low values were expected for landscapes with low patch type diversity, and high values for landscapes with a higher number of different patch types and a more equitable proportional distribution of area among patch types. Low values (i.e. SIDI <0.3) were observed at El Karama and Swara (Figure 28). The highest values (i.e. SIDI>0.7) were found at Nakuru, KNP-North, and KNP-South, suggesting a higher patch type diversity in these localities. Land cover analyses for Mpala and Welgevonden both yielded intermediate-high SIDI values (SIDI=0.59), indicating a moderately high patch type diversity in these localities.

3.3.2.2.1.4 C_4 -Index

The value of the C_4 -Index represents the relative proportion of C_4 -vegetation identified in the landscape, as opposed to C_3 -vegetation. Low values (i.e. C_4-Index <20%) were observed at KNP-South, Welgevonden and KNP-North, indicating environments dominated by C_3 -vegetation (Figure 29). The highest values (i.e. C_4-Index >~60%) were found at El Karama, Swara, and Mpala, indicating habitats with a dominating C_4 -

component. The intermediate value at Nakuru (C_4 -Index=41.15%) suggested a more heterogeneous landscape likely composed of mixed C_3 - C_4 vegetation with a stronger C_3 -component.

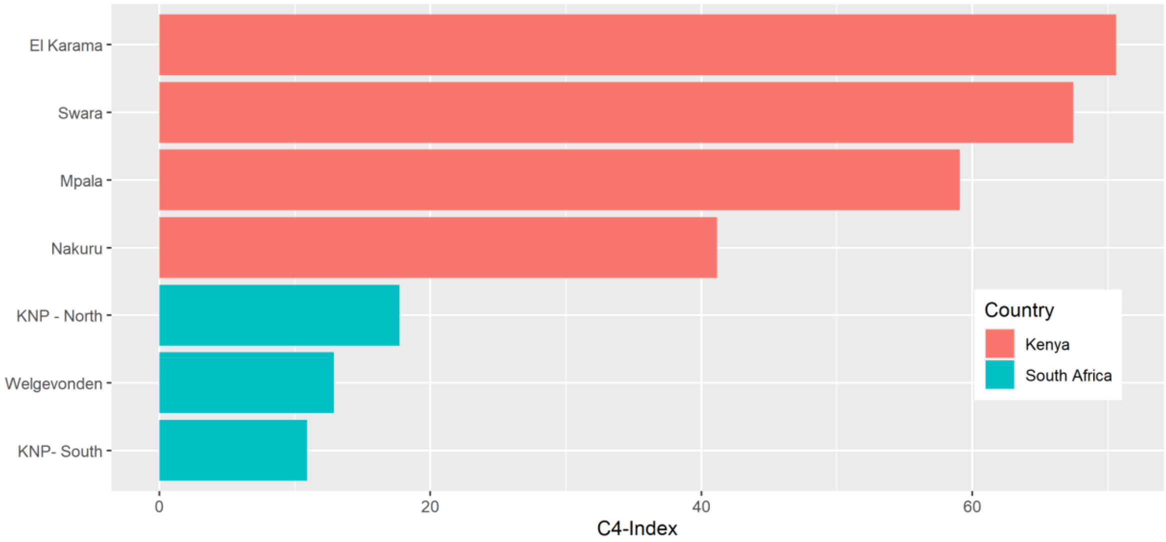

Figure 29: C_4 -Index values per locality.

3.3.2.2.3 Clustering analysis

To check whether some of the studied localities shared similar land cover composition or structure characteristics and could be grouped accordingly, clustering analyses were computed using the k-means algorithm and the relevant landscape variables.

3.3.2.2.3.1 Land cover composition

Results from the K-means clustering analysis using the C_4 -Index as a grouping variable showed that Nakuru alone was attributed to cluster 1 with a low-mid-range C_4-Index value indicative of mixed C_3 - C_4 environments with a slight predominance of C_3 -vegetation (C_4 -Index = 41.15%) (Table 29 and Figure 30). For further analyses, this locality was therefore considered as representing “mixed-habitats”.

Table 29: Results from K-means clustering with 3 clusters using the land cover composition variable C_4-Index.

Cluster	Localities	C4-Index (mean)	Habitat	Within-cluster sum of squares
1	Nakuru	41.15	Mixed-habitats	0
2	KNP-South, KNP-North, Welgevonden	13.84	C_3-habitats	24.74
3	Mpala, Swara, El Karama	65.71	C_4-habitats	70.99
			between_SS / total_SS	97.70%

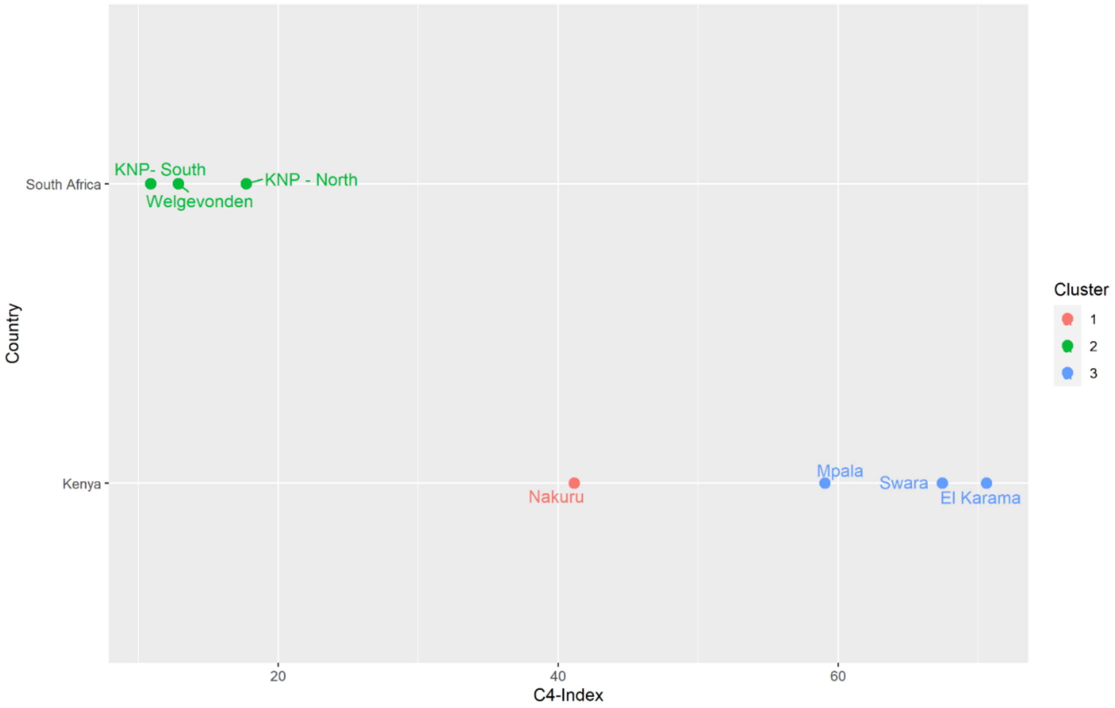

Figure 30: Clusters identified by the K-means algorithm using the land cover composition variable C_4-Index.

All three South African localities were grouped in cluster 2. These localities were characterised by low C_4-Index values (C_4-Index < 20%) indicative of C_3-dominated environments. For further analyses, this cluster of localities was therefore considered as representing "C_3-habitats".

The localities Mpala, Swara, El Karama were grouped into cluster 3 and were characterised by high C_4-Index values (C_4-Index > ~60%) indicative of C_4-dominated environments. For further analyses, this cluster of localities was therefore considered as representing "C_4-habitats".

The clusters identified using the C_4-Index as an indicator of land cover composition were used for further analysis when assessing the relationship between land cover composition and the diet of impalas.

3.3.2.2.3.2 Land cover composition and structure

The results from the K-means clustering analysis using the C_4-Index, SIDI, LPI and DIVISION as grouping variables showed that the localities Nakuru and Mpala were grouped together in cluster 1, characterised by mid-range C_4-Index mean values, mid-range SIDI mean values, high DIVISION mean values, and low LPI mean values (Figure 31 and Table 30). This suggested habitats with small fragmented patches of mixed vegetation, associated with low patch type diversity in the landscape. Based on these observations, this cluster of localities was considered as representing "Mixed/ C_4 - heterogeneous habitats" in subsequent analyses.

All three South African localities were grouped together in cluster 2. This cluster was characterised by localities with a low C_4-Index mean value, a mid-range SIDI mean value, a high DIVISION mean value, and a mid-range LPI mean value. This suggested habitats with a predominance of fragmented medium-size patches of C_3-vegetation, associated with a moderate patch type diversity in the landscape. Based on these observations, this cluster of localities was therefore considered as representing "C_3-heterogeneous to intermediate-mosaic habitats" in subsequent analyses.

Table 30: Results from K-means clustering with 3 clusters using all landscape variables C_4 -Index, LPI, DIVISION and SIDI.

Cluster	Localities	C4-Index (mean)	SIDI (Mean)	DIVISION (mean)	LPI (mean)	Habitat	Within-cluster sum of squares
1	Nakuru, Mpala	50.12	0.69	0.87	24.75	Mixed/ C_4-Heterogeneous	0.64
2	KNP-North, KNP-South, Welgevonden	13.84	0.66	0.80	41.92	C_3-Heterogeneous/ intermediate-mosaic	0.76
3	Swara, El Karama	69.03	0.22	0.25	86.09	C_4-Homogeneous	0.35
						between_SS / total_SS	92.70%

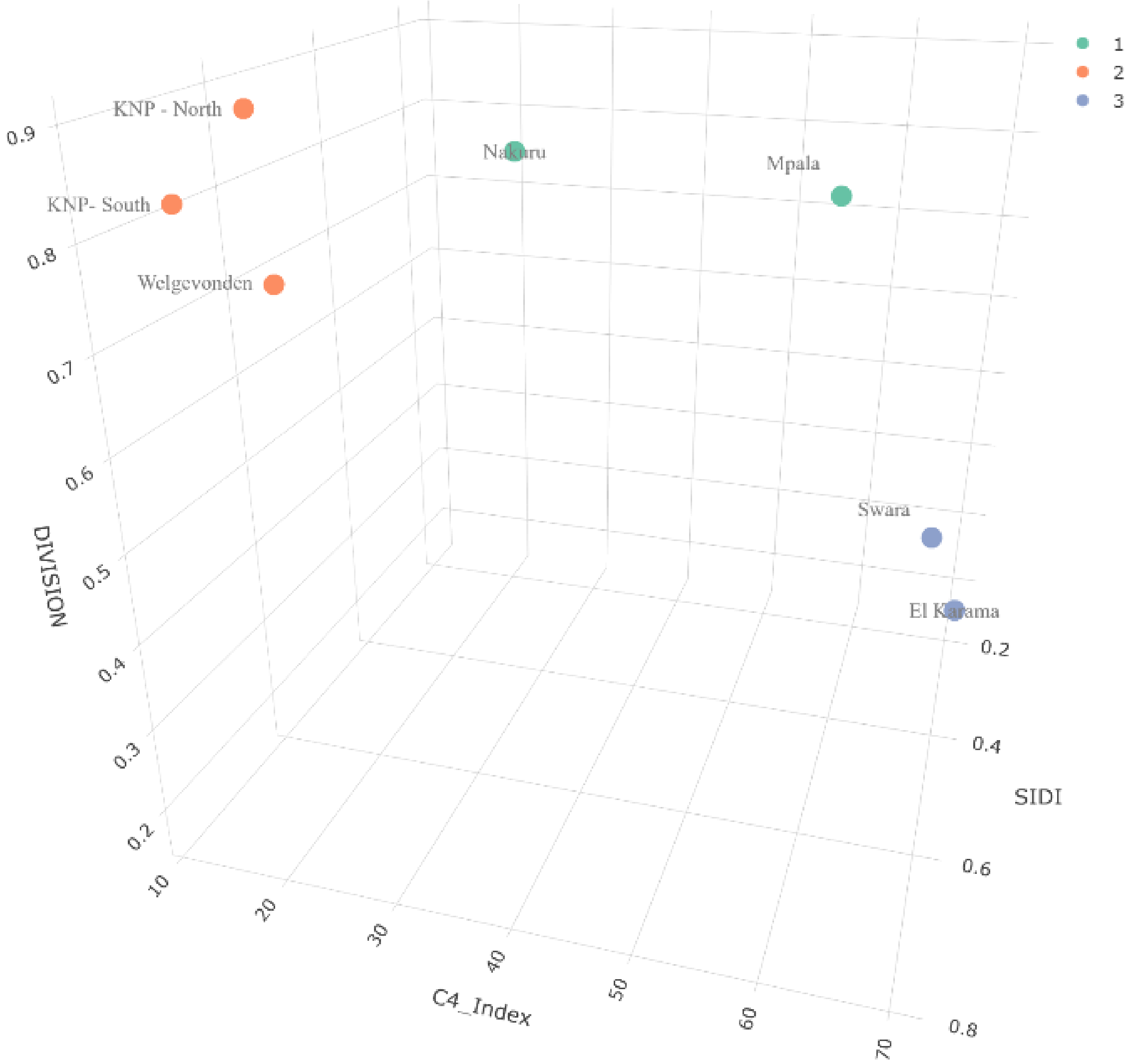

Figure 31: Clusters identified by the K-means algorithm using the land cover pattern variables C_4 -Index, LPI, SIDI and DIVISION.

Finally, the localities Swara and El Karama were grouped together in cluster 3, and were characterised by a high C_4-Index mean value, a low SIDI mean value, a low DIVISION mean value, and a high LPI mean value. These suggested habitats dominated by large compact patches of C_4-vegetation, associated with low patch type diversity. Based on these observations, this cluster of localities was therefore considered as representing "C_4-homogeneous habitats" in subsequent analyses.

The results from the K-means analysis performed on the studied localities using the land cover variables C_4-Index, SIDI, LPI and DIVISION as indicators of combined land cover composition and structure highlighted similarities between some of the studied localities and provided new clusters that can be used for further analysis when assessing the relationship between general land cover patterns and the diet of impalas.

Both sets of clusters were used to assess the relationship between general land cover patterns and the diet of impalas, and their outcome was compared.

3.3.3 Dietary patterns and land cover

In this section, the land cover data and stable carbon isotope data are explored together using multinomial logistic regression to assess whether relationships could be observed between specific land cover types/structures and the dietary signatures from modern impala populations.

3.3.3.1 Model 1: Stable carbon isotopes and land cover composition

Results from the first model showed that a statistically significant positive relationship could be observed between $\delta^{13}C$ values and habitats of mixed-vegetation (as opposed to C_3-vegetation) ($p=0.010$) (Table 31; Figure 32). This means that higher $\delta_{13}C$ values in the teeth of *A. melampus* indicated a higher probability of living in mixed-habitats (or a lower probability of living in a C_3-habitat). For every one-unit increase in $\delta^{13}C$, the odds of being associated to a mixed habitat increased by approximately 1.75 (Table 32 and Figure 33).

No significant relationship was observed between $\delta^{13}C$ values and habitats dominated by C_4-vegetation ($p=0.243$), suggesting that that these types of habitats cannot be easily differentiated from habitats dominated by C_3-vegetation when using the model. Furthermore, the overlap in confidence intervals between the mixed- and C_4-vegetation classes showed that although the 'mixed-vegetation' category could be differentiated from the C_3-vegetation class, the mixed- and C_4-vegetation classes can be difficult to differentiate from each other when using $\delta^{13}C$ as a predictor (Figure 34).

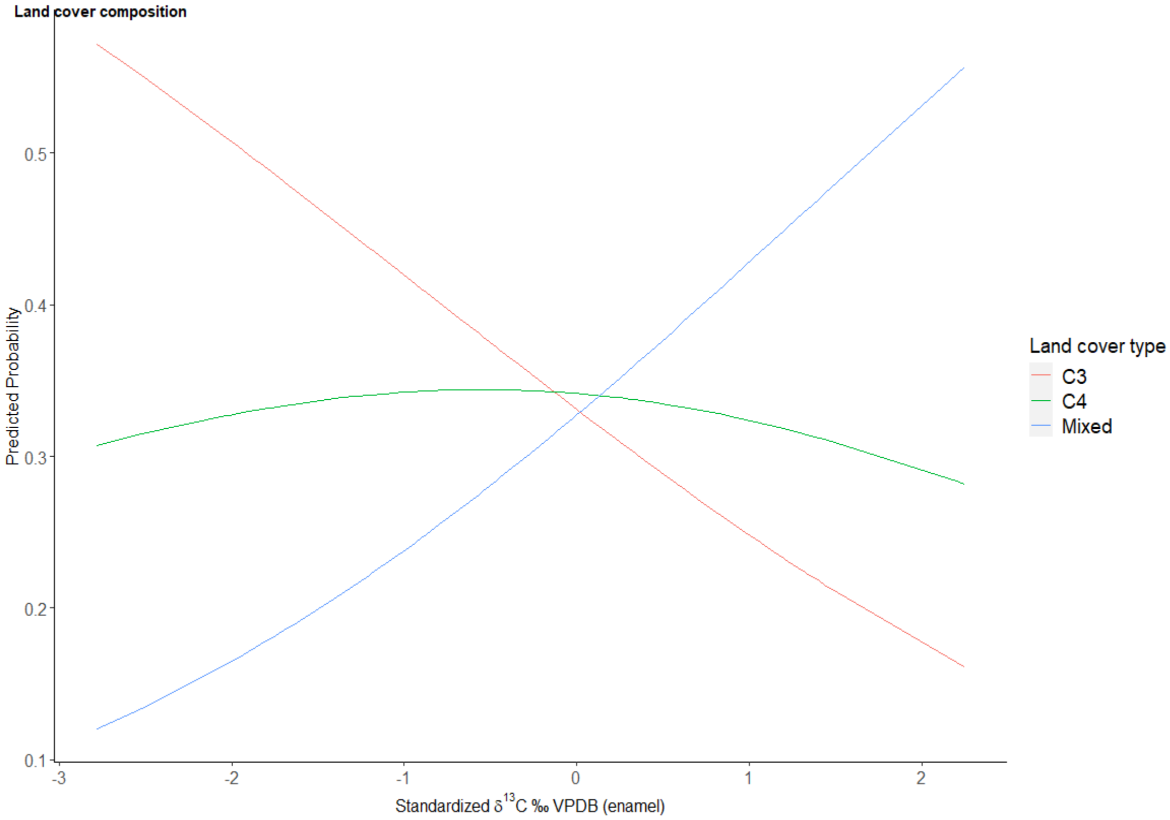

Figure 32: The marginal effect plot for $\delta^{13}C$ - land composition model.

Table 31: Results from the land composition model.

	Intercept estimate	Intercept p-value	Parameter estimate	Parameter p-value
C_4	0.03137	0.8772	0.2346	0.2433
Mixed	-0.01059	0.9593	0.5562	0.009956

Table 32: Odds Ratios from the land composition model (CI: Confidence interval 95%).

	Odds Ratio	Lower CI	Upper CI
C_4	1.264	0.8526	1.875
Mixed	1.744	1.143	2.662

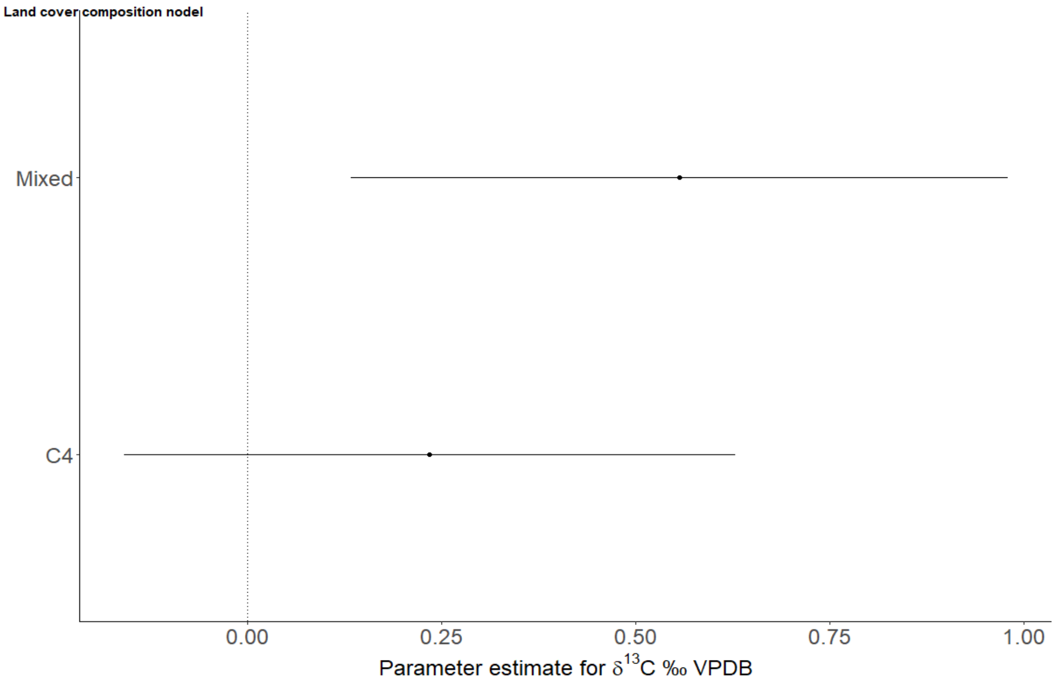

Figure 33: Odds ratios for the effect of diet from the land cover composition model. The points represent the odds ratio, while the lines represent the 95% confidence intervals.

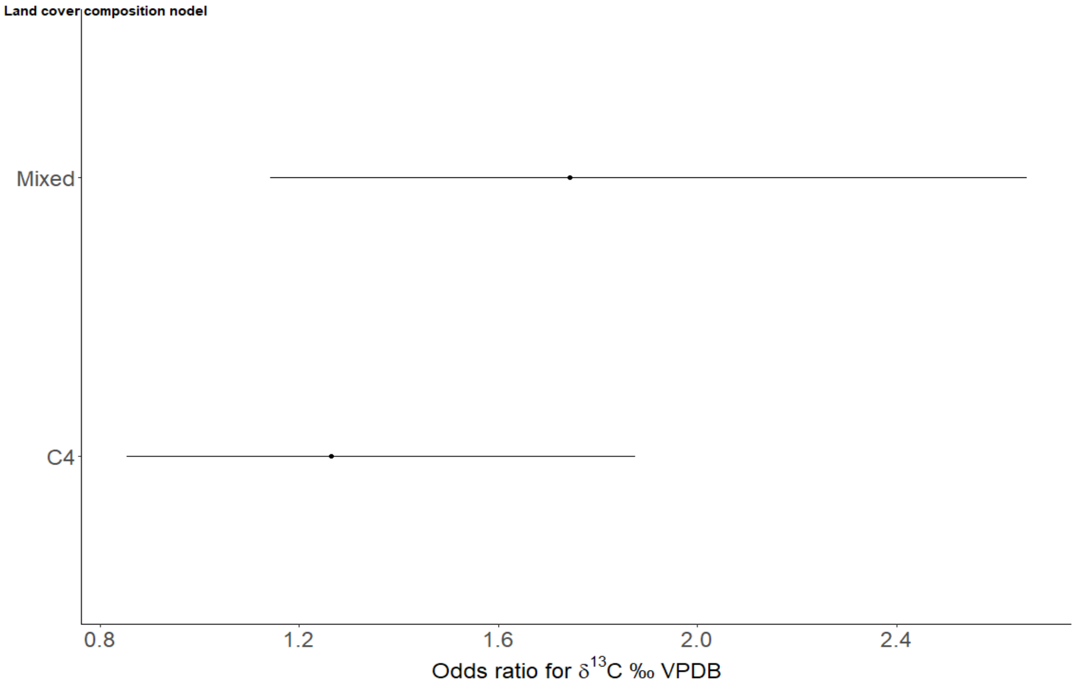

Figure 34: Parameter estimates for the effect of diet from the land cover composition model. The points represent the estimate, while the lines represent the 95% confidence intervals.

3.3.3.2 Model 2: Stable carbon isotopes and general land cover patterns (composition and structure)

A statistically significant positive relationship was observed between $\delta^{13}C$ values and a C_4 -homogeneous habitats (as opposed to a C_3 -heterogeneous/intermediate-mosaic habitat) ($p<0.000$) (Figure 35 and Table 33). This means that high $\delta^{13}C$ values in impala teeth increased the probability of these individuals being associated with C_4 -homogeneous habitats, relative to C_3 -heterogeneous/intermediate-mosaic habitats. For every one-unit increase in $\delta^{13}C$, the odds of being associated to a C_4-homogeneous habitat increased by approximately 2.03 (Table 34 and Figure 36). There is little overlap in confidence intervals between the "Mixed / C_4 – Heterogeneous vegetation" and "C_4 -homogeneous habitats" groups, suggesting that the model should be able to differentiate these two land cover categories when using $\delta^{13}C$ as a predictor (Figure 37).

However, no significant relationship was observed between $\delta^{13}C$ values and habitats dominated by Mixed/C_4–Heterogeneous vegetation ($p=0.838$), suggesting that these types of habitats might be difficult to differentiate from habitats dominated by C_3-heterogeneous/intermediate-mosaic habitat when using the model.

Table 33: Results from the land cover model.

	Intercept estimate	Intercept p-value	Parameter estimate	Parameter p-value
C_4 - Homogeneous	-0.09137	0.6688	0.7101	0.00191
Mixed / C_4 - Heterogeneous	-0.008865	0.9655	-0.04155	0.838

Table 34: Odds Ratios from the land cover model (CI: Confidence interval 95%).

	Odds Ratio	Lower CI	Upper CI
C_4 - Homogeneous	2.034	1.299	3.185
Mixed / C_4 - Heterogeneous	0.9593	0.6441	1.429

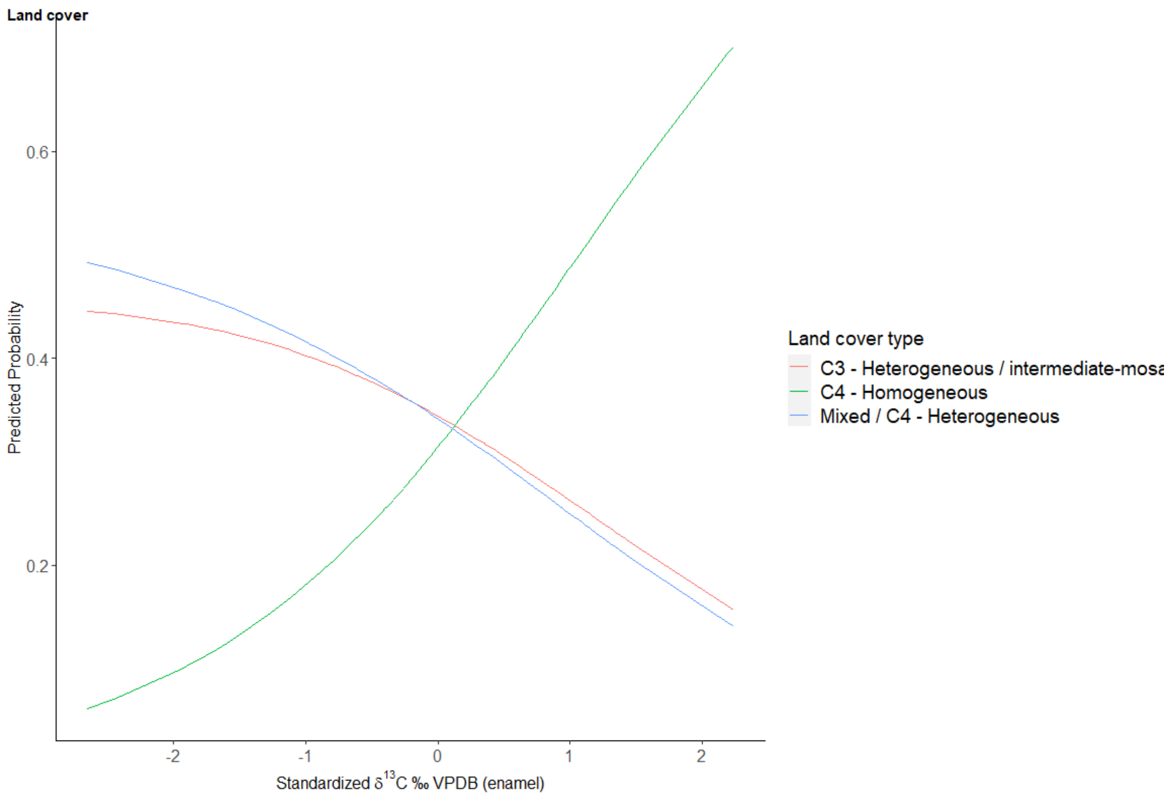

Figure 35: The marginal effect plot for δ13C - land cover model.

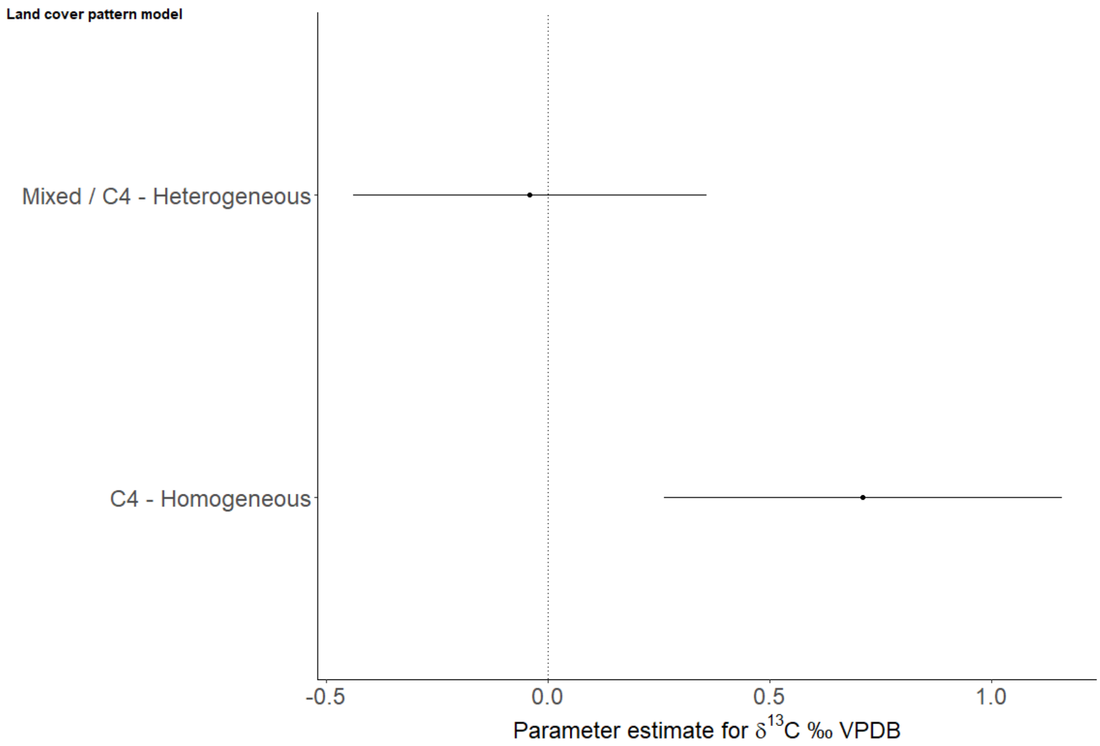

Figure 36: Odds ratios for the effect of diet from the land cover model. The points represent the odds ratio, while the lines represent the 95% confidence intervals.

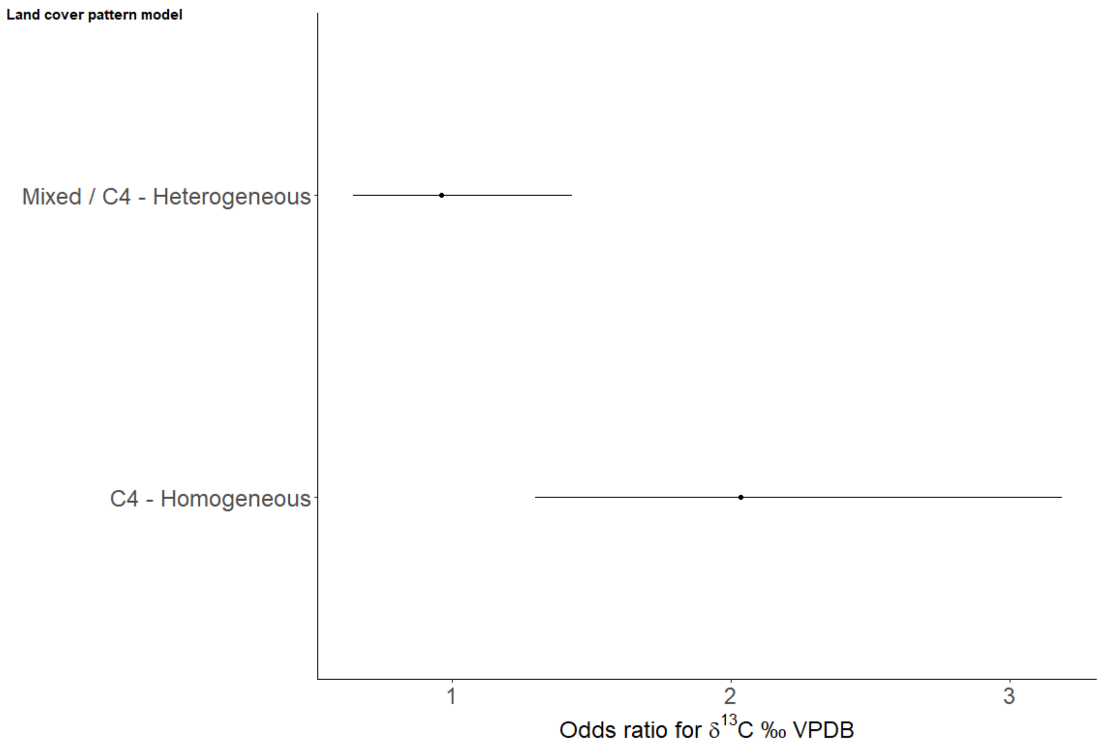

Figure 37: Parameter estimates for the effect of diet from the land cover model. The points represent the estimate, while the lines represent the 95% confidence intervals.

The two multinomial logistic regression models presented above therefore appeared to be able to successfully help predict association to habitat land cover types based on stable carbon isotope data from *Aepyceros melampus* specimens inhabiting the selected study areas, but only to differentiation C_3-dominated habitats from either mixed-vegetation habitats (model 1), or from C_4-homogeneous habitats (model 2). However, both models struggle to differentiate some of the land cover classes, highlighting limits to the approach that will be discussed further in this chapter.

These models were subsequently tested on a new dataset of stable carbon isotope data from impala specimens of unknown associated habitats: fossil *Aepyceros* specimens from the Plio-Pleistocene Omo-Turkana basin.

3.3.4 Predicting land cover type from paleo-dietary data

The multinomial logistic regression models produced were tested on stable carbon isotope data from fossil *Aepyceros melampus*. This was to assess what types of land cover patterns could potentially be inferred from paleo-dietary data in the Omo-Turkana basin, based on the data collected from modern populations and their habitats. The resulting predictions are presented for each model, summarizing predictions for the entire fossil dataset (i.e. per species), and for each site and member represented in the assemblage.

3.3.4.1 Predictions from model 1: Land cover composition model

3.3.4.1.1 Predictions per fossil species

The predictions from the land cover composition model suggest that fossil *Aepyceros melampus* as well as fossil *Aepyceros* sp. specimens tended to be associated to C_3-dominated habitats (Table 35 and Figure 38). Nearly half of the *Aepyceros shungurae* specimens were predicted to be associated to mixed-vegetation (46%), while 43.9% were predicted to be associated to C_3 -vegetation. This suggested differences in associated habitats when comparing *A. shungurae* to *A. melampus* and *Aepyceros* sp. specimens, with a potentially wider habitat range for *Aepyceros shungurae*.

Table 35: δ^{13}C values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimen per category) for fossil *Aepyceros* samples (per species) from the land cover composition model.

Sample		δ13C (‰)					Land cover type (n)		
Species	n	mean	s.d.	s.e.m.	min	max	C_4 - vegetation	Mixed - vegetation	C_3 - vegetation
Aep. melampus	14	-0.25	1.31	0.35	-2.61	2.35	0	**11**	3
Aep. shungurae	139	-1.75	2.39	0.20	-8.00	2.61	14	**64**	**61**
Aepyceros sp.	29	-0.79	1.81	0.34	-5.90	2.30	5	**17**	7

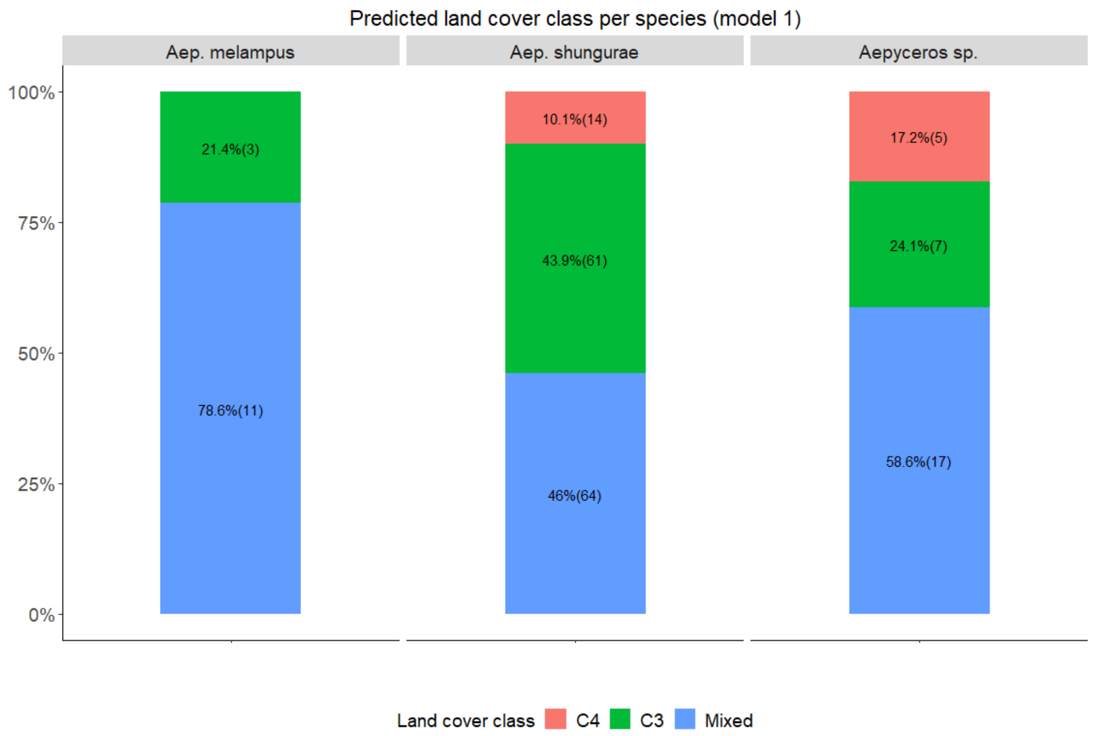

Figure 38: Land cover composition model predictions per species: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in brackets) attributed to each land cover type, per species.

While *A. melampus* specimens were represented in samples from the Koobi Fora and Nachukui formations, *A. shungurae* specimens were represented in samples from the Shungura and Nachukui (Lomekwi member only) formations. The differences in diet and predicted associated habitats observed between these fossil species might therefore reflect different dietary behaviours across the Omo-Turkana basin during the Plio-Pleistocene for genus *Aepyceros*, rather than necessarily species-specific behaviours. These potential spatio-temporal variations in dietary patterns and predicted associated habitats can be explored further from the results of this model.

However, when observing the predicted classifications for all specimens with their associated $\delta^{13}C$ values (Figure 39), the range of $\delta^{13}C$ values associated to the mixed- or the C_4 -vegetation habitat types were contrary to expectation as they suggested that higher $\delta^{13}C$ values tended to be associated to mixed-vegetation while these would have been expected to be associated to C_4 -dominated habitats. This could relate to the limitations of the model that were highlighted previously which showed that individuals associated to either mixed- or C_4 -habitats would likely be difficult to differentiate from each other accurately when fitting the model to new datasets. These limitations must therefore be taken into account when interpreting results acquired using this model. Only predictions for the C_3 -vegetation land cover type can be held to be accurate, as the model was shown previously to be able to efficiently differentiate C_3 -habitats, from C_4 - or mixed-habitats.

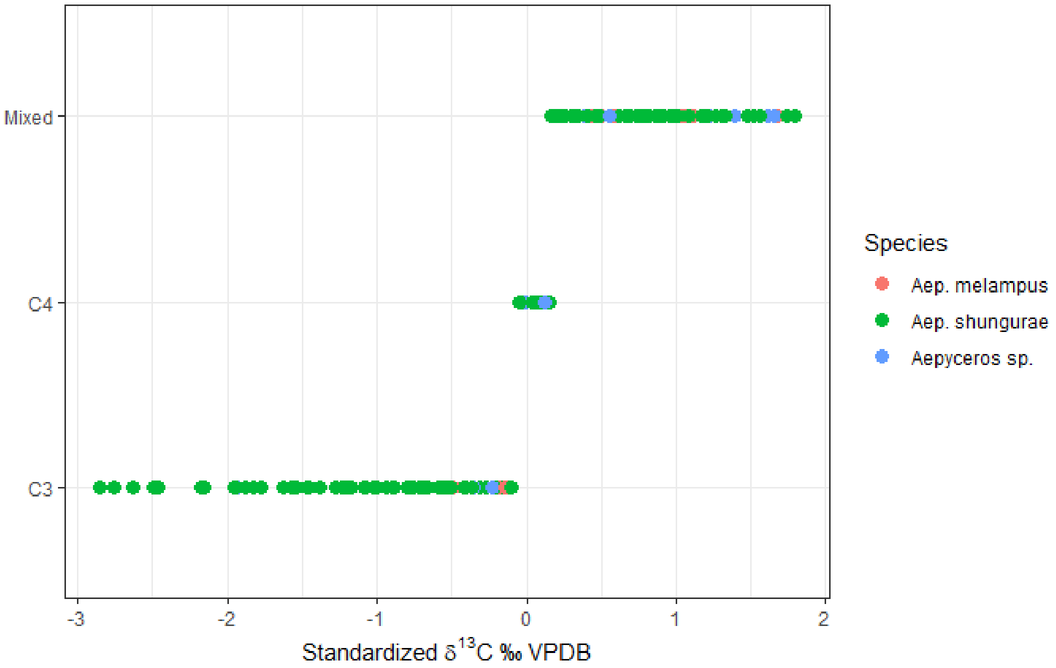

Figure 39: Predicted classification for all fossil specimens, per species, and their $\delta^{13}C$ values, based on the land cover composition model (model 1).

Consequently, the only pattern that can be highlighted with confidence from this model is that most fossil *Aepyceros melampus* as well as fossil *Aepyceros* sp. specimens were predicted to be associated to either mixed- or C_4 -vegetation dominated habitats, while nearly half of the *Aepyceros shungurae* specimens were predicted to be associated to C_3 -habitats. This would suggest a stronger reliance on C_3 -vegetation for *Aepyceros shungurae* and more varied associated habitats.

3.3.4.1.2 Predictions for genus Aepyceros per site

As expected from the predictions for each fossil species and the provenance of these specimens, the predictions from the land cover composition model suggested that fossil *Aepyceros* specimens from Koobi Fora and Nachukui tended to be associated to mixed-vegetation habitats while the majority of specimens from Shungura were associated to either mixed- (44.5%) or C_3-vegetation (45.3%) (Table 36 and Figure 40). It confirmed that, according to this model, more fossil impalas from Shungura were more likely to be feeding from C_3-dominated environments than impalas from Koobi Fora and Nachukui, and are likely to have been associated to a wider range of habitats.

However, as highlighted previously, because the model was likely to misclassify individuals from mixed- and from C_4-habitats, it remains uncertain that individuals predicted to be associated to mixed-habitats were classified accurately. Consequently, the only pattern that can be highlighted with confidence from this model is that most fossil *Aepyceros* specimens from Koobi Fora and Nachukui were predicted to be associated to either mixed- or C_4-vegetation dominated habitats, while nearly half of the *Aepyceros* specimens from Shungura are predicted to be associated to C_3-habitats. This would suggest habitats with a stronger C_3-vegetation component in the lower Omo river valley compared to habitats in the Turkana basin.

Table 36: $\delta^{13}C$ values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimen per category) for fossil *Aepyceros* (per site) from the land cover composition model.

Sample		**δ13C (‰)**					**Land cover type (n)**		
Provenance	**n**	**mean**	**s.d.**	**s.e.m.**	**min**	**max**	**C_4 - vegetation**	**Mixed - vegetation**	**C_3 - vegetation**
Koobi Fora	24	-0.82	1.83	0.37	-5.90	2.30	2	**15**	7
Nachukui	30	-0.61	1.49	0.27	-3.76	2.35	4	**20**	6
Shungura	128	-1.81	2.44	0.22	-8.00	2.61	13	**57**	**58**

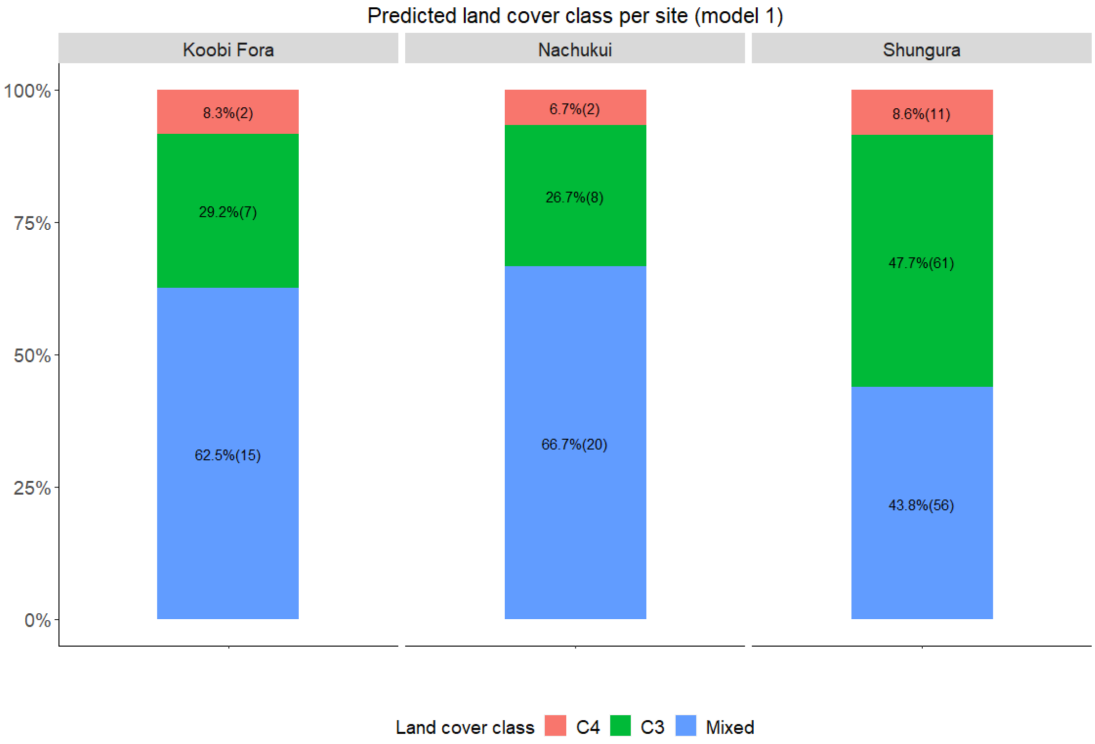

Figure 40: Land cover composition model predictions per site: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in brackets) attributed to each land cover type, per site.

3.3.4.1.3 Predictions for genus Aepyceros per member

Little variation through time in associated land cover type was suggested for *Aepyceros* specimens from Koobi Fora based on the predictions from the land cover composition model for each member, with the predictions suggesting a predominance of mixed habitats in the Burgi and KBS members (2.64 Ma to 1.61 Ma) (

Table 37 and Figure 41). In the Nachukui sample, predictions suggest association with mixed habitats for most specimens, and while very few individuals were predicted to be associated to C_3-habitats in the Kalochoro and Kaitio members (2.33 Ma to 1.61 Ma), 28% of the specimens from the Lomekwi member were predicted to be associated to C_3-habitats, suggesting a stronger C_3-component in the landscape of the Nachukui formation between 3.44 and 2.53 Ma. Similarly, the majority of the impala specimens from the Shungura members B and C were predicted to be associated to C_3-habitats, potentially suggesting a stronger C_3-component in the landscape of the Shungura formation between 3.44 and 2.52 Ma.

Table 37: δ13C values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimens per category) for fossil *Aepyceros* (per site and member) from the land cover composition model.

Sample				**δ13C (‰)**					**Land cover type (n)**		
Provenance	**Member**	**Time (Ma)**	**n**	**mean**	**s.d.**	**s.e.m.**	**min**	**max**	**C_4 - vegetation**	**Mixed - vegetation**	**C_3 - vegetation**
Koobi Fora	Tulu Bor	3.44-2.64	1	-1.81	/	/	/	/	0	0	1
	Burgi	2.64-1.87	12	-0.61	1.54	0.45	-3.20	2.30	2	**7**	3
	KBS	1.87-1.61	11	-0.97	2.21	0.67	-5.90	1.70	0	**8**	3
Nachukui	Lomekwi	3.44-2.53	18	-1.13	1.27	0.30	-3.76	0.60	3	**10**	5
	Kalochoro	2.33-1.9	7	0.31	1.35	0.51	-1.50	2.20	1	**6**	0
	Kaitio	1.9-1.61	5	-0.04	1.87	0.84	-2.40	2.35	0	**4**	1
Shungura	B	3.44-2.91	21	-2.69	2.65	0.58	-7.50	2.50	0	7	**14**
	C	2.91-2.52	23	-3.42	2.64	0.55	-8.00	1.24	2	5	**16**
	D	2.52-2.4	24	-0.88	1.98	0.40	-5.18	1.90	4	**13**	7
	E	2.4-2.32	13	-2.12	2.33	0.65	-6.46	1.20	3	**5**	**5**
	F	2.32-2.27	24	-0.80	1.91	0.39	-4.15	2.08	0	**15**	9
	G	2.27-1.9	23	-1.23	2.07	0.43	-4.83	2.61	4	**12**	7

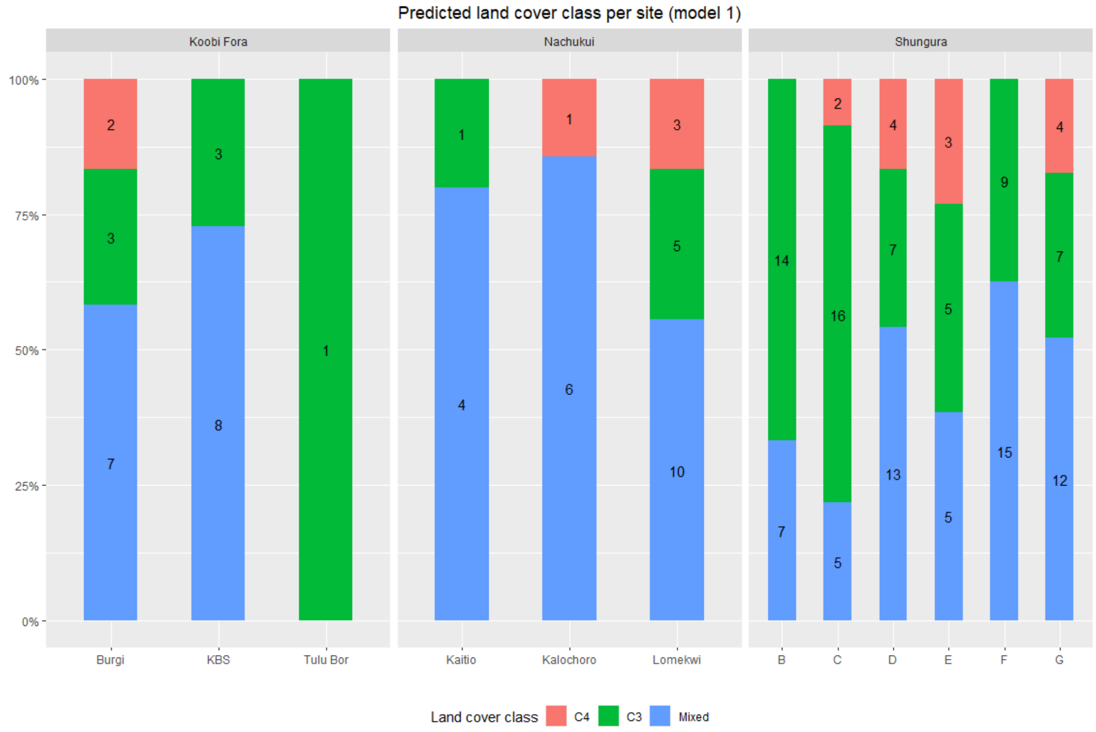

Figure 41: Land cover composition model predictions per site and member: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in bar) attributed to each land cover type, per site and member.

3.3.4.2 Predictions from model 2: General land cover model

3.3.4.2.1 Predictions per fossil species

The predictions from the general land cover model suggested that all fossil *Aepyceros* species tended to be associated to C_3 -heterogeneous habitats (Table 38 and Figure 42). Few specimens were predicted to be associated with C_4 -homogeneous habitats, with 8.7% of *A. melampus* specimens predicted to be associated with this habitat type, and 1.7% of *A. shungurae* specimens. No individual was predicted to be associated to mixed/ C_4 -heterogeneous habitats. This could suggest differences in associated habitats when comparing *A. shungurae* to *A. melampus* specimens, with a slightly stronger reliance on C_3 -vegetation for *A. shungurae*.

Similarly to results from model 1, it is likely that the differences in diet and predicted associated habitats observed between these fossil species reflect different dietary behaviours across the Omo-Turkana basin during the Plio-Pleistocene for genus *Aepyceros* since *A. melampus* specimens were represented in samples from the Koobi Fora and Nachukui formations, while *A. shungurae* specimens were represented in samples from the Shungura and Nachukui (Lomekwi member only) formations.

Table 38: δ13C values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimen per category) for fossil *Aepyceros* (per species) from the general land cover model.

Sample		**δ13C (‰)**					**Land cover type (n)**		
Species	**n**	**mean**	**s.d.**	**s.e.m.**	**min**	**max**	**C4-Homogeneous**	**Mixed/C4-Heterogeneous**	**C3-Heterogeneous**
Aep. melampus	14	-0.25	1.31	0.35	-2.61	2.35	0	1	**2**
Aep. shungurae	139	-1.75	2.39	0.20	-8.00	2.61	0	**55**	20
Aepyceros sp.	29	-0.79	1.81	0.34	-5.90	2.30	0	**7**	5

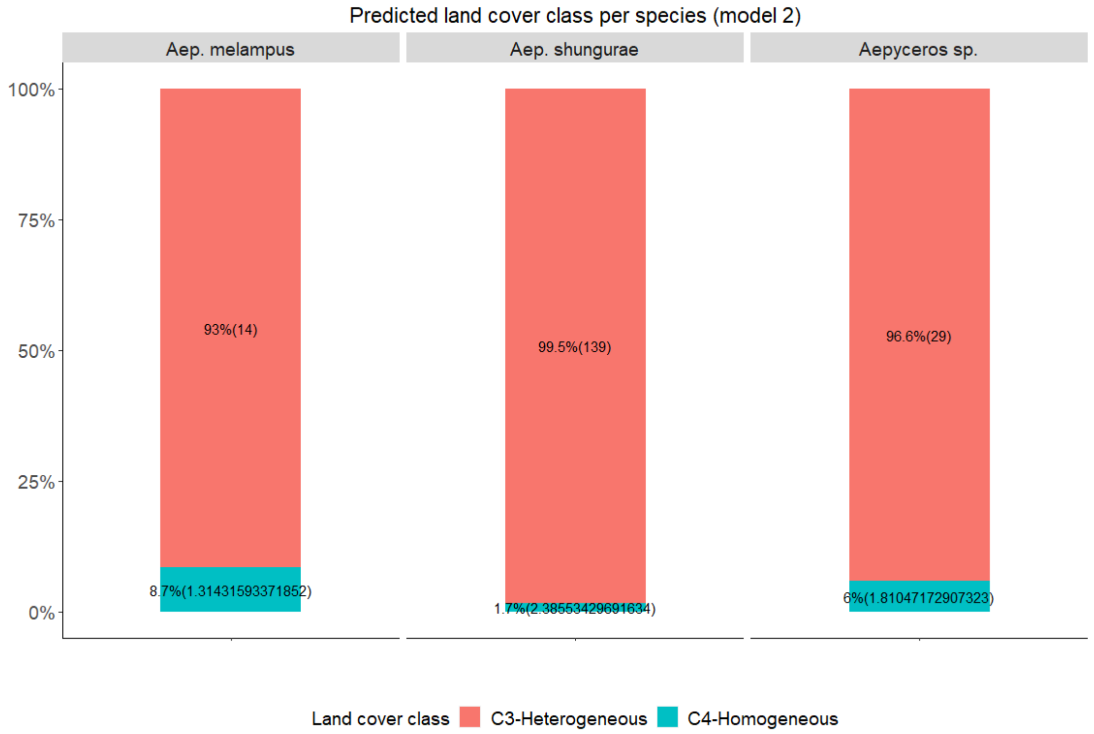

Figure 42: General land cover model predictions per species: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in brackets) attributed to each land cover type, per species.

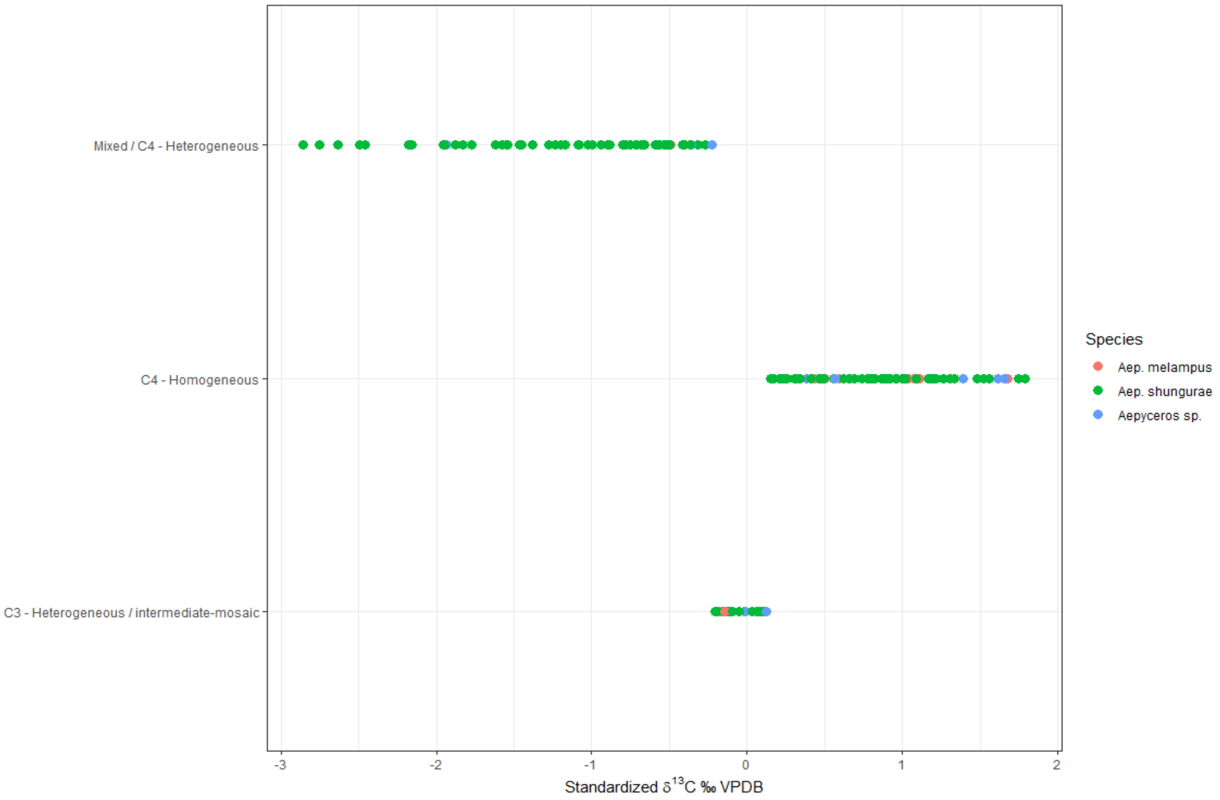

Figure 43: Predicted classification for all fossil specimens, per species, and their δ13C values, based on the general land cover model.

When observing the predicted classifications for all specimens with their associated δ^{13}C values (Figure 43), the range of δ^{13}C values associated to the mixed/ C_4 -heterogeneous or the C_4 -homogeneous habitat types were in agreement with previous research suggesting that higher δ^{13}C values tend to be associated to C_4 -dominated habitats. However, the δ^{13}C values associated with the individuals predicted to be associated to C_3-heterogeneous are surprising and contrary to expected patterns, with much higher values than expected for habitats assumed to be dominated by C_3-vegetation. This could be due to the limitations highlighted previously for this model, which suggested that individuals associated to either mixed/ C_4 -heterogeneous or C_3-heterogeneous habitats could be misclassified when fitting the model to new data. Consequently, the only pattern that could be highlighted with confidence from this model was that most fossil *Aepyceros* specimens were predicted to be associated to either mixed/ C_4-heterogeneous or to C_3 -heterogeneous habitats, with more *A. melampus* specimens predicted to be associated to C_4 -homogeneous habitats than *A. shungurae* specimens. This could reflect a stronger reliance on C_3 -vegetation for *Aepyceros shungurae*, which is in agreement with results of model 1, although it does not provide additional insights into associated land cover structure.

3.3.4.2.2 Predictions for genus *Aepyceros* per site

The predictions of model 2 suggested that while most fossil *Aepyceros* specimens from all three sites tended to be associated to C_3 -heterogeneous habitats, fewer specimens were predicted to be associated with C_4 -homogeneous habitats in the Shungura assemblage (1.9%), compared to the Koobi Fora (7.3%) and Nachukui (4.8%) assemblages (Table 39 and Figure 44). It confirmed that, according to this model, more fossil impalas from Shungura were likely to be feeding from environments dominated by heterogeneous C_3 -vegetation or more varied habitats than impalas from Koobi Fora and Nachukui, suggesting, in turn, habitats with a stronger C_3 -vegetation component in the lower Omo river valley compared with habitats in the Turkana basin.

Table 39: δ¹³C values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimen per category) for fossil *Aepyceros* (per site) from the general land cover model.

Sample		**δ13C (‰)**					**Land cover type (n)**		
Provenance	**n**	**mean**	**s.d.**	**s.e.m.**	**min**	**max**	**C4-Homogeneous**	**Mixed/C4-Heterogeneous**	**C3-Heterogeneous**
Koobi Fora	24	-0.82	1.83	0.37	-5.90	2.30	0	**5**	**4**
Nachukui	30	-0.61	1.49	0.27	-3.76	2.35	0	**6**	4
Shungura	128	-1.81	2.44	0.22	-8.00	2.61	0	**52**	19

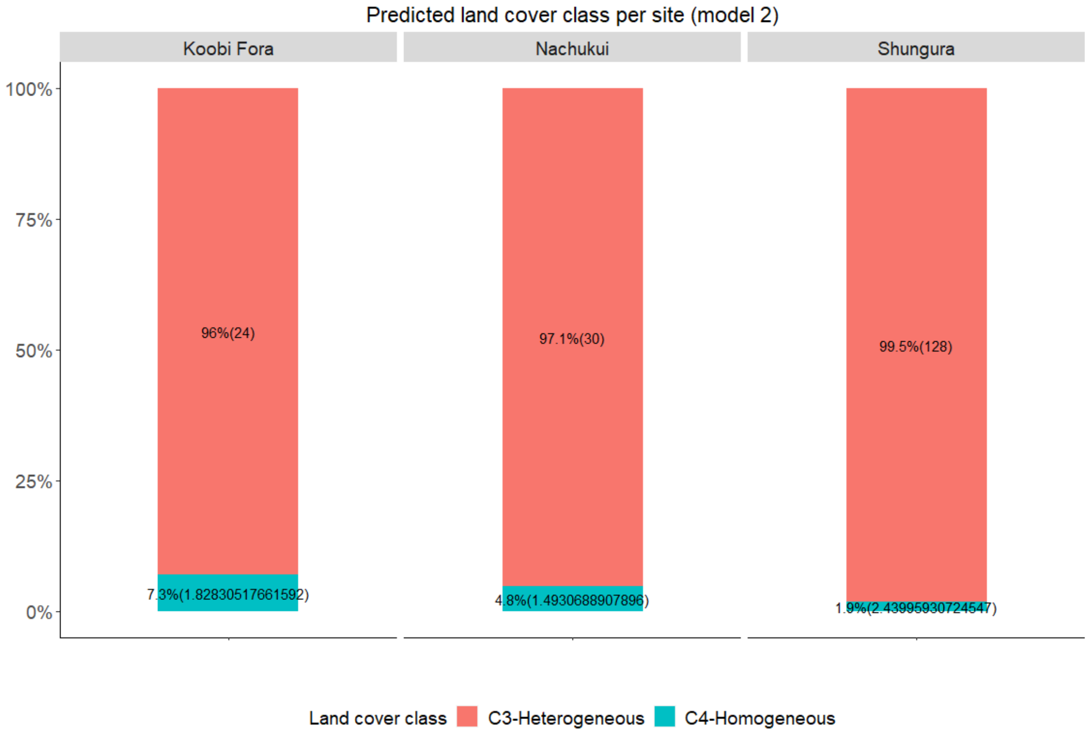

Figure 44: General land cover model predictions per site: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in brackets) attributed to each land cover type, per site.

With no specimen predicted to be associated to mixed/ C_4 -heterogeneous habitats in any of the studied fossil localities, results from this model could suggest that heterogeneous C_3-vegetation tended to dominate the landscape in the Plio-Pleistocene Omo-Turkana basin. However, as noted previously, the uncertainty in the degree of misclassification generated by this model when trying to differentiate the mixed/ C_4 -heterogeneous from the C_3-heterogeneous habitat types prevents from drawing such conclusion with confidence, although it suggests the presence of vegetation conditions rather heterogeneous in structure.

3.3.4.2.3 Predictions for genus Aepyceros per member

Little variation through time in associated land cover type could be observed for *Aepyceros* specimens from Koobi Fora and Nachukui based on the predictions from the general land cover model (model 2) for each member, although specimens from Burgi (2.64 – 1.87 Ma) and Lomekwi (3.44 – 2.64 Ma) appeared to be associated with a wider range of habitats, with specimens predicted to be associated to homogeneous-C_4-habitats and to heterogeneous-C_3-habitats (Table 40 and Figure 45). The majority of the impala specimens from the Shungura members were predicted to be associated to homogeneous-C_4 habitats, although a relatively higher number of specimen was predicted to be associated with heterogeneous-C_3-habitats in members D, E and G. These results could suggest varied environments across Shungura Fm, with a stronger C_3-component and vegetation heterogeneity between 2.52 and 2.32 Ma and between 2.27 and 21.9 Ma.

Table 40: δ^{13}C values (mean, standard deviation, standard error of the mean, minimum and maximum value) and predicted associated land cover type (number of specimen per category) for fossil *Aepyceros* (per site and member) from the general land cover model.

Sample				δ13C (‰)					Land cover type (n)		
Provenance	Member	Time (Ma)	n	mean	s.d.	s.e.m.	min	max	C_4-vegetation	Mixed - vegetation	C_3-vegetation
Koobi Fora	Tulu Bor	3.44-2.64	1	-1.81	/	/	-1.81	-1.81	0	0	1
	Burgi	2.64-1.87	12	-0.61	1.54	0.45	-3.20	2.30	0	**2**	**3**
	KBS	1.87-1.61	11	-0.97	2.21	0.67	-5.90	1.70	0	**3**	0
Nachukui	Lomekwi	3.44-2.53	18	-1.13	1.27	0.30	-3.76	0.60	0	**5**	**3**
	Kalochoro	2.33-1.9	7	0.31	1.35	0.51	-1.50	2.20	0	0	1
	Kaitio	1.9-1.61	5	-0.04	1.87	0.84	-2.40	2.35	0	1	0
Shungura	B	3.44-2.91	21	-2.69	2.65	0.58	-7.50	2.50	0	**14**	0
	C	2.91-2.52	23	-3.42	2.64	0.55	-8.00	1.24	0	**16**	2
	D	2.52-2.4	24	-0.88	1.98	0.40	-5.18	1.90	0	**5**	**6**
	E	2.4-2.32	13	-2.12	2.33	0.65	-6.46	1.20	0	**4**	**4**
	F	2.32-2.27	24	-0.80	1.91	0.39	-4.15	2.08	0	**7**	2
	G	2.27-1.9	23	-1.23	2.07	0.43	-4.83	2.61	0	**6**	**5**

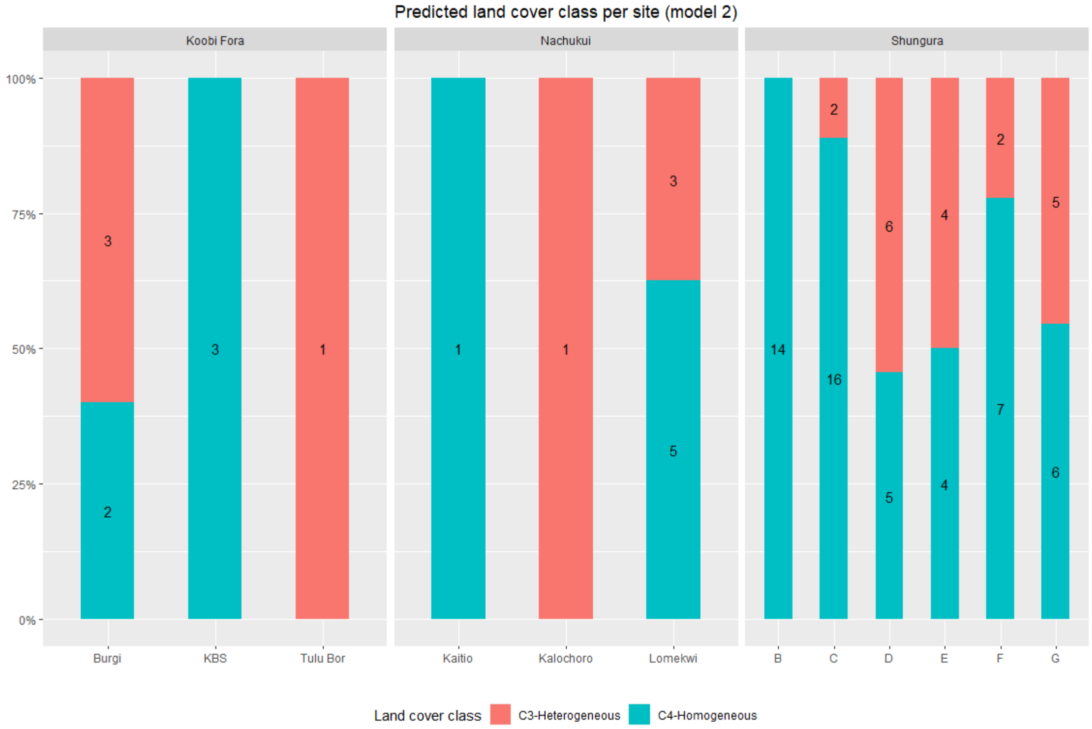

Figure 45: General land cover model predictions per site and member: Relative proportion of fossil *Aepyceros* specimens (with number of specimens in bar) attributed to each land cover type, per site and member.

3.4 Discussion

3.4.1 Dietary variation in modern impala specimens: summary of findings

The results from the dietary analysis of the studied modern impala populations highlighted differing patterns between the samples, suggesting diets rich in C_4-vegetation in the Kenyan localities, and mixed C_3-C_4 diets in some of the South African localities (Kruger National Park-North and Welgevonden). Within the southern African assemblage, significant differences were observed between KNP-South and both KNP-North and Welgevonden, suggesting diets richer in C_4-vegetation in KNP-South, more similar to those of populations from the Kenyan localities.

While these differences in stable carbon isotope content between populations could reflect varying proportions of C_3/C_4-vegetation included in the animals' diet, it could also relate to the geochemical properties of the plants themselves, which might differ between regions of significantly different environmental conditions. As mentioned in chapter 2, previous studies have shown that variation in $\delta^{13}C$ values can be observed among C_3- and C_4 -plants depending local environmental conditions, such as soil properties and aridity conditions (Hattersley, 1982; Ehleringer and Dawson, 1992; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Ehleringer, 2005; J. Codron *et al.*, 2005; Cerling *et al.*, 2015; Cacefo *et al.*, 2019). For instance, C_4-mesic grasses (i.e. adapted to more humid environments) tend to be enriched in ^{13}C by ~ 1-2 ‰ compared to arid-adapted C_4-grasses found in xeric savannas and bushlands (i.e. ecoregions where evaporation exceeds rainfall) (Hattersley, 1982). While such small differences might be difficult to identify statistically in most datasets, it is important to consider that slight variations in $\delta^{13}C$ values observed between samples might reflect the consumption of plants of differing composition, from one locality to the other.

In the present case, it could mean for instance that the significant difference in $\delta^{13}C$ values observed between impalas from KNP-North (South Africa) and Swara (Kenya) might not solely be due to differing proportions of C_3-C_4 plants in the animals' diet, but also to differing geochemical composition of C_3 and C_4 plants in Kenya compared to South Africa, with more arid-adapted vegetation represented in eastern Africa due to drier environmental conditions, as opposed to the presence of more mesic grasses and vegetation in southern Africa, where the climate is cooler and more temperate. However, the significant differences highlighted between populations from KNP-South compared to KNP-North and Welgevonden should likely reflect differences in dietary behaviours with little variation in plant geochemical composition between localities, as these are located close to each other in the same climatic zone.

The similarity in the range of $\delta^{13}C$ values observed for the impala populations from KNP-South, Nakuru, Swara, and El Karama suggest diets dominated by C_4-vegetation in these localities, as opposed to C_3-C_4 mixed diets in KNP-North. The wide range of values observed but relatively high mean values observed within the samples from Mpala and Welgevonden could suggest mixed diets with a relatively high amount of C_4-vegetation in these localities.

Although results for some of the studied samples suggested similar dietary behaviours between localities, some degree of dietary variability could be observed across all impala specimens, both within and between the different samples. This highlights the dietary plasticity of *Aepyceros melampus* and could reflect differing dietary behaviours between the various populations studied. While dietary behaviours can vary between specimens due to various factors (such as season, sex, niche competition), diet can also vary due to differences in habitats and differences in the plant resources available to each individual animal. To assess whether the dietary patterns observed among the selected impala specimens did reflect elements of their habitats, the land cover composition and structure of each of the studied localities must first be evaluated.

3.4.2 Land cover data from modern impala habitats: summary of findings

The observations made from land cover analyses were, overall, in agreement with previously published studies and descriptions of the studied localities. For instance, the dominance of shrubland observed on the Kruger National Park (KNP) land cover maps was consistent with mopane veld being the most dominant ecosystem in the park, taking the form of mopane woodland in the north-west (on granite and gneiss soils), mopane shrub veld in the central northern plains and in the north-east (on basalt soils), or mopane thickets (on ecca shales) (Pty) Ltd 2020). Vegetation in the Kruger National Park (KNP) was previously described as very diverse throughout the park, with predominantly mopane veld in the north, broadleaved trees on the southern granites, and fine-leaved tree species on southern basalts (Codron, Codron, Lee-Thorp, *et al.* 2005, p.1759). Similarly , the predominance of shrubland observed on the Welgevonden land cover map was consistent with published studies of the area which described the area as a mountainous savanna 'bushveld' (Codron *et al.*, 2005; Kilian, 2006; Ramsay *et al.*, 2013). Similarly, the main land cover types identified from land cover data for the habitats of Nakuru National Park, as well as the diversity of land cover classes identified in this area, were in agreement with published literature on the Nakuru National Park which described habitats consisting of grassland, scrub woodland, acacia woodland, marshes, and vegetation characteristic of saline water ecosystems (Kutilek, 1974; Thuo *et al.*, 2015). Results from land cover analysis showed the Nakuru area to be dominated by land cover dominated by patches of closed to open herbaceous vegetation (grassland, savannas, or lichens/mosses), and of mosaic forest or shrubland. The results showed that modern *Aepyceros melampus* can inhabit a wide range of habitat types, ranging from heterogeneous C_3 -dominated habitats to homogenous C_4 -grassland biomes.

When land cover composition in each locality was assessed based on the land cover C_4 -Index variable (i.e. which evaluates the relative proportion of C_4 -vegetation observed in the studied landscape), significantly higher values were found in the Kenyan localities Mpala, Swara, El Karama, suggesting the predominance of C_4 -vegetation in these study areas. On the contrary, C_3-vegetation appeared to prevail in the South African localities where C_4-Index values were the lowest. With a mid-range C_4-Index value, the Kenyan locality Nakuru stood out from the other localities, suggesting mixed-vegetation in this area.

When land cover structure was considered alongside land cover composition (i.e. using the C_4-Index), the Largest Patch Index (LPI), the landscape Division Index (DIVISION) and Simpson's Diversity Index (SIDI)) to assess the general land cover patterns of each studied locality, results of the clustering analyses showed that all three South African localities were characterised by a very heterogeneous vegetation structure dominated by C_3-

vegetation, in contrast to the more homogeneous C_4-dominated vegetation conditions observed for the Kenyan localities Swara and El Karama. The Kenyan localities Nakuru and Mpala were shown to present somewhat intermediate land cover conditions, with a rather heterogeneous land cover structure, with either mixed-vegetation or dominated by C_4-vegetation.

3.4.3 Dietary pattern and land cover: summary of findings

If mixed-feeding herbivores such as impalas (*Aepyceros melampus*) adapt their diet to the vegetation-types prevailing in their habitat, as hypothesized in this study, it would be expected that the differences and similarities in dietary patterns observed via stable carbon isotope analysis between the studied modern impala samples (3.4.1) would be related, to some degree, to the differences in land cover composition and/or structure that were identified across the studied localities using land cover data (3.4.2). To verify this hypothesis, the relationship between impala $\delta^{13}C$ data and land cover structure and/or composition was explored using multinomial logistic regression models to see if isotopic data from mixed-feeding herbivores such as impalas could help predict the type of habitats inhabited by the antelope individuals sampled. It was hypothesized that impala individuals with high $\delta^{13}C$ values would be more likely to be associated with C_4 habitats, while individuals with low $\delta^{13}C$ values would be more likely to be associated with C_3 -vegetation.

The results from the land cover composition model (model 1) showed a statistically significant positive relationship between $\delta^{13}C$ values and being associated to a habitat of mixed-vegetation (as opposed to C_3 -vegetation), but not between $\delta^{13}C$ values and being associated to a habitat dominated by C_4-vegetation. This is at odds with previous studies suggesting that increasing $\delta^{13}C$ values tend to reflect an increase in the inclusion of C_4 -plant material in the diet relative to C_3-plant material. However, results suggested that although the mixed- and C_4 -vegetation classes could be differentiated from the C_3 -

vegetation class, these two classes could not be differentiated from each other when using $\delta^{13}C$ as a predictor. The results from this model therefore suggested that land cover composition could be predicted using $\delta^{13}C$ values from *Aepyceros melampus* specimens, but that individuals associated to either mixed- or C_4-habitats are likely to be difficult to differentiate from each other and might be misclassified. Caution must therefore be applied when interpreting results from predictions generated by this model.

The results from the general land cover patterns model (model 2) showed a statistically significant positive relationship between $\delta^{13}C$ values and being associated to a C_4-dominated homogeneous habitat (as opposed to a C_3-heterogeneous/intermediate-mosaic habitat), but suggested that mixed/ C_4-heterogeneous habitats could not be differentiated from C_3-heterogeneous habitats based on stable carbon isotope data. The direction of the relationships between $\delta^{13}C$ values and the 'C_3-heterogeneous' and 'C_4-heterogeneous ' land cover categories were in agreement with part of the initial hypothesis, as they highlight that increasing $\delta^{13}C$ values tend to reduce the probability of being associated to one of the different C_3-habitat types, and increase the probability of being associated to one of the different C_4-habitat types. However, although results from this model suggested that general land cover patterns could be predicted using $\delta^{13}C$ values from *Aepyceros melampus* specimens of unknown habitat when using the most conservative model, the model could not differentiate effectively individuals associated to C_3-heterogeneous habitats from individuals associated to mixed/ C_4-heterogeneous habitats. The outcome of this model was therefore similar to the outcome of the land cover composition model (model 1), and caution must be applied when interpreting results from predictions generated by this model.

Overall, while both models did not show statistically significant relationships between $\delta^{13}C$ values and the probability of being associated to all specific land cover types, results from this study were in agreement with part of the initial hypothesis that impala individuals with high $\delta^{13}C$ values would be more likely to be associated to C_4-vegetation, while individuals with low $\delta^{13}C$ values will be more likely to be associated to C_3-vegetation. Land cover structure seemed to have some degree of influence on the diet of impalas when studied alongside land cover composition, as illustrated by model 2, highlighting potentially different dietary behaviours in localities with heterogeneous vegetation conditions, compared to localities with homogenous vegetation structure: individuals with the most negative $\delta^{13}C$ values tended to be associated to heterogeneous and highly fragmented C_3 -habitats (i.e. habitats similar to those observed in KNP-North), while individuals with the least negative $\delta^{13}C$ values were associated to homogeneous, poorly fragmented C_4-habitats (i.e. habitats similar to those observed in Swara and El Karama). This could suggest that variations in $\delta^{13}C$ values can potentially reflect not only the relative proportion of C_3-C_4 vegetation included in the diet, but also the structure and diversity of the vegetation present in the landscape.

3.4.4 Modern impala dietary ecology and associated habitats

3.4.4.1 Comparisons between stable carbon isotope data and land cover data

When comparing results from the dietary analysis of the modern impala with the results from the land cover composition and/or structure analysis of their habitats, results were against expectations. While most of stable carbon isotope samples suggested diets dominated by C_4-vegetation, especially for the Kenyan localities, the land cover maps from the regions studied showed more diverse habitats, with C_4-dominated environments in the Kenyan localities, mixed-environments in the Nakuru National Park (Kenya), and C_3-dominated environments in the South African localities (Figure 46).

While part of the results from dietary analysis and land cover composition analysis were consistent with the hypothesis of a positive relationships between the amount of C_4-vegetation present in the landscape and the amount of C_4-vegetation included in the diet for localities such as Swara, El Karama, Mpala, and KNP-North, it was not the case for the other three localities (Nakuru, Welgevonden and KNP-South). This could suggest that the diet of modern impalas does not always reflect the vegetation types prevailing in their environments, and that other aspects of their foraging behaviour might influence the content of their diet. For instance, the differences in dietary behaviours between impalas from the north and from the south of Kruger National Park have been suggested to relate to a reduced availability of herbaceous forage in the north of the park compared to the south, associated to a preference for herbaceous forage over browse due to the higher protein content of C_4-vegetation (Sponheimer, Grant, *et al.*, 2003). Similarly, the high C_4-content observed in the diet of impalas from Nakuru National Park (Copeland *et al.*, 2009) could relate to a preference for C_4-vegetation for its higher protein content that led impala populations to favour areas of the park where grassland is abundant, even in a rather diverse habitat, in a region where rich soils support grasses of high nutritional content all year-round. A study by Mwangi and Western (1997) observed that, in Nakuru, impalas were found predominantly in areas of wooded grassland and grassland, rather than in areas of woodland, shoreline grassland and bush grassland. This is consistent with previous studies that have suggested that impalas tend to favour grass over browse, especially during the wet season when grass nutritional quality is at its highest (Monro, 1980; Meissner, Pieterse and Potgieter, 1996; Codron *et al.*, 2006; Copeland *et al.*, 2009). In turn, impalas would tend to include more browse in their diet when and where high-quality grass is not available to them in their habitats in sufficient quantities.

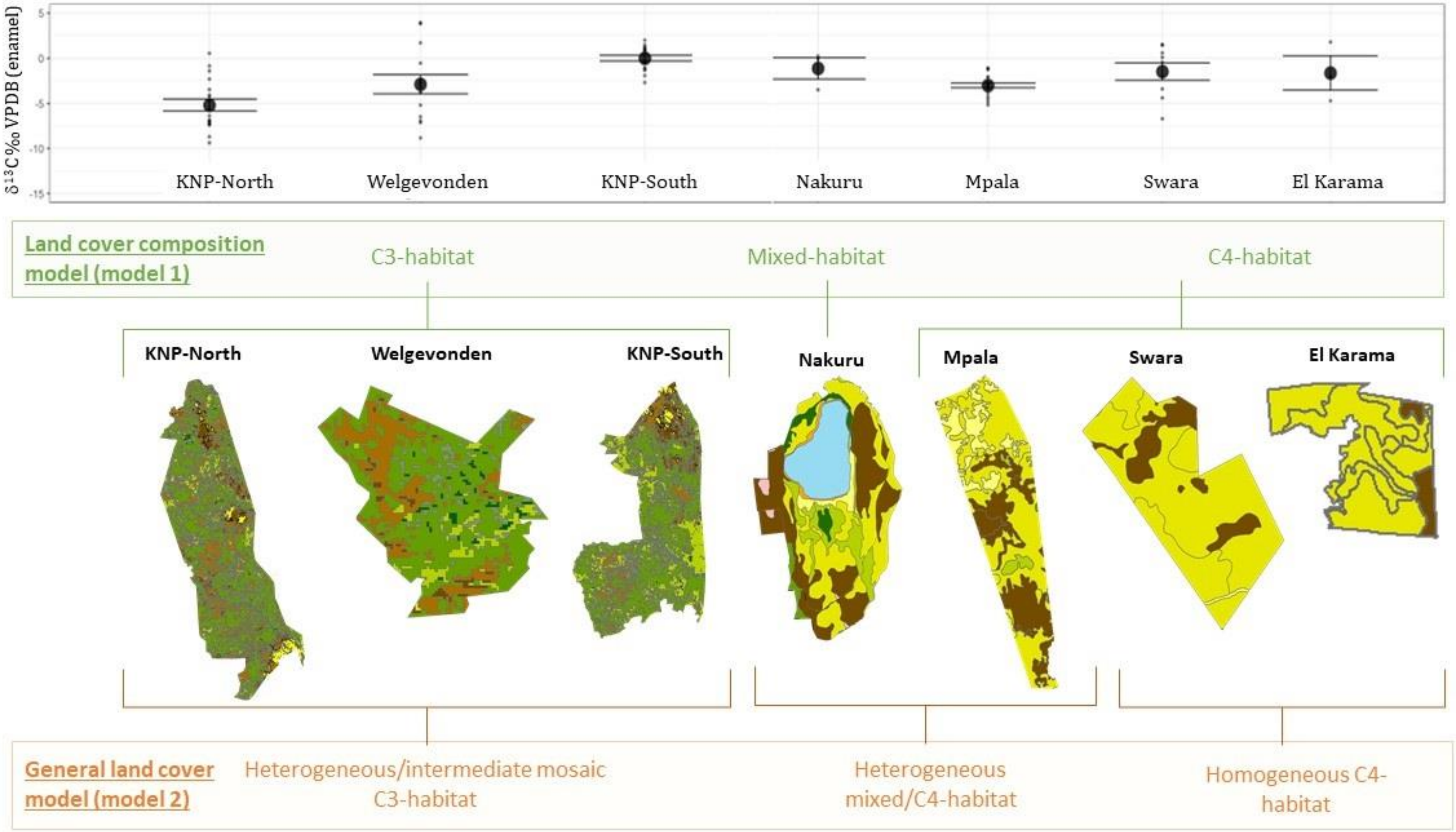

Figure 46: Modern impala diet and associated habitats: summary of the modern *Aepyceros melampus* stable carbon isotope data and of the associated land cover types suggested by k-means clustering analyses, for each studied locality.

Consequently, it could be hypothesized that, based on previous studies and on the comparisons between stable carbon isotope data and land cover data from the seven studied localities, that while the diet of modern impalas can reflect the prevailing vegetation in their environment to a certain extent, it is also likely that their diet is also influenced by the quality of the forage available to the impala populations in their habitat. If impalas do prefer C_4 -vegetation to C_3 -vegetation due to their protein content, it could mean that impalas tend to feed predominantly on browse only in areas and/or seasons where herbaceous vegetation is scarce or of poor quality. While such results would make paleo-habitats reconstructions based on the diet of fossil impala individuals more complex, it does raise interesting points in highlighting that impalas, although considered mixed-feeders, are actually selective feeders that prefer C_4 -vegetation and tend to switch to C_3 -browse only when their preferred foods are not available in sufficient quantities. Similar foraging behaviours could potentially apply as well to fossil impala species.

Such complex relationships between the diet of impalas and the observed land cover composition of their habitats could explain the difficulties encountered by the logistic regression models built in this study to accurately differentiate associated habitats based on stable carbon isotope analysis beyond the general C_3 -C_4 habitats dichotomy. With three localities (i.e. KNP-South, Nakuru and Welgevonden) used in the models training set where individuals were observed to prefer, overall, C_4-vegetation regardless of the prevailing vegetation in the landscape, it is not surprising that the models could not identify a clear logistic relationship between the amount of C_4 -vegetation likely included in the diet and the amount of C_4 -vegetation observed in the habitat, to help identify intermediate habitats such as mixed-vegetation or heterogeneous-C_4-habitats.

3.4.4.2 Models limitations and biases

While the multinomial logistic regression models were shown to be able to successful help predict habitat land cover types based on stable carbon isotope data from *Aepyceros* *melampus* specimens inhabiting the selected study areas for some of the land cover types identified in the studied localities, caution should be applied when fitting these models to new datasets and interpreting the resulting predictions due to several potential biases related to the modern dataset.

In addition to the preference of impalas for high quality grasses highlighted above that likely clouds the identifiable relationship between diet and habitat land cover patterns for this species, it is likely that the models suffer originally from the nature of the training dataset and potentially introduced biases and weaknesses. For instance, the efficiency of the models could very likely be improved by larger sample sizes for $\delta^{13}C$ data for each impala population studied as well as a wider range of study areas to build the models based on modern data that reflects more faithfully the dietary variation of impalas as well as the diversity of habitats they inhabit. More study areas as well as larger stable carbon isotope samples would allow to avoid potential biases in the models due to class unbalance. Furthermore, a more uniform land cover dataset would likely improve the model, with land cover maps produced using the same remote sensing data and the same method to reduce potential bias due to remotely sensed data processing.

3.4.5 Predicting Plio-Pleistocene land cover from fossil impala stable carbon isotope data

3.4.5.1 Fossil species and predicted associated habitats

Predictions from the different models built for this study suggest that, in the studied assemblage, fossil *Aepyceros melampus* specimens were predominantly associated to either mixed habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2). *Aepyceros shungurae* specimens were predicted to be associated to a wider variety of habitats, either to a mixture of C_3- or mixed habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2), suggesting more heterogeneous habitats and/or a stronger reliance on C_3-vegetation for species *Aepyceros shungurae*.

Furthermore, results from model 1 showed that association to C_3-habitats was predicted for a large number of individuals, more particularly in the Shungura formation and in the Nachukui formation member Lomekwi, where only the species *A. shungurae* is represented. These results were in agreement with previous studies which suggested, based on its morphology (straighter, less lyrated and more gracile horn cores, shorter and thicker limb bones), that *A. shungurae* might have inhabited preferentially more closed woodland habitats than *A. melampus* (Harris, 1991; Bobe and Eck, 2001).

3.4.5.2 Predicted associated habitats of the Plio-Pleistocene Omo-Turkana basin

3.4.5.2.1 Koobi Fora and Nachukui formations

Predictions for *Aepyceros* specimens per locality suggested that most specimens from Koobi Fora and Nachukui were likely associated to either mixed-habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2). When comparing the range of $\delta^{13}C$ values from these two fossil deposits to the range of values observed in each of the studied modern localities (Figure 47 and Figure 48), it could be seen that modern impala individuals from most localities yielded a range of $\delta^{13}C$ values similar to fossil impala individuals, regardless of the variety of habitat types that the modern individuals were associated to (C_4-homogeneous, heterogeneous mixed/C_4-heterogeneous, C_3-heterogeneous). However, the ranges of stable carbon isotope ratios observed in these fossil assemblages differed from those observed at KNP-North (C_3-heterogeneous) and Welgevonden (C_3-heterogeneous) where a wider range of values was captured. This suggests that the diet of impalas from Koobi Fora and Nachukui were likely to reflect local environments similar to most of the modern localities studied where C_4-vegetation is dominant (e.g. Swara, El Karama, Mpala), or where high quality C_4-vegetation is available in sufficient quantities all year-round in either mixed or C_3 -dominated habitats (e.g. Nakuru, and KNP-South). The larger range of $\delta^{13}C$ values observed in KNP-North and Welgevonden, likely reflecting a stronger reliance on C_3 -vegetation, is not mirrored in these two fossil assemblages, suggesting the absence of C_3 -dominated habitats in the landscape of the Koobi Fora and Nachukui formations during the Plio-Pleistocene.

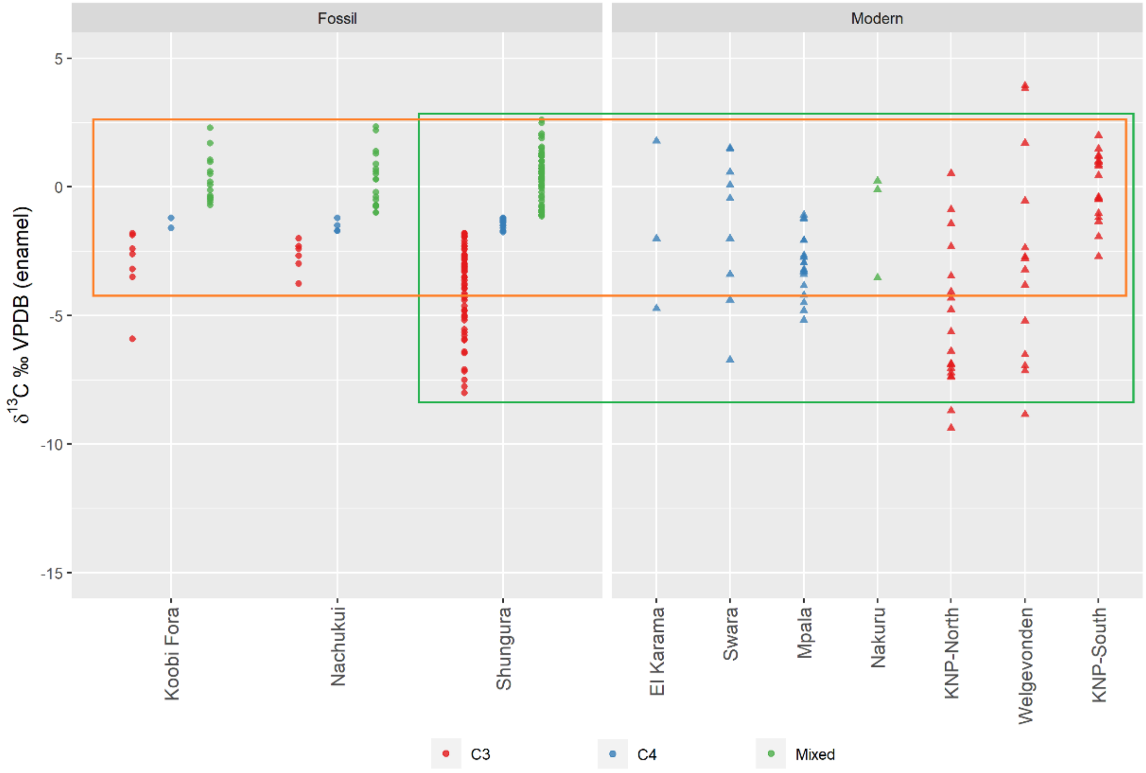

Figure 47: Land cover predictions, per site, based on results from the land cover composition model (model 1): Measured $\delta^{13}C$ values for all fossil and modern specimens and associated habitats as predicted by the general land cover model (least conservative - model 4). The orange box highlights the range of $\delta^{13}C$ values observed in the Koobi Fora and Nachukui formations. The green box highlights the range of $\delta^{13}C$ values observed in the Shungura formation.

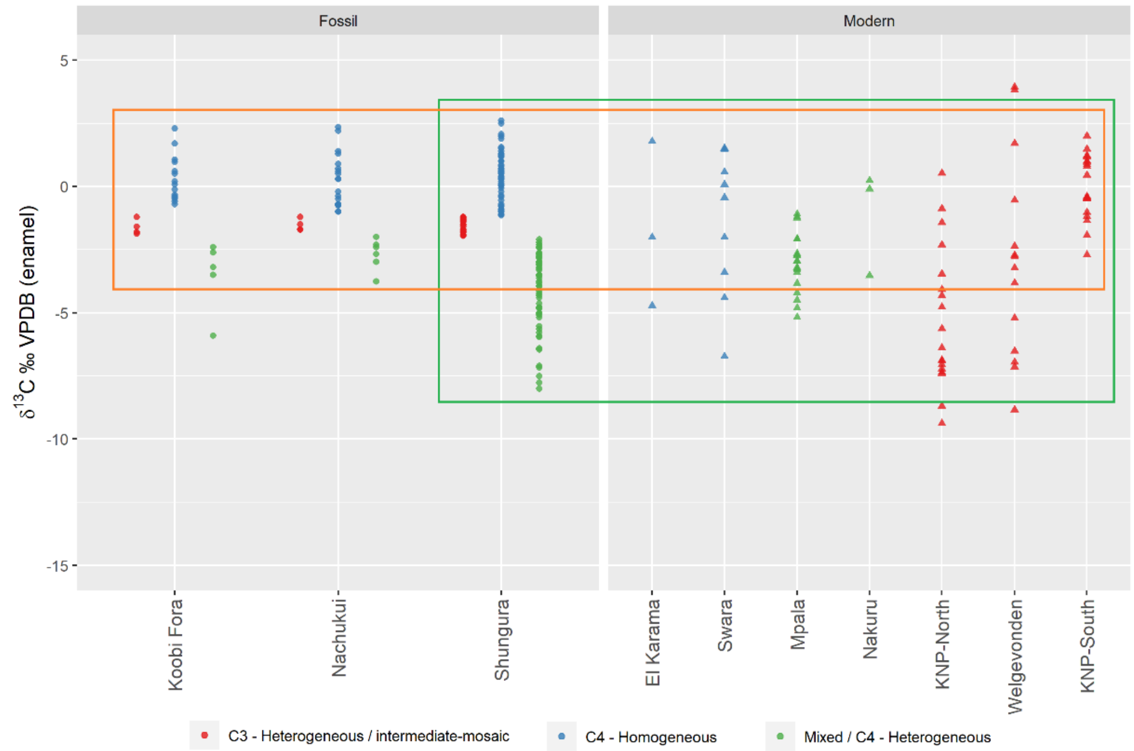

Figure 48: Land cover predictions, per site, based on results from the general land cover model (model 2): Measured δ13C values for all fossil and modern specimens and associated habitats as predicted by the general land cover model (least conservative - model 4). The orange box highlights the range of δ13C values observed in the Koobi Fora and Nachukui formations. The green box highlights the range of δ13C values observed in the Shungura formation.

Little variation through time in predicted associated land cover types was observed across the members from Koobi Fora, although a slight decrease in associated habitat diversity is suggested between the Burgi (2.64 – 1.87 Ma) and KBS (1.87 – 1.61 Ma) members, based on both models (Figure 49 and Figure 50). These predictions would be in agreement with previous paleo-environmental reconstructions for the Burgi member which suggested that this locality sustained a rather heterogeneous environment between 2.64 Ma and 1.61 Ma, with more closed woodlands in the north and more open habitats in the south providing a mixture of woodland and grassland areas (Harris, 1991; Reed, Fleagle and Leakey, 2007). KBS member has been suggested to document a lacustrine phase of the basin (Brown and Feibel, 1991; McDougall and Brown, 2008) with a grassland or shrubland environment dominated by C_4-plants (Bonnefille, 1984; Cerling, Bowman and O'Neil, 1988; Harris, 1991; Kaye E Reed, 1997; Bobe, 2011; Levin *et al.*, 2011). These previous paleo-environmental reconstructions are in agreement with the predominance of homogeneous C_4-dominated habitats predicted by model 2 for KBS member, although at odds with the predominance of mixed-habitats predicted by model 1 for this member.

Overall, the land cover type predictions for the Nachukui formation suggesting that most *Aepyceros* specimens were predominantly associated to homogeneous C_4-habitats (model 2) (Figure 47 and Figure 48), are consistent with the faunal composition study by Bobe *et al.* (2007), which concluded that relatively open and arid environments prevailed in western Turkana during the Plio-Pleistocene. However, predictions from model 1 suggested instead that most *Aepyceros* specimens from Nachukui were predominantly associated to mixed habitats, which would be in agreement with other studies that proposed more complex habitat reconstructions for West Turkana, with diverse habitats and a mosaic pattern of vegetation cover across the area where C_3-woodlands remained an important component of the vegetation throughout the sequence (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013).

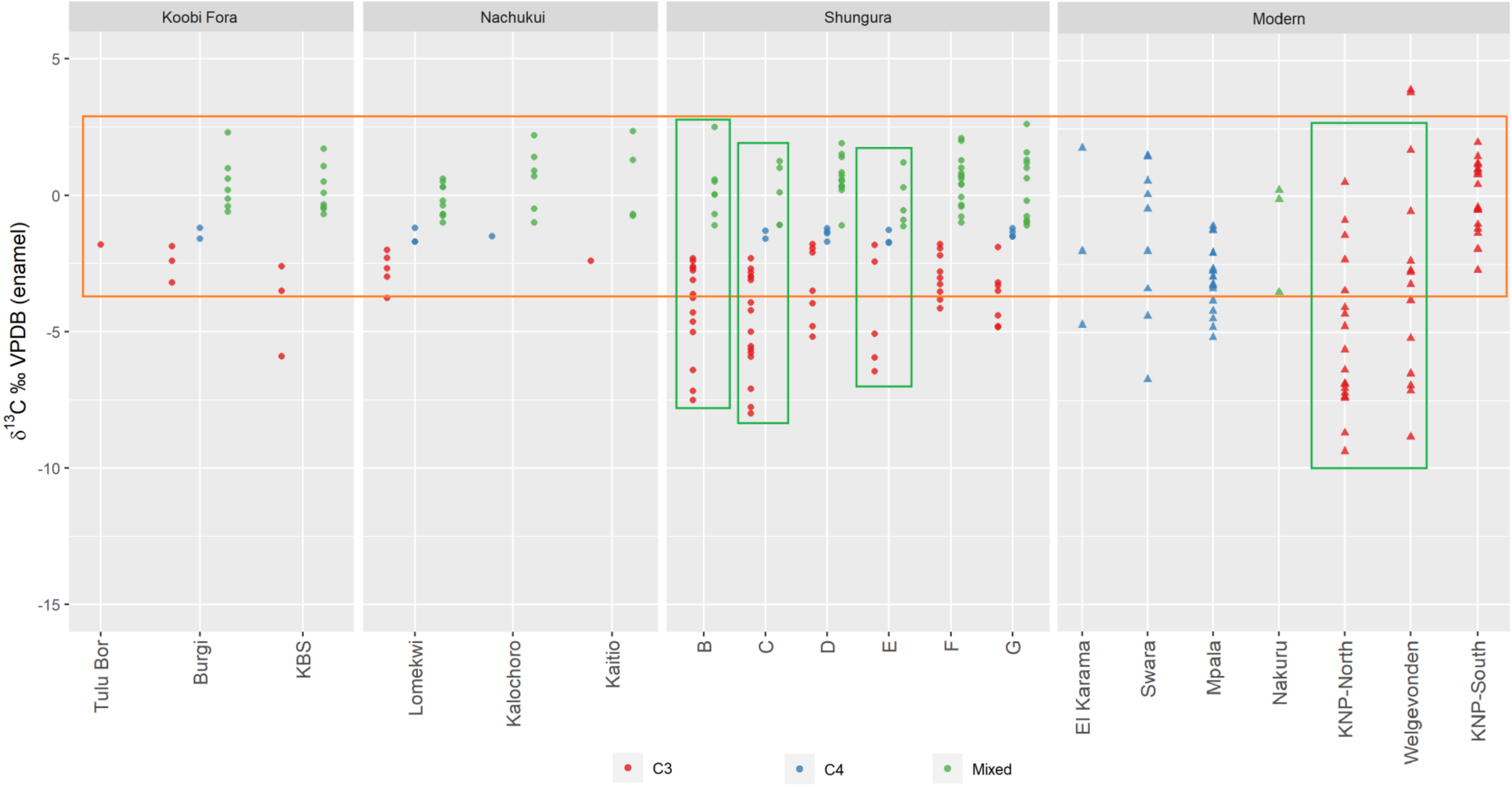

Figure 49: Land cover predictions, per member, based on the land cover composition model (model 1): Measured δ13C values for all fossil and modern specimens and associated habitats as predicted by the general land cover model (least conservative - model 4). The orange box highlights the range of δ13C values observed in the Koobi Fora and Nachukui formations. The green boxes highlight the largest ranges of δ13C values observed in the Shungura formation and in the modern localities.

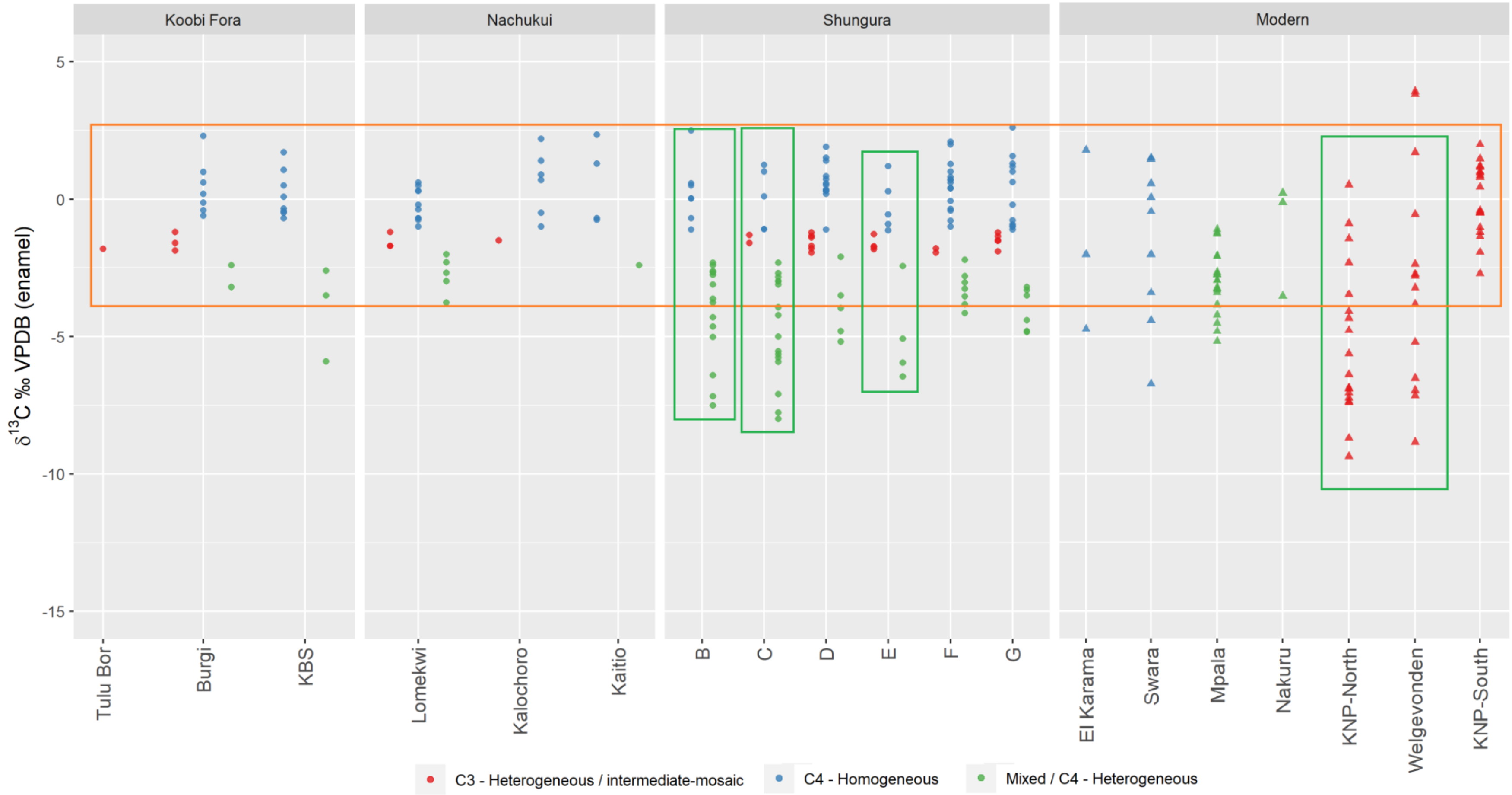

Figure 50: Land cover predictions, per member, based on the general land cover model (model 2): Measured δ13C values for all fossil and modern specimens and associated habitats as predicted by the general land cover model (least conservative - model 4). The orange box highlights the range of δ13C values observed in the Koobi Fora and Nachukui formations. The green boxes highlight the largest ranges of δ13C values observed in the Shungura formation and in the modern localities.

In the Nachukui sample, very few individuals were predicted by the land cover composition model (model 1) to be associated to C_3-habitats in the Kalochoro (2.33-1.9 Ma) and Kaitio members (1.9-1.775 Ma), but nearly 40% of the specimens in the Lomekwi member were predicted to be associated to C_3-habitats, suggesting a stronger reliance on C_3-vegetation in the Nachukui formation between 3.44 and 2.53 Ma (Figure 49 and Figure 50). Similarly, predictions from model 2 suggested a decreasing number of specimens likely associated to heterogeneous C_3-habitats across the Nachukui members. Such differences in the dietary behaviours of fossil impalas before and after ~2.5 Ma would be consistent with paleosol carbonate studies that suggested a rapid increase in C_4-plant biomass in the Turkana basin at around 2.52 Ma (Wynn, 2004; Levin *et al.*, 2011).

The discrepancies between the outputs from the two models, and the dominant association to mixed or C_4 habitats suggested for fossil impalas in both Koobi Fora and Nachukui, could reflect the presence of complex habitats with a strong dominance of C_4-biomass but rather heterogeneous vegetation conditions. However, it could also reflect a preference for C_4-vegetation in heterogeneous localities even when C_3-vegetation dominates the landscape, as observed for modern impala populations for localities such as KNP-South and Welgevonden.

3.4.5.2.2. Shungura formation

Predictions for genus *Aepyceros* specimens in the Shungura formation suggested a stronger C_3-vegetation component in their diet and their associated habitats (model 1), or habitats dominated either by heterogeneous mixed-/C_4-habitats or by heterogeneous C_3-habitats (model 2), suggesting a greater land cover diversity in the lower Omo river valley compared to the other studied fossil localities of the Turkana basin (Figure 47 and Figure 48). This is in agreement with published literature describing environments dominated by C_3-vegetation and closed-wooded habitats for a long part of the sequence (up to ~2.0 Ma) as well as mosaic habitats (Alemseged, 2003; Barr, 2015; Plummer *et al.*, 2015).

Previous studies have suggested the presence of mosaic habitats ranging from forests to open woodlands in the Shungura formation between ~3.4 and 2 Ma, with a gradual increase in C_4 vegetation through time (Jaeger and Wesselman, 1976; Bonnefille and Dechamps, 1983; Wesselman, 1984; Bobe and Eck, 2001; Alemseged, 2003; Levin *et al.*, 2011; Bibi *et al.*, 2013; Barr, 2015; Plummer *et al.*, 2015; Negash *et al.*, 2015; Blondel *et al.*, 2018; Martin *et al.*, 2018). More particularly, according to previous studies, Member B was characterised by a predominance of wet and relatively closed habitats, with little open habitats (Jaeger and Wesselman, 1976; Bonnefille, 1984; Kaye E Reed, 1997; Alemseged, 2003). Similarly, Member C was described as a bushland–woodland regime with a riverine forest and edaphic grasslands (Reed, 1997; Alemseged, 2003). Member E is also thought to have been characterised by a well-watered woodland–bushland with a riparian woodland or forest. In contrast, a change in local climatic conditions from member F to G was observed with more open and drier conditions and habitats dominated by areas of edaphic grasslands, bushlands, and more open woodlands than in the previous members (Jaeger and Wesselman, 1976; Bonnefille, 1984; Reed, 1997). Results from model 1 agree with these studies, with the majority of the impala specimens from the Shungura members B, C and E predicted to be associated to C_3 -habitats in relation to a stronger C_3 -component in their diet between 3.44 and 2.52 Ma and between 2.4 and 2.32 Ma (Figure 49). Similarly, predictions from model 2 suggest a wider range of habitats associated with these members, with a predominance of either heterogeneous mixed-/C_4-habitats or heterogeneous C_3-habitats (Figure 50). The range of $\delta^{13}C$ values observed for impala specimens in these members is similar to the range of values observed in modern specimens from Welgevonden and KNP-North where C_3 -vegetation dominated, and less C_4 -plant material was likely available to impalas in the landscape. A smaller range of $\delta^{13}C$ values and less specimens predicted to be associated to C_3 -habitats or heterogeneous habitats were observed for members F and G, which is consistent with the more open and drier conditions suggested by previous studies for these members.

3.5 Conclusion and perspectives

This study aimed at assessing the dietary variability of modern impala (*Aepyceros melampus*) as well as the variability of the land cover composition and structure of their habitats to explore the relationship between diet and land cover in an extant mixed-feeding antelope species. By comparing case study areas using both land cover metrics derived from remote sensing, and published stable carbon isotope data, this project was designed to test whether it could be possible to predict the types of land cover patterns that are associated with specific dietary patterns observed from dental samples. Despite the limitations and potential biases highlighted previously for the models built based on combined land cover data and impala stable carbon isotope data, interesting patterns were underlined in this study.

First, the high variability in $\delta^{13}C$ values observed among modern impala specimens and the wide range of habitats they inhabit highlighted that, while impalas are often considered as mixed-feeders and are known to be able to adapt to a wide range of habitats and food resources, their diet tends to rely heavily on palatable grasses and forbs, suggesting a preference for C_4-plants for their higher protein content. Comparisons between the dietary behaviour of impala populations studied and the land cover composition of their habitats were consistent with previous studies that observed that impala populations tend to include C_3-vegetation in their diet where and when high quality C_4-vegetation is not available in sufficient quantities in their habitats, either all-year round or seasonally. The diet of modern impalas therefore does not always reflect the vegetation types prevailing in their environments, as availability of their preferred foods can be influenced not only by local year-round land cover patterns (which is itself influenced, for instance, by local geology, hydrology, and soil quality) but also by seasonal fluctuations in climate as well as potential niche competition with other herbivores. Future models using modern dietary ecology and land cover data should therefore seek to include additional information on the habitats inhabited by the impala populations studied to inform on aspects of their foraging behaviour that might influence the content of their diet. Such variables to be included in future models could be: local climatic conditions (temperature and annual rainfall), soil quality, topography, herbivore population estimates (to estimate niche competition), or wildfire regimes (which have been shown to impact grass quality; Young 1972, Bouxin 1975b, Bucini *et al.* 2009). Seasonal variation in diet and in land cover patterns should also be taken into account as much as possible to reduce risks of biasing the models through time averaging,

Although the models built for this study revealed some limitations, the predictions generated for fossil *Aepyceros* samples for the Omo-Turkana basin were partly consistent with previous paleo-environmental studies for this region, which demonstrates the potential of this method. Future work using a modelling approach to reconstructing paleo-environments from paleo-dietary data could improve the precision and relevance of the predictions by including in the model additional variables that can help identify patterns of dietary plasticity in extinct species. For instance, the dietary ecology of fossil impalas could be studied in more detail by combining several dietary proxies to inform on their diet throughout their life (mesowear), during their growth (stable isotopes) and just before death (dental microwear). Additionally, information on local climatic conditions (with stable oxygen isotopes), soil quality (through paleosol carbonates), and herbivore population estimates (through palaeontological studies) for the fossil localities studied could be used and integrated into a model to inform on the broader paleo-environmental context in which fossil impalas were evolving.

Future work could therefore focus on building a strong and detailed modern dataset to record the dietary variability of extant impalas in carefully selected localities, ideally using dietary proxies that can easily be compared with data from the fossil record (i.e. stable isotopes, or dental use-wear). By also recording detailed information on their habitats and the local conditions experienced by the studied populations (climate, seasonal changes, niche competition, etc) combined to information on the land cover composition and structure obtained through remote sensing, the models tested in this study could be improved and provide more accurate predictions to help evaluate in more detail what types of habitats and land cover patterns once characterised the landscapes of eastern Africa during the Plio-Pleistocene.

The use of models built on modern land cover and dietary data was a novel approach which showed promising results. Improved models could be used on other mammal taxa for which isotope data is available for both extant and extinct populations to explore how faunal communities directly relate to their environments and how dietary studies can inform on their habitats depending on their feeding ecology. More particularly, it could be interesting to test this method on carnivores (which might feed on more browsing or grazing herbivore species depending on their ecological niche) and on primates (which have varied omnivorous diets that vary depending on the taxon studied) to build a strong modern baseline to compare with the fossil record. This could allow to explore local Plio-Pleistocene environments from a different angle by testing if models calibrated for various groups would converge in similar environmental reconstructions when fitted to a same fossil depositional context.

Chapter 4: Dental mesowear analysis

4.1 Introduction

The Omo-Turkana basin has been widely studied over the past seventy years, with various studies focusing on the geologic and palaeo-environmental history of this region as a way to better understand the habitats and climatic conditions experienced by hominin species during the Plio-Pleistocene in eastern Africa (see chapter 2.2). Previous studies have suggested that a high diversity of habitats is likely to have been available to hominins in this region between 3.4 Ma and 1.6 Ma, and that several major climatic events might have had an important impact on the local environments, and, in turn, on the faunal communities inhabiting the region at the time. This chapter presents analyses that were designed to test these hypotheses using evidence from herbivore feeding ecology, to see if high habitat heterogeneity and major shifts in environmental conditions were reflected to some extent in the dietary patterns of selected fossil taxa in the Omo-Turkana basin during the Plio-Pleistocene.

For this purpose, the palaeo-dietary behaviours of two mixed-feeding antelope taxa were investigated using fossil teeth from the Plio-Pleistocene deposits of the Omo-Turkana basin, the impala (genus *Aepyceros*) and the springbok (genus *Antidorcas*), which are abundant in the African fossil record, and whose extant relatives are known for their high dietary plasticity. The dietary flexibility of these two fossil taxa could prove to be interesting indicators of vegetation conditions in the past, as mixed-feeders are able to adapt their diet according to the availability of food resources. Their diet can vary seasonally, or when facing niche competition or environmental change, although each taxa are likely to have had dietary preferences that influenced their feeding behaviours regardless of the prevailing vegetation conditions in their habitats (see chapter 3).

The palaeo-diet of these abundant, adaptable antelopes is explored in this chapter, alongside the palaeo-diet of fossil representatives of the giraffid (genus *Giraffa*) and equid (genus *Equus*) mammalian families, to help evaluate the extent of the dietary spectrum of fossil herbivores in the Omo-Turkana basin between 3.44 and 1.6 Ma. To evaluate the dietary ecology of each specimen, dental mesowear analysis was used on data collected from fossil specimens of the studied taxa from the Koobi Fora, Nachukui, and Shungura formations, from members ranging between 3.44 and 1.61 Ma, as well as from modern specimens from different African regions.

Mesowear refers to macroscopic wear on teeth, which results from accumulated attrition and abrasion on molar teeth acquired through life or during the last months/years of an individual's life (Fortelius and Solounias, 2000; Rivals *et al.*, 2007; Louys *et al.*, 2012; Loffredo and DeSantis, 2014; Ackermans *et al.*, 2018; Ackermans, 2020; Ackermans, Martin, *et al.*, 2020). Mesowear is an approach derived from the observations of tooth morphology, occlusal height (relief), and occlusal profile (cusp shape), which can be observed and/or measured from the buccal outlines of specific teeth according to a method defined by Fortelius and Solounias (2000) (see chapter 2.4.1 for more detail on the method). By evaluating the relative proportion of these two types of wear on molars, one can assess whether an animal was predominantly grazing or browsing throughout its life (Fortelius and Solounias, 2000; Mihlbachler and Solounias, 2006; Rivals and Semprebon, 2006; Semprebon and Rivals, 2007; Kaiser *et al.*, 2009; Ackermans, Martin, *et al.*, 2020). High levels of dental abrasion are likely related to the proportion of grass or abrasive matters present in the food resources of the animals, as suggested in previous studies which demonstrated that diets rich in phytoliths (such as grass blades) tend to result in more rounded cups and lower occlusal relief, as opposed to diets depleted of abrasives (such as browsing habits) that result in sharper cusps and higher relief (e.g. Ackermans *et al.,* 2018).

Although some studies have suggested that the dietary signals recorded on the teeth can sometimes be blurred from external non-dietary factors, such as dust or grit, the mesowear method has been shown nonetheless to be able to inform on the overall degree of toughness and abrasiveness of the consumed food items, and to presents the advantages of being quick, inexpensive, non-destructive, relatively taxon-independent, and easy to record directly on fossil material (Loffredo and DeSantis, 2014; Green and Croft, 2018).

The material (4.2) and methods (4.3) used for mesowear analysis are therefore presented in this chapter, followed by results (4.4), divided around the following objectives:

1) Assess the overall dietary signatures of each studied species (extant and extinct), to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and evaluate inter-specific variations between species of the same taxa.
2) Evaluate the degree of variation in dietary patterns within each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time.

These results are presented and briefly interpreted around these themes, before being summarised (4.5). They will be further interpreted and discussed in chapter 7, alongside the other methods for dietary analyses employed in this study.

4.2 Material

Fossil dental remains of the selected taxa (genera *Aepyceros, Antidorcas, Equus* and *Giraffa*) from the Koobi Fora and the Nachukui formations were studied for mesowear analysis at the National Museums of Kenya (Nairobi), as well as specimens from the Shungura formation, held at the National Museum of Ethiopia (Addis-Ababa) (Table 41). The samples were collected from the maximum number of specimens available/allowed for each locality and member under study (see appendix A.9 for the detailed database).

For comparison purposes, data for mesowear analysis were collected on modern dental specimens from the following institutions: the National Museums of Kenya (NMK), the Ditsong Museums of South Africa (Transvaal), Pretoria, and the Bavarian State Collection of Zoology (Munich, Germany) (Table 42- see appendix A.10 for the detailed database).

Table 41: Number of fossil specimens analysed for mesowear analysis, per genus and per member.

Provenance	**Member**	**Dates (Ma)**	**Number of specimens (per genus)**				**Totals**
			Aepyceros	***Antidorcas***	***Equus***	***Giraffa***	
Koobi Fora, Kenya (National Museums of Kenya, Nairobi)	Tulu Bor	3.44 - 2.64	0	0	0	0	30
	Burgi	2.64 - 1.87	3	1	2	1	
	KBS	1.87 - 1.61	8	1	9	5	
Nachukui, Kenya (National Museums of Kenya, Nairobi)	Lomekwi	3.44 - 2.53	6	0	0	0	13
	Lokalalei	2.53 - 2.33	0	0	0	0	
	Kalochoro	2.33 - 1.9	1	0	3	0	
	Kaitio	1.9 - 1.61	2	0	1	0	
Shungura, Ethiopia (National Museum of Ethiopia, Addis-Abeba)	B	3.44 - 2.91	6	0	0	2	50
	C	2.91 - 2.52	7	0	0	2	
	D	2.52 - 2.4	5	0	0	2	
	E	2.4 - 2.32	8	0	0	0	
	F	2.32 - 2.27	10	0	0	0	
	G	2.27 - 1.9	8	0	0	0	
Modern	/		33	10	9	11	63
						Total	**156**

Table 42: Numbers of modern specimens analysed for mesowear analysis, per species and per institution.

Source	**Information available**	**Number of specimens**			
		Aepyceros melampus	***Antidorcas marsupialis***	***Equus quagga***	***Giraffa camelopardalis***
National Museums of Kenya, Nairobi	**Sex; Provenance** (Kenya)	6	3	0	0
Ditsong Museum, Pretoria, South Africa	**Age; Sex; Provenance** (South Africa, Namibia and Botswana localities)	25	7	0	0
Bavarian State Collection of Zoology, Munich, Germany	**Sex; Provenance** (Kenya, and Tanzania localities)	9	0	0	0
Royal Museum for Central Africa, Tervuren, Belgium	**Sex; Provenance** (Congo, Kenya, Rwanda, Sudan and Tanzania localities)	39	0	11	12
Totals		**79**	**10**	**11**	**12**

4.3. Methods

4.3.1 Selected teeth

Upper molars were selected for mesowear analysis, focusing in priority on M^2-M^3 as advised in previous studies (see 2.4.1). M^1 and upper molars of undetermined row were also used to increase sample size. Differences between molar rows were evaluated statistically before any further analysis to ensure the dietary signal would not be averaged by significant differences in mesowear scores between the different molars (see appendix A.10). Following this, all upper first, second and third molars were included in the analyses. A total of 93 fossil specimens and 63 modern specimens were selected for mesowear analysis.

4.3.2 Mesowear Scoring

Each tooth was scored for occlusal relief and cusp shape through visual assessment during data collection in each of the museums visited, following the categories described in Figure 18. To reduce potential scoring biases for occlusal relief (and as advised by Fortelius and Solounias (2000) for "borderline cases"), measurements were also taken a posteriori on each specimen from digital photographs of the specimens, using the software program ImageJ (version 1.52a; Rasband 1997).

A "relief-index" was then constructed by dividing occlusal relief (defined as the vertical distance between a line connecting two adjacent cusp tips and the bottom of the valley between them – see Figure 18) by the length of the tooth; low relief was attributed to specimens with an index value lower than 0.1, and high relief to index scores higher than 0.1 (Fortelius and Solounias, 2000). The results obtained from that index were then compared to the scores obtained through visual assessment. When the results disagreed, the scores obtained quantitatively were favoured against the ones obtained qualitatively, to reduce potential observer bias and ensure consistency in the occlusal relief scoring. Out of the 156 teeth scores for mesowear analysis, only 14 specimens were scored differently between the two methods. A scale from 0 to 4 was used, where 0 represents the most attrition-dominated mesowear signature (suggested to represent browsing habits), and 4 represents the most abrasion-dominated signature (suggested to represent grazing habits) (Figure 51).

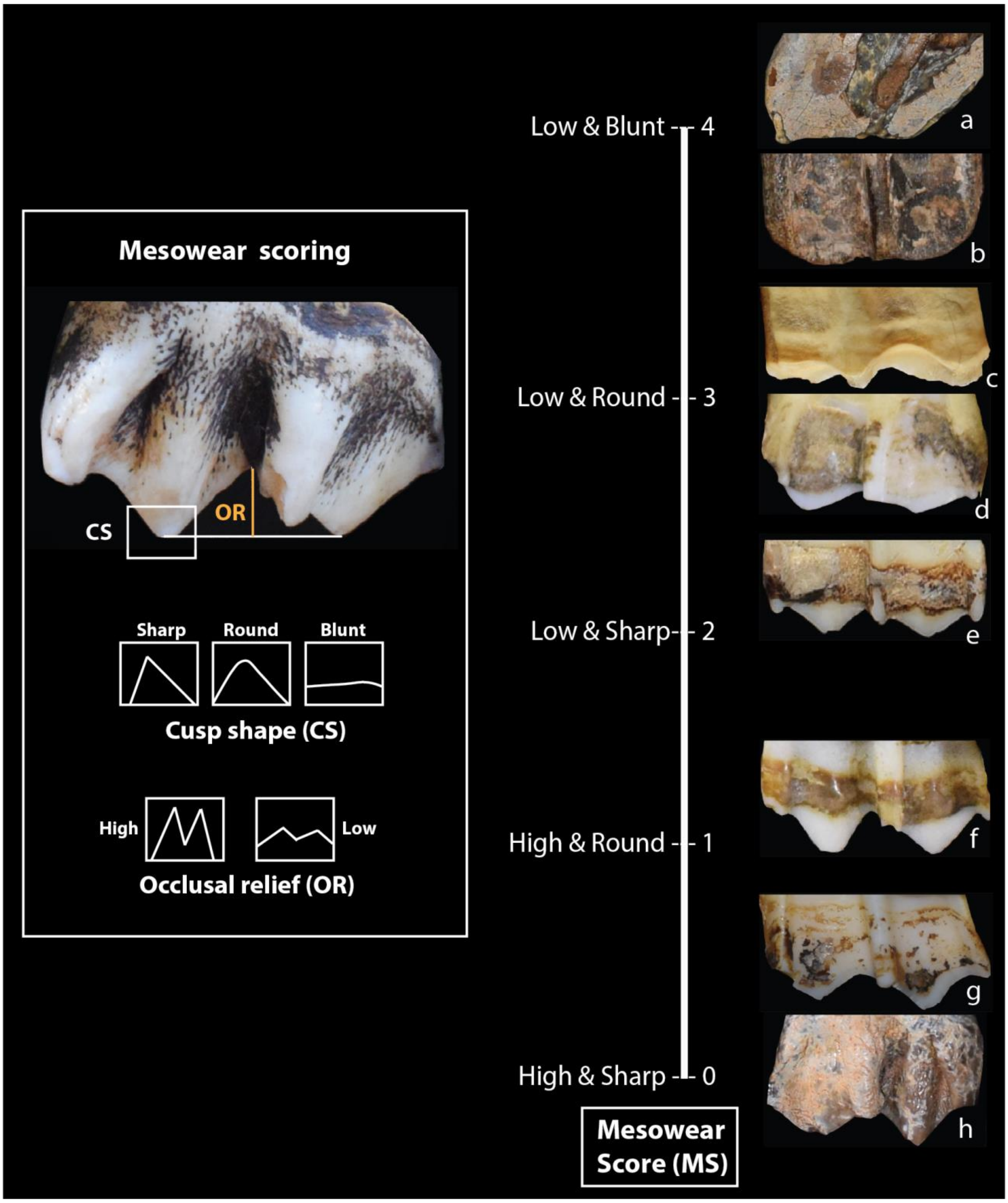

Figure 51: Mesowear scoring of molar relief (into 'low' or 'high') and cusp shape (into 'sharp', 'rounded' or 'blunt') (specimen RMCA 3747, *Giraffa camelopardalis*), and examples of mesowear scores (MS). Specimens: (a) *Equus sp.* (KNM-ER 4056); (b) *Equus sp.* (KNM-WT 14691); (c) *Equus quagga* (RMCA 3607); (d) *Antidorcas marsupialis* (TM-2437); (e) *Aepyceros melampus* (TM-17673); (f) *Aepyceros melampus* (TM-4236); (g) *Antidorcas marsupialis* (TM-3140); and (h) *Giraffa stillei* (KNM-ER 3909); not to scale. From the following institutions: KNM: National Museums of Kenya, Nairobi; TM: Ditsong Museums of South Africa, Pretoria; RMCA: Royal Museum for Central Africa, Tervuren (Belgium).

4.3.2 Statistical analyses

The dietary patterns were analysed for each taxon to assess if significant differences in dietary patterns could be observed between fossil and modern specimens of each species, but also to see if differences between locality and/or member could be found within each studied taxon. For this, a series of statistical analyses were performed using the software R Studio (version 1.2.1335; R version 3.6.3; R Core Team 2013) (see appendix A.6 for detail of all R packages used in this study).

Prior to analysis, the ordinal variable mesowear score was tested for normality (Shapiro-Wilk test) and for homogeneity of variance (Levene Test for Homogeneity of Variance). Because the assumptions of parametric tests were not met, the Kruskal-Wallis test was used to assess significant differences within and between groups. Where the Kruskal–Wallis test was significant, post-hoc analyses were performed to determine which groups significantly differ from the others, using Dunn's test with adjustments to the p-value (Holm's correction) to control for familywise error rates.

The dataset was analysed once to check for significant dietary differences within each genus depending on samples sorted by provenance (i.e. Koobi Fora, Nachukui and modern samples), and a second time to check for significant differences in dietary patterns through time within each fossil locality for each genus, based on subsets sorted by members

For general comparisons between fossil and modern samples (regardless of provenance and member), statistical analyses were run at the species level to assess the dietary preferences of the studied fossil species, in comparison with those of modern specimens. Due to small numbers of specimens per sample for some subsets, analyses were run at the genus level (i.e. species from same genus altogether) when comparing samples by provenance or member, for more statistical power.

4.4 Results and interpretations

Firstly, the differences and similarities in dietary patterns between fossil species and modern species of known diet are examined to assess the dietary preference of each studied fossil taxon, regardless of the provenance and dates of fossil specimens (i.e. interspecific variation) (4.4.1). This is to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and to evaluate inter-specific variations between species of the same taxa. Variations in dietary patterns are then evaluated for each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time (4.4.2).

4.4.1 Dietary variation among taxa: Interspecific comparisons

To investigate the type and degree of accumulated dental use-wear for each of the studied taxa, and, by inference, the relative proportion of grass or of abrasive matters present in their food, mesowear scores of each fossil and modern species were compared (Table 43, Table 44, and Figure 52). Results showed significant differences between species within the studied samples (fossil and modern).

Table 43: Descriptive statistics for each species, for fossil and modern samples. Mean, median, standard deviation and standard error to the mean are represented for mesowear score, as well as the frequencies for each mesowear feature observed (Cusp relief: Low, High; Cusp shape: Sharp, Round, Blunt).

			Mesowear score (1-4)				Frequencies (%)				
Species	**Sample**	**N**	**mean**	**median**	**SD**	**SEM**	**Low**	**High**	**Sharp**	**Round**	**Blunt**
Aepyceros shungurae	Fossil	49	2.02	3	1.09	0.16	55.1	44.9	8.16	91.84	0
Aepyceros melampus	Fossil	14	1.07	1	0.92	0.25	14.29	85.71	21.43	78.57	0
Aepyceros sp.	Fossil	1	3	3			100	0	0	100	0
Aepyceros melampus	Modern	33	1.91	1	1.04	0.18	51.52	48.48	3.03	96.97	0
Antidorcas recki	Fossil	2	2	2	1.41	1	50	50	0	100	0
Antidorcas marsupialis	Modern	10	1.7	1	1.16	0.37	40	60	10	90	0
Equus sp.	Fossil	15	2.67	3	1.11	0.29	80	20	0	80	20
Equus quagga	Modern	9	3.11	3	0.33	0.11	100	0	0	88.89	11.11
Giraffa gracilis	Fossil	3	1.33	1	1.53	0.88	33.33	66.67	33.33	66.67	0
Giraffa pygmaea	Fossil	2	2	2	1.41	1	50	50	0	100	0
Giraffa stillei	Fossil	6	0.83	1	0.41	0.17	0	100	16.67	83.33	0
Giraffa sp.	Fossil	1	1	1			0	100	0	100	0
Giraffa camelopardalis	Modern	11	1.36	1	1.12	0.34	27.27	72.73	18.18	81.82	0

Table 44: Kruskal-Wallis test to explore variation in mesowear score between species (fossil and modern samples). DF=Degrees of freedom. (See appendix A.12.1 table-A 14 for pairwise comparisons table).

	Chi-square	**DF**	**P-value**
Fossil/Modern species	29.786	11	**0.002**

As expected, significant differences were found between *Equus* and *Giraffa* specimens. Mesowear scores are typical of browsing species for the *Giraffa* specimens, with low values (i.e. MS < 1.5) indicative of a poorly abrasive diet. On the contrary, mesowear scores are typical of grazing species for modern plain zebra specimens with high scores (*Equus quagga* mean = 3.11), and fossil equid specimens display medium-high scores which could indicate mixed-diets with a predominance of abrasive food items (*Equus* sp. mean = 2.67). This difference in dietary pattern between giraffids and equids is confirmed by results from Dunn tests, showing that there are significant differences between *G. camelopardalis* and *E. quagga* specimens in the modern samples (p=0.048), as well as between fossil *G. stillei* and modern *E. quagga* specimens (p=0.0002). No significant difference was found between fossil and modern species within each of these genera.

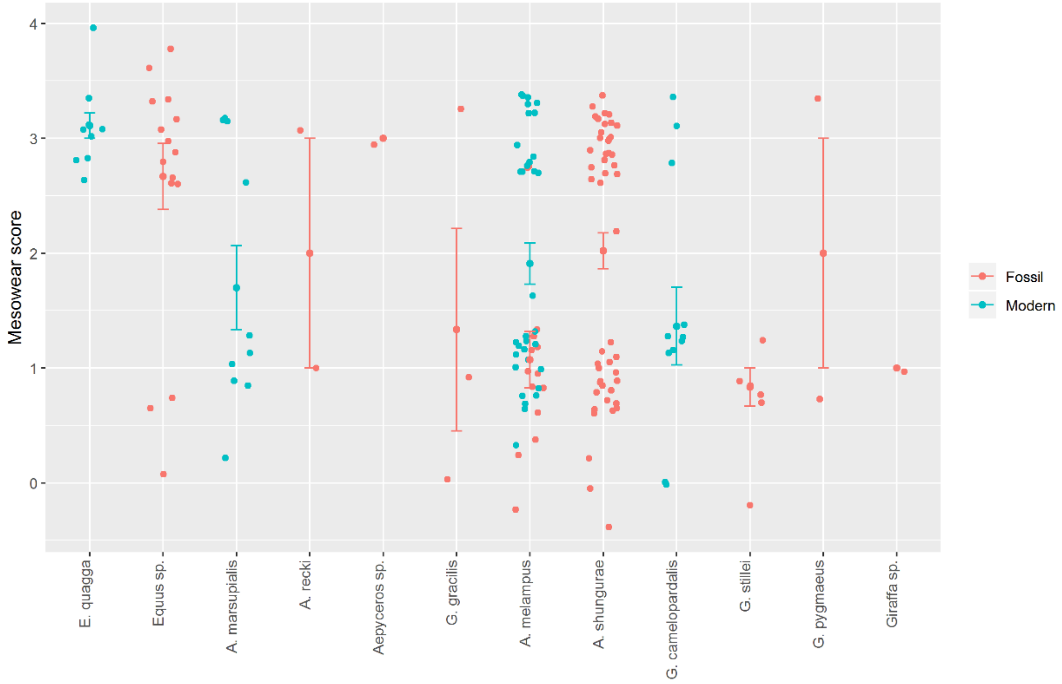

Figure 52: Distribution of mesowear scores per species (mean and standard error of the mean), for fossil and modern samples. This figure highlights the differences between browsers (MS between 0-1) and grazers (MS between 3-4).

Mesowear scores (MS) for specimens from genus *Aepyceros* vary depending on the species and the samples. While modern *Aepyceros melampus* specimens (mean = 1.91) and fossil *Aepyceros shungurae* specimens (mean = 2.02) demonstrate a large spread of values along the grazing-browsing spectrum typical of mixed-feeders, fossil *A. melampus* specimens display lower MS values (mean = 1.07), more similar to browsers. However, no significant difference was found between the various *Aepyceros* species. While no significant difference was identified between modern *A. melampus* and other modern species, fossil *A. melampus* was found to significantly differ from the modern *Equus quagga* sample (p=0.002) and from fossil *Equus sp.* specimens (p=0.012), with lower mean MS for fossil impalas compared to modern plain zebras and fossil equids. This could suggest the inclusion of a large amount of browse in the diet of most of the fossil *A. melampus* specimens, resulting in poorly abrasive diets, compared to grazing equids. No significant difference was found between fossil *A. shungurae* and other species.

Similarly to modern *A. melampus* specimens, modern *Antidorcas marsupialis* (mean = 1.7) and fossil *Antidorcas recki* (mean =2) individuals demonstrate mean mesowear scores typical of mixed-feeders, with values spread across the dietary spectrum. Results from Dunn's tests showed no significant differences between *Antidorcas* samples and other species.

4.4.2 Intra-generic spatio-temporal variation in diet in the Omo-Turkana basin

Intra-generic dietary comparisons were performed on mesowear scores at the genus level to assess whether spatial and/or temporal differences in dietary practices could be observed within each of the studied taxa (Table 45, Table 46, Figure 53, Figure 54). No significant difference was found between localities, or between members within each locality, for any of the studied taxa.

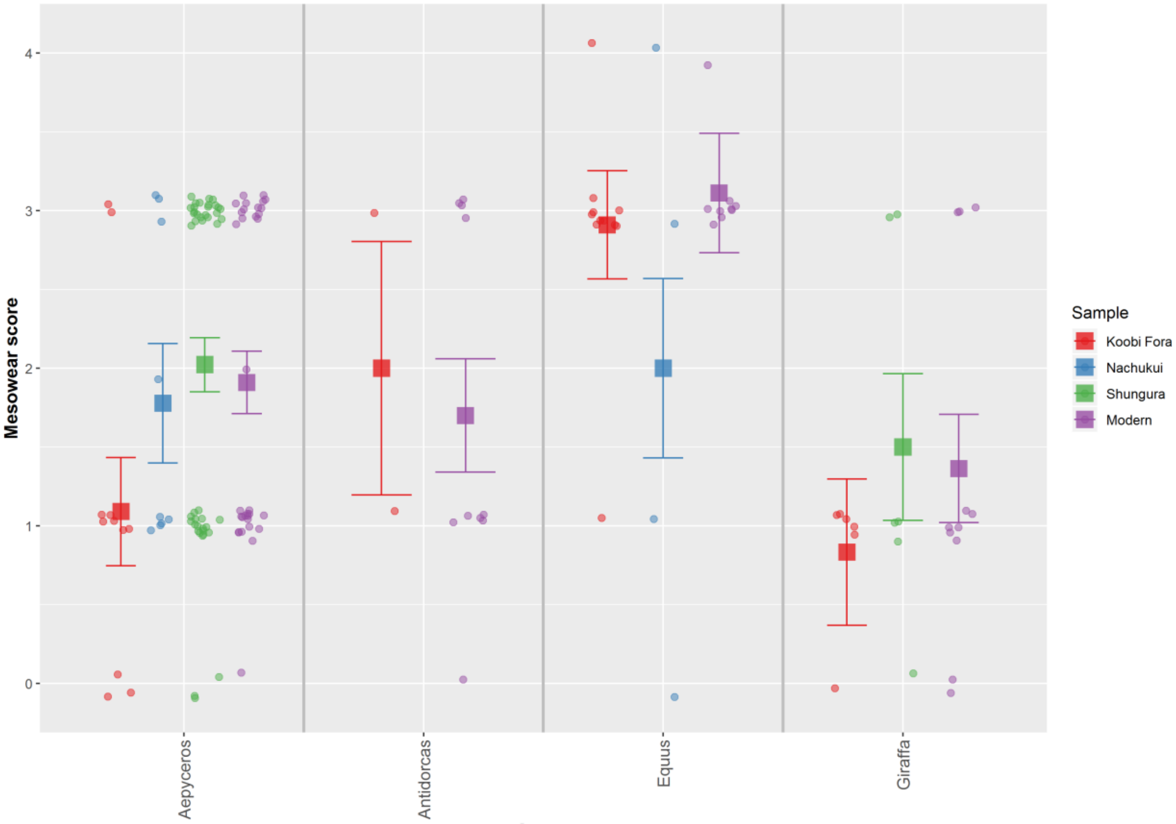

Figure 53: Distribution of mesowear scores per genus (mean and standard error of the mean), for fossil (i.e. Koobi Fora, Nachukui and Shungura) and modern samples. Points represent individual specimen, squares with error bars represent the mean value and standard deviation of each sample.

Table 45: Descriptive statistics for each genus, for fossil and modern samples, for each studied subset (locality and member). Mean, median, standard deviation (S.D.) and standard error of the mean (S.E.M.) are represented for mesowear score, as well as the frequencies for each mesowear feature observed (Cusp relief: Low, High; Cusp shape: Sharp, Round, Blunt).

				Mesowear score (1-4)				Frequencies (%)				
Species	**Subset**	**Member (Ma)**	**N**	**mean**	**median**	**SD**	**SEM**	**Low**	**High**	**Sharp**	**Round**	**Blunt**
Aepyceros	**Koobi Fora**	**All**	**11**	**1.09**	**1**	**1.04**	**0.31**	**18.18**	**81.82**	**27.27**	**72.73**	**0**
		Burgi (2.68 - 1.88)	3	1	1	0	0	0	100	0	100	0
		KBS (1.88 -1.6)	8	1.13	1	1.25	0.44	25	75	37.5	62.5	0
	Nachukui	**All**	**9**	**1.78**	**1**	**0.97**	**0.32**	**44.44**	**55.56**	**11.11**	**88.89**	**0**
		Lomekwi (3.35 -2.5)	6	2.17	2.5	0.98	0.40	66.67	33.33	16.67	83.33	0
		Kalochoro (2.35 - 1.9)	1	1	1			0	100	0	100	0
		Kaitio (1.9 -1.65)	2	1	1	0	0	0	100	0	100	0
	Shungura	**All**	**44**	**2.02**	**3**	**1.11**	**0.17**	**54.55**	**45.45**	**6.818**	**93.18**	**0**
		B (3.44 - 2.91)	5	2.2	3	1.10	0.49	60	40	0	100	0
		B-C	1	3	3			100	0	0	100	0
		C (2.91 - 2.52)	7	1.43	1	1.13	0.43	28.57	71.43	14.29	85.71	0
		D (2.52 - 2.4)	5	2.60	3	0.89	0.40	80	20	0	100	0
		E (2.4 - 2.32)	5	1.80	1	1.10	0.49	40	60	0	100	0
		E-F	3	1.67	1	1.15	0.67	33.33	66.67	0	100	0
		F (2.32 - 2.27)	10	2.10	3	1.20	0.38	60	40	10	90	0
		G (2.27 - 1.9)	8	2.13	3	1.25	0.44	62.5	37.5	12.5	87.5	0
	Modern	/	**33**	**1.91**	**1**	**1.04**	**0.18**	**51.52**	**48.48**	**3.03**	**96.97**	**0**
Antidorcas	**Koobi Fora**	**All**	**2**	**2**	**2**	**1.41**	**1**	**50**	**50**	**0**	**100**	**0**
		Burgi (2.68 - 1.88)	1	1	1			0	100	0	100	0
		KBS (1.88 -1.6)	1	3	3			100	0	0	100	0
	Modern	/	**10**	**1.70**	**1**	**1.16**	**0.37**	**40**	**60**	**10**	**90**	**0**
Equus	**Koobi Fora**	**All**	**11**	**2.91**	**3**	**0.70**	**0.21**	**90.91**	**9.091**	**0**	**90.91**	**9.09**
		Burgi (2.68 - 1.88)	2	3	3	0.00	0	100	0	0	100	0
		KBS (1.88 -1.6)	9	2.89	3	0.78	0.26	88.89	11.11	0	88.89	11.11
	Nachukui	**All**	**4**	**2**	**2**	**1.83**	**0.91**	**50**	**50**	**0**	**50**	**50**
		Kalochoro (2.35 - 1.9)	3	2.33	3	2.08	1.20	66.67	33.33	0	33.33	66.67
		Kaitio (1.9 -1.65)	1	1	1			0	100	0	100	0
	Modern	/	**9**	**3.11**	**3**	**0.33**	**0.11**	**100**	**0**	**0.00**	**88.89**	**11.11**
Giraffa	**Koobi Fora**	**All**	**6**	**0.83**	**1**	**0.41**	**0.17**	**0**	**100**	**16.67**	**83.33**	**0**
		Burgi (2.68 - 1.88)	1	0	0			0	100	100	0	0
		KBS (1.88 -1.6)	5	0	0	0	0	0	100	0	100	0
	Shungura	**All**	**6**	**1.5**	**1**	**1.22**	**0.5**	**33.33**	**66.67**	**16.67**	**83.33**	**0**
		B (3.44 - 2.91)	2	2	2	1.41	1	50	50	0	100	0
		C (2.91 - 2.52)	2	1.5	1.5	2.12	1.5	50	50	50	50	0
		D (2.52 - 2.4)	2	1	1	0	0	0	100	0	100	0
	Modern	/	**11**	**1.36**	**1**	**1.12**	**0.34**	**27.27**	**72.73**	**18.18**	**81.82**	**0**

Impala specimens from the Koobi Fora formation appear to have lower mesowear scores than specimens from both Nachukui and Shungura formations, which could suggest a lifetime-diet dominated by browse for most *Aepyceros* specimens in the Koobi Fora formation, as opposed to more varied dietary practices among specimens from the other two localities. Little variation through time can be observed within the Koobi Fora and Nachukui formations for this taxon, apart from a higher dietary variability among specimens from the KBS (represented by *A. melampus*) and Lomekwi (represented by *A. shungurae*) members, as opposed to browsing signals in members Burgi, Kalochoro and Kaitio. A high dietary variability can also be observed between specimens from Shungura (represented by *A. shungurae*), and some degree of variation can be noticed across members, with lower mean mesowear scores for specimens from members C and E, suggesting a dominance of specimens predominantly browsing throughout their life. This could suggest variation in the diet of fossil impala specimens through time in the Omo-Turkana basin. However, none of these differences was confirmed by statistical analyses.

Potential spatial and temporal variation in diet could not be assessed for fossil *Antidorcas* specimens, due to small sample sizes.

Equid specimens from the Koobi Fora formation appear to have higher mesowear scores than specimens from the Nachukui formation, which could suggest an overall diet more typical of grazing herbivores in Koobi Fora, and a larger range of dietary practices in specimens from Nachukui, ranging between grazing and browsing. However, the small sample size available for the Nachukui formation does not permit to explore further this pattern, and none of these observations were confirmed by statistical analyses.

Little variation in mesowear scores can be observed for the *Giraffa* samples, with mean scores typical of browsing species in all three localities, and little variation through time in each locality. Small sample sizes did not allow to explore further the potential dietary variability of fossil giraffids in the studied deposits.

Table 46: Results from the Kruskal Wallis tests to explore variation in mesowear score within each genus between samples a) per locality and b) per member within each locality. DF=Degrees of freedom.

	Locality		
	Chi-square	**DF**	**P-value**
a) *Aepyceros*	0.138057076	1	0.710
Antidorcas	0.128571429	1	0.720
Equus	0.679939668	1	0.410
Giraffa	0.124539744	1	0.724

	Member			
	Sample	**Chi-square**	**DF**	**P-value**
b) *Aepyceros*	*Koobi Fora*	0.11	1	0.735
	Nachukui	3.00	2	0.223
	Shungura	4.90	7	0.672
Antidorcas	*Koobi Fora*	1.00	1	0.317
Equus	*Koobi Fora*	0.00	1	1.000
	Nachukui	0.20	1	0.655
Giraffa	*Koobi Fora*	5.00	1	0.055
	Shungura	0.58	2	0.747

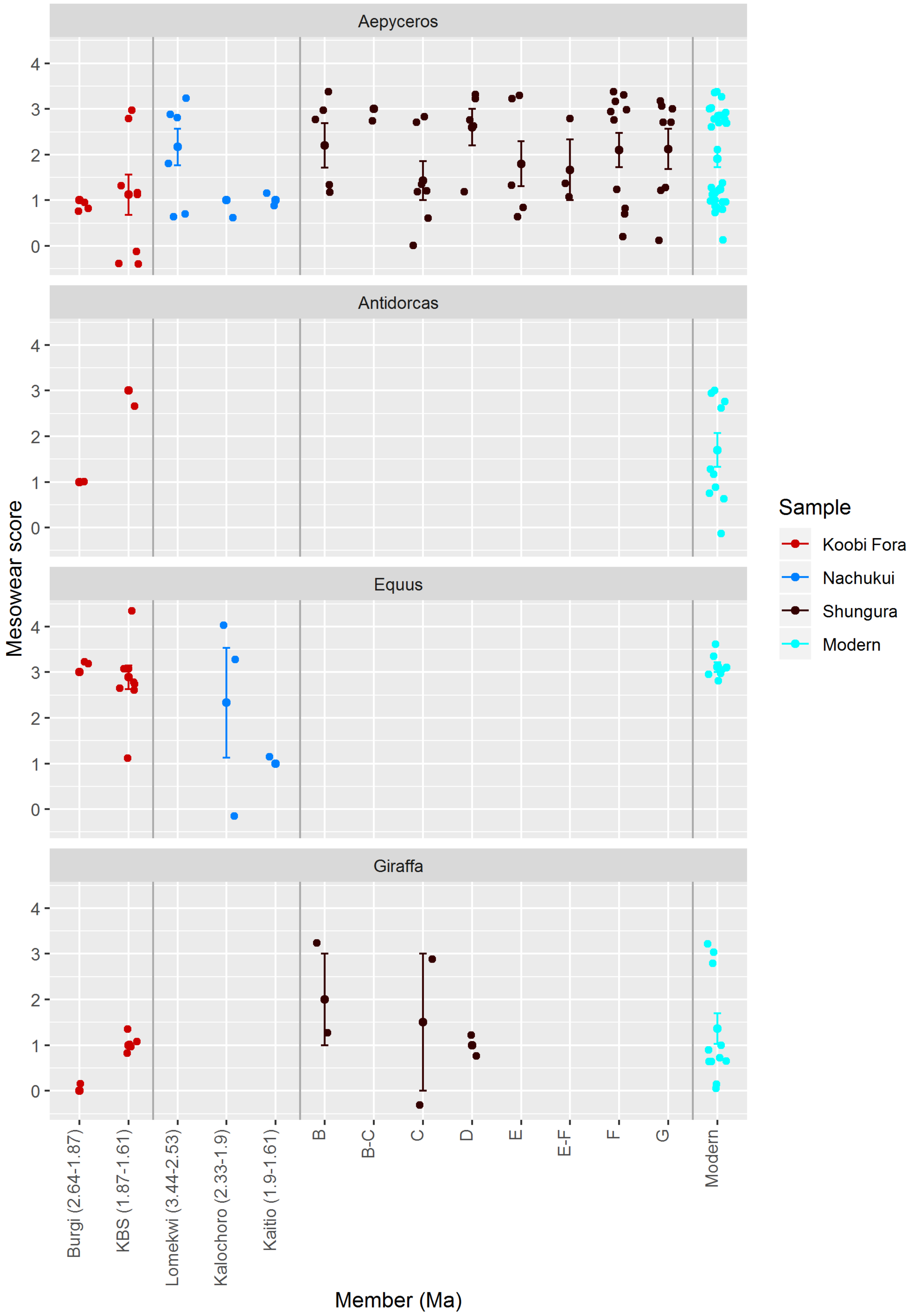

Figure 54: Distribution of mesowear scores per genus through time (mean and standard error of the mean), for modern and fossil (i.e. Koobi Fora and Nachukui) samples, with subsets by member.

4.5 Summary of findings

Species-specific mesowear patterns:

- *Giraffa*: low mesowear score (MS) for all species. This signal is typical of browsers.
- *Equus*: high MS for modern *E. quagga*, but high to mid-range MS for fossil *Equus*. This might indicate more individuals with mixed-feeding behaviours in fossil equids compared to modern specimens.
- *Aepyceros shungurae*: wide range of values for MS. This suggests varied dietary patterns across fossil specimens, from grazing to browsing.
- *Aepyceros melampus*: wider range of values among modern specimens, compared to fossil specimens; lower MS score for fossil specimens, potentially indicating a dominance of browsing diets.

Intra-generic variations in mesowear patterns:

- *Aepyceros*: lower MS in Koobi Fora compared to other samples, which suggests less abrasive diets in East Turkana. Varying mesowear scores across members observed in Shungura, with higher mean mesowear scores for specimens from members B, D, F and G, where scores are more typical of mixed-feeders, while scores from the other members are more typical of browsing species.
- *Equus*: lower MS in Nachukui compared to other samples, which could suggest mixed-feeding patterns in West Turkana equids.
- *Giraffa*: Little variation in mesowear scores was observed for the *Giraffa* samples, with mean scores typical of browsing species in Koobi Fora and Shungura, although the mean mesowear scores in Shungura are slightly higher.

Overall, results from mesowear analysis suggest that fossil *Aepyceros* might have favoured browse in Koobi Fora, as opposed to graze in Nachukui. This could potentially reflect a difference in habitat composition and/or heterogeneity between East and West Turkana, with a more heterogeneous vegetation structure in the East compared to the West, and less wooded areas in the West. Indeed, the Koobi Fora samples show the presence of both grazing and browsing species in the area, while the Nachukui samples suggest a prevalence of grazing practices, with evidence of browse consumption only between 2.5 and 1.9 Ma in Kalochoro member. This change in feeding preference among impalas from the Kalochoro member could potentially reflect a change in resource availability or in niche competition at Nachukui. However, the very small sample size for this member (*Aepyceros* n=1) does not allow for robust analyses and interpretations.

Inter-generic dietary comparisons per locality and per member

Results from mesowear analysis suggest that East Turkana *Aepyceros* and *Antidorcas* specimens differed in their dietary practices, with impalas including a smaller amount of abrasive food items in their diet compared to springboks, resulting in lower mesowear scores. This is especially highlighted at Koobi Fora, where they are both represented in the same members (i.e. while in Nachukui they are represented in different members). This could potentially reflect the vegetation heterogeneity of the area, providing each mixed-feeding taxon with a variety of food resources to choose from. The difference in dietary preference among the two antelope species could potentially reflect as well niche partitioning behaviours, with impala predominantly browsing and springbok predominantly grazing in the same area to reduce dietary competition, although this hypothesis cannot be confirmed.

Chapter 5: Dental microwear textural analysis

5.1 Introduction

As described in previous chapters, published studies of the Omo-Turkana basin have suggested that a high diversity of habitats is likely to have been available to hominins in this region between 3.4 and 1.6 Ma, and that several major climatic events might have had an important impact on the local environments, and, in turn, on the faunal communities inhabiting the region at the time. Alike the mesowear analyses presented in chapter 4, this chapter presents analyses that were designed to test these hypotheses using evidence from herbivore feeding ecology, to assess whether high habitat heterogeneity and major shifts in environmental conditions were reflected in the dietary patterns of selected fossil taxa in the Omo-Turkana basin during the Plio-Pleistocene. The palaeo-dietary behaviours of the mixed-feeding antelope taxa *Aepyceros* (impala) and *Antidorcas* (springbok) are investigated, alongside those of fossil representatives of the giraffid (genus *Giraffa*) and equid (genus *Equus*) mammalian families, to help evaluate the extent of the dietary spectrum of fossil herbivores in the Omo-Turkana basin between 3.44 and 1.6 Ma.

To evaluate the dietary ecology of each specimen, dental microwear textural analysis was used on data from fossil specimens of the studied taxa from the Koobi Fora, Nachukui and Shungura formations, from members ranging between 3.44 and 1.61 Ma, as well as from modern specimens from different African regions.

Dental microwear refers to the microscopic tooth-wear that results from dental use, different food types yielding differing marking patterns on the enamel surface due to how various food types differ in resistance to structural breakdown during mastication (Walker and Teaford, 1989; Teaford, 1994). Dental microwear texture analysis (DMTA) is based on three-dimensional surface measurements taken using white-light confocal microscopy and scale-sensitive fractal analysis, producing surface parameters that allow quantitative characterizations of three-dimensional surfaces that are repeatable and free of observer measurement error (Ungar *et al.*, 2003; Scott *et al.*, 2006; Green and Croft, 2018) (see 2.4.2.3 Textural parameters). Previous studies have showed that microwear, similarly to mesowear, is closely impacted by the properties of the consumed foods, especially its toughness and siliceous content, but also to other food properties, such as particle size (Lucas *et al.*, 2008; Scott, 2012; Ramdarshan *et al.*, 2016) (see chapter 2.4.2 for more detail). Unlike mesowear, microwear does not reflect a cumulative use-wear produced over months to years, but instead informs on the structural characteristics of the food items consumed up to two weeks before the animal's death, due to the rapid turnover rate of the traces imprinted on the enamel surface (Kaiser and Brinkmann, 2006; Ungar, 2015; Calandra and Merceron, 2016; Bignon-lau *et al.*, 2017; Green and Croft, 2018). Dental microwear textural analysis can therefore provide information on individual feeding behaviour in greater detail and on a different temporal scale than mesowear analysis, and therefore can be used to evaluate variation in dietary behaviours within and between populations of a species, as well as seasonal and temporal changes in feeding ecology at the species, taxa or palaeo-community-level (e.g. Rivals and Solounias 2007, Merceron *et al.* 2010, 2014, Rivals *et al.* 2015, Bignon-lau *et al.* 2017, Berlioz *et al.* 2018).

As for mesowear analysis in chapter 4, the material (5.2) and methods (5.3) used for this analysis are presented in this chapter, followed by the results (5.4), divided around the following objectives:

1) Assess the overall dietary signatures of each studied species (extant and extinct), to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and evaluate inter-specific variations between species of the same taxa.

2) Evaluate the degree of variation in dietary patterns within each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time.

These results are presented and briefly interpreted around these themes, before being summarised (5.5). They will be further interpreted and discussed in chapter 7, alongside the other methods for dietary analyses employed in this study.

5.2 Material

Fossil dental remains of the selected taxa (genera *Aepyceros, Antidorcas, Equus* and *Giraffa*) from the Koobi Fora and the Nachukui formations were moulded for microwear analysis at the National Museums of Kenya (Nairobi). For specimens from the Shungura formation, held at the National Museum of Ethiopia (Addis-Ababa), microwear data were not collected, as this aspect of the palaeo-ecology of the studied species was already under study by project collaborators (i.e. Dr. Gildas Merceron and Dr Cécile Blondel, University of Poitiers, France, PALEVOPRIM, UMR 7262 CNRS INEE). However, dental microwear data for *Aepyceros* specimens were kindly shared by G. Merceron to be included in this project, and allow for comparison with the microwear data collected for the Koobi Fora and Nachukui formations. The samples were collected from the maximum number of specimens available/allowed for each locality and member under study (Table 47 – see appendix A.9 for the detailed dataset).

To allow for comparisons with modern specimens, moulds for microwear analysis were collected on modern dental specimens from the following institutions: the National Museums of Kenya (NMK), the Ditsong Museums of South Africa (Transvaal), Pretoria, and the Bavarian State Collection of Zoology (Munich, Germany). (Table 48 - see appendix A.10 for the detailed database).

DMTA data from a set of modern specimens of different African bovid species, whose diets are known and should reflect the main dietary categories studied, was provided by project collaborator G. Merceron (PALEVOPRIM, UMR CNRS 7262 - Université de Poitiers, France) and used for comparative analyses. Additional data for the leaf-browsing giraffe (*Giraffa camelopardalis* – 17 specimens) was provided, as well as data for the obligate grazing hartebeest (*Alcelaphus buselaphus* – 28 specimens), and the fruit-browsing yellow-backed duiker (*Cephalophus silvicultor* – 27 specimens). Among the 86 modern impala specimens (*Aepyceros melampus*) scanned for this study, 14 casts had been collected by G. Merceron's team at the Natural History Museum of Berlin (Germany).

Table 47: Number of fossil specimens analysed for dental microwear textural analysis, per genus and per member.

Provenance	Member	Dates (Ma)	Number of specimens (per genus)			
			Aepyceros	*Antidorcas*	*Equus*	*Giraffa*
Koobi Fora, Kenya (National Museums of Kenya, Nairobi)	Tulu Bor	3.44 - 2.64	1	3	1	3
	Burgi	2.64 - 1.87	7	9	7	6
	KBS	1.87 - 1.61	20	17	10	14
Nachukui, Kenya (National Museums of Kenya, Nairobi)	Lomekwi	3.44 - 2.53	20	3	0	3
	Lokalalei	2.53 - 2.33	0	2	0	0
	Kalochoro	2.33 - 1.9	3	1	4	1
	Kaitio	1.9 - 1.61	7	0	3	0
Shungura, Ethiopia (National Museum of Ethiopia, Addis-Abeba)	B	3.44 - 2.91	15	/	/	/
	C	2.91 - 2.52	20	/	/	/
	D	2.52 - 2.4	12	/	/	/
	E	2.4 - 2.32	20	/	/	/
	F	2.32 - 2.27	46	/	/	/
	G	2.27 - 1.9	15	/	/	/
Total	/		186	35	25	27

Table 48: Numbers of modern specimens for which moulds were collected for dental microwear textural analysis, per species and per institution.

Source	Information available	Number of specimens			
		Aepyceros melampus	***Antidorcas marsupialis***	***Equus quagga***	***Giraffa camelopardalis***
National Museums of Kenya, Nairobi	**Sex; Provenance** (Kenya)	6	3	0	0
Ditsong Museum, Pretoria, South Africa	**Age; Sex; Provenance** (South Africa, Namibia and Botswana localities)	25	7	0	0
Bavarian State Collection of Zoology, Munich, Germany	**Sex; Provenance** (Kenya, and Tanzania localities)	9	0	0	0
Royal Museum for Central Africa, Tervuren, Belgium	**Sex; Provenance** (Congo, Kenya, Rwanda, Sudan and Tanzania localities)	39	0	11	12
Totals		**79**	**10**	**11**	**12**

5.3 Method

5.3.1 Selected specimens

Following previous studies (see 2.4.2) (Semprebon *et al.*, 2004; Merceron *et al.*, 2012; Scott, 2012; Rivals *et al.*, 2015; Ramdarshan *et al.*, 2017), data for dental microwear textural analysis was collected preferentially on upper- and lower-second molars. Analyses focused on the disto-labial facet of the protoconid (or of the hypoconid, if the protoconid was broken), the mesio-lingual facet of the protocone and the mesio-lingual facet of the paracone (Figure 20).

5.3.2 Moulding and scanning protocols

Data for dental microwear analysis was collected following the TRIDENT protocol used in similar studies (e.g. Francisco *et al.* 2016, Merceron, Blondel, *et al.* 2016, Ramdarshan *et al.* 2016, Berlioz *et al.* 2017, Bignon-lau *et al.* 2017, Blondel *et al.* 2018) to ensure output comparability. First, each occlusal surface was cleaned using acetone with a toothbrush and a cotton swab, to remove any remaining organic material (especially for modern specimens) and sediment. Moulds were then made using a polyvinylsiloxane elastomer (Regular Body President, ref 6015 - ISO 4823, medium consistency, polyvinylsiloxane addition type; Coltene Whaledent) (Figure 55).

The facets of interest were scanned at the PALEVOPRIM laboratory (UMR CNRS 7262 - Université de Poitiers, France) with a Leica DCM8 confocal profilometer using white light confocal technology with a Leica 100 objective (Numerical Aperture = 0.90; working distance= 0.9 mm) (Figure 56). The centre of the selected facets was preferably targeted for scanning, to ensure consistency and repeatability, and avoid biases related to study area selection (Ramdarshan *et al.* 2017). However, other areas of the facet had to be targeted for scanning when the centre of the cast was not preserved, either due to microscopic overlaying sediment or organic matter that was present on the tooth surface, or due to microscopic bubbles formed in the silicone while casting, which can happen in regions with high altitudes, such as in Nairobi, Kenya (1661 m) and in Addis-Ababa, Ethiopia (2300-2600 m) (pers. Com. G. Merceron, May 2017). Analyses were based on the association of the protocone and the protoconid facets, which were the most represented facets in the assemblage.

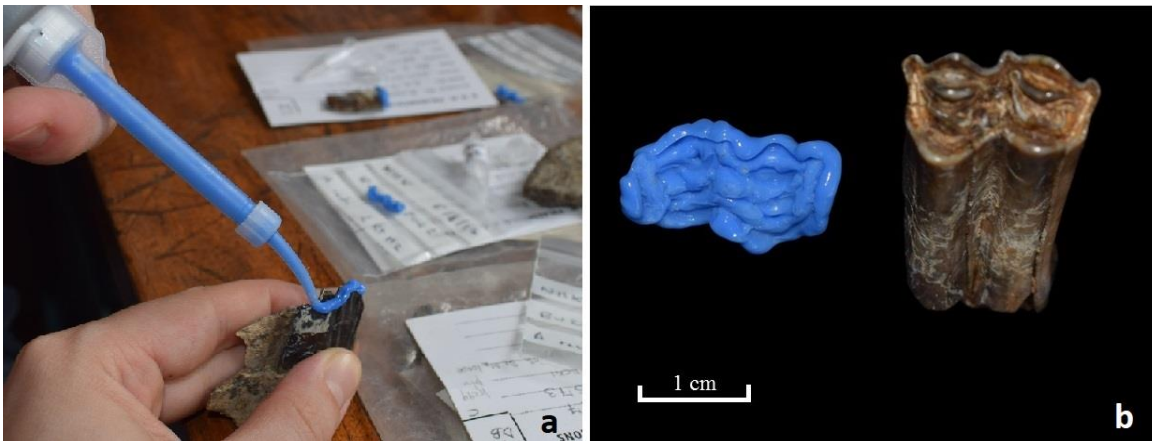

Figure 55: Dental microwear casting (April 2017). a) dental casting b) resulting mould.

5.3.3 Textural parameters

Following previous studies (e.g. Merceron *et al.* 2012, Scott 2012, Rivals *et al.* 2015), this study focused on the parameters that have proven to be the most reflective of the animal's feeding patterns and are therefore relevant for dietary analysis: complexity (area scale of fractal complexity - Asfc), heterogeneity of complexity (heterogeneity of the area scale of fractal complexity - HAsfc), scale of maximum complexity (Smc), anisotropy (exact proportion of length scale anisotropy of relief - epLsar), and textural fill volume (Tfv) (see 2.4.2.4 for more detail).

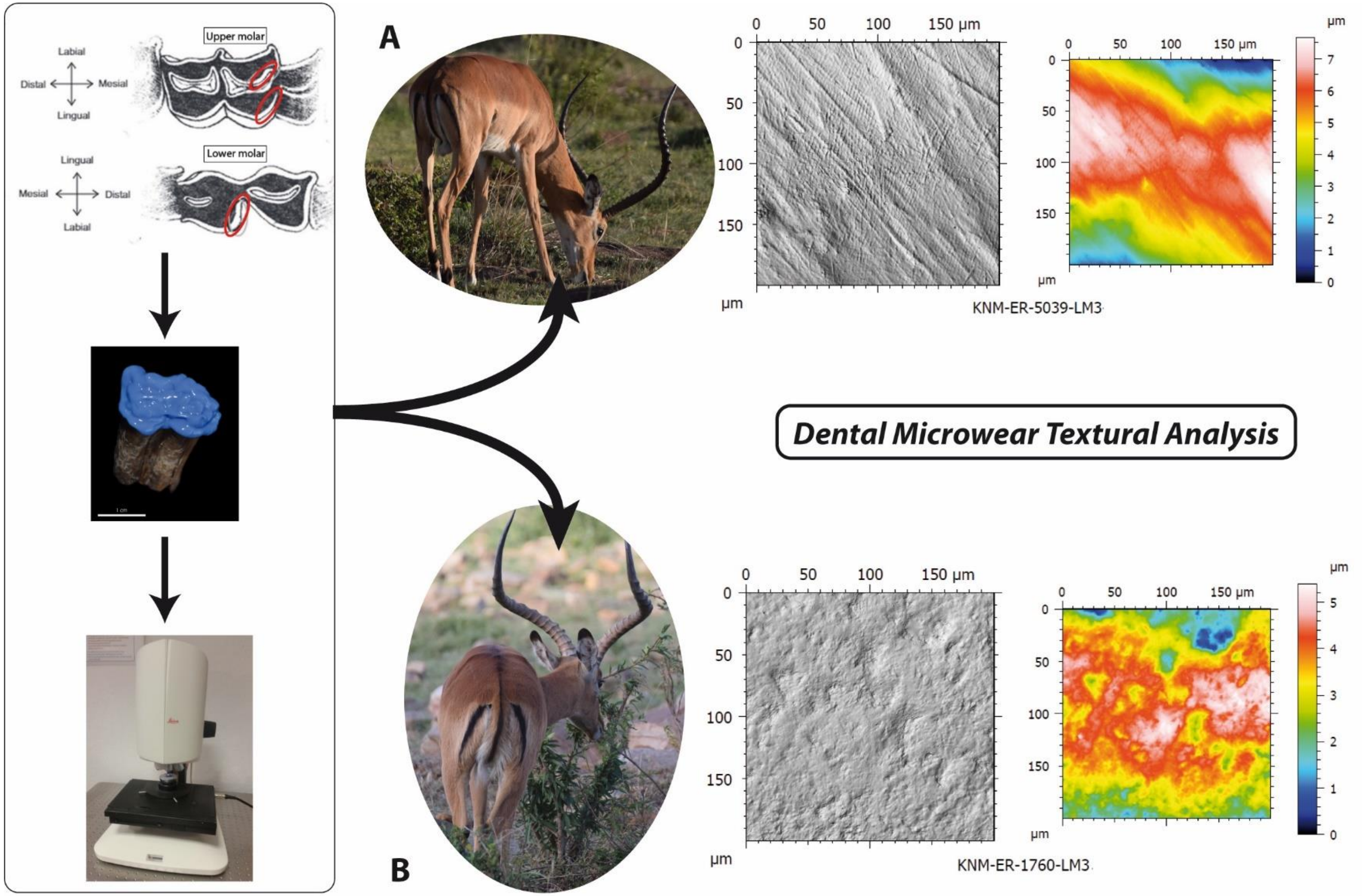

Figure 56: Dental Microwear Textural Analysis (DMTA), from data collection to scanned surfaces. Examples A and B belong to *Aepyceros melampus* specimens from the same formation and member (Koobi Fora formation, KBS member) on which the protoconid of the lower M3 was scanned and analysed using the Leica DCM8 3D Optical Surface Metrology System and the software ToothFrax. These two specimens demonstrate the dietary adaptability of the fossil impala, with A) suggesting a preference for grazing and B) a preference for browsing (based on combined DMTA parameters, such as complexity and anisotropy).

5.3.4 Statistical analyses

As for mesowear analysis, the dietary patterns were analysed for each taxon to assess if significant differences in dietary patterns could be observed between fossil and modern specimens of each species, but also to see if differences between locality and/or member could be found within each studied taxon. For this, a series of statistical analyses were performed using the software R Studio (version 1.2.1335; R version 3.6.3; R Core Team 2013) (see appendix A.6 for detail of all R packages used).

Prior to each analysis, each variable was tested for normality (Shapiro-Wilk test) and for homogeneity of variance (Levene Test for Homogeneity of Variance). Because the assumptions of parametric tests were not met for the dental microwear textural parameters studied, all data were rank-transformed (Conover and Iman, 1980, 1981) following methods from previous DMTA studies (Merceron, Ramdarshan, *et al.*, 2016; Berlioz *et al.*, 2017; Ramdarshan *et al.*, 2017; Lazagabaster, 2019). Results from the Levene Test showed that there were equal variances between groups for each variable, allowing the use of parametric tests on the DMTA dataset. After rank-transforming each variable, the data were therefore analysed using a series of one-way analyses of variance (ANOVAs), for each textural parameter. Corresponding post-hoc Tukey's Honest Significant Difference (HSD) tests were performed where relevant.

The dataset was analysed once to check for significant dietary differences within each genus depending on samples sorted by provenance (i.e. Koobi Fora, Nachukui, Shungura, and modern samples), and a second time to check for significant differences in dietary patterns through time within each fossil locality for each genus, based on subsets sorted by members. For general comparisons between fossil and modern samples (regardless of provenance and member), statistical analyses were run at the species level to assess the dietary preferences of the studied fossil species, in comparison with those of modern specimens. Due to small numbers of specimens per sample for some subsets, analyses were run at the genus level when comparing samples by provenance or member, for more statistical power.

5.4 Results and interpretations

Firstly, the differences and similarities in dietary patterns between fossil species and modern species of known diet are examined to assess the dietary preference of each studied fossil taxon, regardless of the provenance and dates of fossil specimens (i.e. interspecific variation) (5.4.1). This is to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and to evaluate inter-specific variations between species of the same taxa. Variations in dietary patterns are then evaluated for each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time (5.4.2).

5.4.1 Dietary variation among taxa: Interspecific comparisons

To evaluate the dietary patterns of specimens from each studied fossil species during their last feeding events (i.e. up to two weeks prior death), statistical analyses were performed on each dental microwear textural parameter (Table 49 and Figure 58 - Figure 63). The results from the one-way ANOVAs (Table 50) and relevant post-hoc tests (appendix A12.2 table A-15) showed that there were significant differences between species within the studied samples (fossil and modern), for all variables (i.e. Asfc, epLsar, HAsfc81 and Tfv).

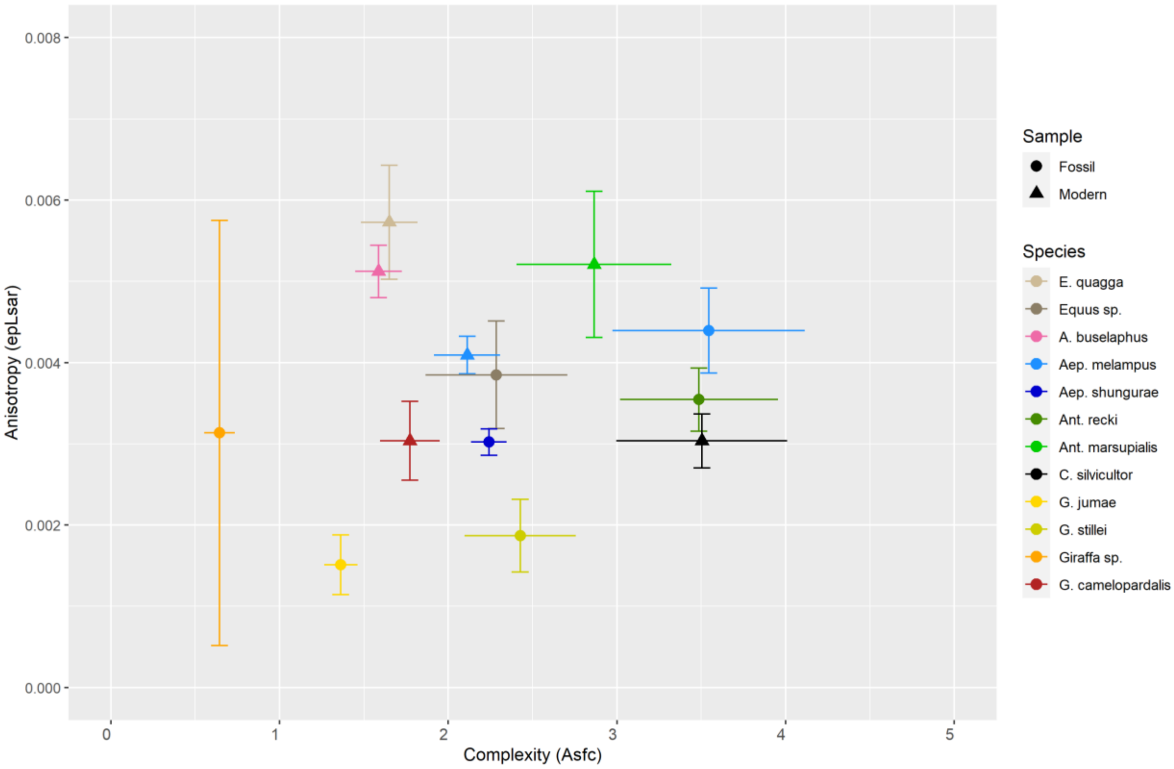

Figure 58: Distribution (mean and standard error of the mean) of the fossil and modern samples for each studied species depending on the anisotropy (epLsar) and the complexity (Asfc) of the dental facets. Following Scott (2012), obligate grazers demonstrate a combination of high anisotropy and low complexity, while obligate browsers and fruit-browsers demonstrate a combination of low anisotropy and high complexity. Mid-range anisotropy associated with low complexity is found among variable grazers, and low anisotropy associated with mid-range complexity is found among mixed-feeders.

Table 49: Descriptive statistics for each genus and species for fossil and modern samples, for each DMTA variable (mean, standard deviation and standard error of the mean).

	Sample		Asfc			epLsar			HAsfc81			Tfv		
		N	mean	s.d.	s.e.m	mean	s.d.	s.e.m	mean	s.d.	s.e.m	mean	s.d.	s.e.m
Fossil	***Aepyceros***	**160**	**2.39**	**1.48**	**0.12**	**0.00318**	**0.00200**	**0.00016**	**0.547**	**0.259**	**0.020**	**47042.2**	**11391.9**	**900.6**
	Aep. melampus	18	3.54	2.42	0.57	0.00439	0.00222	0.00052	0.664	0.489	0.115	51695.3	12757.2	3006.9
	Aep. shungurae	142	2.24	1.26	0.11	0.00302	0.00192	0.00016	0.532	0.212	0.018	46452.4	11117.9	933.0
	Antidorcas													
	Ant. recki	26	3.49	2.39	0.47	0.00355	0.00198	0.00039	0.505	0.148	0.029	47950.2	15548.2	3049.3
	Equus													
	Equus sp.	15	2.29	1.63	0.42	0.00385	0.00256	0.00066	0.495	0.155	0.040	47486.9	10925.4	2820.9
	Giraffa	**19**	**2.07**	**1.23**	**0.28**	**0.00195**	**0.00174**	**0.00040**	**0.427**	**0.121**	**0.028**	**37780.5**	**15156.2**	**3477.1**
	G. jumae	3	1.36	0.17	0.10	0.00151	0.00064	0.00037	0.408	0.140	0.081	31129.0	19724.7	11388.1
	G. stillei	14	2.43	1.23	0.33	0.00187	0.00168	0.00045	0.425	0.128	0.034	41466.8	11938.8	3190.8
	Giraffa sp.	2	0.65	0.13	0.09	0.00313	0.00370	0.00262	0.471	0.064	0.045	21953.6	26072.6	18436.1
Modern	*A. buselaphus*	27	1.59	0.72	0.14	0.00512	0.00168	0.00032	0.595	0.232	0.045	50576.9	8843.0	1701.8
	E.quagga	9	1.65	0.51	0.17	0.00573	0.00211	0.00070	0.575	0.099	0.033	47825.0	6200.9	2067.0
	Aep. melampus	84	2.11	1.80	0.20	0.00409	0.00212	0.00023	0.695	0.307	0.034	45827.2	13101.0	1429.4
	Ant. marsupialis	9	2.86	1.37	0.46	0.00521	0.00270	0.00090	0.720	0.350	0.117	61649.6	16165.3	5388.4
	C. silvicultor	27	3.5	2.63	0.51	0.00304	0.00173	0.00033	0.61	0.205	0.039	40349.2	9066.44	1744.84
	G. camelopardalis	23	1.77	0.85	0.18	0.00304	0.00233	0.00049	0.705	0.456	0.095	27510.1	19852.9	4139.61

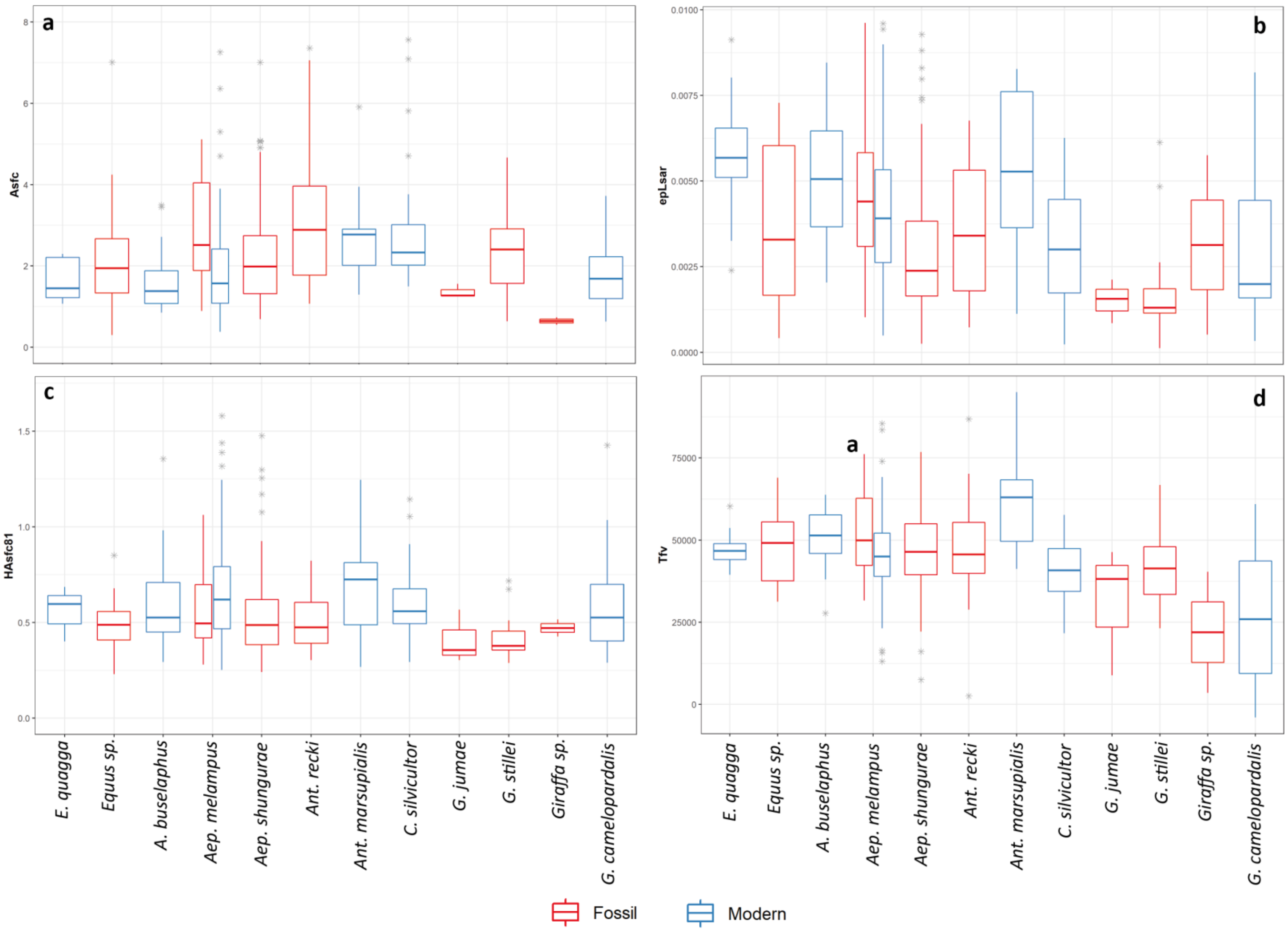

Figure 59: Mean and standard error of the mean for each species and for each DMTA variable analysed. a) Asfc: Area scale of complexity; b) epLsar: anisotropy; c) HAsfc81: Heterogeneity of complexity 9x9 cells; c) Tfv: Textural fill volume. These figures particularly highlight the differences between fossil and modern *Aepyceros* species (for the variables epLsar and Asfc) and between fossil and modern *Antidorcas* species (for the variables epLsar, Tfv and HAsfc81).

Table 50: One-way ANOVA on dental microwear textural parameters to explore variations between the studied fossil and modern species (df: degrees of freedom; SS: Sum of Squares; MS: Mean squares; Fval: F-value, Pval: P-value). (See appendix A.12.2 table-A15 for pairwise comparisons table).

Var		df	SS	MS	Fval	Pval
Asfc	Species	12	733352.3	61112.7	5.173	**4.60E-08**
	Residuals	386	4560047.7	11813.6		
epLsar	Species	12	824796.5	68733.0	5.937	**1.62E-09**
	Residuals	386	4468597.0	11576.7		
HAsfc81	Species	12	545900.3	45491.7	3.699	**2.69E-05**
	Residuals	386	4747495.2	12299.2		
Tfv	Species	12	661855.9	55154.7	4.597	**5.68E-07**
	Residuals	386	4631544.1	11998.8		

5.4.1.1 Genus *Equus*

The modern plain zebra (*E. quagga*) sample studied displayed values typical of grazing species, with low complexity (mean Asfc = 1.65), high anisotropy (mean epLsar = 0.00573), low heterogeneity of complexity (mean HAsfc81 = 0.575) and mid-range textural fill volume (mean Tfv = 47825.1µm^3). These values were similar to the values displayed by the obligate grazer *A. buselaphus*. Results from the HSD test confirmed, as expected, significant differences in anisotropy (epLsar) between modern grazing *E. quagga* and modern leaf-browsing *G. camelopardalis* (p=0.050).

Fossil equid specimens from Koobi Fora and Nachukui formations have all been identified to genus only. The dental microwear textures of these specimens suggest a variable grazing diet, with mid-range values for complexity (mean Asfc = 2.29), anisotropy (mean epLsar = 0.00385), heterogeneity of complexity (mean HAsfc81 = 0.495), and textural fill volume (mean Tfv = 47486.9 µm^3). Fossil equids show no significant differences for any of the variables when compared to the other fossil and extant species. This could indicate variable grazing dietary practices among fossil equids, with a preference for graze but the inclusion of harder food items when necessary.

5.4.1.2 Genus *Giraffa*

The modern giraffe sample (*Giraffa camelopardalis)* studied displayed values typical of soft-leaf browsing species, with low complexity (mean Asfc = 1.77), anisotropy (mean epLsar = 0.00304) and textural fill volume (Tfv = 27,510.1 µm^3), combined with high values of heterogeneity of complexity (mean HAsfc81 = 0.705). As expected, modern *G. camelopardalis* has significantly lower values for anisotropy than grazing *Alcelaphus buselaphus* (p=0.005) and *Equus quagga* (p=0.050), with a soft-leaf diet that is poorly abrasive compared to the monocots eaten primarily by modern hartebeests and plain zebras. Modern giraffes are also shown to have significantly lower complexity values than modern fruit-browsing *C. silvicultor* (p=0.024) as well as significantly lower textural fill volume values than *A. buselaphus* (p<0.000), *A. marsupialis* (p<0.000) and modern *A. melampus* (p=0.012). This confirms diets dominated by soft-food items for the modern giraffe assemblage.

Genus *Giraffa* is represented in the fossil dataset by three different species: *Giraffa jumae*, *Giraffa stillei*, and *Giraffa* specimens of unknown species (i.e. referred to as *Giraffa sp.*). *Giraffa stillei* is the most represented species in the assemblage (n=14). When looking at dental microwear textural parameters for fossil giraffids at the genus level (i.e. combining all three *Giraffa* samples), fossil *Giraffa* specimens display mean values suggesting a soft leaf-browsing diet similar to that of modern giraffes, with low Asfc (mean = 2.07), low epLsar (mean = 0.00195), low HAsfc (mean HAsfc81 = 0.427) and medium-low Tfv (mean = 37780.5 µm^3). *G. stillei* specimens have higher Tfv values than *G. jumae* specimens, while *Giraffa sp*. specimens demonstrate higher epLsar values than the other two fossil giraffid samples. This could suggest slight differences in dietary preferences, but none of these differences were shown to be statistically significant following post-hoc tests (table A-14).

Overall, the dental microwear textural patterns observed for fossil *Giraffa* specimens suggest dietary behaviours similar to those of modern giraffes. However, it is interesting to note that fossil *Giraffa* specimens, contrary to the modern *G. camelopardalis* specimens studied, do not significantly differ in textural complexity from modern fruit-browsing *C. silvicultor*. This could suggest that fossil giraffids (more particularly *G. stillei*) might have included more hard items in their diet such as fruits and seeds than their modern counterparts, although modern giraffes are known to also include some hard food items in their diet such as Acacia seeds, fruits and pods (Schulz, Calandra and Kaiser, 2013).

5.4.1.3 Genus *Aepyceros*

The dental microwear textures of modern impalas (*Aepyceros melampus)* displayed values expected for mixed-feeders and/or generalists, with relatively high values for heterogeneity of complexity (mean HAsfc81 = 0.695), as well as medium values for anisotropy (mean epLsar = 0.00409), complexity (mean Asfc = 2.11) and textural fill volume (mean Tfv = 45827.2 μm^3). Modern impala specimens have significantly lower Asfc values (p=0.002) than modern fruit-browsing yellow-backed duiker (*Cephalophus silvicultor*), suggesting diets including less hard items such as seeds compared to *C. silvicultor*. However, modern *A. melampus* samples also significantly differed from modern leaf-browsing giraffe specimens (*G. camelopardalis*) in having higher Tfv values (p=0.012), indicative of wear surfaces dominated by large pits or deep scratches, such as the ones produced when ingesting hard food items such as seeds and browse. These results confirm mixed-feeding patterns among the studied modern impala specimens, with the inclusion of both graze and browse in their diet.

Fossil *A. melampus* specimens demonstrated textural complexity values (Asfc) similar to those of modern fruit-browser *C. silvicultor* (Figure 58), and were found to have significantly higher Asfc values than *A. buselaphus* (p=0.004) and modern *A. melampus* (p=0.019). This suggests diets richer in browse in fossil *A. melampus* compared to modern impala and hartebeest. Alike modern impala specimens, fossil *A. melampus* specimens significantly differed from modern leaf-browsing giraffes in having higher Tfv values (p=0.002), confirming that fossil *A. melampus* likely included hard food items in their feeding regime.

When compared to the other fossil taxa studied, the fossil *Aepyceros melampus* sample significantly differed from *Giraffa stillei* specimens, with higher anisotropy values. This likely reflects more tough and abrasive foods (such as grass blades) in the diet of the antelope species, compared to that of fossil giraffids.

A. shungurae demonstrated Asfc values similar to those observed in modern *A. melampus*. However, *A. shungurae* specimens were shown to significantly differ from modern A. *melampus* by having lower anisotropy values (epLsar; p=0.006) and lower heterogeneity of complexity values (HAsfc81; p=0.004). This likely suggests less varied diets and a lower reliance on tough abrasive food items such as grass in fossil *A. shungurae* specimens compared to their extant relatives. Indeed, *A. shungurae* specimens yielded epLsar values similar to those observed for modern browsers such as giraffes and yellow-backed duikers (Figure 58). These epLsar values were confirmed to be significantly lower than those observed in modern grazing species *A. buselaphus* (p<0.000) and *E. quagga* (p=0.017). Alike modern and fossil *A. melampus* specimens, *A. shungurae* specimens significantly differed from modern leaf-browsing giraffes in having higher Tfv values (p=0.001), suggesting that fossil *A. shungurae* likely included hard food items in their feeding regime. No significant difference was found between the two fossil impala species, *A. melampus* and *A. shungurae*.

Overall, these results point towards mixed-feeding behaviours in modern and fossil impalas, although some differences in textural patterns were highlighted between fossil *A. melampus* and *A. shungurae*. While *A. shungurae* specimens were suggested to have had dietary patterns resembling those of modern impala specimens, their diet was likely less varied and included less graze than the diet of their extant relatives. In contrast, the dietary patterns observed for fossil *A. melampus* specimens suggest mixed-feeding habits with a stronger reliance on browse compared to modern impalas, with the consumption of more hard items such as twigs, seeds and/or fruits in addition to tough and abrasive items such as grass blades.

5.4.1.4 Genus *Antidorcas*

The dental microwear textures of modern springbok (*Antidorcas marsupialis*) displayed high values for complexity (mean Asfc = 2.86), heterogeneity of complexity (mean HAsfc81 = 0.720) and textural fill volume (mean Tfv = 61649.5 μm^3). Values for anisotropy (mean epLsar = 0.00521 μm) are similar to those of grazing *A. buselaphus and E. quagga* samples, suggesting the consumption of tough and abrasive foods such as monocots. *A. marsupialis* displays significantly higher textural fill volume values than *C. silvicultor* (p=0.004) and *G. camelopardalis* (p=0.012), suggesting wear-surfaces dominated by larger pits and deeper scratches in modern springboks compared to the browsing giraffe and yellow-backed duiker. As previous studies have suggested that smaller seed size tend to generate higher Tfv values (Ramdarshan *et al.*, 2016), the higher Tfv values observed in modern springbok compared to modern fruit-browsing *C. silvicultor* could suggest that modern springbok consume hard items of smaller seed-size than yellow-backed duikers do. These variables suggest a mixed-feeding diet among modern springbok specimens, with a wide range of food items of different properties, both tough (i.e. grass blades) and hard (i.e. seeds/fruits) items.

No significant difference was found between fossil *A. recki* and modern *A. marsupialis* specimens, nor between *A. recki* and the other fossil taxa. However, when considering anisotropy (epLsar) and complexity (Asfc) values for fossil and modern *Antidorcas* species, values for fossil *A. recki* were shown to be similar to the values observed the modern fruit-browser *C. silvicultor*, while modern *A. marsupialis* displayed anisotropy values closer to the grazer *A. buselaphus* (Figure 58). Fossil *A. recki* displayed significantly higher complexity values than modern *A. melampus* (p=0.004), *A. buselaphus* (p=0.001) and *G. camelopardalis* (p=0.035). These observations suggest the inclusion of a significant amount of hard food items such as seeds and fruits in the diet of fossil springbok species *A. recki.* Similarly to modern springbok specimens, *A. recki* specimens differed from *G. camelopardalis* by having significantly higher Tfv values (p=0.012), confirming the consumption of hard food items.

Overall, modern *Antidorcas* specimens present dental microwear textural values that seem to fall within the range of expected values for mixed-feeders and/or generalists. The range of values observed for fossil *Antidorcas recki* suggests dietary habits more similar to those of fruit-browsing species, with a prevalence of fruits and/or seeds in their diet.

5.4.1.5 Results summary

The results from the analyses performed on dental microwear textural parameters seem to demonstrate, in the fossil record, a stronger browsing signal for giraffids and a stronger grazing signal for fossil *Equus*, when compared to *Aepyceros* and *Antidorcas* specimens, as expected. No significant difference in dietary patterns was observed between the two antelope taxa *Aepyceros* and *Antidorcas*, in neither the modern nor the fossil record. Both fossil *Aepyceros* and *Antidorcas* samples showed DMTA values suggesting mixed-feeding or generalist behaviours, although fossil *Aepyceros melampus* and *Antidorcas recki* displayed microwear textural patterns more similar to those of modern fruit-browsing species, highlighting the likely inclusion of large amounts of seeds and/or fruits in the diet of these extinct species.

5.4.2 Intra-generic spatio-temporal variation in diet in the Omo-Turkana basin

For this part of the dietary analysis, statistical tests were performed at the genus level for intra-generic dietary comparisons though space and time, to assess whether spatial and/or temporal differences in dietary practices could be observed within each of the studied taxa(Table 51 - Table 53 ; appendix A12.2 tables A 16 and A 17; and Figure 60 - Figure 61).

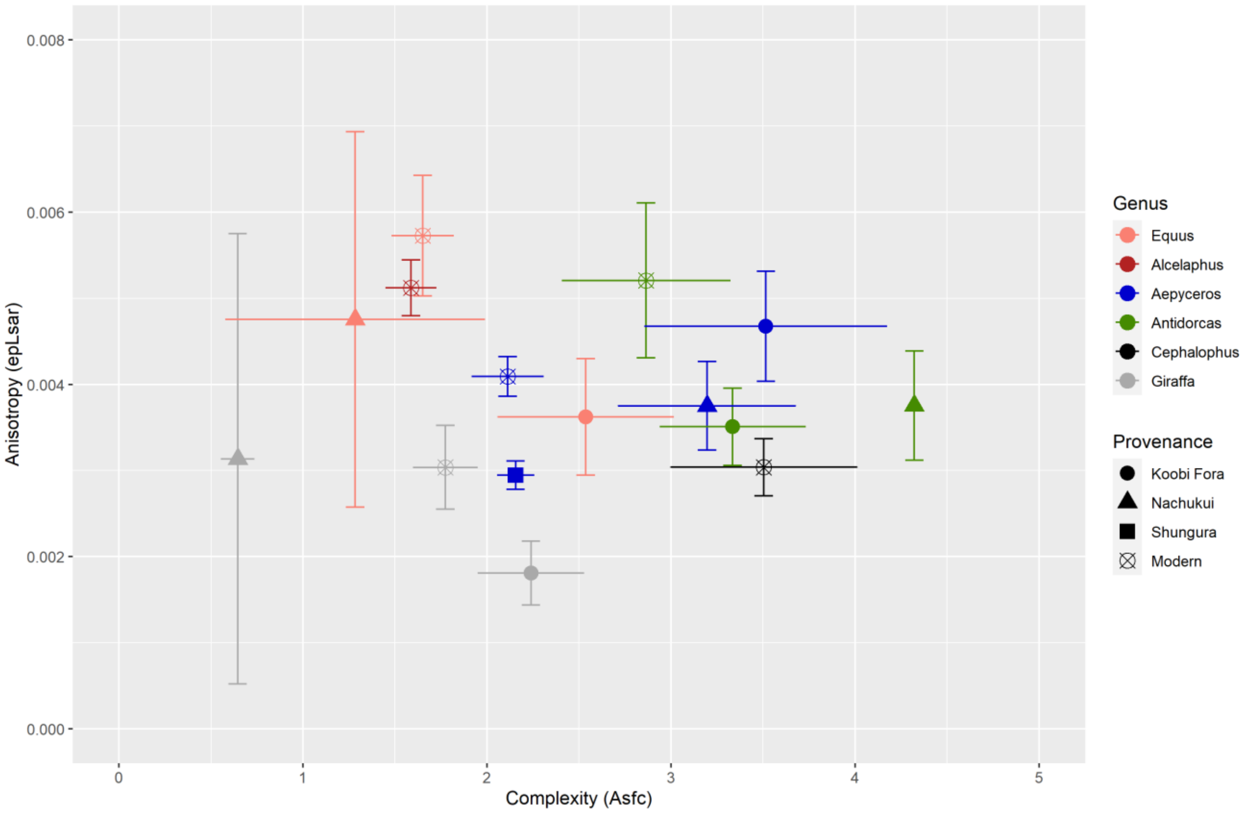

Figure 60: Distribution (mean and standard error of the mean) of each studied taxon, per locality, depending on the anisotropy (epLsar) and the complexity (Asfc) of the dental facets.

Table 51: Descriptive statistics for each taxon studied (grouped by genus for more statistical power) for each DMTA variable (mean, standard deviation and standard error of the mean), per provenance (i.e. Koobi Fora, Nachukui and modern samples – fossil localities in bold) and per member (i.e. time deposits).

Genus	Provenance	Member	Ma		Asfc			epLsar			HAsfc81			Tfv		
				N	mean	s.d.	s.e.m	mean	s.d.	s.e.m	mean	s.d.	s.e.m	mean	s.d.	s.e.m
Aepyceros	**Koobi Fora**			**12**	**3.52**	**2.28**	**0.66**	**0.00467**	**0.00222**	**0.00064**	**0.549**	**0.224**	**0.065**	**53703.5**	**12725.3**	**3673.5**
		Tulu Bor	3.44-2.64	1	9.67	/	/	0.00426	/	/	0.661	/	/	59675.4	/	/
		Burgi	2.64-1.87	3	3.67	1.31	0.76	0.00559	0.00425	0.00245	0.425	0.241	0.139	54255.5	19486.3	11250.4
		KBS	1.87-1.61	8	2.69	1.23	0.43	0.00438	0.00144	0.00051	0.582	0.229	0.081	52750.0	11820.0	4179.0
	Nachukui			**20**	**3.20**	**2.16**	**0.48**	**0.00375**	**0.00230**	**0.00051**	**0.632**	**0.451**	**0.101**	**47655.9**	**10883.4**	**2433.6**
		Lomekwi	3.44-2.53	14	3.02	1.86	0.50	0.00372	0.00237	0.00063	0.519	0.135	0.036	47646.0	10415.5	2783.6
		Kalochoro	2.33-1.9	3	1.89	0.78	0.45	0.00440	0.00280	0.00161	0.665	0.366	0.211	46970.9	18157.8	10483.4
		Kaitio	1.9-1.61	3	5.31	3.40	1.96	0.00327	0.00220	0.00127	1.122	1.108	0.640	48387.2	9429.1	5443.9
	Shungura			**128**	**2.16**	**1.15**	**0.10**	**0.00295**	**0.00186**	**0.00016**	**0.533**	**0.219**	**0.019**	**46321.8**	**11223.0**	**992.0**
		B	3.44-2.91	15	2.21	1.36	0.35	0.00345	0.00230	0.00059	0.493	0.146	0.038	47212.0	5604.5	1447.1
		C	2.91-2.52	20	2.50	1.27	0.28	0.00186	0.00096	0.00022	0.504	0.194	0.043	43626.8	7922.8	1771.6
		D	2.52-2.4	12	2.09	1.66	0.48	0.00275	0.00195	0.00056	0.559	0.192	0.056	39892.4	13136.3	3792.1
		E	2.4-2.32	20	2.12	1.18	0.26	0.00356	0.00216	0.00048	0.587	0.307	0.069	50315.8	11648.3	2604.6
		F	3.32-2.27	46	2.12	0.95	0.14	0.00317	0.00185	0.00027	0.529	0.202	0.030	49017.1	10648.8	1570.1
		G	2.27-1.9	15	1.85	0.83	0.21	0.00252	0.00130	0.00034	0.533	0.257	0.066	40577.8	14598.2	3769.2
		Modern	/	**84**	**2.11**	**1.80**	**0.20**	**0.00409**	**0.00212**	**0.00023**	**0.695**	**0.307**	**0.034**	**45827.2**	**13101.0**	**1429.4**
Antidorcas	**Koobi Fora**			**22**	**3.33**	**1.86**	**0.40**	**0.00351**	**0.00211**	**0.00045**	**0.502**	**0.147**	**0.031**	**48007.0**	**10697.0**	**2280.6**
		Tulu Bor	3.44-2.64	2	1.60	0.25	0.17	0.00299	0.00004	0.00003	0.362	0.038	0.027	45414.2	6027.9	4262.4
		Burgi	2.64-1.87	6	3.35	2.08	0.85	0.00371	0.00274	0.00112	0.463	0.082	0.034	51347.2	12325.0	5031.7
		KBS	1.87-1.61	14	3.57	1.84	0.49	0.00350	0.00205	0.00055	0.539	0.164	0.044	46945.8	10780.8	2881.3
	Nachukui			**4**	**4.32**	**4.70**	**2.35**	**0.00375**	**0.00127**	**0.00063**	**0.520**	**0.176**	**0.088**	**47638.2**	**34834.1**	**17417.1**
		Lomekwi	3.44-2.53	3	5.17	5.37	3.10	0.00434	0.00060	0.00034	0.540	0.210	0.121	44940.0	42147.8	24334.1
		Lokalalei	2.53-2.33	1	1.78	/	/	0.00200	/	/	0.459	/	/	55732.8	/	/
		Modern	/	**9**	**2.86**	**1.37**	**0.46**	**0.00521**	**0.00270**	**0.00090**	**0.720**	**0.350**	**0.117**	**61649.6**	**16165.3**	**5388.4**
Equus	**Koobi Fora**			**12**	**2.54**	**1.66**	**0.48**	**0.00362**	**0.00234**	**0.00068**	**0.489**	**0.166**	**0.048**	**45728.5**	**11536.5**	**3330.3**
		Tulu Bor	3.44-2.64	1	1.72	/	/	0.00178	/	/	0.441	/	/	31262.8	/	/
		Burgi	2.64-1.87	4	3.29	2.62	1.31	0.00404	0.00262	0.00131	0.457	0.157	0.078	54224.6	13755.5	6877.8
		KBS	1.87-1.61	7	2.22	1.01	0.38	0.00365	0.00244	0.00092	0.513	0.191	0.072	42940.1	7571.3	2861.7
	Nachukui			**3**	**1.28**	**1.22**	**0.71**	**0.00476**	**0.00378**	**0.00218**	**0.520**	**0.128**	**0.074**	**54520.5**	**3284.0**	**1896.0**
		Kalochoro	2.33-1.9	2	0.60	0.42	0.30	0.00693	0.00051	0.00036	0.537	0.176	0.125	56416.5	18.3	13.0
		Kaitio	1.9-1.61	1	2.65	/	/	0.00041	/	/	0.488	/	/	50728.5	/	/
		Modern	/	**9**	**1.65**	**0.51**	**0.17**	**0.00573**	**0.00211**	**0.00070**	**0.575**	**0.099**	**0.033**	**47825.0**	**6200.9**	**2067.0**
Giraffa	**Koobi Fora**			**17**	**2.24**	**1.19**	**0.29**	**0.00181**	**0.00154**	**0.00037**	**0.422**	**0.126**	**0.031**	**39642.5**	**13451.5**	**3262.5**
		Tulu Bor	3.44-2.64	1	1.26	/	/	0.00212	/	/	0.355	/	/	38184.2	/	/
		Burgi	2.64-1.87	5	2.54	1.30	0.58	0.00217	0.00231	0.00103	0.468	0.145	0.065	40580.6	17291.2	7732.9
		KBS	1.87-1.61	11	2.19	1.20	0.36	0.00161	0.00123	0.00037	0.408	0.123	0.037	39348.7	13006.5	3921.6
	Nachukui	**Lomekwi**	**3.44-2.53**	**2**	**0.65**	**0.13**	**0.09**	**0.00313**	**0.00370**	**0.00262**	**0.471**	**0.064**	**0.045**	**21953.6**	**26072.6**	**18436.1**
		Modern	/	**23**	**1.77**	**0.85**	**0.18**	**0.00304**	**0.00233**	**0.00049**	**0.7053**	**0.4559**	**0.0951**	**27510.1**	**19852.9**	**4139.6**

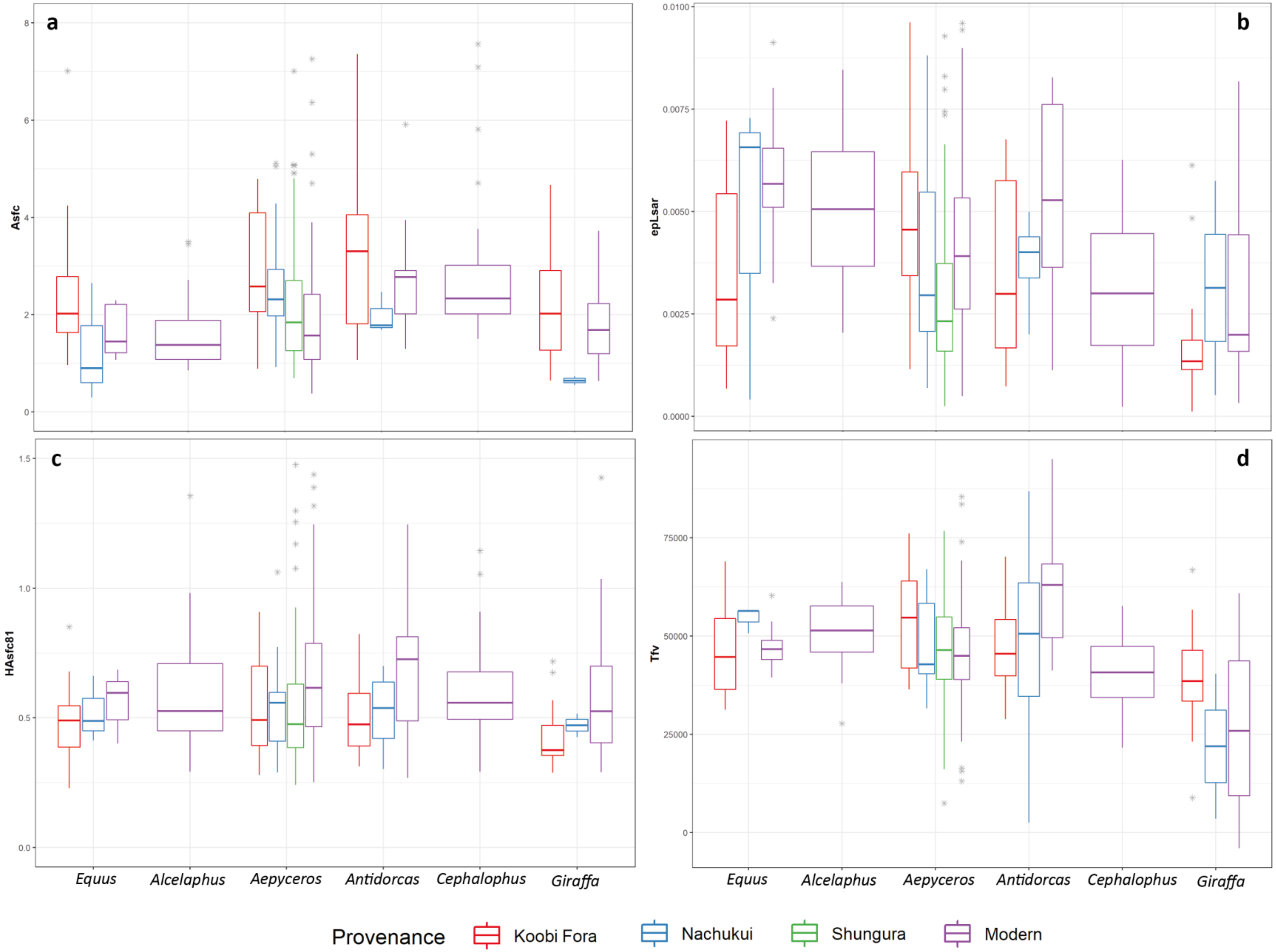

Figure 61: Mean and standard error of the mean per taxon studied (grouped by genus) and per fossil localities, for each DMTA variable analysed. a) Asfc: Area scale of complexity; b) epLsar: anisotropy; c) HAsfc81: Heterogeneity of complexity 9x9 cells; c) Tfv: Textural fill volume.

Table 52: Results of the one-way ANOVAs performed to investigate differences within each taxon between samples by provenance (i.e. Koobi Fora, Nachukui and modern samples). Significant differences are shown in bold. (df: degrees of freedom; SS: Sum of Squares; MS: Mean squares; Fval: F-value, Pval: P-value). (See appendix A.12.2 table-A16 for pairwise comparisons table).

Sample	Var	df	SS	MS	Fval	Pval
Aepyceros	Asfc	3	215419.3	71806.4	5.646	**9.39E-04**
	Residuals	240	3052539.0	12718.9		
	epLsar	3	250176.3	83392.1	7.517	**7.91E-05**
	Residuals	240	2662583.8	11094.1		
	HAsfc81	3	294264.4	98088.1	7.819	**5.32E-05**
	Residuals	240	3010835.5	12545.1		
	Tfv	3	48050.3	16016.8	1.271	2.85E-01
	Residuals	240	3024995.6	12604.1		
Antidorcas	Asfc	2	1405.6	702.8	0.061	9.40E-01
	Residuals	32	365893.4	11434.2		
	epLsar	2	35506.8	17753.4	1.188	3.18E-01
	Residuals	32	478066.8	14939.6		
	HAsfc81	2	41797.5	20898.7	1.512	2.36E-01
	Residuals	32	442337.1	13823.0		
	Tfv	2	63486.4	31743.2	2.527	9.57E-02
	Residuals	32	401939.5	12560.6		
Equus	Asfc	2	40724.9	20362.4	1.990	1.62E-01
	Residuals	21	214914.5	10234.0		
	epLsar	2	58469.4	29234.7	1.906	1.74E-01
	Residuals	21	322113.9	15338.8		
	HAsfc81	2	23762.4	11881.2	1.341	2.83E-01
	Residuals	21	185996.9	8857.0		
	Tfv	2	29546.4	14773.2	1.514	2.43E-01
	Residuals	21	204942.9	9759.2		
Giraffa	Asfc	2	74018.0	37009.0	3.064	5.81E-02
	Residuals	39	471050.1	12078.2		
	epLsar	2	52741.6	26370.8	1.919	1.60E-01
	Residuals	39	535847.3	13739.7		
	HAsfc81	2	119849.5	59924.7	4.393	**1.90E-02**
	Residuals	39	532021.3	13641.6		
	Tfv	2	26446.7	13223.4	1.026	3.68E-01
	Residuals	39	502607.3	12887.4		

Table 53: Results of the one-way ANOVAs performed to investigate differences within each taxon between samples by member (i.e. time), within each of the studied fossil localities. Significant differences are shown in bold. (df: degrees of freedom; SS: Sum of Squares; MS: Mean squares; Fval: F-value, Pval: P-value). (See appendix A.12.2 tables-A 17 for results from the HSD test).

Genus	Provenance	Var	df	SS	MS	Fval	Pval
Aepyceros	**Shungura**	Asfc	5	40745.1	8149.0	0.662	6.53E-01
		Residuals	122	1500742.2	12301.2		
		epLsar	5	124213.9	24842.8	2.430	**3.88E-02**
		Residuals	122	1247016.8	10221.4		
		HAsfc81	5	16436.1	3287.2	0.245	9.42E-01
		Residuals	122	1639974.4	13442.4		
		Tfv	5	146299.2	29259.8	2.536	**3.20E-02**
		Residuals	122	1407339.7	11535.6		
	Koobi Fora	Asfc	2	25490.5	12745.2	1.179	3.51E-01
		Residuals	9	97267.5	10807.5		
		epLsar	2	27.1	13.5	0.001	9.99E-01
		Residuals	9	108749.6	12083.3		
		HAsfc81	2	28201.6	14100.8	0.729	5.09E-01
		Residuals	9	174070.7	19341.2		
		Tfv	2	9653.8	4826.9	0.288	7.56E-01
		Residuals	9	150834.9	16759.4		
	Nachukui	Asfc	2	30250.8	15125.4	1.302	2.98E-01
		Residuals	17	197526.9	11619.2		
		epLsar	2	5557.3	2778.7	0.187	8.31E-01
		Residuals	17	252879.9	14875.3		
		HAsfc81	2	10268.2	5134.1	0.394	6.80E-01
		Residuals	17	221464.8	13027.3		
		Tfv	2	1601.1	800.5	0.053	9.48E-01
		Residuals	17	254971.9	14998.3		
Antidorcas	**Koobi Fora**	Asfc	2	31725.3	15862.7	1.272	3.03E-01
		Residuals	19	236974.5	12472.3		
		epLsar	2	238.1	119.1	0.007	9.93E-01
		Residuals	19	314632.7	16559.6		
		HAsfc81	2	33273.3	16636.7	1.676	2.14E-01
		Residuals	19	188654.5	9929.2		
		Tfv	2	7468.5	3734.2	0.300	7.44E-01
		Residuals	19	236685.3	12457.1		
	Nachukui	Asfc	1	7105.3	7105.3	0.513	5.48E-01
		Residuals	2	27716.7	13858.3		
		epLsar	1	14421.3	14421.3	20.770	**4.49E-02**
		Residuals	2	1388.7	694.3		
		HAsfc81	1	1976.3	1976.3	0.085	7.98E-01
		Residuals	2	46512.7	23256.3		
		Tfv	1	9576.8	9576.8	0.247	6.69E-01
		Residuals	2	77618.0	38809.0		
Equus	**Nachukui** (Kalochoro and Kaitio)	Asfc	1	48420.2	48420.2	115.149	5.92E-02
		Residuals	1	420.5	420.5		
		epLsar	1	87362.7	87362.7	891.456	**2.13E-02**
		Residuals	1	98.0	98.0		
		HAsfc81	1	433.5	433.5	0.024	9.02E-01
		Residuals	1	17860.5	17860.5		
		Tfv	1	2440.2	2440.2	4880.333	**9.11E-03**
		Residuals	1	0.5	0.5		
Giraffa	**Koobi Fora**	Asfc	2	17192.0	8596.0	0.557	5.85E-01
		Residuals	14	215996.4	15428.3		
		epLsar	2	5643.3	2821.7	0.296	7.48E-01
		Residuals	14	133512.5	9536.6		
		HAsfc81	2	9067.9	4533.9	0.478	6.30E-01
		Residuals	14	132881.6	9491.5		
		Tfv	2	2691.2	1345.6	0.094	9.11E-01
		Residuals	14	200517.7	14322.7		

5.4.2.1 Genus *Equus*

When observing anisotropy (epLsar) and complexity (Asfc) values for *Equus* samples from the Koobi Fora and Nachukui formations, it appears that while equid specimens from Nachukui yield values similar to those of modern plain zebra (*E. quagga*), equid specimens from Koobi Fora yield mid-range values more similar to those of mixed-feeding species (Figure 60). This could suggest that fossil equids from East Turkana included more hard food items in their diet than West Turkana and modern specimens, whose DMTA values suggest pure grazing behaviours. However, these potential differences in dietary patterns between fossil equids from the Koobi Fora and Nachukui formations were not confirmed by statistical analyses (Table 52).

Significant differences across members were suggested by results from one-way ANOVAs for *Equus* specimens from the Nachukui formation (Table 53), with equids from Kalochoro (2.33-1.9 Ma) showing significantly higher epLsar and Tfv values than *Equus* specimens from Kaitio (1.9-1.61 Ma). However, because fossil *Equus sp*. is represented in this fossil locality by very small sample sizes for both members (n<3), results from statistical analyses cannot be interpreted further, as the small sample sizes may not accurately reflect the range of dietary variation in the living assemblage.

5.4.2.2 Genus *Giraffa*

Analysis of *Giraffa* specimens from the Koobi Fora formation showed that these specimens yield anisotropy values (epLsar) similar to modern giraffes, but mid-range complexity values (Asfc) more similar to those of modern mixed-feeding *A. melampus* along with mid-range textural fill volume values (Tfv) and heterogeneity of complexity values (HAsfc81). Significant differences in HAsfc81 were observed between *Giraffa* specimens from Koobi Fora and modern specimens (p=0.0014). These observations suggest browsing behaviours for fossil giraffids from east Turkana, with slightly less varied diets but with the inclusion of more hard food items in their diet compared to modern giraffes. No significant variation in diet was observed through time for giraffids from this formation (Table 53).

The dietary patterns of *Giraffa* specimens from the Nachukui formation are difficult to gage due to a very small sample size (n=2) and a large within-sample variation for two of the textural parameters (i.e. epLsar and Tfv) (Table 51). Giraffids from west Turkana, therefore, cannot be compared to giraffids from east Turkana to assess difference in dietary behaviours across the Omo-Turkana for this taxon. Similarly, variations in dietary practices through time could not be investigated for the Nachukui formation, as the two specimens sampled from this locality derive from the same member (i.e. Lomekwi).

5.4.2.3 Genus *Aepyceros*

Significant differences within the *Aepyceros* assemblage were highlighted by statistical analyses (Table 52), between modern specimens and the two fossil localities, as well as between specimens from the Koobi Fora and the Shungura formations (Table 53 and appendix A12.2 table A-16).

Aepyceros specimens from Koobi Fora and Nachukui were found to have significantly higher complexity values than modern *A. melampus* specimens (p=0.009 and p=0.012, respectively). This suggests that fossil impalas from these two localities included more browse in their diet than modern impalas, with values more similar to those observed in fruit-browsing *C. silvicultor*. These two *Aepyceros* samples also yield similar anisotropy values (epLsar) than the modern yellow-backed duiker sample (Figure 31). Although *Aepyceros* specimens from Shungura are shown to yield similar Asfc values than modern impalas, they are shown to differ from their extant relatives by having significantly lower epLsar values (p<0.000) and HAsfc81 values (P<0.000), suggesting less varied mixed-feeding behaviours with a reduced grazing-component compared to modern impalas. When observed epLsar and Asfc values, it can be noticed that impala specimens from Shungura yield values similar to those of modern giraffes. Results from statistical analyses showed as well that *Aepyceros* specimens from the Koobi Fora formation had significantly higher anisotropy values than specimens from the Shungura formation (p=0.025), suggesting diets with a higher graze-component for impalas in East Turkana compared to impalas from the lower Omo-river valley.

When observing Asfc and epLsar values across members, some degree of variation can be observed, more particularly for the Nachukui formation with an increase in anisotropy and a decrease in complexity in the Kalochoro member (2.33-1.9 Ma), compared to Asfc and epLsar values observed for *Aepyceros* in Lomekwi (3.44-2.53 Ma) and in Kaitio (1.9-1.61 Ma) (Figure 33). However, this trend cannot be confirmed statistically as no significant difference was found through time for *Aepyceros* specimens within the Koobi Fora nor the Nachukui formations. The absence of significant differences across members identified between *Aepyceros* specimens from these localities could also be due to small sample sizes for most members (i.e. n<5).

A wider range of variation in textural parameter values can be observed for *Aepyceros* specimens from the Shungura formation, more particularly when considering anisotropy (epLsar) (Figure 33). A sharp decrease in epLsar values can be observed between member B (3.44-2.91 Ma) and member C (2.91-2.52 Ma), followed by a gradual increase in anisotropy values from members D to E (2.52 to 2.32 Ma), and another gradual decrease in epLsar values from members F to G (2.32 to 1.9 Ma). Results from statistical analyses show that *Aepyceros* specimens from member C yield significantly lower epLsar values than specimens from member E (p=0.041) (appendix A12.2 table A-17). These observations and results suggest dietary behaviours fluctuating through time among fossil impalas from the Shungura formation, and more particularly temporal variations in the amount of tough and abrasive food items included in their diet (i.e. monocots, grass blades).

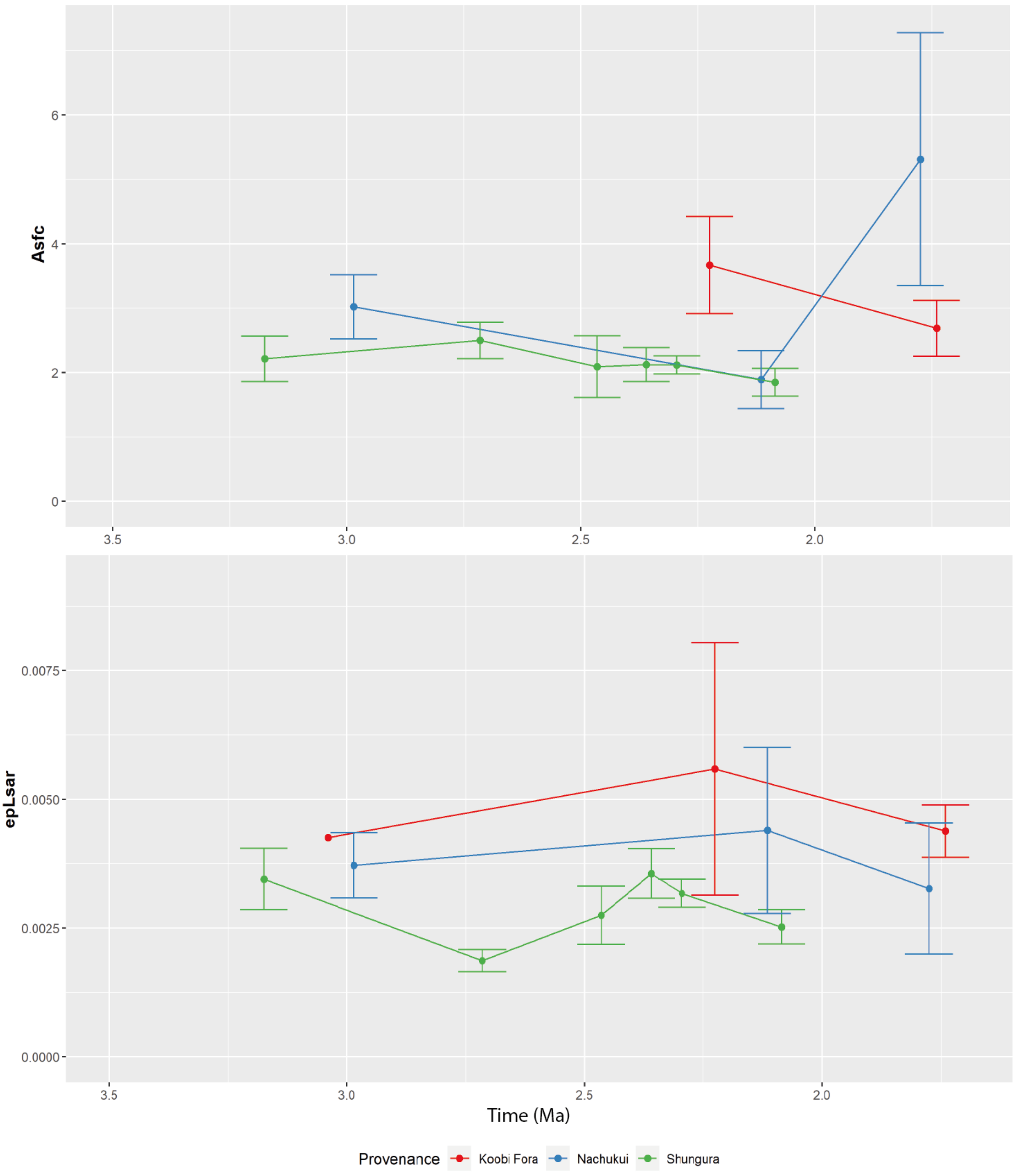

Figure 62: Distribution of complexity (Asfc) and anisotropy (epLsar) values (mean and standard error of the mean) through time for *Aepyceros* specimens from the Koobi Fora, Nachukui, Shungura formations.

5.4.2.4 Genus *Antidorcas*

When observing the mean values for anisotropy and complexity (Figure 60), springbok specimens from Koobi Fora appear to have values similar to those found in fruit-browsing Cephalophus silvicultor. Although higher complexity values (Asfc) can be observed among Antidorcas specimens from the Nachukui formation when compared to fossil springbok from Koobi Fora (Figure 60), both Antidorcas samples yield similar values for the other textural parameters (Figure 61). No significant difference in dietary patterns between the assemblages from these two fossil localities was highlighted by statistical analyses (Table 52).

No significant difference through time was highlighted among Antidorcas specimens from the Koobi Fora formation, despite an apparent increase in complexity (Asfc) between the Tulu Bor (3.44-2.64 Ma) and Burgi (2.64-1.87 Ma) (Figure 34). This could be due, as mentioned previously, the small sample sizes for some of these samples.

Results from statistical analyses suggests that temporal variation in diet can be observed between Antidorcas specimens from the Nachukui formation, with significantly lower anisotropy values for specimens from Lokalalei (2.53-2.33 Ma) compared to specimens from Lomekwi (3.44-2.53 Ma) ($p=0.041$) (Table 53 and appendix A12.2 table A-17). However, because Antidorcas specimens are represented in this locality by very small sample sizes for both members ($n<4$), results from statistical analyses cannot be interpreted further, as the small sample sizes may not accurately reflect the range of dietary variation in the living assemblage.

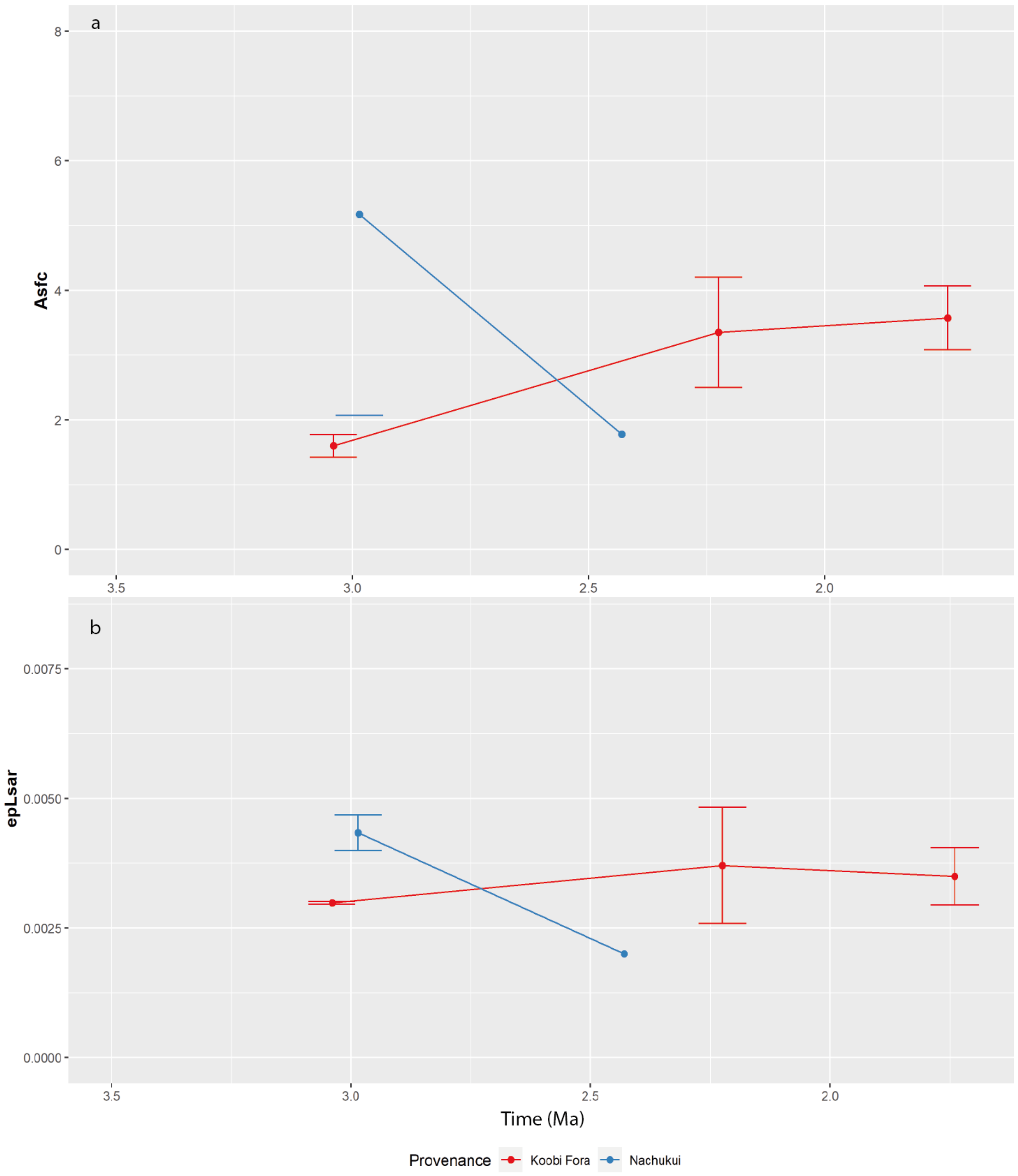

Figure 63: Distribution of complexity (Asfc) and anisotropy (epLsar) values (mean and standard error of the mean) through time for *Antidorcas* specimens from the Koobi Fora and Nachukui formations.

5.4.2.5 Results summary

While no or little spatio-temporal variation in dietary behaviours could be observed within the Omo-Turkana basin during the Plio-Pleistocene for most of the studied taxa, interesting patterns were highlighted when studying the fossil impala assemblages, which benefit from larger sample sizes and greater spatio-temporal detail. More particularly, dietary behaviours were shown to differ between *Aepyceros* specimens from the Koobi Fora and Shungura formations, suggesting diets with a higher graze-component for impalas in East Turkana compared to impalas from the lower Omo-river valley. Temporal variation in feeding behaviours were highlighted for fossil impalas from the Shungura formation, suggesting that, in the lower Omo-river valley, the relative amount of tough and abrasive food items that was included in the diet of fossil *Aepyceros* specimens fluctuated through time between 3.4 and 1.6 Ma.

5.5 Summary of results

Inferred dietary behaviours of the studied taxa:

- *Aepyceros*: mixed-feeding behaviours suggested in modern and fossil impalas, with the consumption of more hard items such as twigs, seeds and/or fruits in the diet of fossil impalas, more comparable to the diet of modern fruit-browsing species such as the yellow-backed duiker.
- *Antidorcas*: modern and fossil *Antidorcas* specimens present DMTA values that seem to fall within the range of expected values for mixed-feeders and/or generalists, suggesting similar dietary preferences to modern and fossil impalas, with potentially more fruits and/or seeds in springbok’s diet.
- *Giraffa*: dietary patterns dominated by soft-leaf-browsing for the modern and fossil Giraffa samples, although fossil *G. stillei* specimens might have included more seeds and pods in their diet than their extant relatives.

- *Equus*: variable grazing dietary practices suggested among fossil equids, with a preference for graze but the inclusion of harder food items in some specimens.

The results from the analyses performed on dental microwear textural parameters seem to demonstrate, in the fossil record, a stronger browsing signal for giraffids and a stronger grazing signal for fossil *Equus*, when compared to *Aepyceros* and *Antidorcas* specimens, as expected. No significant difference in dietary patterns was observed between the two antelope taxa *Aepyceros* and *Antidorcas*, in neither the modern nor the fossil record. Both fossil *Aepyceros* and *Antidorcas* samples showed DMTA values suggesting mixed-feeding or generalist behaviours, although fossil *Aepyceros melampus* and *Antidorcas recki* displayed microwear textural patterns more similar to those of modern fruit-browsing species, highlighting the likely inclusion of large amounts of seeds and/or fruits in the diet of these extinct species.

Intra-generic variation in inferred diet:

While no or little spatio-temporal variation in dietary behaviours could be observed within the Omo-Turkana basin during the Plio-Pleistocene for most of the studied taxa, interesting patterns were highlighted when studying the fossil impala assemblages, which benefit from larger sample sizes and greater spatio-temporal detail. More particularly, dietary behaviours were shown to differ between *Aepyceros* specimens from the Koobi Fora and Shungura formations, suggesting diets with a higher graze-component for impalas in East Turkana compared to impalas from the lower Omo-river valley. Temporal variation in feeding behaviours were highlighted for fossil impalas from the Shungura formation, suggesting that, in the lower Omo-river valley, the relative amount of tough and abrasive food items that was included in the diet of fossil *Aepyceros* specimens fluctuated through time between 3.4 and 1.6 Ma.

Chapter 6: Stable isotope analyses

6.1 Introduction

As described in previous chapters, the Omo-Turkana basin has been widely studied using multiple methods and environmental proxies, with various studies focusing on the palaeo-environmental history of the region to better understand the habitats and climatic conditions experienced by hominin species during the Plio-Pleistocene in eastern Africa (see chapter 2). Previous studies have suggested that a high diversity of habitats is likely to have been available to hominins in this region between 3.4 and 1.6 Ma, related to several major climatic events that likely had a strong impact on local environments, and on the faunal communities inhabiting the region at the time. Alike the dental use-wear analyses presented in chapters 4 and 5, this chapter presents analyses aiming to test this hypothesis, using stable isotope evidence to investigate the feeding ecology of mixed-feeding herbivores, whose diet might have been influenced by local vegetation conditions, such as high habitat heterogeneity and major shifts in environmental conditions.

The palaeo-dietary behaviours of the mixed-feeding antelope taxa *Aepyceros* (impala) and *Antidorcas* (springbok) are therefore investigated, alongside those of fossil representatives of the giraffid (genus *Giraffa*) and equid (genus *Equus*) mammalian families, to help evaluate the extent of the dietary spectrum of fossil herbivores in the Omo-Turkana basin between 3.44 and 1.6 Ma. This is to assess whether the studied mixed-feeding antelope taxa showed evidence for variations in inferred dietary behaviours, which might relate to variations in the availability of local food resources, either due to seasonal change, niche competition or environmental change. Carbon and oxygen stable isotope analyses are used on data collected from fossil specimens of the studied taxa from the Koobi Fora, Nachukui and Shungura formations, from members ranging between 3.44 and 1.61 Ma, as well as from modern specimens from different African regions.

As described in more detail in chapter 2.4.3, carbon stable isotopes in body tissues of herbivores are thought to reflect the relative proportion of leaves and grasses that were integrated in their diet, as the carbon isotopic compositions of the plans are assimilated through ingestion, with an additional fractionation process (Lee-Thorp and Van der Merwe, 1987; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Passey *et al.*, 2005). Previous studies have demonstrated that pure browsers (C_3 consumers) have $\delta^{13}C$ values which differ significantly from those of pure grazers (C_4 consumers), and that these values can vary depending on the canopy cover (e.g. Lee-Thorp *et al.* 2007, Louys *et al.* 2012). Similarly, previous studies have suggested that variation in $\delta^{13}C$ values can be observed among C_4-plants between mesic grasses and arid-adapted C_4 -grasses (Hattersley, 1982; Cerling and Harris, 1999; Cerling, Harris and Passey, 2003; Ehleringer, 2005; J. Codron *et al.*, 2005; Cerling *et al.*, 2015; Cacefo *et al.*, 2019). Stable carbon isotope data is therefore thought in this study to help assess the relative composition of the studied taxa's diet, in term of C_3-C_4 vegetation.

The oxygen isotope composition ($\delta^{18}O$ values) of mammalian body tissue is directly related to the composition of ingested water at a constant body temperature (Longinelli, 1984; Luz, Kolodny and Horowitz, 1984; Iacumin *et al.*, 1996; Koch, 2002; Chenery *et al.*, 2012). The composition of ingested water can reflect, in turn, the oxygen composition of local meteoric water (Daniel Bryant and Froelich, 1995; Chenery *et al.*, 2012) or can be modified by evaporative processes (Kohn, 1996). The $\delta^{18}O$ values of meteoric water are believed to vary due to changes in air temperature, humidity and precipitation/evaporation balance within an ecosystem (McCrea, 1950; Dansgaard, 1964; Schmidt, LeGrande and Hoffmann, 2007). As $\delta^{18}O$ reflects local evaporation and meteoric water composition through precipitation, it can be used to analyse climate changes as experienced by local species during a specific time period. Water-dependent animals usually have $\delta^{18}O$ values closely correlated with that of local precipitation (Bernard *et al.*, 2009).

As for the palaeo-dietary analyses presented in chapters 4 and 5, the material (6.2) and methods (6.3) used for this analysis are described in this chapter, followed by results (6.4), divided around the following objectives:

1) Assess the overall dietary signatures of each studied species (extant and extinct), to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and evaluate inter-specific variations between species of the same taxa.
2) Evaluate the degree of variation in dietary patterns within each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time.
3) Explore the impact of seasonal variation on the dietary patterns observed among Plio-Pleistocene impala populations.

As for previous data chapters, these results are presented and briefly interpreted around these themes, before being summarised (6.5). They will be further interpreted and discussed in chapter 7, alongside the other methods for dietary analyses employed in this study.

6.2 Material

Fossil dental remains of the selected taxa (genera *Aepyceros, Antidorcas, Equus* and *Giraffa*) from the Koobi Fora and the Nachukui formations were sampled for isotopic studies at the National Museums of Kenya (Nairobi). For specimens from the Shungura formation, held at the National Museum of Ethiopia (Addis-Ababa), data were only collected for isotopic analysis for the genera *Aepyceros* and *Giraffa*, as *Equus* specimens were already under study (i.e. Dr. Tiphaine Coillot, member of the Omo Group Research Expedition (OGRE)). The samples were collected from the maximum number of specimens available/allowed for each locality and member under study (Table 54 – see appendix A.9 for the detailed dataset).

Table 54: Number of fossil specimens sampled for isotopic analyses, per genus and per member.

Provenance	**Member**	**Dates (Ma)**	**Number of specimens (per genus)**			
			Aepyceros	***Antidorcas***	***Equus***	***Giraffa***
Koobi Fora, Kenya (National Museums of Kenya, Nairobi)	Tulu Bor	3.44 - 2.64	1	2	1	2
	Burgi	2.64 - 1.87	10	11	8	7
	KBS	1.87 - 1.61	20	21	10	15
Nachukui, Kenya (National Museums of Kenya, Nairobi)	Lomekwi	3.44 - 2.53	25	3	0	3
	Lokalalei	2.53 - 2.33	0	1	0	0
	Kalochoro	2.33 - 1.9	4	1	5	1
	Kaitio	1.9 - 1.61	8	0	3	0
Shungura, Ethiopia (National Museum of Ethiopia, Addis-Abeba)	B	3.44 - 2.91	20 (16 bulk/2 serial)	Not enough specimens	Already under study by the Omo Group Research Expedition	5
	C	2.91 - 2.52	20(16 bulk/4 serial)			5
	D	2.52 - 2.4	20(16 bulk/ 5 serial)			5
	E	2.4 - 2.32	20 (16 bulk/4 serial)			5
	F	2.32 - 2.27	20 (16 bulk / 4 serial)			5
	G	2.27 - 1.9	21 (17 bulk/5 serial)			5
Modern	/		2 (serial)	0	0	2 (serial)

Most of the modern data used for comparative analysis were drawn from published literature (Sponheimer, Lee-Thorp, *et al.* 2003, Copeland *et al.* 2009; see appendix A.8), as well as data from four modern specimens (i.e. two *Aepyceros melampus* specimens, and two *Giraffa camelopardalis* specimens) which were sampled for intra-tooth isotopic analysis at the Royal Museum for Central Africa (Tervuren, Belgium) (see appendix A.10 for the detailed dataset).

6.3 Method

6.3.1 Sampling protocols and teeth sampled

Prior to sampling, selected areas of the teeth were cleaned: adhering loose matrix was removed using a damp cotton swab, and acetone was used locally for glue residues if necessary.

6.3.1.1 Bulk sampling

Bulk sampling was the main method used in the present study, which consisted in the extraction of 7-9 mg of enamel powder from the tooth surface using a 1mm diameter diamond-tipped drill bit. Slow-medium drilling speed was applied to prevent local heating (Lee-Thorp *et al.,* 1997). This left a light scratch on the fossil tooth (Figure 64 and Figure 65). The orientation of the samples varied depending on the museums' curatorial preferences (i.e. along broken edges at the National Museums of Kenya; following the mesio-distal width of the tooth at the National Museum of Ethiopia). A total of 259 bulk samples were collected on the fossil assemblage.

Figure 65: Enamel sampling using a hand-held drill (National Museums of Kenya,

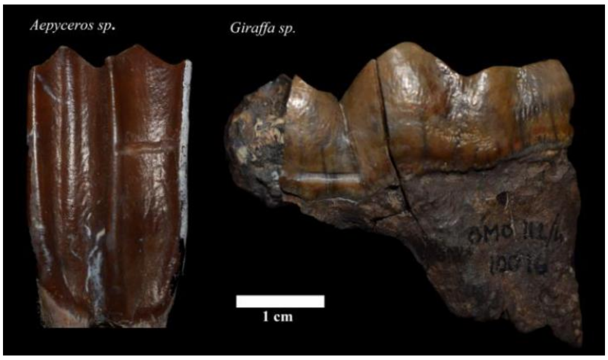

Figure 64: Examples of bulk sampling on an *Aepyceros* sp. specimen (OMO33 69-2029) and a *Giraffa* sp. specimen (OMO112/4 10016).

6.3.1.2 Intra-tooth sampling

Intra-tooth sampling was performed on selected teeth (3-4 individuals per member where possible) to assess the seasonality of diet changes among these species. The sampling process required repeated sampling on a tooth (P4; M2-M3) or on a dental sequence (up to 7-9 times per tooth), to extract small bands of 7-9 mg of enamel powder from the occlusal surface to the enamel-dentine junction (Figure 66). The number of samples, their position and the amount of enamel powder collected was evaluated on a tooth-by-tooth basis with guidance from the curatorial team. A total of 236 serial samples were collected at the National Museum of Ethiopia (Addis-Ababa), from 24 *Aepyceros* specimens from the Shungura formation. No serial sampling was possible on the material from Koobi Fora and Nachukui, hosted at the National Museums of Kenya (Nairobi).

Figure 66: Example of serial sampling performed on an *Aepyceros* sp. specimen in May 2017 (OMO11.2 67-724, National Museum of Ethiopia).

The position of each sample relative to the cervix (i.e. crown-root junction) was measured prior analysis using ImageJ (version 1.53e) to take into account the distance between samples and potential time-averaging for specimens on which a limited number of intra-tooth samples could be collected. Because the apex of tooth (i.e. top of the crown) forms before the cervix, the x-axis was reversed on plots to represent the relative temporal sequence represented by the samples, from a younger age (i.e. at the beginning of crown formation) to an older age (i.e. toward the end of crown formation). Where two adjacent teeth were sampled for intra-tooth analysis, the results were plotted next to each other to gauge the extent of seasonal variability on a longer time-sequence (Figure 67).

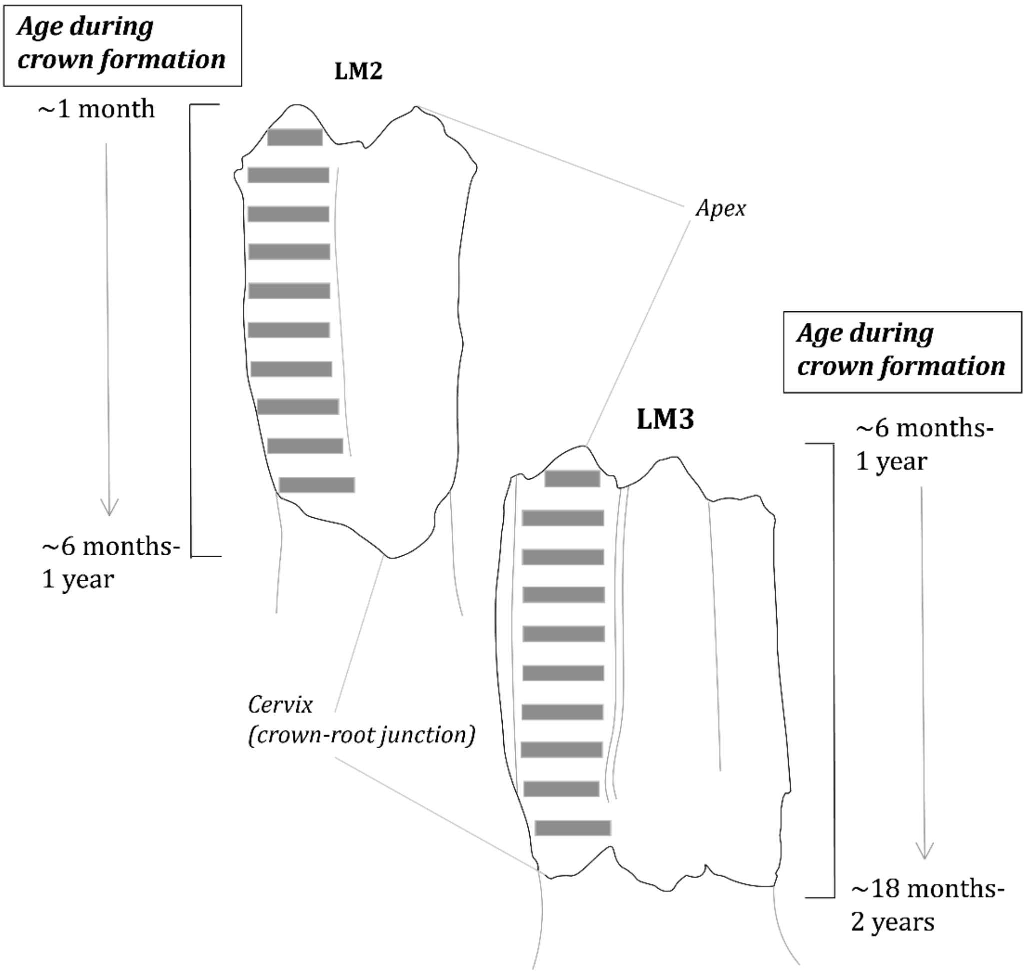

Figure 67:Intra-tooth sampling and schematic chronology of crown mineralisation in second and third molars (based on data for cattle from Brown 1960). When intra-tooth samples can be collected from two adjacent teeth for a same individual, the dietary signal that can be assessed via isotopic analyses cover a larger time-span than individual teeth.

6.3.1.3 Additional data

For comparison purposes, previously published data were also used in this study, from other fossil species represented in the Omo-Turkana basin (Cerling *et al.*, 2013, 2015; Negash *et al.*, 2015; Du *et al.*, 2019) , as well as from modern *Aepyceros melampus* populations (Sponheimer, Lee-Thorp, *et al.*, 2003; Copeland *et al.*, 2009) (see appendix A.8).

When comparing fossil and modern isotopic values, modern values were corrected using atmospheric δ^{13}C data for the change in isotopic ratio of atmosphere due to human activities (Francey *et al.*, 1999; Ferrio *et al.*, 2005; Long *et al.*, 2005; Keeling *et al.*, 2010), where the

$\delta^{13}C_{1750}$ value for atmospheric CO^2 (i.e. pre-industrial era) is taken to be -6.3‰ (e.g. $\delta^{13}C$ +0.8‰ for specimens collected in 1968-1969, +1.6‰ for modern specimens collected between 1997-1999, and $\delta^{13}C$ +1.7‰ for specimens collected between 2000-2003). This correction allows to take into account the "fossil fuel effect" (or Suess Effect) that led to a depletion of ambient atmospheric $\delta^{13}C$ values compared to values from the pre-industrial era (Keeling, Mook and Tans, 1979; Marino and McElroy, Michael, 1991; Kingston and Harrison, 2007; Bocherens, Grandal-d'Anglade and Hobson, 2014). This correction is essential to enable accurate comparison between modern and fossil isotope data.

6.3.2 Sample pre-treatment

The enamel powder collected on the studied specimens was cleaned using standard pre-treatment methods for the removal of organic and carbonate contaminants. In addition to the enamel samples collected for this study, enamel samples of known isotopic composition were also pre-treated (FBS and LES equid, provided by P. Hopley, Birkbeck), to be used as internal standards during isotopic analysis, and to check for the impact of pre-treatment on the expected values. Powdered enamel is typically pre-treated with dilute sodium hypochlorite (NaOCl) or hydrogen peroxide (H_2O_2) to remove organic matter, followed by leaching with a solution of acetic acid (0.1M) to dissolve secondary mineral contaminants (Koch, Tuross and Fogel, 1997; Rowland, 2006). This pre-treatment should only leave purified structural carbonate for analysis.

Each enamel sample therefore went through a first wash using 1ml dilute sodium hypochlorite (NaOCl - bleach 2%- rest for 45min), followed by 3 rinses using deionised water (ultra-pure), to remove organic matter. Each sample was then washed a second time using 0.5 ml dilute acetic acid (0.1M – rest for 15min), followed by 3 rinses using deionised water, to dissolve secondary mineral contaminants. The samples were centrifuged between each wash to facilitate the removal of the liquid elements and were dried overnight in a drying oven at low temperature (70°C).

To control for the effect of pre-treatment procedures on the samples, two internal enamel standards of known isotopic composition (LES and FBS standards, provided by Philip Hopley, UCL Birkbeck; see appendix A.9) were pre-treated and analysed alongside the studied samples.

6.3.2 Mass-spectrometry data acquisition

Part of these samples (i.e. all bulk samples, and serial samples for modern *G. camelopardalis*) was analysed at the Stable Isotope Ratio Mass-Spectrometry (SIRMS) Laboratory (University of Southampton, National Oceanography Centre; procedure performed by Megan Spencer) using a Kiel Carbonate Device coupled to a MAT253 Isotope Ratio Mass Spectrometer (both Thermo Fisher Scientific, Bremen, Germany). 0.3-0.6 mg of each sample was weighed out into borosilicate glass vials according to their $CaCO_3$ concentration in order to match ~30-40 µg of pure $CaCO_3$. During subsequent analysis, they reacted with 106% phosphoric acid at 90°C for 800 seconds. After cryogenic removal of water vapour and other gases, the resulting CO_2 was measured multiple times against a reference gas. Following data reduction and corrections, data were normalised using a two-point calibration with NBS 18 and NBS 19 (IAEA, Vienna, Austria) and reported relative to VPDB (Vienna PeeDee Belemnite). The $\delta^{18}O$ and $\delta^{13}C$ values were obtained from these analyses using the following calculation:

Equation 3. 2: $\delta x = 1000[(R_{sample}/Rs_{tandard}) - 1]$

(where δx is either $\delta^{13}C$ or $\delta^{18}O$, and R is either $^{13}C/^{12}C$ or $^{18}O/^{16}O$.)

In-house reference material (GS1) was used for quality assurance purposes and to report instrument precision (Coplen, 1994). Long-term instrument precision is 0.05‰ for $\delta^{13}C$ and 0.09‰ for $\delta^{18}O$ (Thermo Scientific, 2009).

The second part of the samples (i.e. fossil and modern serial samples) was analysed at the NERC Isotope Geosciences Facilities (NIGL, British Geological Survey, Keyworth; procedure performed by Hilary Sloane) on an IsoPrime 100 dual inlet mass spectrometer plus Multiprep device. This analysis was permitted by the collaborative support granted by the NERC Isotope Geosciences Facilities Steering Committee (IP-1865-1118; work in collaboration with Dr Angela Lamb and Hilary Sloane). Approximately 1 mg of carbonate material was weighed out into glass vials and sealed with septa. The automated system evacuated vials and delivered anhydrous phosphoric acid to the carbonate at 90°C. The evolved CO_2 was collected for 15 minutes, cryogenically cleaned and passed to the mass spectrometer. Isotope values ($\delta^{13}C$, $\delta^{18}O$) were reported as per mil (‰) deviations of the isotopic ratios ($^{13}C/^{12}C$, $^{18}O/^{16}O$) calculated to the VPDB scale using a within-run laboratory standard calibrated against NBS-19 (Coplen, 1994). $\delta^{18}O$ values were then converted to the VSMOW scale using the following formula:

Equation 3. 3: $\delta^{18}O\text{-VSMOW} = 1.03091 * \delta^{18}O\text{-VPDB} + 30.92$ ‰

The calcite-acid fractionation factor applied to the gas values was 1.00798 (Sharma and Clayton, 1965; Friedman and O'Neil, 1977). Due to the long run time of 21 hours, a drift correction was applied across the run, calculated using the standards that bracket the samples. The Craig correction was also applied to account for $\delta^{17}O$ (Craig, 1957). The average analytical reproducibility of the standard calcite (KCM) is <0.1‰ for $\delta^{13}C$ and $\delta^{18}O$.

For comparative purposes, $\delta^{18}O$ values were converted from the VSMOW standard (Vienna Standard Mean Ocean Water) to the VPBD standard where necessary, using the following formula (Brand *et al.*, 2014):

Equation 3. 4: $\delta^{18}O\text{-VPDB} = 0.970017 * \delta^{18}O\text{-VSMOW} - 29.98$

Both stable carbon and oxygen isotopes results are therefore presented in this work using standard δ‰ notation relative to VPDB.

6.3.4 Correction of intra-tooth data

Due to concerns regarding higher-than-expected $\delta^{13}C$ and $\delta^{18}O$ values measured at the NIGL when analysing the first batches of serial samples (see appendix A.13.1), only a selected number of samples were analysed for this project to serve as a pilot study (i.e. 9 specimens out of the 25 specimens sampled for intra-tooth analysis; one modern specimen and 8 fossil specimens, one from each member). Future analyses will focus on the remaining 16 specimens and the methodological concerns raised by collaborators Dr Angela Lamb and Hilary Sloane from the NIGL.

Calibration issues were considered, because an offset in the $\delta^{13}C$ and $\delta^{18}O$ values measured for the internal enamel standards could be observed between previous analyses and analyses conducted at the NIGL for these standards (see appendix A.13.2). This offset appeared more pronounced for high $\delta^{13}C$ values, as reflected in the measurements retrieved from the LES-equid standard (i.e. Previous analyses: mean $\delta^{13}C$ = -1.26‰, s.d.=1.20, and mean $\delta^{18}O$= -0.13‰, s.d.=1.73, n=40; NIGL analyses: mean $\delta^{13}C$= 1.2‰, s.d.=1.11, and mean $\delta^{18}O$= 3.23‰, s.d.= 2.88, n=5).

To correct for this offset and calibrate the measurements obtained at the NIGL on the intra-tooth samples, a two-point calibration curve was generated based on the two internal standards used during analyses (see appendix A.13.3 for more detail) (Jardine and Cunjak, 2005; Debajyoti, Grzegorz and Istvan, 2007; Szpak, Metcalfe and Macdonald, 2017). This enabled corrected measurements for the NIGL data to be proposed using the following formulae:

Equation 3. 5: $\delta^{13}C\text{-corr} = 0.85281*\delta^{13}C_{sample} -1.97587$

Equation 3. 6: $\delta^{18}O\text{-corr} = 0.5428*\times\delta^{18}O_{sample} - 1.6455$

Both uncorrected and corrected $\delta^{13}C$ and $\delta^{18}O$ values are presented in this chapter.

6.3.5 Estimated percentage of C_4-vegetation included in the diet

To facilitate interpretation of carbon isotope values, the dietary classification suggested by Lee-Thorp *et al.* (2007) was used on the studied dataset to estimate for each sample the relative proportions of C_3-browsers ($\delta^{13}C < -9‰$), mixed-feeders ($9‰ > \delta^{13}C < -3‰$) and C_4 -grazers ($\delta^{13}C > -3‰$).

To estimate the minimum percent C_4 -vegetation indicated by enamel $\delta^{13}C$ values, the parameters for linear equations published by Passey *et al.* (2009) were used, with varying formulas depending on the age of the sample (Table 55). This equation represents a linear mixed model between the 'max C_3' and C_4 endmembers for each sample (see Passey *et al.* 2009 for more detail).

Table 55: Formulas used to estimate the minimum percent C_4 -vegetation based on individual enamel $\delta^{13}C$ values, using the parameters for linear equations from Passey *et al.* (2009).

Age-range (Ma)	Samples	Formula (based on Passey *et al.* 2009)
present	Modern	$8.46 * \delta^{13}C$ sample + 87.48
1.5-1.99	KBS Kaitio	$8.44 * \delta^{13}C$ sample + 72.05
2.0-2.49	Burgi Kalochoro Lolakalei D to G	$8.44 * \delta^{13}C$ sample + 73.05
2.5-2.99	Lomekwi (upper and middle) C	$8.44 * \delta^{13}C$ sample + 72.45
3.0-3.49	Tulu Bor Lower Lomekwi B	$8.44 * \delta^{13}C$ sample + 72.61
General equation: $\%C_4$ = slope * $\delta^{13}C$ sample + intercept		

6.3.6 Statistical analyses

The geochemical content of the studied samples was analysed for each taxon, to assess whether significant differences could be observed between fossil and modern specimens of each species, but also to see if differences between locality and/or member could be found within each studied taxon. For this, a series of statistical analyses were performed using the software R Studio (version 1.2.1335; R version 3.6.3; R Core Team 2013) (see appendix A.6 for detail of all R packages used in this study).

Prior to each analysis, each variable was tested for normality (Shapiro-Wilk test) and for homogeneity of variance (Levene Test for Homogeneity of Variance). Because the assumptions of parametric tests were not met for both carbon and oxygen isotopic data, the Kruskal-Wallis test was used to assess significant differences within and between groups. Where the Kruskal–Wallis test was significant, post-hoc analyses were performed to determine which groups significantly differ from the others, using Dunn's test with adjustments to the p-value (Holm's correction) to control for familywise error rates.

As for previous dietary analyses presented in this thesis, the dataset was analysed once to check for significant differences in isotopic content within each genus depending on samples sorted by provenance (i.e. Koobi Fora, Nachukui, Shungura, and modern samples), and a second time to check for significant differences in dietary patterns through time within each fossil locality for each genus, based on subsets sorted by members. For general comparisons between fossil and modern samples (regardless of provenance and member), statistical analyses were run at the species level to assess the dietary preferences of the studied fossil species, in comparison with those of modern specimens. Due to small numbers of specimens per sample for some subsets, analyses were run at the genus level (i.e. species from same genus altogether) when comparing samples by provenance or member, for more statistical power.

To appraise the degree of seasonal variability in diet within the specimens studied for stable isotope analyses, summary statistics were computed for each tooth. As serial-tooth data displayed non-normal distributions, correlations between intra-tooth $\delta^{18}O$ and $\delta^{13}C$ sequences was evaluated for each specimen using Spearman's coefficient.

6.4 Results and interpretations

An overview of the stable isotope data is presented first, combining carbon and oxygen data (6.4.1). Results from stable carbon (6.4.2) and oxygen (6.4.3) analyses are then presented, focusing first on the differences and similarities in inferred dietary patterns between fossil species and modern species of known diet (to assess the dietary preference of each studied fossil taxon, regardless of the provenance and dates of fossil specimens), before evaluating the degree of variations in isotopic signals that can be observed for each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time. Finally, seasonal variation in isotopic signals is evaluated for the studied specimens, using intra-tooth data (6.4.4).

6.4.1 Stable carbon and oxygen isotope analyses – overview of the data

When observing the carbon and oxygen isotopic signals of all studied extinct and extant species, two clusters appear, likely reflecting differences in ecology (Figure 68). On one end of the spectrum, *Giraffa* specimens are shown to yield low stable carbon isotope ratios ($\delta^{13}C$), with mean values ranging between -12.44 ‰ (*G. pygmaea*) and -10.72 ‰ (*G. stillei*) for fossil species, and a mean value of -9.39 ‰ for modern *G. camelopardalis* (see Table 56 for more detail). These are associated with relatively high stable oxygen isotope ratios ($\delta^{18}O$), ca. +4 ‰ (see Table 60 for more detail). These patterns are likely indicative of browsing behaviours, as expected for giraffids, which tend to yield negative $\delta^{13}C$ values due to diets rich in C_3-vegetation, and rather high $\delta^{18}O$ values due to non-obligate drinking patterns. Indeed, modern giraffes are known today to be evaporation sensitive (ES), due to their independence to water-sources and their ability to obtain their daily water requirements from the water content of the consumed plants (Levin *et al.*, 2006; Blumenthal *et al.*, 2017) (see 6.4.3.1 for more detail).

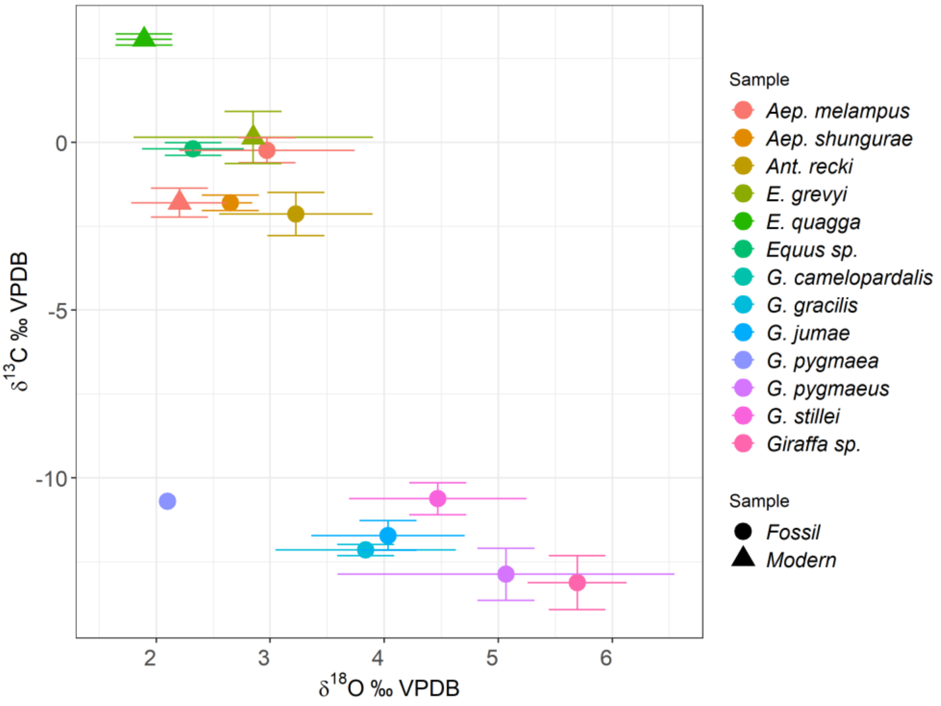

Figure 68: Carbon (δ^{13}C) and oxygen (δ^{18}O) stable isotope values for the fossil species and the comparative modern species studied. Modern data corrected for fossi-fuel effect.

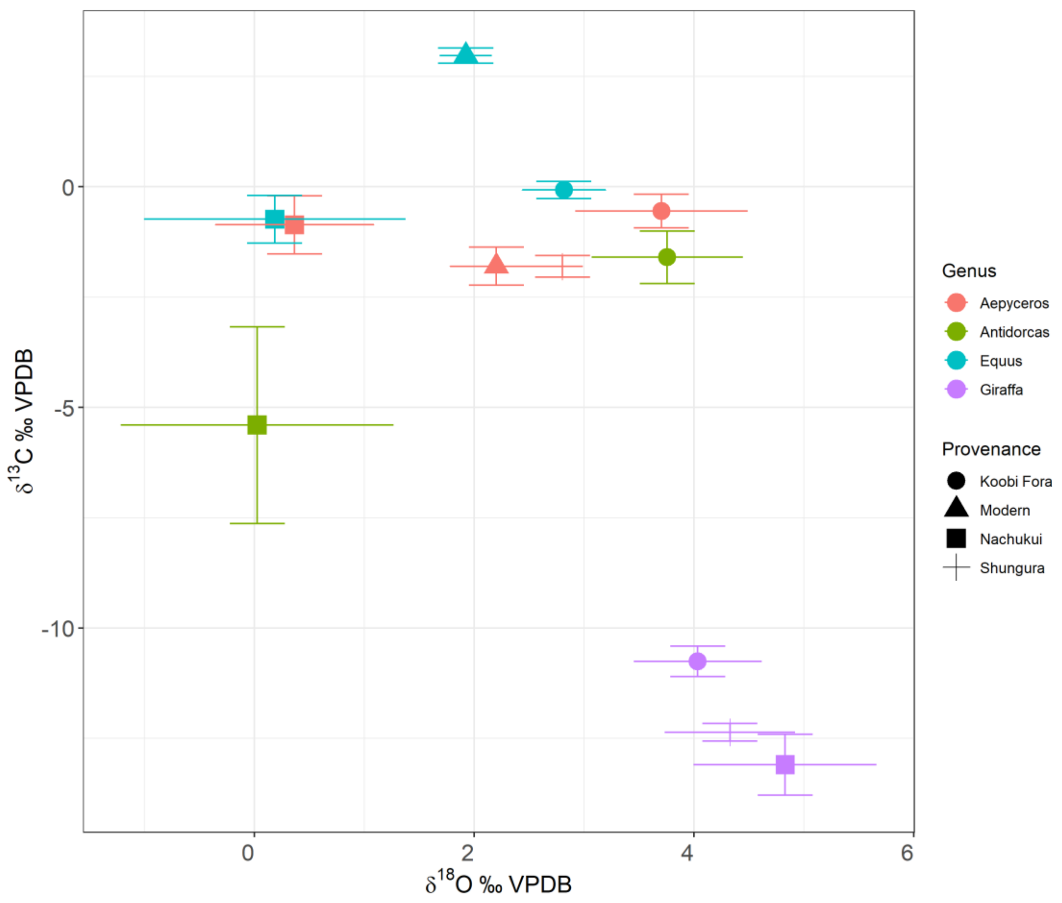

Figure 69: Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotope values for the fossil taxa studied from the Plio-Pleistocene deposits of the Omo-Turkana Basin, and for the comparative modern taxa studied. Modern data corrected for fossi-fuel effect.

On the other end of the spectrum, equid specimens yield the highest $\delta^{13}C$ values, more particularly modern species *E. grevyi* (mean $\delta^{13}C$ = +1.69 ‰) and *E. quagga* (mean $\delta^{13}C$ = +3.03 ‰), while fossil *Equus* sp. specimens yield lower $\delta^{13}C$ values than their modern relatives (mean $\delta^{13}C$ = -0.04 ‰). These species are associated with a lower range of $\delta^{18}O$ values, ca. +2‰. As opposed to giraffids, these patterns likely reflect grazing behaviours, with high $\delta^{13}C$ values indicative of diets rich in C_4-plants, potentially associated to obligate-drinking behaviours, as freshwater sources tend to yield rather low stable oxygen isotope ratios.

The mixed-feeding antelopes yield mean carbon and oxygen values resembling those observed amongst equids. Indeed, modern impalas (*A. melampus*) are shown to yield relatively high $\delta^{13}C$ values (mean = -1.92 ‰), although less clearly dominated by C_4-graze than among modern equids, likely indicative of variable diets relatively rich in C_4-plants. The fossil impala species show similar patterns, with carbon and oxygen stable isotope ratios similar to the modern populations for *A. shungurae*, but more similar to modern *Equus grevyi* for fossil *A. melampus.* Fossil springbok (*A. recki*) yield $\delta^{13}C$ values similar to those of modern impala specimens (mean $\delta^{13}C$ = -2.14 ‰), likely indicative of variable diets relatively rich in C_4-plants. However, the $\delta^{18}O$ values observed for fossil *A. recki* appear to have a larger spread and slightly higher ratios than modern equids, making it difficult to assess whether fossil springbok were likely obligate-drinkers (like equids) or water-independent (like giraffids), although their extant relatives (*Antidorcas marsupialis*) have been reported to be water-independent.

When observing the carbon and oxygen isotopic signals of all studied taxa per provenance (i.e. fossil sites and modern assemblage) (Figure 69), three main clusters appear, likely reflecting differences in taxa behavioural ecology, but also local environmental conditions, as oxygen isotope ratios have been previously shown to vary according to geography, altitude, and rainfall patterning in addition to drinking behaviour (Kohn, 1996; Sponheimer and Lee-Thorp, 1999). While the giraffids remain separated from the other samples by yielding low $\delta^{13}C$ values paired with high $\delta^{18}O$ values regardless of the provenance of the assemblage, the other samples demonstrate more variation across samples, more particularly when considering stable oxygen isotope content. Indeed, while *Aepyceros*, *Antidorcas*, and *Equus* specimens from Nachukui are shown to yield, on average, relatively low $\delta^{18}O$ values (ca. +0 ‰), the *Aepyceros*, *Antidorcas*, and *Equus* specimens from Koobi Fora are shown to yield much higher mean $\delta^{18}O$ values (ca. +3-4 ‰). These patterns could relate to differences in local environmental conditions, as well as to differences in drinking-water sources, as previous studies have showed that lake waters tend to provide obligate drinkers with relatively higher $\delta^{18}O$ values than river waters (Quinn, 2015).

These observed patterns are explored further in the following sections.

6.4.2 Stable carbon isotopes

6.4.2.1 Dietary variation among taxa: Interspecific comparisons

To investigate the relative proportion of C_3 - C_4 plant items ingested by specimens of the studied taxa during the early years of their lives (i.e. during tooth formation), the stable carbon isotope ratios of each fossil and modern species were studied and compared (Table 56-Table 57 and Figure 70-Figure 71). Results showed significant differences between species within the studied samples (fossil and modern).

The distribution of $\delta^{13}C$ values for the modern and fossil samples suggests slightly different patterns between the two assemblages (Figure 70). The modern specimens display a multimodal distribution with three modes that seem to correspond to the three main dietary categories expected for the modern species represented in the assemblage (i.e. browsers, mixed-feeders and grazers, from more negative to more positive values). The fossil specimens display a bimodal distribution that suggests the dominance of only two main dietary categories among the studied fossil species (i.e. browsers and grazers), although the mode centred around the most positive values, more typical of C_4 -plant feeders, is slightly skewed to the left, potentially suggesting the presence of more variable grazing and/or mixed-feeding behaviours in the fossil assemblage compared to the modern assemblage.

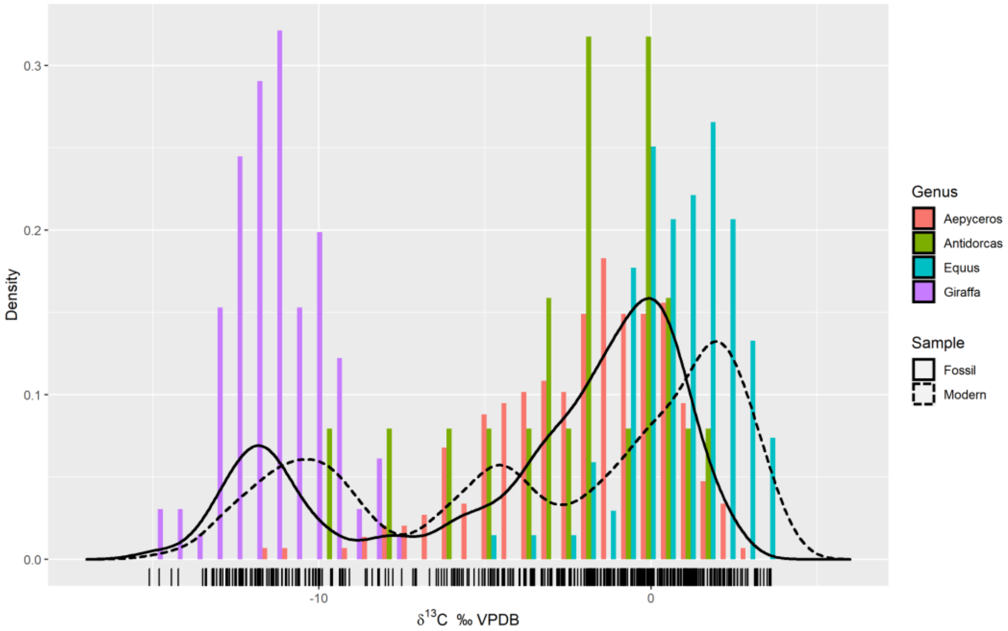

Figure 70: Kernel density estimates (Gaussian) for fossil and modern samples of all taxa (lines), and density per genus (fossil and modern combined; histogram). Modern δ13C data was corrected to take into account the "fossil fuel effect".

When observing and interpreting the carbon isotopic mean values using the dietary classification suggested by Lee-Thorp *et al.* (2007), the *Equus* sp. sample shown to be dominated by grazing signals, with 97.56% of the fossil specimens classifying as C_4 -grazers (Figure 71 and Table 56). The average proportion of C_4 -plants included in the diet suggests however a diet not entirely composed of C_4 -vegetation for *Equus* sp., with an average of only 72.2% of C_4 -plant accounted for in the diet of these specimens. At the other end of the dietary spectrum, fossil *Giraffa* specimens appear clearly dominated by C_3 -browsing signals, as expected, with most species being classified in the browsing category for 100% of their specimens, with 0% of C_4 -plants in their diet. Only *Giraffa stillei* presents more variability in the measured $\delta^{13}C$ values, with 81.8% classified as browsers, and 18.2% classified as mixed-feeders. This could suggest a slightly more varied diet for this fossil species, compared to other giraffid taxa.

When observing the $\delta^{13}C$ values measured for the studied mixed-feeding antelope species, *Aepyceros* samples appear dominated by C_4 -grazing signals, for fossil *Aepyceros melampus*, *Aepyceros shungurae* and *Aepyceros sp*. samples (respectively 100%, 70.8% and 89.7% of specimens classified as C_4-grazers). This differs from the modern *A. melampus* sample, where the proportion of grazers, mixed-feeders and browsers (henceforth referred to as G:MF:B) is 42.4: 52.5: 5.1. This suggests differences in overall dietary patterns between modern and fossil impalas, where fossil impalas relied on more C_4-vegetation than modern impalas, which appear to be dominantly mixed-feeders.

The *Antidorcas recki* sample appears dominated by grazing signals (G:MF:B : 71.4: 23.8: 4.8). However, the estimated proportions of C_4-plant included in the diet appear to vary between species, with a higher percentage of C_4-plants in the overall diet of fossil *A. melampus* (70.3 %) and *Aepyceros sp*. specimens (65.9 %) than in the overall diet of *A. shungurae* (57.7 %), *A. recki* (54.5 %) and modern *A. melampus* (58.3%).

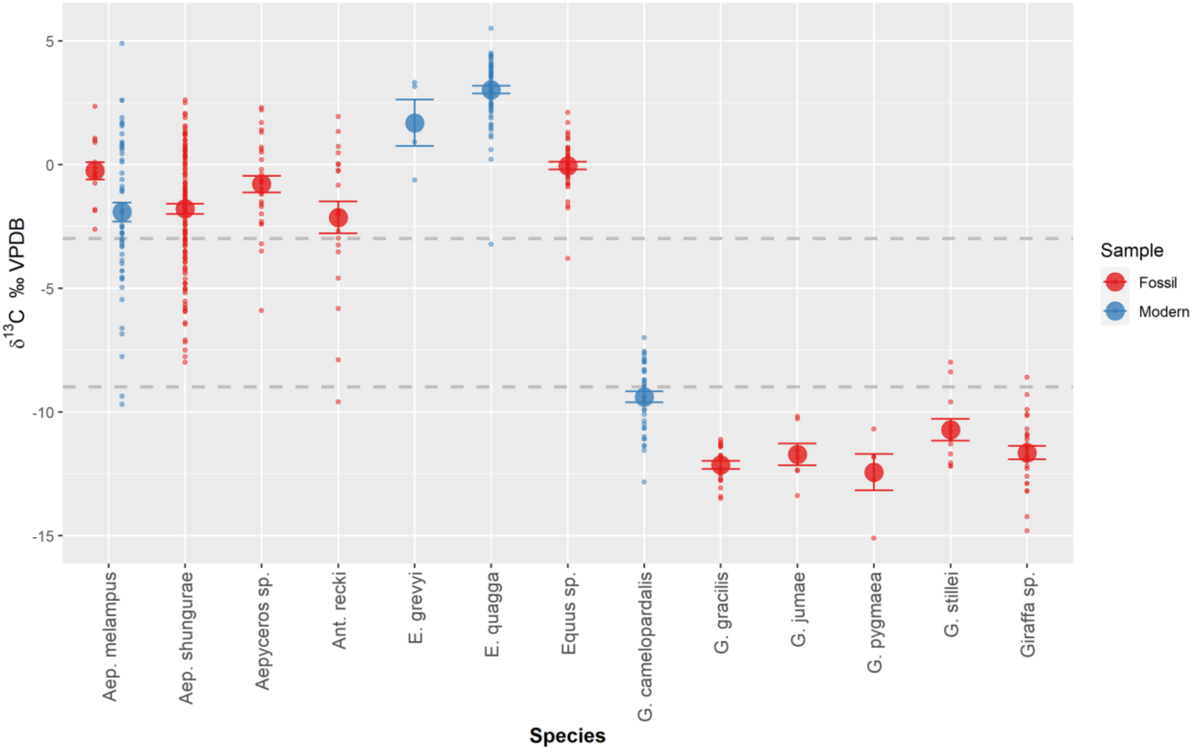

Figure 71: Distribution of $\delta^{13}C$ values (mean and standard error of the mean) for all species sampled from the Koobi Fora, Nachukui and Shungura formations, as well as modern *G. camelopardalis* specimens. (Note: modern $\delta^{13}C$ values were corrected for the "fossil fuel effect"). Smaller points represent values per individual specimen.

Table 56: Descriptive statistics for all species studied for stable carbon isotope analysis. Frequencies of grazers, browsers and mixed-feeders in each sample are based on Lee-Thorp *et al.* (2007). The mean percentage of C_4-plant included in the diet was estimated based on the linear mixed model from Passey *et al.* (2002, 2009). Mean, standard deviation (S.D.), standard error of the mean (S.E.M), minimum value (min), maximum value (max). Modern values are corrected for fossil-fuel effect.

			δ^{13}C ‰VPDB Mean					Classification (%)			Estimated min. % C_4		
Sample	**Species**	**N**	**Mean**	**s.d.**	**s.e.m**	**Min**	**Max**	**Grazers**	**Mixed-feeders**	**Browsers**	**Mean**	**Min**	**Max**
Fossil	*Aep. melampus*	14	-0.25	1.31	0.35	-2.61	2.35	100.00	0.00	0.00	70.30	50.01	91.89
	Aep. shungurae	144	-1.79	2.38	0.20	-8.00	2.61	70.83	29.17	0.00	57.72	4.89	95.09
	Aepyceros sp.	29	-0.79	1.81	0.34	-5.90	2.30	89.66	10.34	0.00	65.93	22.23	92.47
	Ant. recki	21	-2.14	2.95	0.64	-9.60	1.95	71.43	23.81	4.76	54.49	0.00	88.52
	Equus sp.	41	-0.04	1.02	0.16	-3.80	2.10	97.56	2.44	0.00	72.23	40.96	89.78
	G. gracilis	20	-12.15	0.74	0.17	-13.50	-11.12	0.00	0.00	100.00	0.00	0.00	0.00
	G. jumae	7	-11.72	1.16	0.44	-13.39	-10.18	0.00	0.00	100.00	0.00	0.00	0.00
	G. pygmaea	5	-12.44	1.66	0.74	-15.10	-10.70	0.00	0.00	100.00	0.00	0.00	0.00
	G. stillei	11	-10.72	1.47	0.44	-12.20	-8.00	0.00	18.18	81.82	0.00	0.00	5.49
	Giraffa sp.	27	-11.65	1.41	0.27	-14.81	-8.60	0.00	3.70	96.30	0.00	0.00	0.42
Modern	*Aep. melampus*	59	-1.92	2.97	0.39	-9.70	4.90	42.37	52.54	5.08	58.29	0.00	100.00
	E. grevyi	4	1.69	1.89	0.95	-0.63	3.31	100.00	0.00	0.00	86.32	66.92	100.00
	E. quagga	68	3.03	1.29	0.16	-3.23	5.50	98.53	1.47	0.00	100.00	46.62	100.00
	G. camelopardalis	39	-9.39	1.36	0.22	-12.84	-7.00	0.00	5.13	94.87	0.00	0.00	18.28

Table 57: Results from the Kruskal-Wallis test to explore variation in carbon isotopic values between a) all studied species (fossil and modern samples) and b) non-browsing species only (i.e. *A. melampus, A. shungurae, Aepyceros sp., A. recki* and *Equus sp.*). DF=Degrees of freedom. (See appendix A.12.3 table-A18 for pairwise comparisons table).

a)

Species level - all specimens			
	Chi-square	**DF**	**P-value**
Fossil/Modern species	355.60	13	**5.14E-68**

b)

Species level - non-browsing species			
	Chi-square	**DF**	**P-value**
Fossil/Modern	167.52	7	**8.37E-33**

Results from statistical analyses (Table 57a) highlighted significant differences between species within the studied samples. Among fossil specimens, the *Aepyceros melampus*, *Aepyceros shungurae*, *Antidorcas recki* and *Equus sp.* samples all significantly differed from the giraffid species (i.e. *Giraffa gracilis*, *Giraffa jumae, Giraffa pygmaea*, *Giraffa stillei*, *Giraffa sp*., and modern *Giraffa camelopardalis*), with lower $\delta^{13}C$ values. These values confirm a clear dichotomy between C_3 -browsers (i.e. giraffids, with $\delta^{13}C$ values > 9‰) and mixed to C_4 -grazing species (i.e. mixed-feeders with $\delta^{13}C$ values between -9 and -3‰, and C_4 grazers with values > -3‰). Fossil species *A. shungurae, Aepyceros* sp. and *A. recki*, as well as modern *A. melampus* specimens, demonstrated also significantly lower $\delta^{13}C$ values than modern *E. quagga*, suggesting a diet poorer in C_4 -plants among these species, compared to modern plain zebra.

When statistical analyses were conducted on all species but *Giraffa* specimens (i.e. to account for potential variability in isotopic values between non-browsing species within a smaller range of isotopic values; Table 57b), significant differences were found for $\delta^{13}C$ values between several species. In this test, *A. shungurae, Aepyceros* sp.*, A. recki* and modern *A. melampus* specimens were found once more to have significantly lower $\delta^{13}C$ values than modern *E. quagga*. Fossil *A. shungurae* and modern *A. melampus* differed also from fossil *Equus sp*. in having lower $\delta^{13}C$ values. Within genus *Aepyceros*, modern *A. melampus* was shown to have significantly lower $\delta^{13}C$ values than fossil *A. melampus* and *Aepyceros* sp.. These results could suggest that both modern *A. melampus* and *A. shungurae* specimens had a diet less heavily dominated by C_4 -plants than fossil *Equus* sp., *Aepyceros* sp. and fossil *A. melampus* specimens, potentially reflecting more mixed-feeding behaviours. This is in agreement with the proportion of C_4 -plants in the diet evaluated above for these species.

6.4.2.2 Intra-generic spatio-temporal variation in diet in the Omo-Turkana basin

To assess whether spatial and/or temporal differences in dietary practices could be observed within each of the studied taxa, δ13C values were studied depending on the locality and the members the specimens came from (Table 58). Significant differences were found between samples per locality for the *Aepyceros*, *Equus* and *Giraffa* assemblages (Table 59). Significant differences between members were found only for genus *Aepyceros* from the Shungura formation (appendix A.12.3 table-A 19).

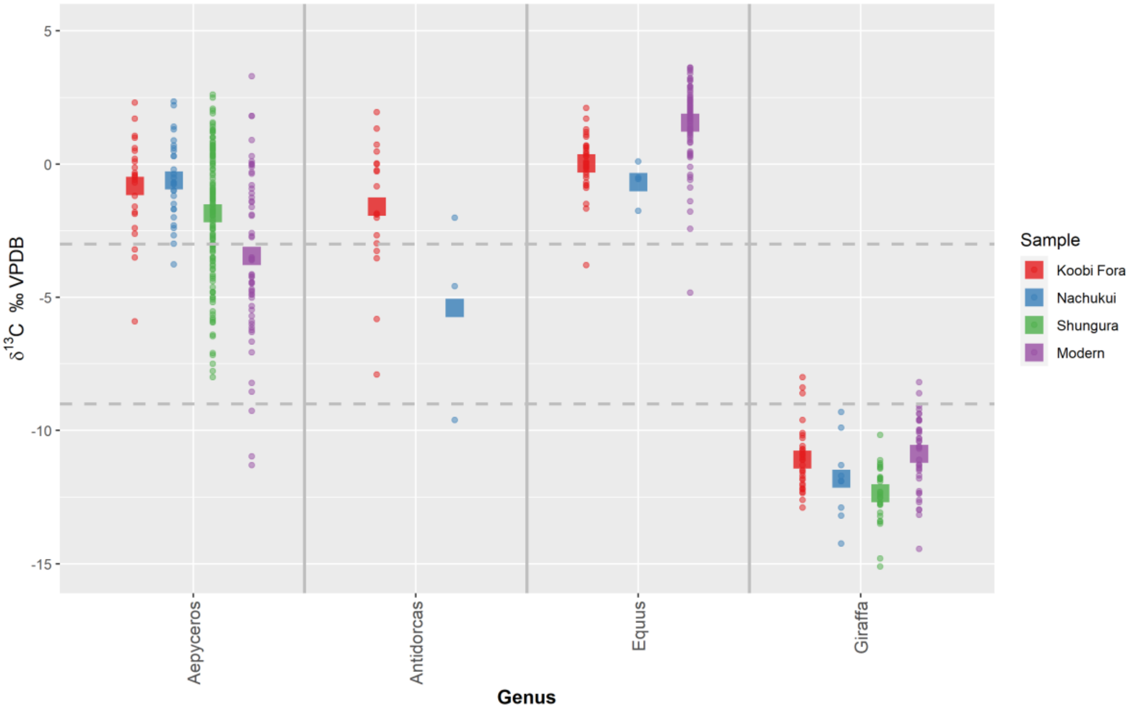

Figure 72: Distribution of δ13C values for the studied taxa from the Koobi Fora, Nachukui and Shungura formations, as well as from modern specimens (previously published data and samples from the present study combined; modern δ13C values corrected for the "fossil fuel effect"). Points represent individual specimen; squares represent the mean value of each sample.

Statistical analyses revealed significant differences in δ13C values between fossil *Equus* specimens and modern *E. quagga*, but no significant difference could be found between equids from Koobi Fora and Nachukui, or between the various members represented (Table 59). The overall dietary signal of *Equus* specimens is dominated by grazing signals in all samples. While *Giraffa* specimens are clearly dominated by browsing signals across all samples, the δ13C values of specimens from the Koobi Fora formation were found to have significantly higher values than specimens from Shungura. No significant difference in δ^{13}C values was found between members for *Giraffa* specimens.

Table 58: Descriptive statistics for carbon stable isotopes, for all taxa studied, per locality and per member. Frequencies of grazers, browsers and mixed-feeders in each sample are based on Lee-Thorp *et al.* (2007). The mean percentage of C_4 -plant included in the diet was estimated based on the linear mixed model from Passey *et al.* (2002, 2009). Mean, standard deviation (S.D.), standard error of the mean (S.E.M), minimum value (min), maximum value (max).

			N	δ13C ‰VPDB Mean					Classification (Lee-thorp et al. 2007)			Estimated
Taxon	Sample	Member		Mean	s.d.	s.e.m	Min	Max	% Grazers	% Mixed-feeders	% Browsers	% C4
Aepyceros	Koobi Fora	**All**	**24**	**-0.82**	**1.83**	**0.37**	**-5.90**	**2.30**	**87.50**	**12.50**	**0.00**	**65.62**
		Tulu Bor	1	-1.81			-1.81	-1.81	100.00	0.00	0.00	57.32
		Burgi	12	-0.61	1.54	0.45	-3.20	2.30	91.67	8.33	0.00	67.90
		KBS	11	-0.97	2.21	0.67	-5.90	1.70	81.82	18.18	0.00	63.90
	Nachukui	**All**	**30**	**-0.61**	**1.49**	**0.27**	**-3.76**	**2.35**	**96.67**	**3.33**	**0.00**	**67.39**
		Lomekwi	18	-1.13	1.27	0.30	-3.76	0.60	94.44	5.56	0.00	62.96
		Kalochoro	7	0.31	1.35	0.51	-1.50	2.20	100.00	0.00	0.00	75.69
		Kaitio	5	-0.04	1.87	0.84	-2.40	2.35	100.00	0.00	0.00	71.71
	Shungura	**All**	**133**	**-1.85**	**2.43**	**0.21**	**-8.00**	**2.61**	**69.17**	**30.83**	**0.00**	**57.23**
		B	21	-2.69	2.65	0.58	-7.50	2.50	57.14	42.86	0.00	49.92
		B-C	1	-5.84			-5.84	-5.84	0.00	100.00	0.00	23.13
		B-D	1	-3.63			-3.63	-3.63	0.00	100.00	0.00	41.79
		C	23	-3.42	2.64	0.55	-8.00	1.24	52.17	47.83	0.00	43.61
		D	24	-0.88	1.98	0.40	-5.18	1.90	83.33	16.67	0.00	65.62
		E	13	-2.12	2.33	0.65	-6.46	1.20	76.92	23.08	0.00	55.13
		E-F	3	-1.89	1.50	0.87	-3.02	-0.19	66.67	33.33	0.00	57.09
		F	24	-0.80	1.91	0.39	-4.15	2.08	79.17	20.83	0.00	66.29
		G	23	-1.23	2.07	0.43	-4.83	2.61	73.91	26.09	0.00	62.68
Antidorcas	Koobi Fora	**All**	**18**	**-1.60**	**2.52**	**0.59**	**-7.90**	**1.95**	**77.78**	**22.22**	**0.00**	**59.03**
		Tulu Bor	1	-2.98			-2.98	-2.98	100.00	0.00	0.00	47.44
		Burgi	8	-3.04	2.74	0.97	-7.90	0.03	50.00	50.00	0.00	47.34
		KBS	9	-0.16	1.49	0.50	-2.68	1.95	100.00	0.00	0.00	70.70
	Nachukui	**All**	**3**	**-5.40**	**3.86**	**2.23**	**-9.60**	**-2.01**	**33.33**	**33.33**	**33.33**	**27.24**
		Lomekwi	1	-2.01			-2.01	-2.01	100.00	0.00	0.00	55.48
		Lokalalei	1	-9.60			-9.60	-9.60	0.00	0.00	100.00	0.00
		Kalochoro	1	-4.59			-4.59	-4.59	0.00	100.00	0.00	34.28
Equus	Koobi Fora	**All**	**37**	**0.02**	**1.02**	**0.17**	**-3.80**	**2.10**	**97.30**	**2.70**	**0.00**	**72.79**
		Tulu Bor	1	-0.79			-0.79	-0.79	100.00	0.00	0.00	65.94
		Burgi	19	-0.02	1.21	0.28	-3.80	1.70	94.74	5.26	0.00	72.85
		KBS	17	0.13	0.81	0.20	-1.50	2.10	100.00	0.00	0.00	73.12
	Nachukui	**All**	**4**	**-0.68**	**0.77**	**0.39**	**-1.75**	**0.10**	**100.00**	**0.00**	**0.00**	**67.08**
		Kalochoro	3	-0.32	0.36	0.21	-0.56	0.10	100.00	0.00	0.00	70.35
		Kaitio	1	-1.75			-1.75	-1.75	100.00	0.00	0.00	57.27
Giraffa	Koobi Fora	**All**	**32**	**-11.09**	**1.20**	**0.21**	**-12.90**	**-8.00**	**0.00**	**9.38**	**90.63**	**0.00**
		Tulu Bor	2	-11.71	0.20	0.14	-11.85	-11.57	0.00	0.00	100.00	0.00
		Burgi	13	-10.94	1.46	0.40	-12.90	-8.00	0.00	15.38	84.62	0.00
		KBS	17	-11.13	1.06	0.26	-12.60	-8.39	0.00	5.88	94.12	0.00
	Nachukui	**All**	**9**	**-11.81**	**1.55**	**0.52**	**-14.24**	**-9.30**	**0.00**	**0.00**	**100.00**	**0.00**
		Lomekwi	8	-11.64	1.56	0.55	-14.24	-9.30	0.00	0.00	100.00	0.00
		Kalochoro	1	-13.19			-13.19	-13.19	0.00	0.00	100.00	0.00
	Shungura	**All**	**29**	**-12.36**	**1.07**	**0.20**	**-15.10**	**-10.16**	**0.00**	**0.00**	**100.00**	**0.00**
		B	5	-12.27	1.79	0.80	-14.81	-10.16	0.00	0.00	100.00	0.00
		C	5	-12.26	0.78	0.35	-13.42	-11.28	0.00	0.00	100.00	0.00
		D	5	-12.70	1.62	0.73	-15.10	-11.12	0.00	0.00	100.00	0.00
		E	4	-12.64	0.71	0.35	-13.50	-11.78	0.00	0.00	100.00	0.00
		F	5	-12.12	0.62	0.28	-12.79	-11.43	0.00	0.00	100.00	0.00
		G	5	-12.22	0.74	0.33	-13.08	-11.23	0.00	0.00	100.00	0.00

Table 59: Results from the Kruskal-Wallis tests to explore variation in carbon isotopic values within each taxon between samples a) per locality and b) per member in each locality. DF=Degrees of freedom. (See appendix A.12.3 tables-A 19 and A 20 for pairwise comparisons tables).

a)

	Locality		
	Chi-square	DF	P-value
Aepyceros	27.94	3	**3.73E-06**
Antidorcas	3.46	1	6.29E-02
Equus	37.71	2	**6.46E-09**
Giraffa	21.78	3	**7.23E-05**

b)

	Member			
	Sample	Chi-square	DF	P-value
Aepyceros	*Nachukui*	5.04	2	0.080
	Shungura	22.63	8	**0.004**
Antidorcas	*Koobi Fora*	5.98	2	0.050
	Nachukui	2.00	2	0.368
Equus	*Koobi Fora*	1.52	2	0.468
	Nachukui	1.80	1	0.180
Giraffa	*Koobi Fora*	0.61	2	0.738
	Nachukui	1.36	1	0.243
	Shungura	0.98	5	0.964

No significant difference in $\delta^{13}C$ values was found between localities or members for *Antidorcas* specimens, although analyses were limited by small sample sizes for some members. For instance, the Nachukui sample is only represented by three specimens with highly different $\delta^{13}C$ values across members: although this variability could be an interesting feature of the dietary ecology of fossil springbok in this locality, the small sample size is not sufficient to allow further interpretation. Variation in $\delta^{13}C$ values across members can be however observed among the *Antidorcas* specimens from the Koobi Fora formation, where $\delta^{13}C$ values appear higher in KBS (G: MF: B = 100: 0: 0) when compared to Burgi (G: MF: B = 50: 50: 0), suggesting a predominance of mixed-feeding patterns in springbok specimens from Burgi (2.64 – 1.87 Ma), which contrasts with the grazing signal suggested by the average $\delta^{13}C$ values of springbok specimens from KBS (1.87 – 1.61 Ma). These differences were however not confirmed by statistical analyses.

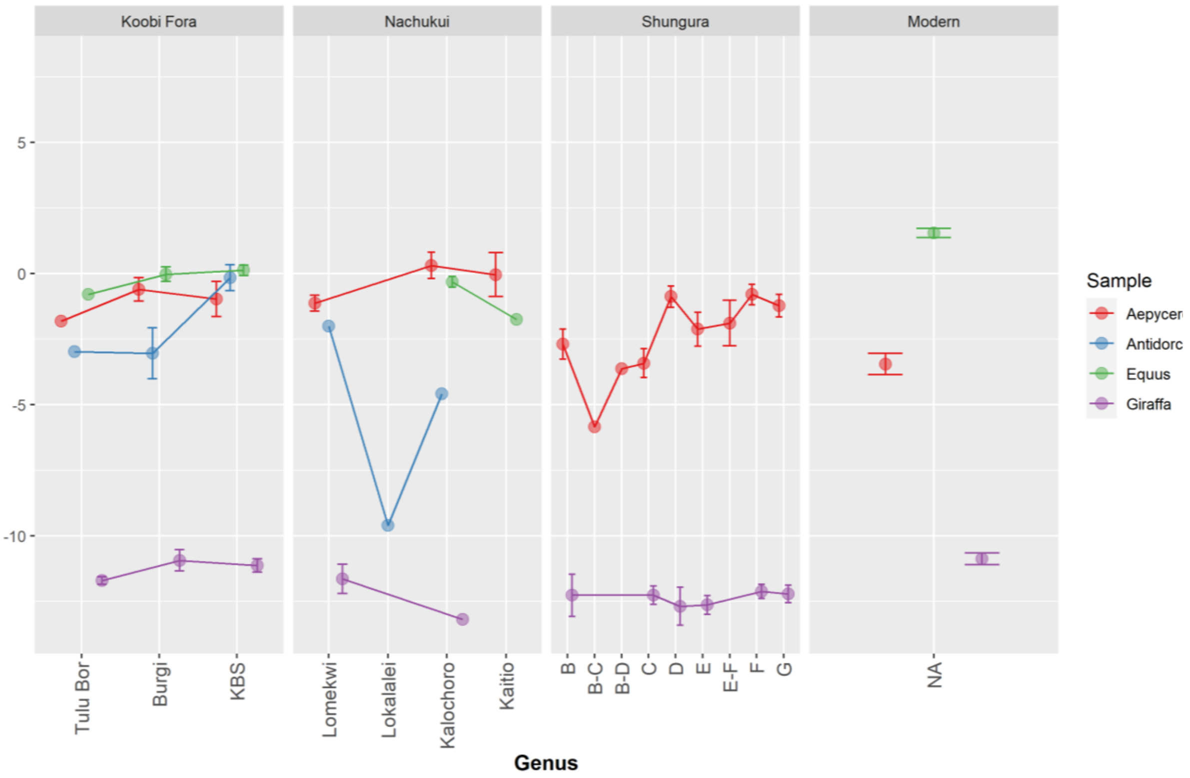

Figure 73: Distribution of δ¹³C values (mean and standard error of the mean) for the studied taxa for the Koobi Fora, Nachukui, Shungura and modern samples, for each member. (Note: modern δ¹³C values corrected for the "fossil fuel effect").

While the diet of fossil impala specimens appears dominated by C$_4$-vegetation and grazing patterns in the Koobi Fora and the Nachukui formation, the average δ¹³C value for specimens from the Shungura formation suggest more varied dietary patterns in that locality. The relative proportion of individuals classified as grazers, mixed-feeders and browsers (G: MF: B) in each sample is 87.5: 12.5: 0 for Koobi Fora, 96.7: 3.3: 0 for Nachukui and 69.2: 30.8: 0 for Shungura. Results from the statistical analyses confirmed that δ¹³C values from *Aepyceros* specimens from the Shungura formation are significantly lower than δ¹³C values from the Nachukui formation. Although variations in δ¹³C values can be observed between members within each locality, significant differences were only highlighted by statistical tests for impala specimens from the Shungura formation (Table 59 and Figure 73).

When exploring carbon isotopic values across members, the *Aepyceros* assemblages from members D (G: MF: B = 83.3: 16.7: 0) and F (G: MF: B = 79.2: 20.8: 0) have the strongest C$_4$-

grazing signals within the Shungura formation. In contrast, *Aepyceros* specimens from member C appear to be predominantly mixed-feeding individuals (G: MF: B = 52.2: 47.8: 0), with an average diet composed of only 43.6% of C_4-plants at minimum in this member. These results could suggest a diet richer in C_4-plants for impalas between 2.53 and 2.4 Ma in Member D, compared to older fossil impala specimens, as well as for impalas between 2.32 and 2.27 Ma (member F), compared to older fossil specimens. These observations were confirmed statistically, with significantly lower $\delta^{13}C$ values for *Aepyceros* specimens from members B and C (3.44-2.52 Ma) compared to members D (2.52-2.4 Ma) and F (2.32-2.27 Ma) (appendix A.12.3 table-A 20). Similarly, significantly lower $\delta^{13}C$ values could be observed between impala specimens from member C compared to specimens from member G (2.27-1.9 Ma). This suggests a significant increase in the consumption of C_4-plants for impala populations from the Shungura formation from ~2.32 Ma.

Overall, these results highlight the dietary adaptability of the *Aepyceros* species in the studied assemblages, with varying degrees of grazing and mixed-feedings habits found through time and throughout the Turkana basin. Impala specimens from the Shungura formation, in the Lower Omo river valley, appear to differ from East and West Turkana specimens, with a higher dietary variability and a stronger mixed-feeding signal, although the assemblage remains dominated by grazing individuals. However, this grazing signal in Shungura varies greatly through time in the Shungura formation: while mixed-diets prevail among impala specimens between 2.91–2.5 Ma in Member C, a clear pattern of increased C_4-grazing behaviours can be observed for this genus from member D, at ~2.32 Ma.

6.4.3 Stable oxygen isotopes

6.4.3.1 Dietary variation among taxa: Interspecific comparisons

To investigate the aridity conditions experienced by the studied specimens during the early years of their lives, the stable oxygen isotope ratios of each fossil and modern species were studied and compared (

Table 60-

Table 61 and Figure 74-Figure 75). Results showed significant differences between species within the studied samples (fossil and modern).

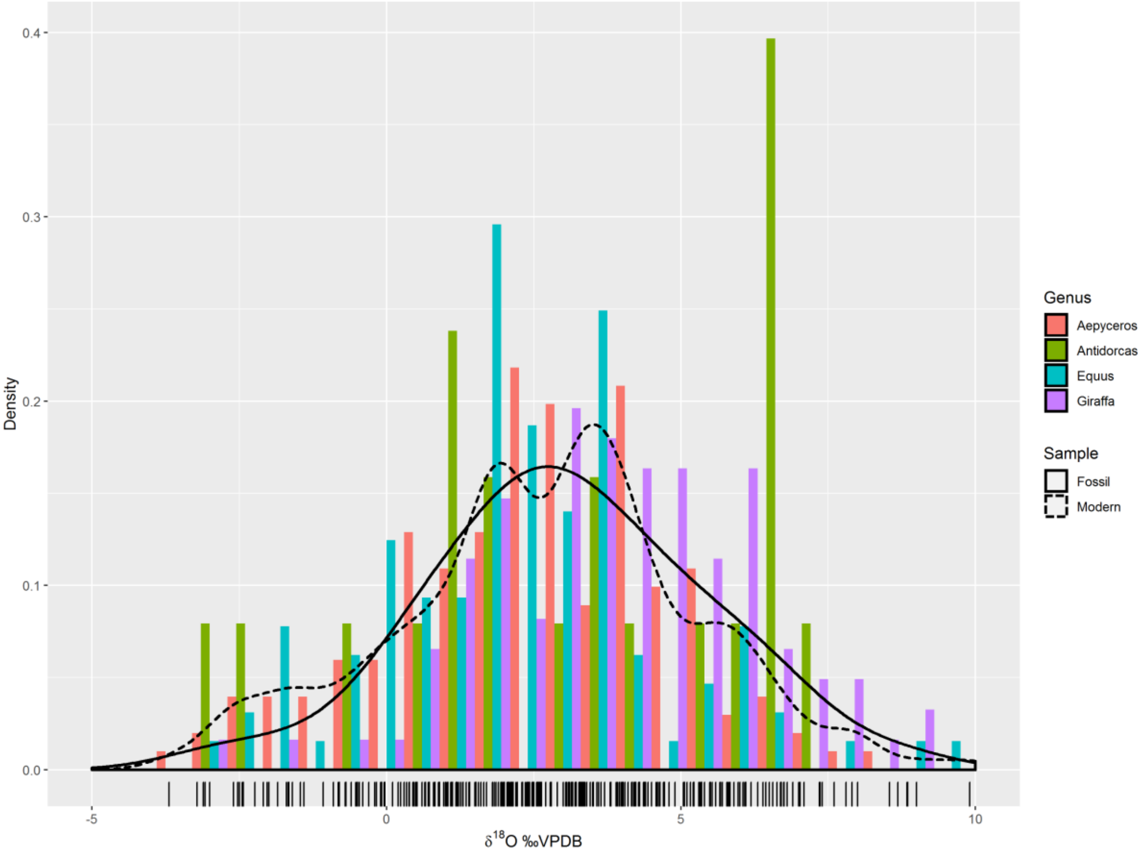

Figure 74: Kernel density estimates (Gaussian) for fossil and modern samples of all taxa (lines), and density per genus (fossil and modern combined; histogram).

The distribution of δ18O values for the modern and fossil samples suggests broadly similar patterns between the two assemblages (Figure 74). Both distributions are unimodal, although the fossil distribution appears more symmetrical than the modern distribution. This difference in distribution might relate to varying aridity conditions reflected in the modern individuals, which come from different localities across Africa between 1900 and 2011. Indeed, previous studies have suggested that oxygen isotope patterns in mammals vary from region to region (Estes, 1991; Sponheimer and Lee-Thorp, 1999). When observing the range δ18O values yielded by the analyses for each studied species (Figure 75), most samples demonstrate a large range of values, most particularly within the modern *Aepyceros melampus* sample.

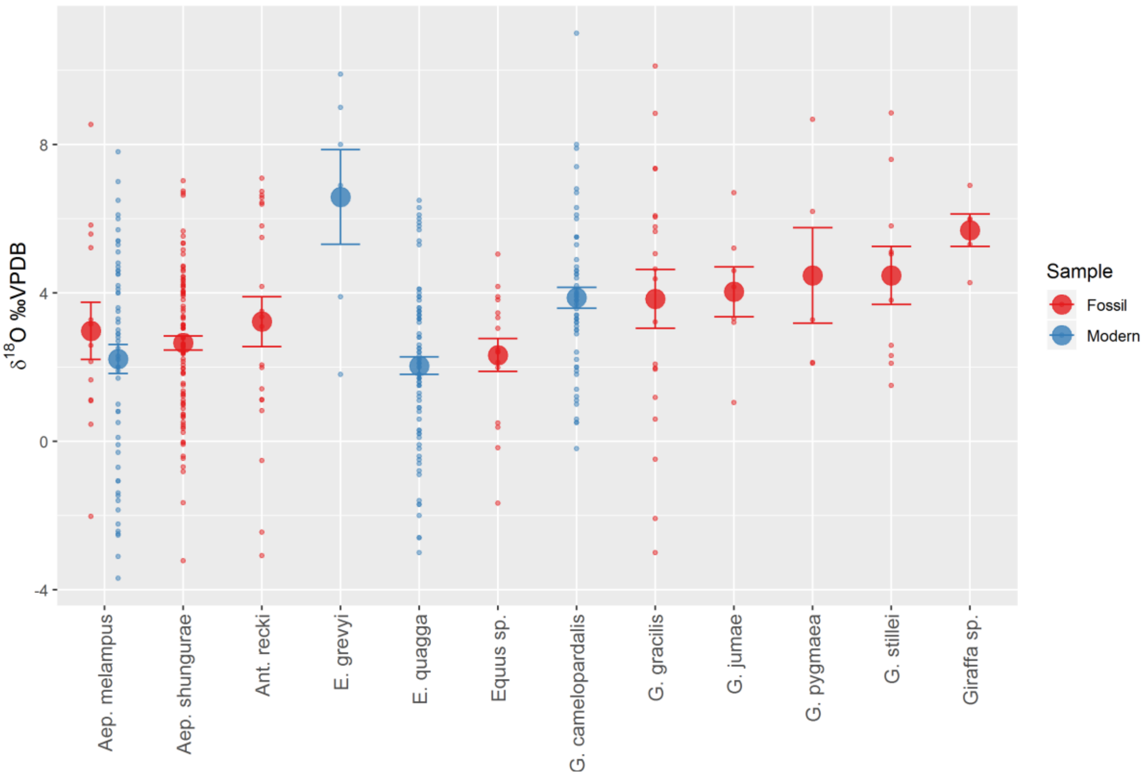

Figure 75: Distribution of δ^{18}O values (mean and standard error of the mean) for all taxa sampled from the Koobi Fora, Nachukui and Shungura formations, as well as modern *G. camelopardalis* specimens. Smaller points represent values per individual specimen.

Table 60: Descriptive statistics for all species studied for stable oxygen isotope analysis. Mean, standard deviation (S.D.), standard error of the mean (S.E.M), minimum value (min), maximum value (max).

Sample	Species	N	δ18O ‰VPDB Mean				
			Mean	s.d.	s.e.m	Min	Max
Fossil	*Aep. melampus*	13	2.97	2.77	0.77	-2.03	8.54
	Aep. shungurae	99	2.65	1.91	0.19	-3.22	7.02
	Ant. recki	21	3.22	3.08	0.67	-3.08	7.09
	Equus sp.	16	2.32	1.79	0.45	-1.67	5.05
	G. gracilis	20	3.84	3.53	0.79	-3.00	10.12
	G. jumae	7	4.03	1.78	0.67	1.04	6.70
	G. pygmaea	5	4.47	2.88	1.29	2.10	8.68
	G. stillei	10	4.47	2.46	0.78	1.50	8.85
	Giraffa sp.	5	5.69	0.97	0.43	4.28	6.90
Modern	*Aep. melampus*	56	2.21	2.93	0.39	-3.69	7.80
	E. grevyi	6	6.58	3.13	1.28	1.80	9.90
	E. quagga	85	2.04	2.14	0.23	-3.00	6.50
	G. camelopardalis	57	3.87	2.10	0.28	-0.20	11.00

Table 61: Results from the Kruskal-Wallis test to explore variation in δ^{18}O values between all studied species (fossil and modern samples). DF=Degrees of freedom. (See appendix A.12.4 table-A 21 for pairwise comparisons table).

Chi-square	DF	P-value
47.03627159	12	4.59E-06

Specimens from fossil *Giraffa sp*, modern *G. camelopardalis* and modern *E. grevyi* were all found to have significantly higher δ^{18}O values than modern *E. quagga* specimens (p=0.037, p=0.00, and p=0.044, respectively). These differences could be related to differing biological processes between taxa.

Indeed, the δ^{18}O values of the food ingested and the mode of water vapour loss (i.e. panting vs sweating) have been shown in previous studies to significantly impact the δ^{18}O values of mammalian body water (Wong *et al.*, 1988; Sponheimer and Lee-Thorp, 1999). Modern giraffes are known today to be evaporation sensitive (ES), due to their independence to water-sources and their ability to obtain their daily water requirements from the water content of the consumed plants (Levin *et al.*, 2006; Blumenthal *et al.*, 2017). Equids are sometimes considered as evaporation-insensitive (EI) (e.g. Bedaso *et al.,* 2013), as they are water-dependant. The enamel oxygen isotopic composition of ES animals has been suggested to reflect local aridity conditions, while the δ^{18}O of EI species tends to reflect that of meteoric water. The significantly higher δ^{18}O values observed in this study in fossil *Giraffa sp*, modern *G. camelopardalis* and modern *E. grevyi* specimens when compared to modern *E. quagga* specimens could therefore potentially reflect differing animal biologics and differences in the main sources of their body-water, with obligate-drinking EI species on one end (here *E. quagga*) and non-obligate drinking ES species on another end (here *Giraffa* sp., *G. camelopardalis* and *E. grevyi*). The difference between modern *E. quagga* and *E. grevyi* could be related to the small sample size for *E. grevyi* specimens, or to differences in ecology, with previous studies suggesting niche partitioning and differences in the type of plants eaten between the two species (e.g. Kartzinel *et al.,* 2015).

Following this hypothesis, the δ18O values observed for the *Aepyceros* species (extinct and extant), being similar to the range of values observed for *Equus quagga*, could suggest obligate-drinking behaviours for this taxon. If that was the case, the δ18O values observed in fossil impala samples will likely reflect the δ18O composition of local meteoric water at the time. *Antidorcas recki* yielded a large range of δ18O values which overlaps with all other species, making it difficult to assess the drinking patterns of this species.

6.4.3.2 Intra-generic spatio-temporal variation in diet in the Omo-Turkana basin

To assess whether spatial and/or temporal differences in the δ18O values of the body water of the studied specimens could be observed within each of the studied taxa, δ18O values were studied depending on the locality and the members the specimens came from (Table 62-Table 63; Figure 76 -Figure 77). Significant differences were found between samples per locality (i.e. Koobi Fora, Nachukui, Shungura and moderns) for *Aepyceros* only. No significant difference in δ18O was found through time for any of the other studied taxa.

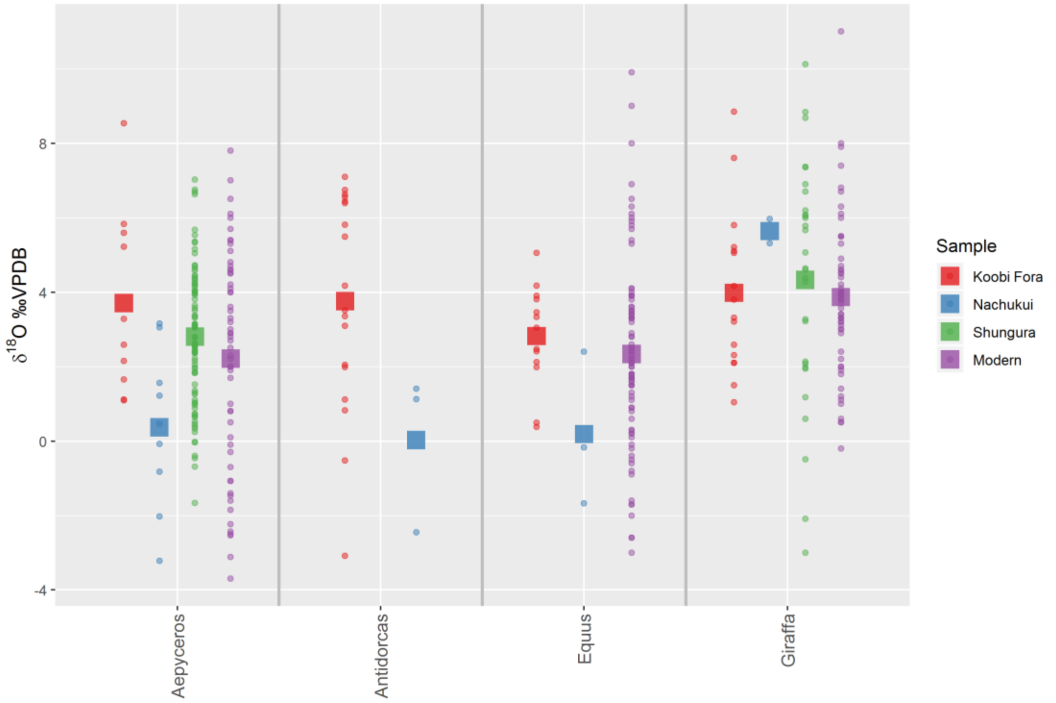

Figure 76: Distribution of δ18O values for the studied taxa from the Koobi Fora, Nachukui and Shungura formations, as well as from modern specimens (previously published data and samples from the present study combined). Points represent individual specimen; Squares represent the mean value of each sample.

Table 62: Descriptive statistics for oxygen stable isotopes, for all taxa studied, per locality and per member. Mean, standard deviation (S.D.), standard error of the mean (S.E.M), minimum value (min), maximum value (max),

				$\delta^{18}O$ ‰VPDB Mean				
Taxon	**Sample**	**Member**	**N**	**Mean**	**s.d.**	**s.e.m**	**Min**	**Max**
Aepyceros	Koobi Fora	**All**	**10**	**3.71**	**2.48**	**0.78**	**1.09**	**8.54**
		Tulu Bor	1	5.22			5.22	5.22
		Burgi	3	2.94	2.35	1.36	1.09	5.59
		KBS	6	3.83	2.83	1.16	1.11	8.54
	Nachukui	**All**	**9**	**0.37**	**2.16**	**0.72**	**-3.22**	**3.16**
		Lomekwi	6	0.29	2.18	0.89	-3.22	3.05
		Kalochoro	1	3.16			3.16	3.16
		Kaitio	2	-0.79	1.76	1.25	-2.03	0.46
	Shungura	**All**	**93**	**2.80**	**1.80**	**0.19**	**-1.66**	**7.02**
		B	13	3.23	1.49	0.41	0.65	5.67
		B-C	1	4.23			4.23	4.23
		B-D	1	6.69			6.69	6.69
		C	15	2.17	1.74	0.45	-0.69	4.63
		D	16	3.00	2.19	0.55	-1.66	6.75
		E	13	3.13	1.52	0.42	0.66	7.02
		E-F	3	1.87	0.73	0.42	1.10	2.56
		F	16	3.06	1.87	0.47	-0.46	6.63
		G	15	2.14	1.63	0.42	-0.04	5.04
Antidorcas	Koobi Fora	**All**	**18**	**3.76**	**2.92**	**0.69**	**-3.08**	**7.09**
		Tulu Bor	1	1.11			1.11	1.11
		Burgi	8	4.90	3.42	1.21	-3.08	7.09
		KBS	9	3.04	2.27	0.76	-0.52	6.56
	Nachukui	**All**	**3**	**0.03**	**2.15**	**1.24**	**-2.45**	**1.41**
		Lomekwi	1	1.41			1.41	1.41
		Lokalalei	1	-2.45			-2.45	-2.45
		Kalochoro	1	1.12			1.12	1.12
Equus	Koobi Fora	**All**	**13**	**2.82**	**1.37**	**0.38**	**0.38**	**5.05**
		Tulu Bor	1	3.81			3.81	3.81
		Burgi	5	2.11	1.65	0.74	0.38	4.17
		KBS	7	3.18	1.10	0.42	1.99	5.05
	Nachukui	**All**	**3**	**0.19**	**2.06**	**1.19**	**-1.67**	**2.40**
		Kalochoro	2	0.37	2.88	2.04	-1.67	2.40
		Kaitio	1	-0.17			-0.17	-0.17
Giraffa	Koobi Fora	**All**	**16**	**3.98**	**2.19**	**0.55**	**1.04**	**8.85**
		Tulu Bor	2	3.69	0.67	0.48	3.21	4.16
		Burgi	4	4.85	2.52	1.26	1.50	7.60
		KBS	10	3.70	2.32	0.73	1.04	8.85
	Nachukui	**All**	**2**	**5.64**	**0.47**	**0.33**	**5.31**	**5.97**
		Lomekwi	1	5.31			5.31	5.31
		Kalochoro	1	5.97			5.97	5.97
	Shungura	**All**	**29**	**4.33**	**3.19**	**0.59**	**-3.00**	**10.12**
		B	5	6.18	1.71	0.76	4.28	8.68
		C	5	3.85	2.23	1.00	1.98	7.36
		D	5	6.11	1.03	0.46	4.64	7.35
		E	4	2.71	2.87	1.44	-0.49	5.78
		F	5	3.89	2.05	0.92	1.94	6.08
		G	5	2.89	6.17	2.76	-3.00	10.12

Table 63: Results from the Kruskal-Wallis tests to explore variation in oxygen isotopic values within each taxon between samples a) per locality and b) per member for each locality. DF=Degrees of freedom. (See appendix A.12.4 table-A 22 for pairwise comparisons table).

a)

Locality			
	Chi-square	**DF**	**P-value**
Aepyceros	9.01	3	**0.029**
Antidorcas	3.27	1	0.070
Equus	4.02	2	0.134
Giraffa	3.19	3	0.364

b)

Member				
	Sample	**Chi-square**	**DF**	**P-value**
Aepyceros	*Koobi Fora*	0.76	2	0.683
	Nachukui	2.76	2	0.252
	Shungura	10.29	8	0.245
Antidorcas	*Koobi Fora*	4.58	2	0.101
	Nachukui	2.00	2	0.368
Equus	*Koobi Fora*	1.39	2	0.499
	Nachukui	0.00	1	1.000
Giraffa	*Koobi Fora*	0.99	2	0.610
	Nachukui	1.00	1	0.317
	Shungura	5.78	5	0.329

Significant differences within the *Aepyceros* sample were highlighted for $\delta^{18}O$ between specimens from the Nachukui formation and specimens from the other two fossil localities: Koobi Fora and Shungura. Fossil impalas from West Turkana demonstrate lower $\delta^{18}O$ values than impalas from East Turkana and the lower Omo river valley. Similarly, *Equus* and *Antidorcas* specimens from Koobi Fora appear to have higher $\delta^{18}O$ values in average than *Equus* and *Antidorcas* specimens from Nachukui, although these differences were not confirmed statistically. No significant difference was found for *Giraffa* specimens between sites or members. Following the hypothesis stated above in which fossil *Equus* and *Aepyceros* species were likely to have been obligate-drinkers, the variations in $\delta^{18}O$ values observed across the Omo-Turkana basin for these taxa could highlight differing local meteoric water composition between Nachukui and Koobi Fora/Shungura, and, in turn, differing environmental conditions across the basin.

When observing oxygen isotope patterns through time (Figure 77), the patterns of variation in $\delta^{18}O$ values differ between *Equus*, *Antidorcas* and *Aepyceros*, especially when comparing the *Antidorcas* assemblage with the *Aepyceros* and *Equus* assemblages. More particularly, a similar pattern of variation in $\delta^{18}O$ values can be observed between genera *Aepyceros* and *Equus* in the Koobi Fora formation, with $\delta^{18}O$ values decreasing between ~3.0 and ~2.0 Ma, and increasing between ~2.0 and ~1.75 Ma. In the Nachukui assemblage, δ18O values for *Aepyceros* appear to increase between ~3.25 and ~2.5 Ma, and decrease between ~2.0 and ~1.75 Ma. Because fewer specimens were available for genus *Equus* in this formation, the analyses only provide data for a small time-span and show a slight decrease in δ18O values between ~2.0 and 1.75 Ma. Data for *Aepyceros* specimens in the Shungura formation suggest an increase in δ18O values between ~3.25 and ~3.0 Ma and a decrease in values between ~3.0 and ~2.5 Ma, followed by an alternation of slight increases and decreases in values up to ~2.0 Ma. These patterns could suggest a high temporal variability in the isotopic composition of the water ingested by these taxa in the three studied localities, which might relate to changing environmental conditions in the region during the time period studied.

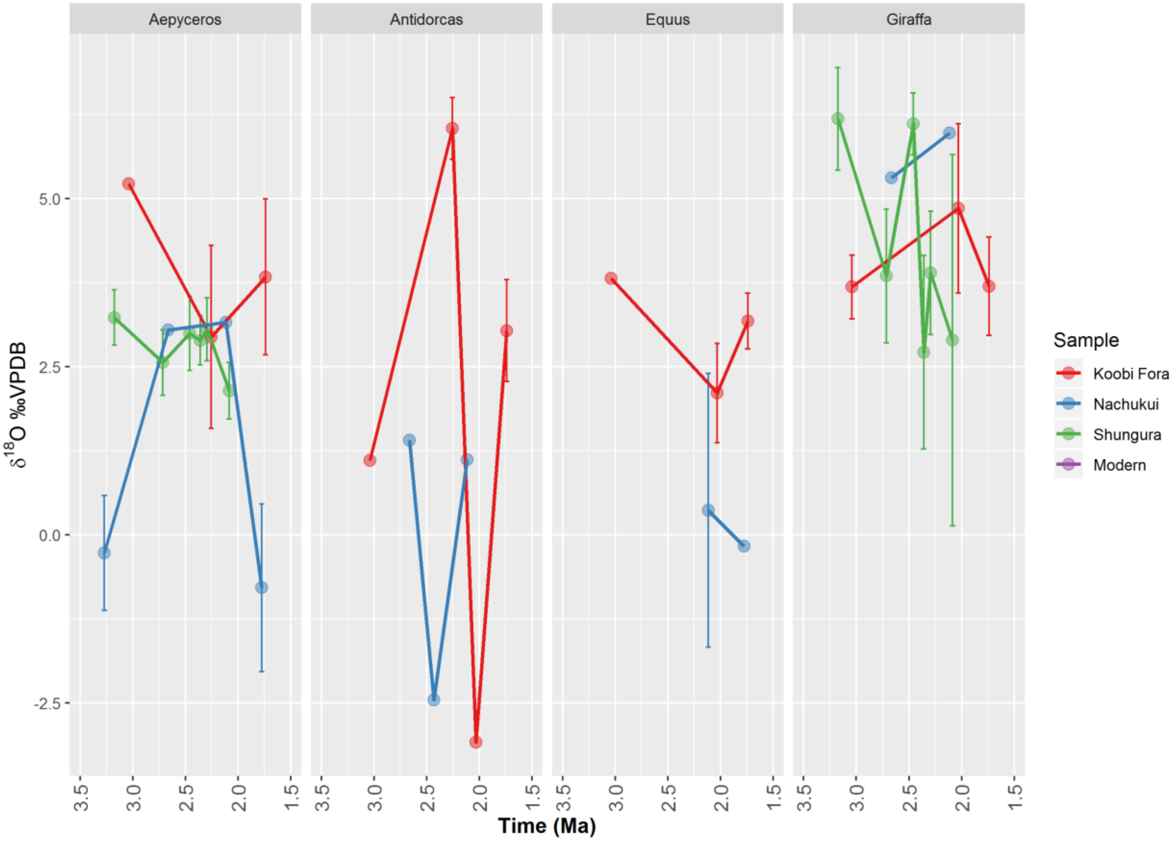

Figure 77: Distribution of δ18O values (mean and standard error of the mean) for the studied taxa for the Koobi Fora, Nachukui, Shungura through time.

6.4.4 Intra-tooth stable isotope analysis: Seasonal variation in diet

To appraise the degree of seasonal variability in diet within fossil impala populations, intra-tooth variability was assessed for selected *Aepyceros shungurae* specimens analysed following serial sampling for stable isotope analyses (Figure 78-Figure 81). Intra-tooth variability was also assessed for modern *Aepyceros melampus* and *Giraffa camelopardalis* specimens. Some specimens displayed intra-tooth variations in both $\delta^{13}C$ and $\delta^{18}O$ values, and a positive correlation between carbon and oxygen stable isotope ratios (Table 64).

As predicted, little variation was observed in stable carbon isotope ratios ($\delta^{13}C$) across the intra-tooth sequence of the modern giraffe specimens ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$ < 1‰), with values typical of browsing species (Figure 78). One *G. camelopardalis* specimen showed little variation in $\delta^{18}O$ as well ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$ < 1‰), while the other displayed a wider range of $\delta^{18}O$ values ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$ = 2.7 ‰). A wider range of $\delta^{13}C$ values was observed within the intra-tooth sequence of the modern impala specimens ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$ = 1.3 to 1.6‰). For both *A. melampus* specimens, the lowest $\delta^{13}C$ values recorded fell within the range of $\delta^{13}C$ values usually observed in mixed-feeders. While the highest $\delta^{13}C$ value observed for RMCA-2193 remained within the range of values associated with mixed-feeders, the highest value observed for the individuals I4 from Copeland *et al.*'s study (2009) fell within the range of $\delta^{13}C$ values usually observed in grazers (-2.4‰). These results indicate mixed-feeding behaviours for both specimens, but a stronger seasonal dietary variability in the I4 specimen (specimen originating from Akagera National Park, Rwanda; Copeland *et al.* 2009) compared to RMCA-2193 (specimen originating from Kenya). Some degree of variation in $\delta^{18}O$ was observed across the sequences of both impala specimen as well (i.e. $\delta^{18}O_{max}$ - $\delta^{18}O_{min}$ = 1.28 to 2.72 ‰), but only the values observed for the impala specimen RMCA-2193 demonstrated a significant positive correlation between $\delta^{18}O$ and $\delta^{13}C$ (tau=1; p=0.001) (Table 64).

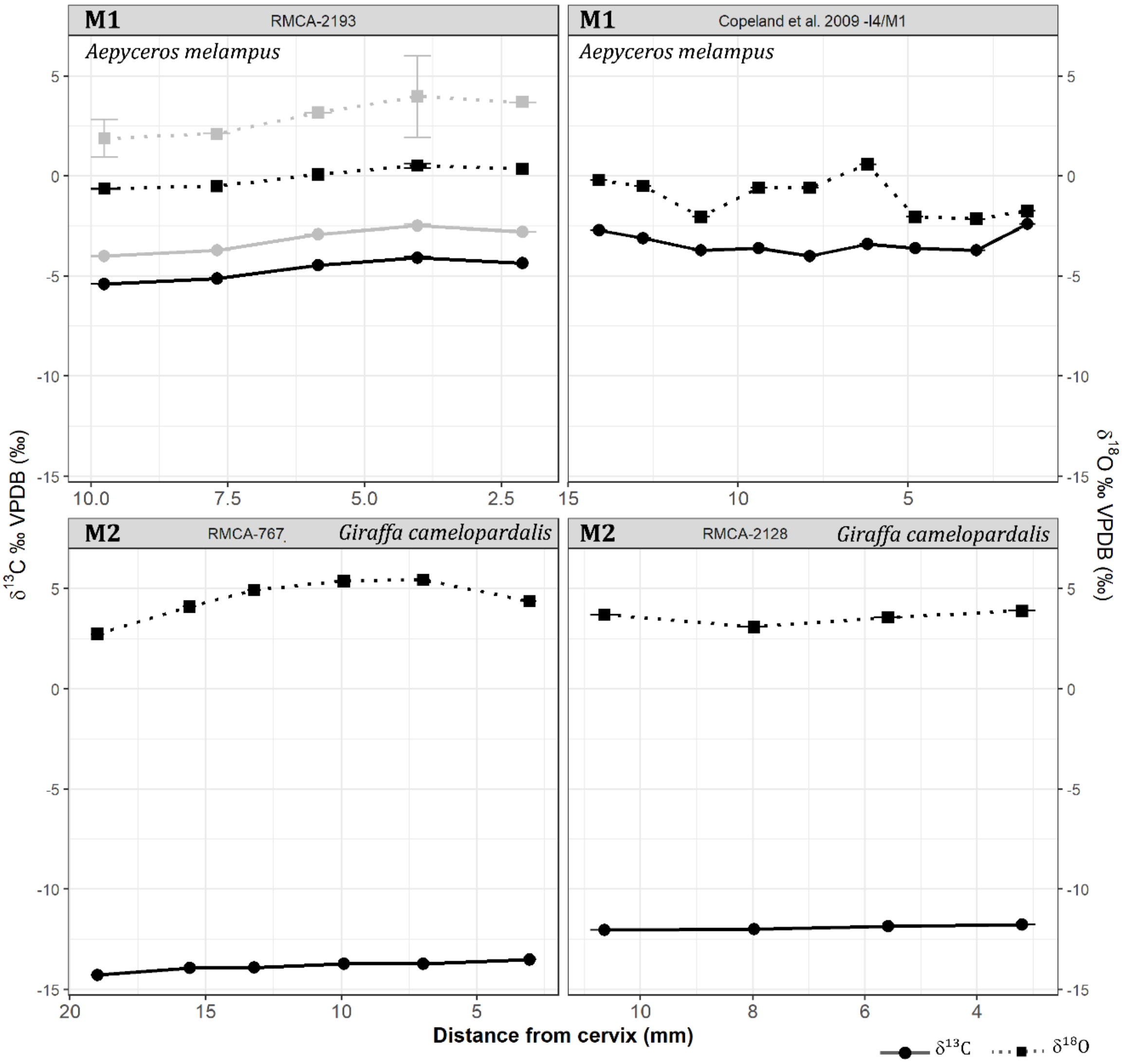

Figure 78: Intra-tooth variation in δ18O and δ13C values for two modern impala specimens (*Aepyceros melampus)* and, for comparison, two modern giraffe specimens (*Giraffa camelopardalis*). All data from the Royal Museum for Central Africa (i.e. RMCA numbers) was collected for the present study. Data for the impala specimen I4, used for comparison, originates from Copeland *et al.,* 2009. Points and lines in grey represent non-corrected NIGL data.

Table 64: Summary statistics for all specimens studied for stable carbon and oxygen isotope intra-tooth analyses, and results from Kendall rank coefficient tests (i.e. Kendall's tau) to evaluate the association between δ^{18}O and δ^{13}C within each intra-tooth sequence. Mean, standard deviation (S.D.), standard error of the mean (S.E.M), minimum value (min), maximum value (max), Kendall correlation coefficient (estimate (tau), significance level (p-value). Corrected values are used for samples analysed at NIGL. See Appendix A-11.5 for detailed results.

Species	Specimen	Member	Tooth	N	δ13C (‰) VPDB Mean	S.D.	S.E.M	Min	Max	Max-Min	δ18O (‰)VPDB Mean	S.D.	S.E.M	Min	Max	Max-Min	Kendall's tau Estimate (tau)	p-value
Aepyceros shungurae	OMO3.0 72-14	B12	UM3	10	-0.25	0.78	0.25	-0.98	+1.55	**2.52**	+3.47	1.58	0.50	+1.24	+6.47	**5.23**	0.56	**0.029**
	L279-10012	C6	UM2	8	-1.76	0.84	0.30	-3.42	-0.82	**2.60**	+6.62	1.58	0.56	+5.00	+9.76	**4.75**	0.65	**0.000**
			UM3	10	-2.80	1.07	0.34	-4.81	-1.16	**3.65**	+3.85	2.71	0.86	+0.63	+8.34	**7.71**		
	OMO11.2 67-730	D1	UM3	16	+1.76	0.69	0.17	-0.13	+2.54	**2.67**	+5.62	1.18	0.29	+4.22	+8.41	**4.19**	0.44	**0.017**
	L147-45	E4	LM1-2	13	-2.16	1.96	0.54	-4.84	+0.80	**5.65**	+7.91	2.51	0.70	+4.14	+13.70	**9.56**	0.36	0.100
	L28-7x	F1	LM1-2	10	+1.45	0.63	0.20	+0.92	+3.12	**2.20**	+5.84	1.15	0.36	+3.82	+7.46	**3.64**	0.64	**0.009**
	L66-1b	F3	UM	10	+2.79	0.86	0.27	+1.44	+4.09	**2.65**	+3.72	1.10	0.35	+1.92	+5.47	**3.55**	0.20	0.484
	F165-18	G13	UM	15	+1.57	1.18	0.31	-0.22	+3.43	**3.65**	+5.11	1.49	0.38	+3.00	+7.55	**4.56**	0.52	**0.006**
	Omo50 68-2389	G3-13	LM2	13	-0.27	2.32	0.64	-3.08	+5.21	**8.29**	+3.17	2.46	0.68	+0.26	+8.77	**8.51**	0.67	**0.000**
			LM3	12	-1.58	2.57	0.74	-6.48	+1.90	**8.37**	+2.49	1.71	0.49	-0.83	+4.86	**5.69**		
	Omo100 70-2260	G28-29	LM3	15	-0.48	1.99	0.51	-3.88	+2.24	**6.11**	+2.61	2.32	0.60	-1.31	+5.75	**7.07**	0.64	**0.001**
Aepyceros melampus	RMCA-2193	Modern	LM1	7	-4.70	0.59	0.22	-5.40	-4.02	**1.37**	-0.04	0.53	0.20	-0.64	+0.63	**1.28**	1.00	**0.000**
	Copeland et al. 2009 -I4	Modern	M1	9	-3.36	0.52	0.17	-4.00	-2.40	**1.60**	-1.03	0.98	0.33	-2.14	+0.58	**2.72**	0.35	0.200
Giraffa camelopardalis	RMCA-2128	Modern	M2	4	-11.91	0.12	0.06	-12.03	-11.77	**0.26**	+3.57	0.34	0.17	+3.10	+3.90	**0.80**	0.33	0.750
	RMCA-767	Modern	M2	6	-13.84	0.26	0.11	-14.28	-13.52	**0.76**	+4.50	1.01	0.41	+2.74	+5.44	**2.70**	0.55	0.126

More significant ranges of intra-tooth variation were observed within the sequences analysed for fossil *Aepyceros* specimens from the Shungura formation, for both carbon and oxygen isotopic ratios (Figure 79-Figure 81). A difference of around 2-4 ‰ was found between the minimum and maximum $\delta^{13}C$ values for impala specimens from members B, C, D and F, while a much larger amplitude of $\delta^{13}C$ values was found for most individuals from members E and G (i.e. $5‰ < \delta^{13}C_{max} - \delta^{13}C_{min} < 9‰$) (Table 64). The mean $\delta^{13}C$ values calculated suggest, overall, diets dominated by C_4-vegetation for all specimens, although specimens from members C, E and G displayed a range of values suggesting at least one shift to a mixed C_3 - C_4 diet within the dietary sequence recorded for these individuals.

A wide range of $\delta^{18}O$ values was observed for most specimens (i.e. $4‰ < \delta^{18}O_{max} - \delta^{18}O_{min} < 10‰$), with one or more peaks in values across each sequence. The highest $\delta^{18}O$ values were observed in specimens from members C and E. A significant positive correlation between $\delta^{18}O$ and $\delta^{13}C$ was found for most fossil specimens, highlighting synchronous increases and decreases in both carbon and oxygen isotopic ratios throughout the intra-tooth sequences studied.

The observed patterns of intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values are consistent with the patterns predicted for mixed-feeding herbivores that vary their diet throughout the year.

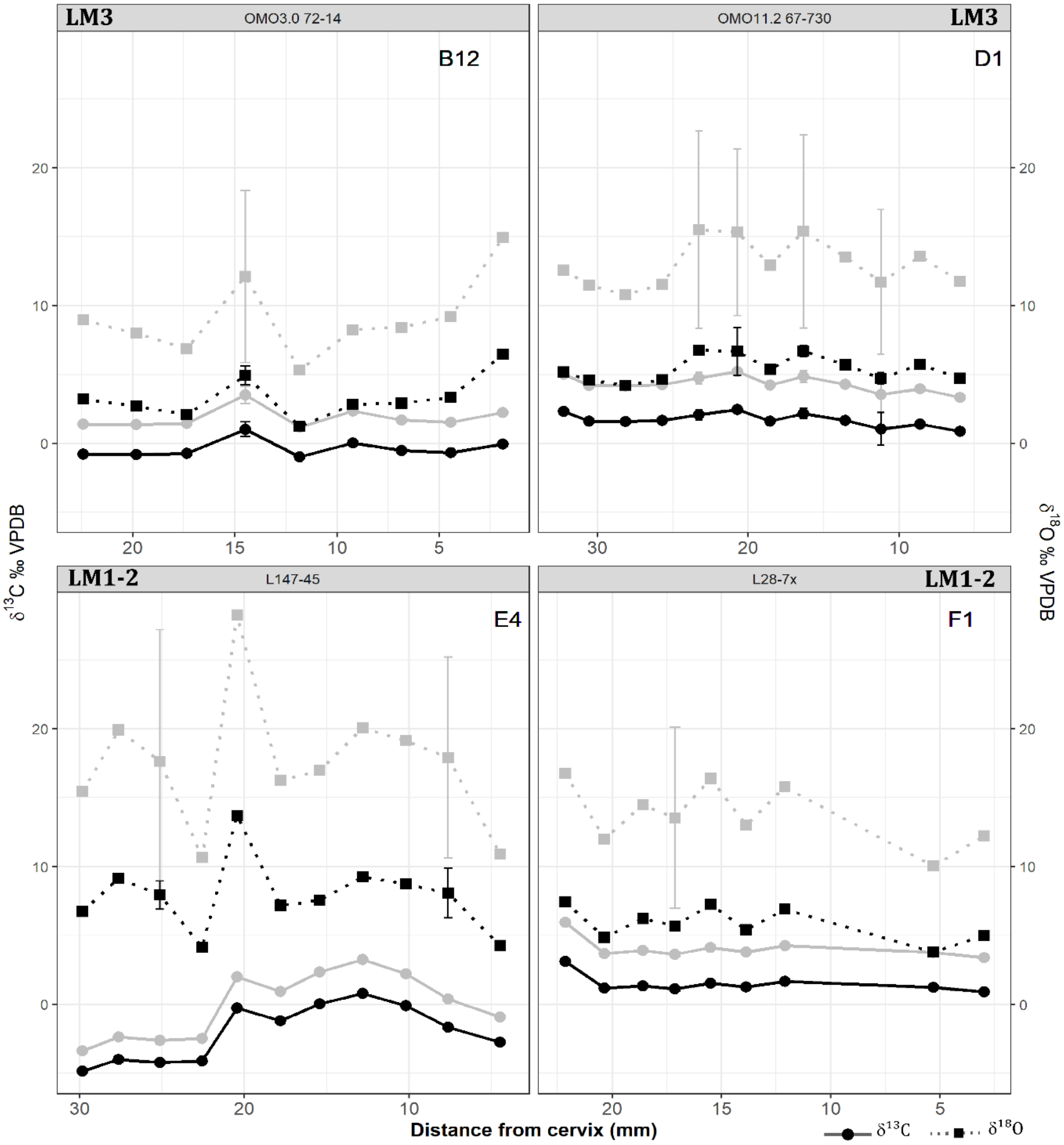

Figure 79: Intra-tooth variation in δ18O and δ13C values for *Aepyceros* specimens from the Shungura formation (members B to F; 3.4-2.32 Ma) that were analysed using a single tooth. The error-bars represent the mean and standard error of the mean for samples for which replicates were analysed. Points and lines in grey represent non-corrected NIGL data.

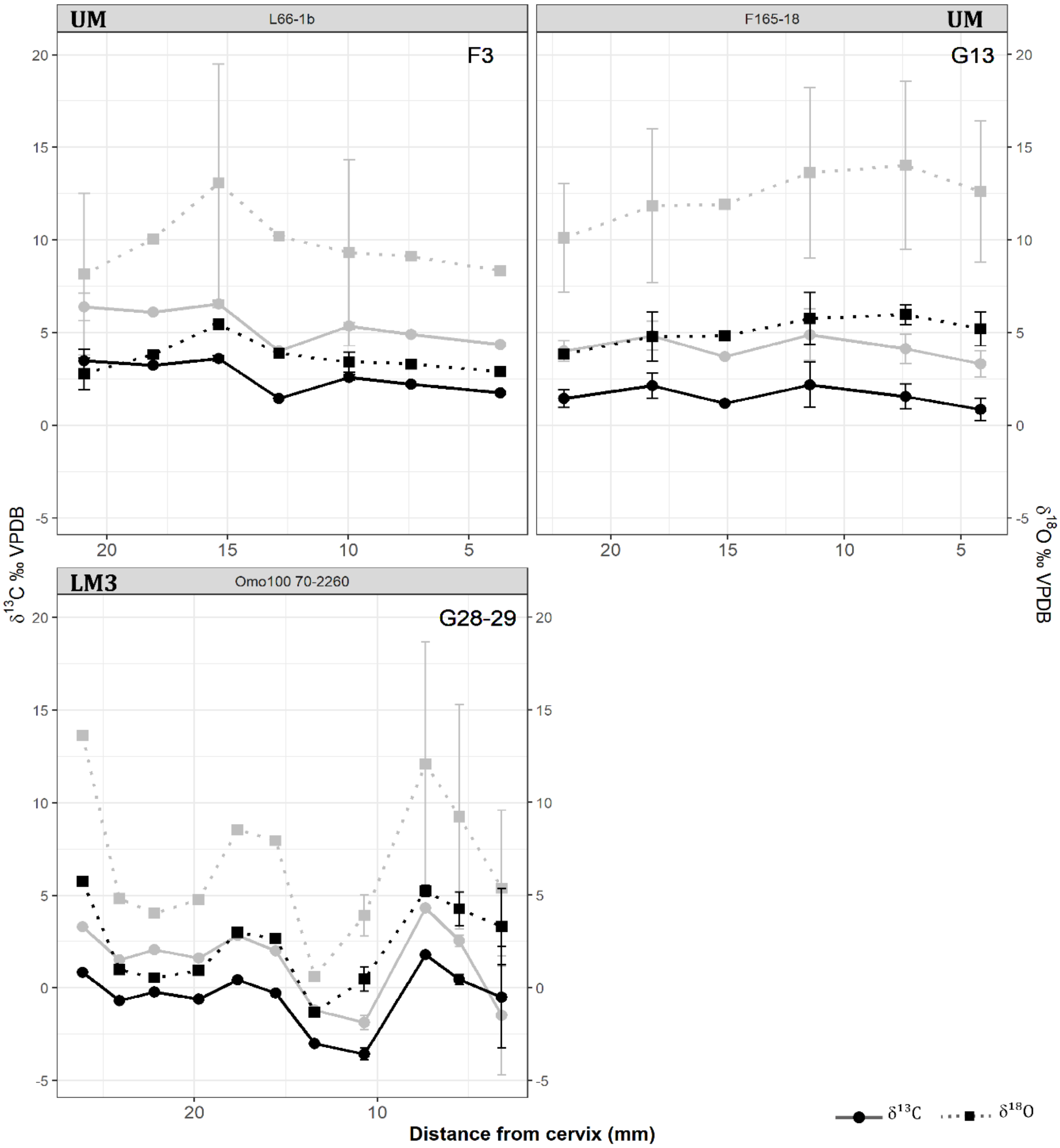

Figure 80: Intra-tooth variation in $\delta^{18}O$ and $\delta^{13}C$ values for *Aepyceros* specimens from the Shungura formation (members F to G; 2.32-1.9 Ma) that were analysed using a single tooth. The error-bars represent the mean and standard error of the mean for samples for which replicates were analysed. Points and lines in grey represent non-corrected NIGL data.

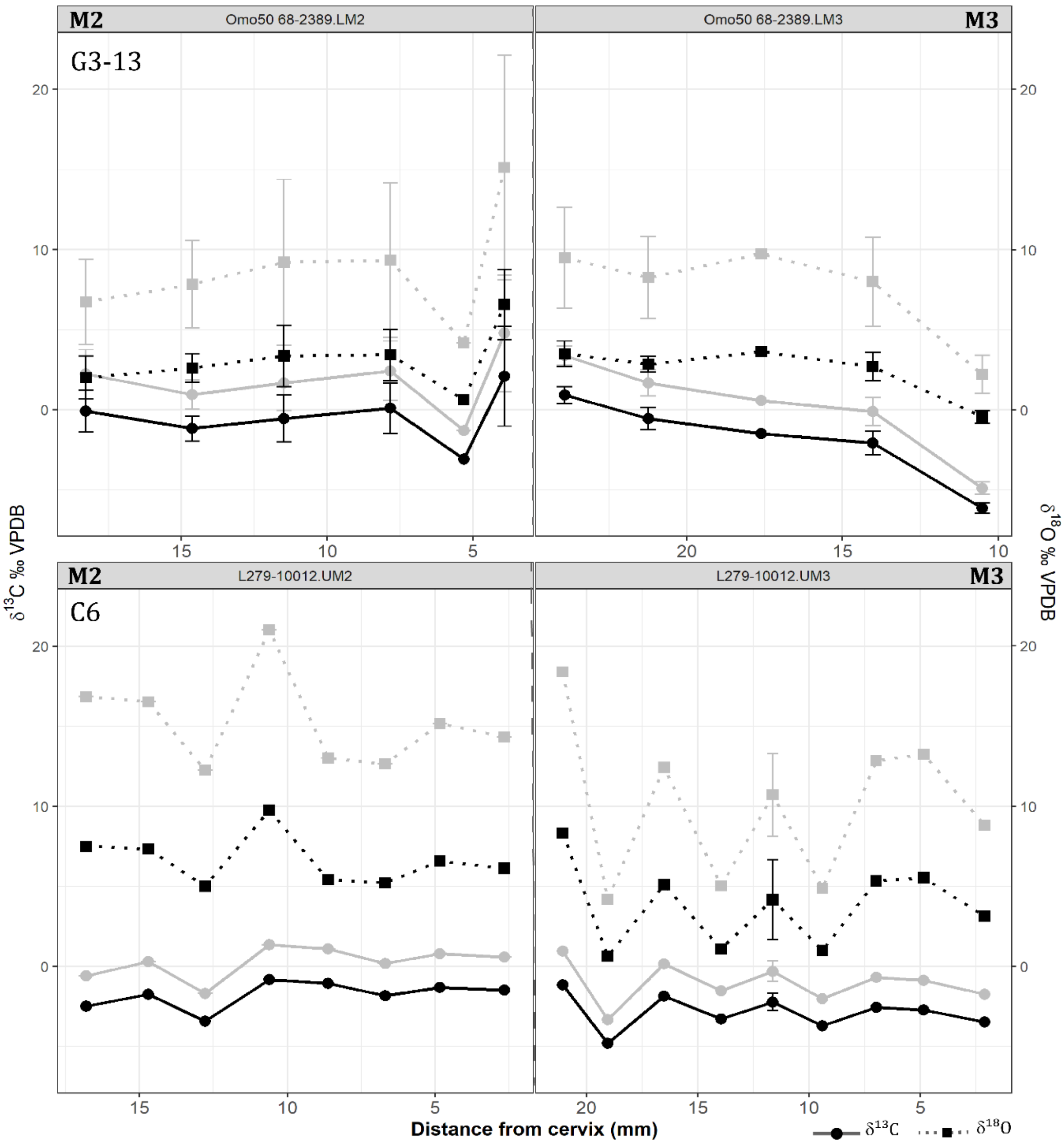

Figure 81: Intra-tooth variation in δ^{18}O and δ^{13}C values for *Aepyceros* specimens from the Shungura formation that were analysed using a combination of two adjacent teeth. The error-bars represent the mean and standard error of the mean for samples for which replicates were analysed. Points and lines in grey represent non-corrected NIGL data.

6.5 Summary of results

Stable carbon isotopes – Interspecific variation in inferred dietary signals:

- *Aepyceros*: samples dominated by C_4-grazing signals, for fossil *Aepyceros melampus*, *Aepyceros shungurae* and *Aepyceros sp*. samples (respectively 100%, 70.8% and 89.7% of specimens classified as C4-grazers). This differs from the modern *A. melampus* sample, where the proportion of grazers, mixed-feeders and browsers (G:MF:B) is 42.4: 52.5: 5.1. This suggests differences in overall dietary patterns between modern and fossil impalas, where fossil impalas rely on more C_4-vegetation than modern impalas, which are dominantly mixed-feeders.

- *Antidorcas*: *Antidorcas recki* sample dominated by C_4- signals (G:MF:B : 71.4: 23.8: 4.8).

- *Giraffa*: *Giraffa* specimens dominated by C_3-browsing signals. Only *Giraffa stillei* presents more variability in the measured $\delta^{13}C$ values, with 81.8% classified as browsers, and 18.2% classified as mixed-feeders. This could suggest a slightly more varied diet for this fossil species, compared to other giraffid taxa.

- *Equus*: *Equus sp*. specimens dominated by grazing signals, with 97.56% of the fossil specimens classifying as C_4-grazers.

Stable carbon isotopes – Intra-generic variation in inferred dietary signals (*Aepyceros*):

Overall, these results highlight the dietary adaptability of the *Aepyceros* species in the studied assemblages, with varying degrees of grazing and mixed-feedings habits found through time and throughout the Turkana basin. Impala specimens from the Shungura formation, in the Lower Omo river valley, appear to differ from East and West Turkana specimens, with a higher dietary variability and a stronger mixed-feeding signal, although the assemblage remains dominated by C_4-grazing individuals. However, this grazing signal in Shungura varies greatly through time in the Shungura formation: while mixed-diets prevail among impala specimens between 2.91–2.5 Ma in Member C, a clear pattern of increased C_4-grazing behaviours can be observed for this genus from member D, at ~2.32 Ma.

Stable oxygen isotopes – species-specific patterns and variations across the Omo-Turkana basin:

While *Aepyceros*, *Antidorcas*, and *Equus* specimens from Nachukui were shown to yield, on average, relatively low δ^{18}O values (ca. +0 ‰), the *Aepyceros*, *Antidorcas*, and *Equus* specimens from Koobi Fora were shown to yield much higher mean δ^{18}O values (ca. +3-4 ‰). These patterns could relate to differences in local environmental conditions, as well as to differences in drinking-water sources, as previous studies have showed that lake waters tend to provide obligate drinkers with relatively higher δ^{18}O values than river waters (Quinn, 2015). Significant differences within the *Aepyceros* sample were indeed highlighted for δ^{18}O between specimens from the Nachukui formation and specimens from the other two fossil localities: Koobi Fora and Shungura, with fossil impalas from West Turkana demonstrating lower δ^{18}O values than impalas from East Turkana and the lower Omo river valley. It was hypothesized that, due to the similarity in their stable isotope content, fossil *Equus* and *Aepyceros* species were likely to have been both obligate-drinkers, suggesting that the variations in δ^{18}O values observed across the Omo-Turkana basin for these taxa could potentially reflect differing local meteoric water composition between Nachukui and Koobi Fora/Shungura, and, in turn, differing environmental conditions across the basin.

Intra-tooth analyses and seasonal variation in diet:

Large ranges of intra-tooth variation were observed for the fossil *Aepyceros* specimens from the Shungura formation studied, for both carbon and oxygen isotopic ratios, with a particularly large amplitude of δ^{13}C values observed for most individuals from members E and G. These large ranges might reflect high seasonal variation in diet, more particularly between 2.4 Ma and 2.32 Ma, and between 2.27 Ma and 1.9 Ma. The mean δ^{13}C values calculated suggest, overall, diets dominated by C_4 -vegetation for all specimens, although specimens from members C, E and G displayed a range of values suggesting at least one shift to a mixed C_3 - C_4 diet within the dietary sequence recorded for these individuals.

Chapter 7: Multiproxy analysis

7.1 Introduction

Following previous chapters which assessed the dietary variability of the studied taxa across the Plio-Pleistocene deposits of the Omo-Turkana basin, inferred from dental mesowear analysis (chapter 4), dental textural microwear analysis (chapter 5), and stable isotope analyses (chapter 6), this chapter seeks to combine the data acquired from these dietary-proxies to test whether a detailed picture of the taxa's feeding ecology can be draw to help make inferences about palaeo-environmental conditions. As in previous chapters, the palaeo-dietary behaviours of the mixed-feeding impala (genus *Aepyceros*) and springbok (genus *Antidorcas*) are the focus of the analyses, hypothesizing that the dietary flexibility of these two fossil taxa might provide relevant information on the vegetation conditions experienced by hominins in the past, as modern mixed-feeders are able to adapt their diet according to the availability of food resources.

To explore in more detail the dietary patterns inferred from the studied specimens, the data acquired from dental use-wear and stable isotope analyses are therefore combined and assessed for each taxon in a multiscale (or multiproxy) approach. As previously mentioned in chapter 2, the use of a multiscale approach can provide detailed information on the dietary behaviours of the studied specimens at different moments of their life, from their early years to the last weeks before their death, and mitigate for some of the limitations of each method. In addition, the use of multiscale approach can help reduce interpretation biases related to sample- and time-averaging by assessing inter-individual dietary variability within each sample.

Indeed, biases such as sample-averaging must be taken into account, as it is one of the main caveats that are inherent to the fossil record. When taxa are analysed using samples per locality or per member, datasets combine information from specimens that likely belonged to different populations, and from populations that potentially lived at varying time periods, resulting in averaged dietary patterns. For instance, what might be interpreted, based on the mean value of a sample, as mixed-feeding patterns related to mosaic habitats or seasonal variation in vegetation cover, could actually be the product of sample-averaging if the sample contained obligate-grazing and obligate-browsing individuals that might have lived at different times, during periods of alternating long-lived open- and closed-canopy habitats. When members span over several hundred thousand years, sample-averaging is likely to lead to climate-averaging, as studies have shown that climate varies significantly through time following various events, which can be stepwise (e.g. volcanic eruptions, tectonism, ocean circulation) or cyclical (e.g. orbital forcing, El Niño/La Niña cycles) (e.g. Bobe *et al.,* 2007; Maslin and Christensen, 2007; Hopley and Maslin, 2010). One way to reduce interpretation biases related to sample- and time-averaging is to assess the inter-individual variability within each sample to evaluate the degree of within-sample variation in dietary patterns. Sample- or time-averaging can be assessed more efficiently for specimens that were analysed with at least two different methods, as the multi-scale approach allows to appraise the degree of dietary variation experienced by each individual through life. Individual dietary patterns and intra-sample variability were therefore assessed in this study for the specimens that could be analysed using multiple methods.

The material and methods (7.2) used for this analysis are presented in this chapter, followed by the results obtained when combining all proxies together, for each taxon (7.3). These results are interpreted and discussed alongside previously published research (7.4), to answer the following research aims:

1) Assess the overall dietary signatures of each studied species (extant and extinct), to appraise whether the diet of the fossil species do or do not mirror that of their extant relatives, and evaluate inter-specific variations between species of the same taxa.

2) Evaluate the degree of variation in dietary patterns within each fossil taxon (i.e. intra-generic variation) across the studied fossil localities and members to detect potential differences in feeding behaviours within the Turkana basin and/or through time.
3) Explore the impact of seasonal variation on the dietary patterns observed among Plio-Pleistocene impala populations.

7.2 Material and method

7.2.1 Fossil specimens

Fossil dental remains of the selected taxa (genera *Aepyceros, Antidorcas, Equus* and *Giraffa*) from the Koobi Fora and the Nachukui formations were studied for mesowear analysis, moulded for microwear analysis, and sampled for isotopic studies at the National Museums of Kenya (Nairobi) (see chapters 4, 5 and 6 for details about data collection). Where possible, data were collected for all three methods on each specimen, but due to poor preservation of some part of the teeth, or due to curatorial limitations, it could not be achieved for all specimens. The samples were collected from the maximum number of specimens available/allowed for each locality and member under study (see appendix A.9 for the detailed database).

7.2.2 Modern specimens

Data for mesowear analysis and moulds for microwear analysis were collected on dental specimens from the following institutions: the National Museums of Kenya (NMK), the Ditsong Museums of South Africa (Transvaal), Pretoria, and the Bavarian State Collection of Zoology (Munich, Germany). No isotopic sampling was allowed on these specimens. Mesowear data and dental moulds were also collected at the Royal Museum for Central Africa (Tervuren, Belgium), as well as samples from four modern specimens (i.e. two *Aepyceros* *melampus* specimens, and two *Giraffa camelopardalis* specimens) for intra-tooth isotopic analysis. (Table 65-- see appendix A.10 for the detailed database).

Table 65: Numbers of modern specimens analysed for mesowear, microwear and isotopic analyses, per species and per institution.

Source	**Information available**	**Number of specimens**				**Analysed for:**			**Totals**
		Aepyceros melampus	***Antidorcas marsupialis***	***Equus quagga***	***Giraffa camelopardalis***	***Mesowear***	***Microwear***	***Stable Isotopes***	
National Museums of Kenya, Nairobi	**Sex; Provenance** (Kenya)	6	3	0	0	✓	✓	✗	9
Ditsong Museum, Pretoria, South Africa	**Age; Sex; Provenance** (South Africa, Namibia and Botswana localities)	25	7	0	0	✓	✓	✗	32
Bavarian State Collection of Zoology, Munich, Germany	**Sex; Provenance** (Kenya, and Tanzania localities)	9	0	0	0	✓	✓	✗	9
Royal Museum for Central Africa, Tervuren, Belgium	**Sex; Provenance** (Congo, Kenya, Rwanda, Sudan and Tanzania localities)	39	0	11	12	✓	✓	✓	62
Totals		**79**	**10**	**11**	**12**				**112**

7.2.5 Multi-scale dietary analysis

Potential discrepancies observed between results from different proxies could be informative as they might relate to the different temporal scales on which each proxy provides information on the dietary behaviour of the studied individuals. Indeed, comparing diets across several temporal scales can help assess how much the diet of the studied individuals changed throughout their lifetime, and inform on their overall and seasonal dietary variability (Davis and Pineda Munoz, 2016). Multi-scale estimates of diet can be obtained by comparing results from dental mesowear analysis (lifetime dietary signal), dental microwear analysis ("last supper effect") and stable isotope analyses (early life dietary signal).

A first step in combining the information gathered from all dietary proxies used in this study to conduct a multi-scale dietary was to compare the general trends observed across the studied samples with each method. For this, the frequencies of individuals associated with specific diets (i.e. browsing, grazing or mixed-feeding) were compared for each dietary proxy and each sample. The overall dietary preferences of specimens in each sample was estimated, for stable carbon isotopes, based on the dietary classification suggested by Lee-Thorp *et al.* (2007) with C_3 -browsers ($\delta^{13}C < -9‰$), mixed-feeders ($9‰ > \delta^{13}C < -3‰$) and C_4 -grazers ($\delta^{13}C > -3‰$). For dental microwear textural analysis, browsing-behaviours were identified by high complexity values (Asfc>2.0) and grazing-behaviours by high anisotropy values (epLsar >0.005). Finally, for mesowear analysis, browsers were identified by high cusp relief, and grazers by low cusp relief. This allowed to pinpoint where several proxies indicate similar dietary patterns for some samples, but also where discrepancies between methods could be observed.

To mitigate for the sample-averaging likely to occur when analysing dietary patterns at the sample-level, multi-scale dietary analysis was also conducted on targeted individuals for which data was available for all of the studied dietary proxies (n=35). For this, the relationships between the various dietary proxies were tested using Kendall's rank-order correlation coefficient (tau) to identify correlations between dietary proxies (Croux and Dehon, 2010). This allowed to identify variables that can successfully be used together to explore the complexity of individual dietary behaviours in the fossil assemblage available in this study and potentially identify multi-scale dietary behaviours specific to the studied taxa (i.e. species or genus level) or to their spatio-temporal origin (i.e. provenance and/or member).

7.3 Results

7.3.1 Multi-scale dietary analysis: general overview for the studied species

Overall, results from the analyses conducted using several dietary proxies showed, as expected, dietary behaviours typical of browsing herbivores for all of the *Giraffa* species studied, across all proxies (Table 66 and Figure 82). Similarly, modern plain zebra specimens (*Equus quagga*) demonstrated, across all proxies, dietary behaviours typical of grazing species (Figure 83). Analysis of fossil equid specimens suggested diets typical of grazing species throughout most of their life, although mixed-feeding behaviours just before death were suggested based on dental microwear textural analysis.

Table 66: Summary table of multiproxy dietary interpretations for all studied species: mesowear scores (MS), dental microwear textural analysis (DMTA), stable carbon isotopes ($\delta^{13}C$), and stable oxygen isotopes ($\delta^{18}O$).

Species	Sample	MS score	DMTA	$\delta^{13}C$	$\delta^{18}O$	Gagnon and Chew 2000
Aepyceros melampus	Fossil	Browser	Mixed-feeder /fruit-browser	C4-diet	Water-dependant	/
	Modern	Mixed-feeder	Mixed-feeder	C3-C4 diet	Water-dependant	Browser-grazer intermediate
Aepyceros shungurae	Fossil	Mixed-feeder	Mixed-feeder	C4 to C3-C4 diets	Water-dependant	/
Antidorcas recki	Fossil	Mixed-feeder	Fruit-browser/ generalist	C4-diet	?	/
Antidorcas marsupialis	Modern	Mixed-feeder	Fruit-browser/ generalist	/	?	Browser-grazer intermediate
Equus sp.	Fossil	Variable grazer	Mixed-feeder	C4-diet	Water-dependant	/
Equus quagga	Modern	Grazer	Grazer	C4-diet	Water-dependant	Obligate grazer
Giraffa jumae	Fossil	/	Soft leaf-browser	C3-diet	Non-water dependant	/
Giraffa gracilis	Fossil	Browser	/	C3-diet	Non-water dependant	/
Giraffa pygmaea	Fossil	Mixed-feeder	/	C3-diet	Non-water dependant	/
Giraffa stillei	Fossil	Browser	Soft leaf-browser	C3-diet	Non-water dependant	/
Giraffa sp.	Fossil	Browser	/	C3-diet	Non-water dependant	/
Giraffa camelopardalis	Modern	Browser	Soft leaf-browser	C3-diet	Non-water dependant	Leaf-browser

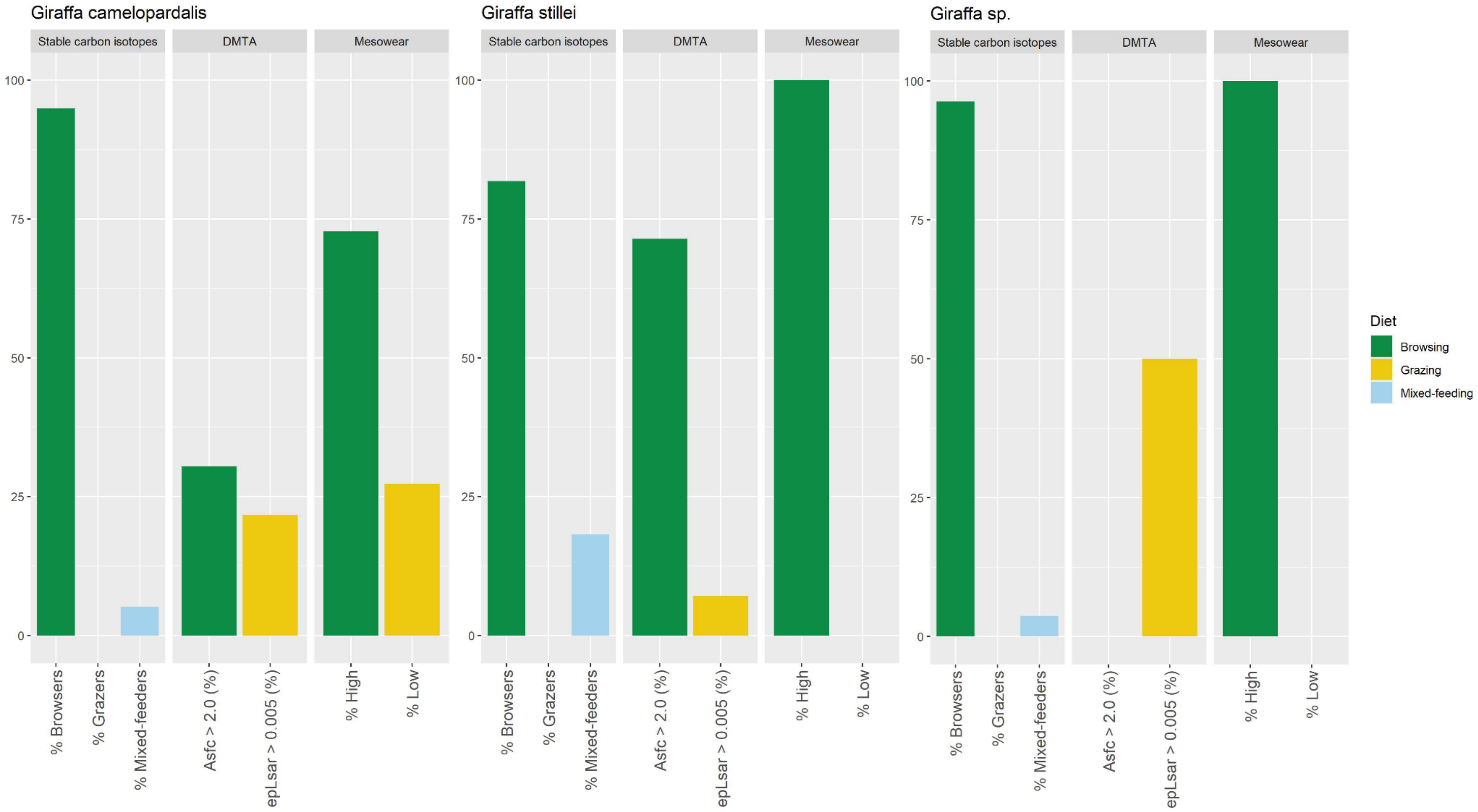

Figure 82: Multi-scale dietary summary for modern and fossil giraffid species (genus *Giraffa*). The frequencies of individuals associated with specific diets (i.e. browsing, grazing or mixed-feeding) are presented for each dietary proxy. Stable isotopes: frequencies based on τηε dietary classification suggested by Lee-Thorp *et al.* (2007) with C_3 -browsers ($\delta^{13}C$ < -9‰), mixed-feeders (9‰ > $\delta^{13}C$ < -3‰) and C_4 -grazers ($\delta^{13}C$ > -3‰); DMTA: browsers identified by high complexity values (Asfc>2.0) and grazers by high anisotropy values (epLsar >0.005); Mesowear: browsers identified by high cusp relief, and grazers by low cusp relief.

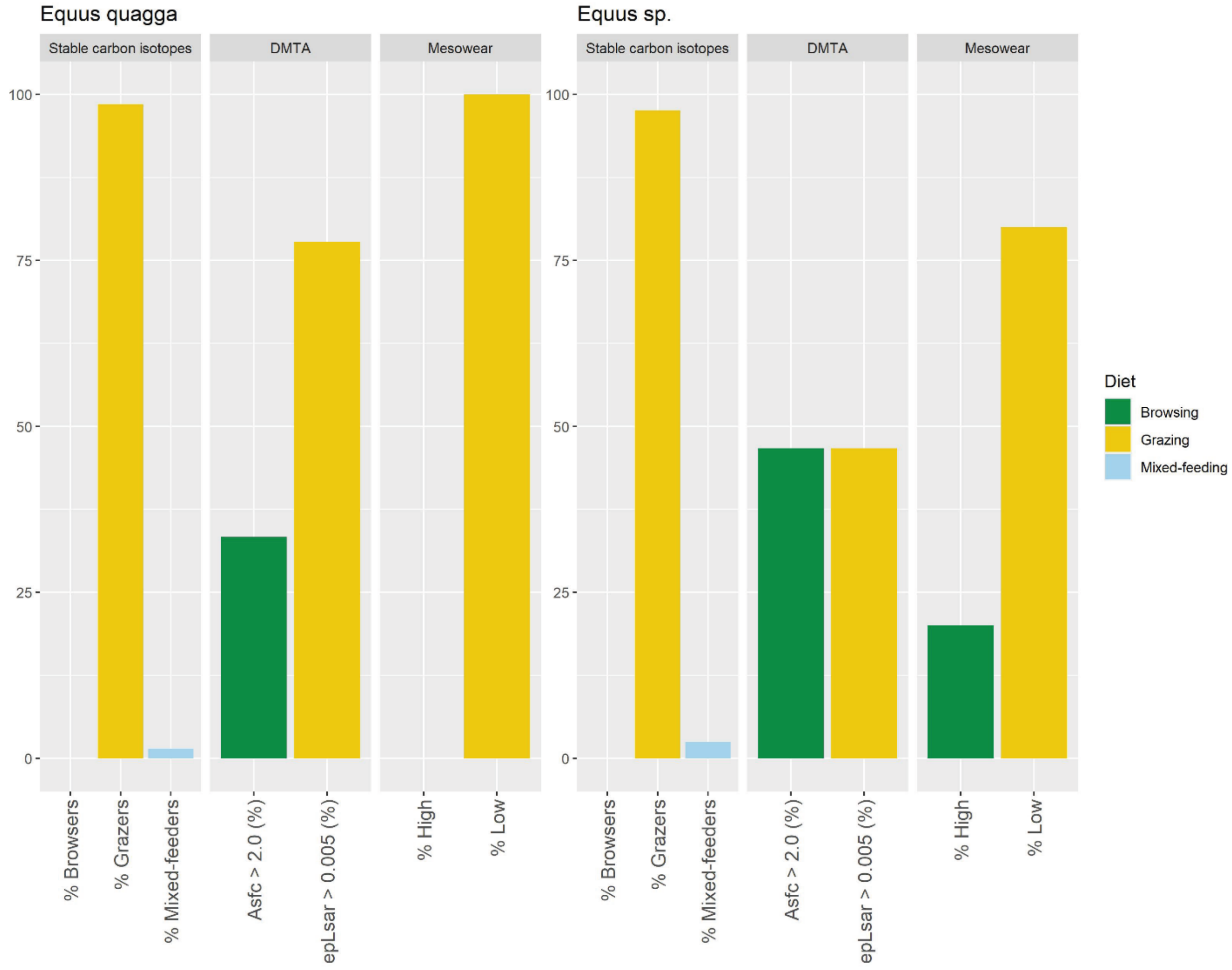

Figure 83: Multi-scale dietary summary for modern and fossil equid species (genus *Equus*). The frequencies of individuals associated with specific diets (i.e. browsing, grazing or mixed-feeding) are presented for each dietary proxy. (See Figure 82 for description of the variables used to evaluate dietary preferences).

While the modern antelope species *Antidorcas marsupialis* and *Aepyceros melampus* demonstrated mixed-feeding behaviours throughout all proxies as expected, more variability in feeding practices was suggested for their extinct relatives.

Results from analyses on the *Antidorcas recki* assemblage suggested variable dietary behaviours throughout their life, with early-life diets dominated by C_4-vegetation, last meals before death dominated by mixed-diets, and an overall mildly abrasive lifetime diet suggesting a predominance of mixed-feeding behaviours throughout their life (Figure 84). This likely highlights the dietary plasticity of this fossil springbok species, as well as potential seasonal variation in diet.

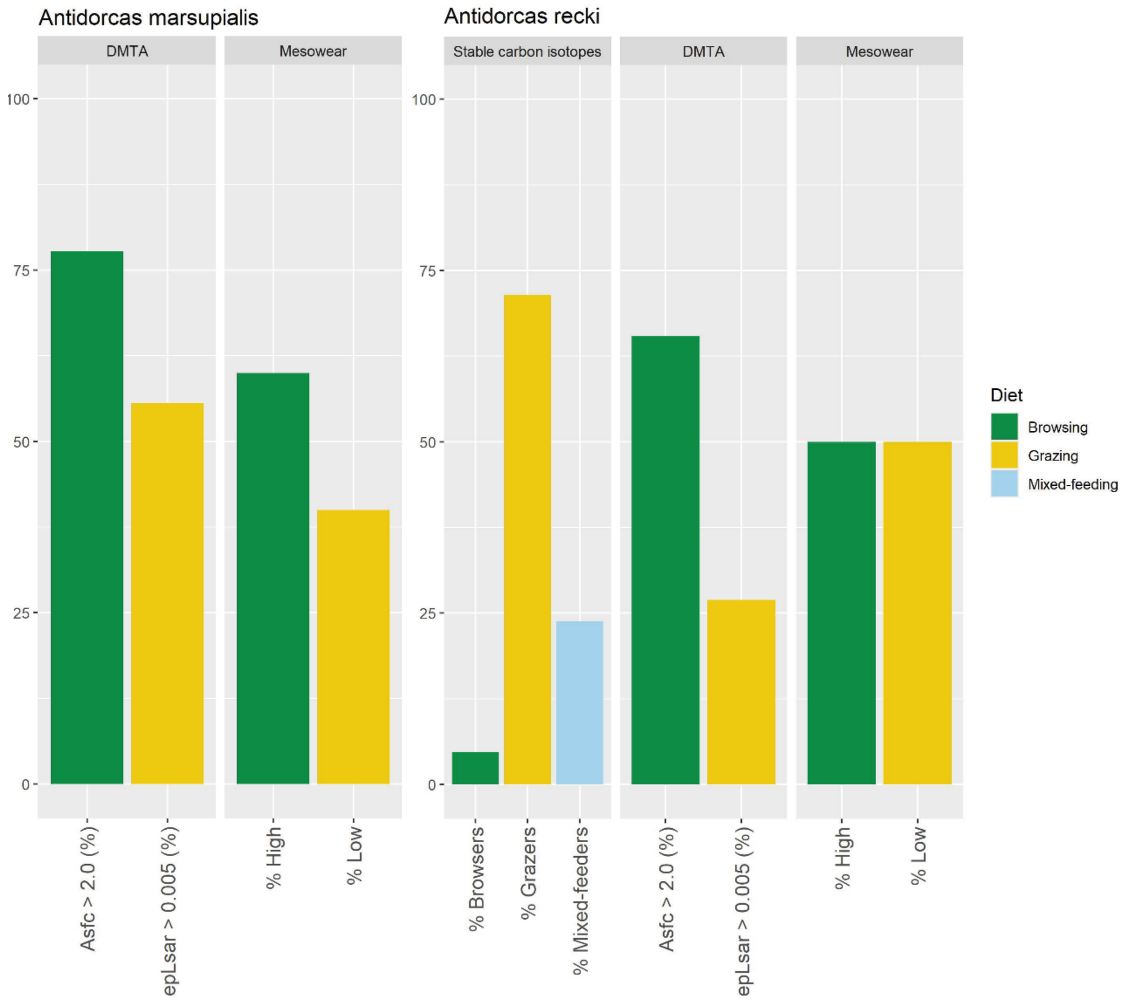

Figure 84: Multi-scale dietary summary for modern and fossil springbok species (genus *Antidorcas*). The frequencies of individuals associated with specific diets (i.e. browsing, grazing or mixed-feeding) are presented for each dietary proxy. (See Figure 82 for description of the variables used to evaluate dietary preferences).

Mixed-feeding diets were suggested for most *Aepyceros shungurae* specimens across all proxies, similar to modern impalas (Figure 85). The wide range of stable isotope values observed for individual specimens studied through intra-tooth analysis indicated significant seasonal variation in diet for this fossil species. Analysis of the fossil *Aepyceros melampus* assemblage suggested lifetime variability in dietary behaviours, with early-life diets dominated by C_4-vegetation, last meals before death dominated by mixed-diets containing a significant amount of fruits and/or seeds, and, overall, a poorly abrasive lifetime diet suggesting a predominance of browsing behaviours throughout their life. Similarly to the *Antidorcas* assemblage, this likely highlights varied diets through life as well as a potentially marked seasonal variation in diet for this fossil species. Results from stable oxygen isotope analyses suggested obligate-drinking patterns for all *Aepyceros* species.

Multiproxy results highlight the clear dichotomy in lifetime dietary behaviours between browsing and grazing species which tend to have relatively homogenous diet behaviours throughout their lives, and the dietary plasticity of mixed-feeding species such as impala and springbok which tend to vary their diet throughout their life. The same patterns were highlighted when investigating individual dietary patterns for selected specimens.

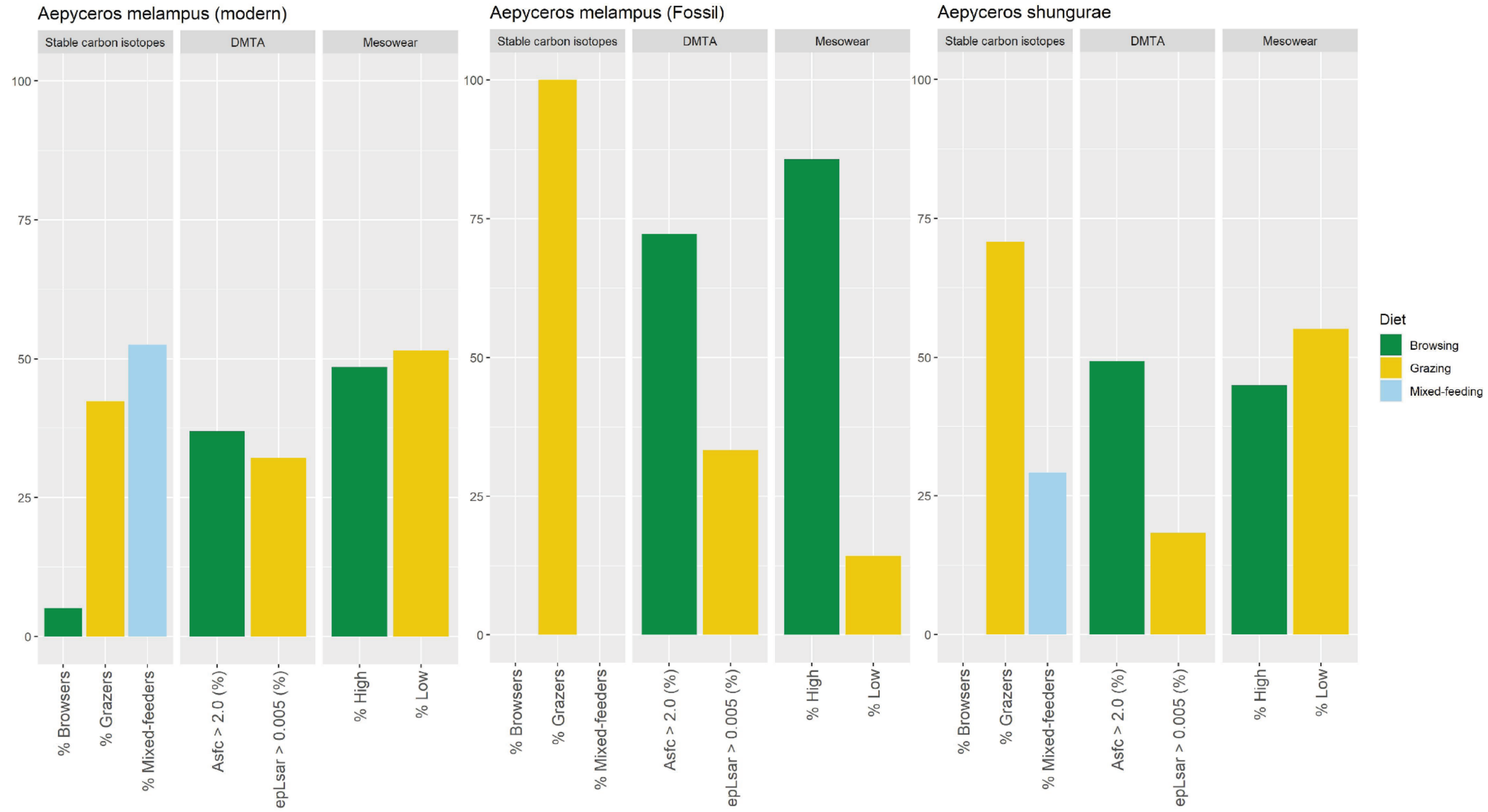

Figure 85: Multi-scale dietary summary for modern and fossil impala species (genus *Aepyceros*). The frequencies of individuals associated with specific diets (i.e. browsing, grazing or mixed-feeding) are presented for each dietary proxy. (See Figure 82 for description of the variables used to evaluate dietary preferences).

When analysing specimens for which data was available for all dietary proxies, correlations could be observed between several proxies (Figure 86). More particularly, correlations were observed between the DMTA variable epLsar (i.e. anisotropy) and mesowear score (tau coefficient: +0.25, p=0.0018), and between epLsar and $\delta^{13}C$ (tau coefficient: +0.19, p=0.0042). Correlations were also observed between mesowear score and textural fill volume (Tfv; tau coefficient: +0.18; p=0.022), as well as between mesowear score and $\delta^{13}C$ (tau coefficient: +0.26; p=0.011). Finally, correlations were observed between $\delta^{13}C$ and $\delta^{18}O$ (tau coefficient: -0.15, p=0.011). The relationships between dietary variables highlighted by these results suggest that as mesowear scores increase, epLsar, Tfv and $\delta^{13}C$ values increase as well. On the contrary, as $\delta^{13}C$ values increase, $\delta^{18}O$ values tend to decrease.

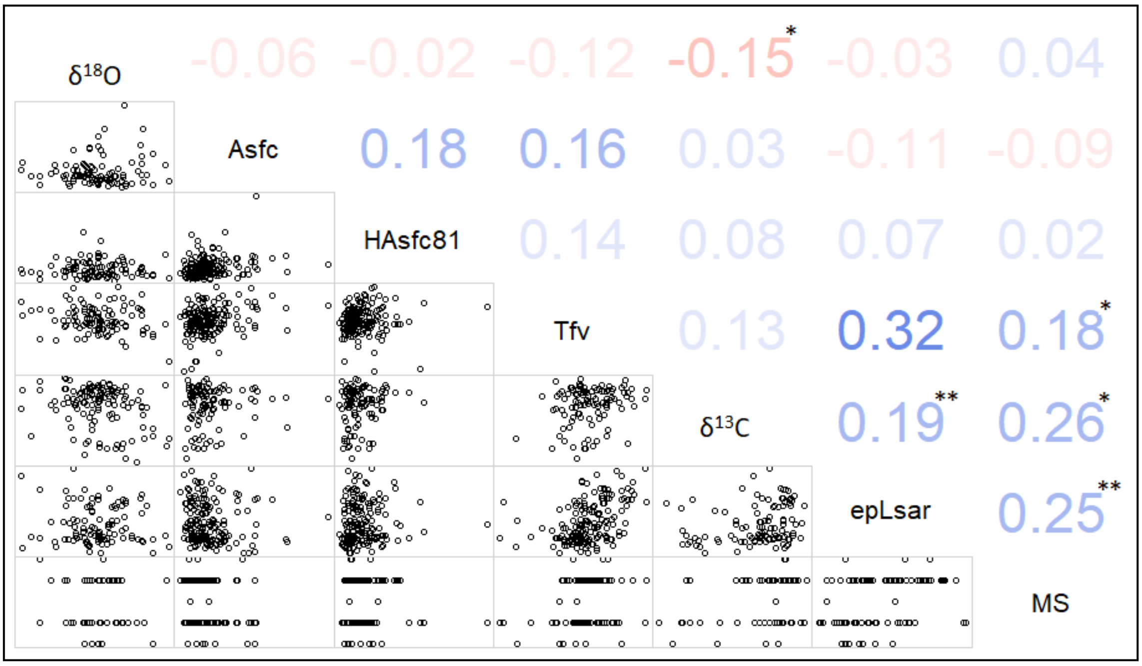

Figure 86: Correlogram showing correlations between dietary proxies, with Kendall's tau coefficient estimates for each paired-variables in the upper panel.

Following these results, the variables epLsar, mesowear score and $\delta^{13}C$ were therefore combined to further explore the fossil assemblage and assess multi-scale dietary behaviours of the studied taxa (Figure 87). The multiproxy dietary patterns observed when combining these three variables confirm the clear dichotomy in lifetime dietary behaviours highlighted above between browsing and grazing species which demonstrate, on an individual-scale, relatively consistent dietary behaviours through life (i.e. *Equus*: high epLsar values combined with high mesowear scores and high δ13C values; *Giraffa*: low epLsar values combined with low mesowear scores and low δ13C values), although some variations in microwear patterns could be observed, likely suggesting some degree of seasonal variation in diet and differing seasons of death.

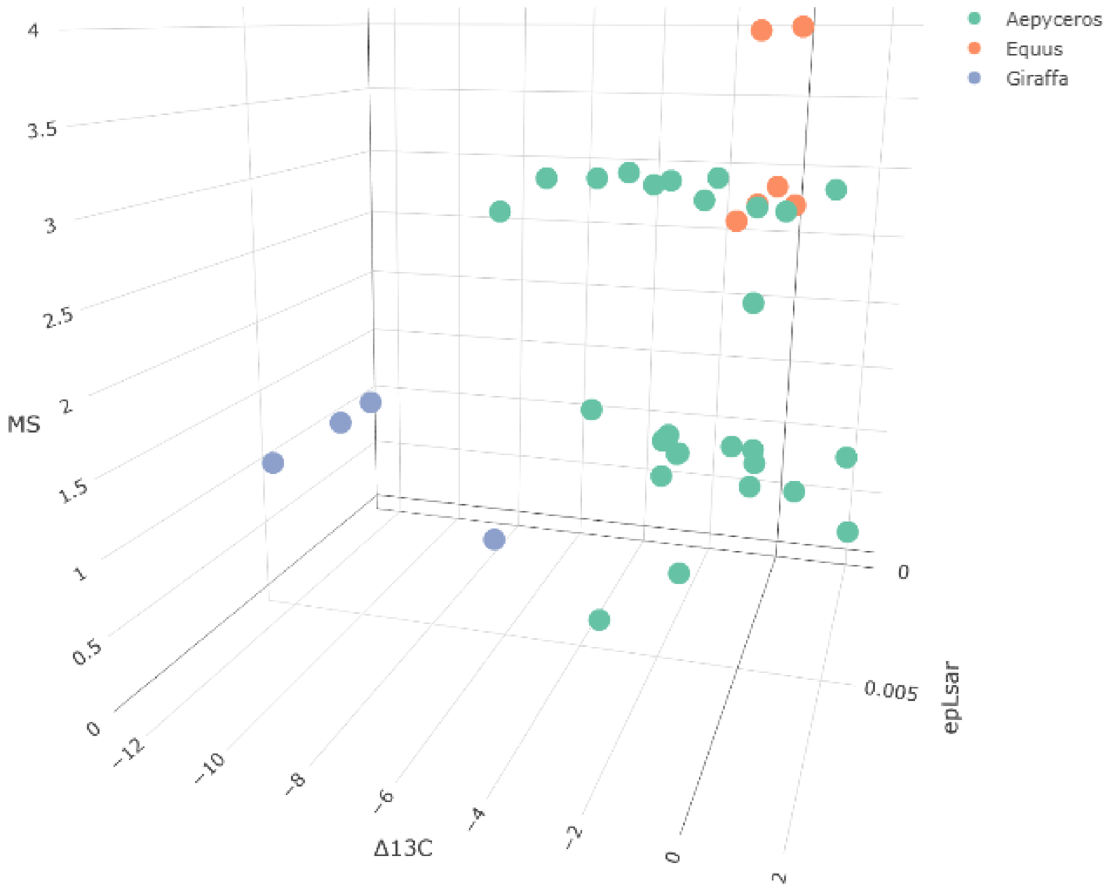

Figure 87: Distribution of anisotropy (epLsar), stable carbon isotope ratios (δ13C) and mesowear score (MS) values for individuals studied for multi-scale dietary analysis, per genus. The assemblage is composed of 27 fossil *Aepyceros*, 6 fossil *Equus*, 3 fossil *Giraffa* and 1 modern *Giraffa* specimens.

As predicted for mixed-feeding taxa, the *Aepyceros* specimens present a large range of values for all three variables with various combinations of dietary patterns suggested throughout their life. Some of these lifetime dietary patterns overlap with those of grazing *Equus* specimens, while combined epLsar/MS/ δ13C values for most specimens suggest intermediate dietary behaviours, confirming the dietary plasticity of fossil impala species and suggesting seasonal variation in diet through life.

7.3.2 Multi-scale dietary analysis per taxon

7.3.2.1 Genus *Giraffa* and genus *Equus*

As expected, mesowear scores, DMTA results as well as stable isotopes ratios observed for *Giraffa* specimens all suggest that, overall, fossil giraffids had browsing/leaf-browsing dietary habits, with no significant change through time and throughout the Omo-Turkana basin when larger samples were considered (i.e. n>3) (Table 67 and Figure 88). When specimens that were studied with two or more methods were assessed individually, the majority of the *Giraffa* specimens presented mesowear, DMTA and carbon isotope results consistent with diets dominated by C_3 -browsing behaviours through life and before death (appendix A.14 Table-A30). Two specimens from the Shungura formation yielded mesowear patterns suggesting relatively abrasive diets associated with C_3 -dominated diets during the early years of their life.

Table 67: Summary table of multiproxy dietary interpretations for genus *Giraffa* (samples per provenance and per member: mesowear scores (MS), dental microwear textural analysis (DMTA), stable carbon isotopes ($\delta^{13}C$).

Genus	Subset	Member (Ma)	MS score (n)	DMTA (n)	δ13C (n)
Giraffa	**Koobi Fora**	**All**	**Browser**	**Leaf-browser**	**C3-diet**
		Tulu Bor (3.44- 2.64)	/	Leaf-browser (2)	C3-diet (2)
		Burgi (2.64- 1.87)	Browser (1)	Leaf-browser (5)	C3-diet (13)
		KBS (1.87 -1.61)	Browser (5)	Leaf-browser (11)	C3-diet (17)
	Nachukui	**All**	**/**	**Leaf-browser**	**C3-diet**
		Lomekwi (3.44 -2.53)	/	Leaf-browser? (2)	C3-diet (8)
		Kalochoro (2.33 - 1.9)	/	/	C3-diet (1)
	Shungura	**All**	**Browser**	**/**	**C3-diet**
		B (3.44 - 2.91)	Mixed-feeder (2)	/	C3-diet (5)
		C (2.91 - 2.52)	Mixed-feeder (2)	/	C3-diet (5)
		D (2.52 - 2.4)	Browser (2)	/	C3-diet (5)
		E (2.4 - 2.32)	/	/	C3-diet (4)
		F (2.32 - 2.27)	/	/	C3-diet (5)
		G (2.27 - 1.9)	/	/	C3-diet (5)
	Modern	**/**	**Browser (11)**	**Leaf-browser (23)**	**C3-diet (39)**

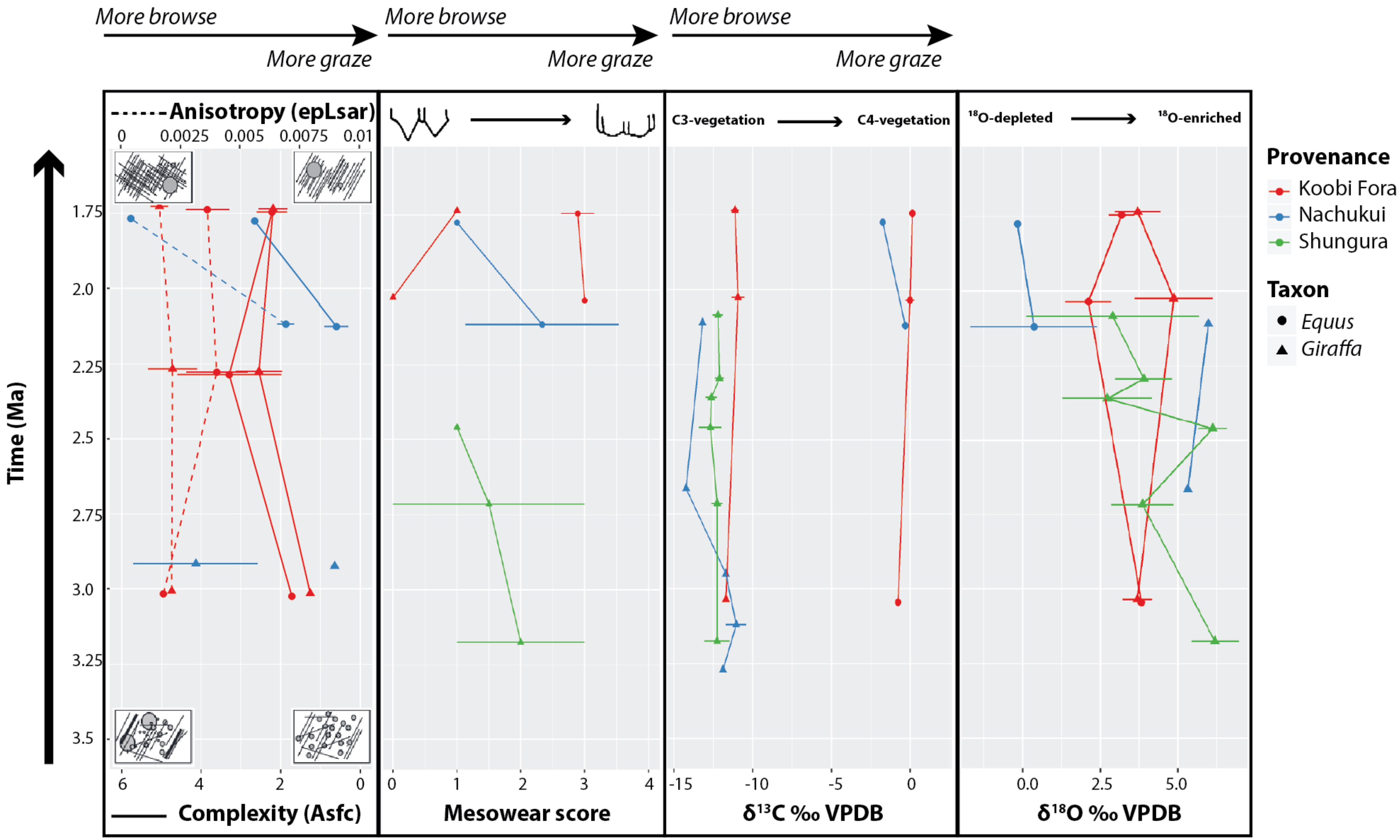

Figure 88: *Equus* (points) and *Giraffa* (triangles) dietary variability though time, as assessed by (from left to right) dental microwear textural analysis (anisotropy and complexity), mesowear analysis (mesowear score), carbon stable isotope analysis ($\delta^{13}C$) and oxygen stable isotope analysis ($\delta^{18}O$).

Mean δ^{13}C values for *Giraffa* specimens were slightly lower in the Shungura formation than in the Koobi Fora formation. δ^{18}O values from the Shungura formation showed a large range of variation through time, with a gradual decrease in values through time, but peaks of ^{18}O-enriched values in members B (~3.44-2.91 Ma) and D (~2.52-2.4 Ma). Mesowear scores were higher for *Giraffa* specimens in Shungura formation for members B and C, suggesting mixed-feeding habits for these specimens dating between ~3.44 and 2.52 Ma. δ^{18}O values for giraffid specimens were consistently higher than the δ^{18}O values observed for equid specimens in the Omo-Turkana basin, probably reflecting the differences in main water-source between the two taxa, with fossil *Giraffa* likely obtaining most of their body water from plant moisture, alike their modern relatives.

Table 68: Summary table of multiproxy dietary interpretations for genus *Equus* (samples per provenance and per member: mesowear scores (MS), dental microwear textural analysis (DMTA), stable carbon isotopes (δ^{13}C).

Genus	Subset	Member (Ma)	MS score (n)	DMTA (n)	δ13C (n)
Equus	**Koobi Fora**	**All**	**Grazer**	**Mixed-feeder**	**C4-diet**
		Tulu Bor (3.44- 2.64)	/	/	C4-diet (1)
		Burgi (2.64- 1.87)	Grazer (2)	Mixed-feeder (4)	C4-diet (19)
		KBS (1.87 -1.61)	Grazer (9)	Mixed-feeder (8)	C4-diet (17)
	Nachukui	**All**	**Mixed-feeder**	**Grazer**	**C4-diet**
		Kalochoro (2.33 - 1.9)	Mixed-feeder(3)	Grazer (2)	C4-diet (3)
		Kaitio (1.9 -1.61)	Browser (1)	Grazer (1)	C4-diet (1)
	Modern	**/**	**Grazer (9)**	**Grazer (10)**	**C4-diet (68)**

Mesowear scores for fossil *Equus sp.* showed, overall, a cumulative use-wear typical of grazing species in the Koobi Fora formation, but scores more typical of mixed-feeders in the Nachukui formation (Figure 89 and Table 66). Stable carbon isotope ratios suggested a pure C_4 -plant based diet among all specimens of this taxon, with very little spatial or temporal variation across the samples. However, according to DMTA, fossil *Equus* specimens from the Koobi Fora formation demonstrated dietary habits closer to those of mixed-feeders, with anisotropy and complexity values close to those observed among mixed-feeding antelopes, and distant from both grazing *A. buselaphus* and fruit-browsing *C. silvicultor* samples. This was more particularly highlighted by the DMTA results for Koobi Fora equids from the Burgi member (~2.64-1.87 Ma).

When specimens that were studied with two or more methods were assessed individually, the majority of *Equus* specimens from Koobi Fora presented mesowear and $\delta^{13}C$ values suggesting life-time diets dominated by abrasive C_4 -food items, associated with either grazing, browsing or mixed-feeding behaviours before death (appendix A.14 Table-A 31). The differences observed between mesowear scores, carbon isotope ratios and DMTA results for the majority of the Koobi Fora *Equus* specimens could reflect differences in the timescales represented by each method, with fossil equid specimens eating primarily graze in during their growth as well as throughout their lives but having a more varied food intake with graze and browse during the last few days/weeks before their death. This could potentially be related to seasonal variation in diet and individuals dying across different seasons, but also to the consumption of fall-back foods during periods of graze-shortage, since mixed-feeding practices were only highlighted in this study by microwear patterns, which only reflect the last few days or weeks before death.

The dietary patterns of fossil equids from the Nachukui formation remain difficult to interpret, due to small samples sizes. Specimens from this locality demonstrated anisotropy and complexity values closer to those of modern grazing *A. buselaphus*, $\delta^{13}C$ values typical of grazing species, and mesowear scores suggesting mixed-feeding to browsing behaviours. $\delta^{18}O$ values for equids in the Nachukui formation were much lower than the $\delta^{18}O$ values observed for equids in the Koobi Fora formation compared to specimens from Nachukui, suggesting differing local groundwater composition and local environmental conditions between East and western West Turkana. However, all interpretations for the Nachukui formation should remain cautious, as genus *Equus* was only represented by three specimens in this locality.

7.3.2.2 Genus *Aepyceros*

When comparing results from stable isotopes, dental microwear textural analysis and mesowear analysis for impala samples using mean values, discrepancies were observed between methods regarding the dietary behaviours suggested for this taxon (Table 69 and Figure 89; appendix A.14 Table-A 32).

Table 69: Summary table of multiproxy dietary interpretations for genus *Aepyceros* (samples per provenance and per member: mesowear scores (MS), dental microwear textural analysis (DMTA), stable carbon isotopes (δ^{13}C).

Genus	Subset	Member (Ma)	MS score (n)	DMTA (n)	δ13C (n)
Aepyceros	**Koobi Fora**	**All**	**Browser**	**Mixed-feeder/Fruit-browser**	**C4-diet**
		Tulu Bor (3.44- 2.64)	/	Browser (1)	C4-diet (1)
		Burgi (2.64- 1.87)	Browser (3)	Mixed-feeder (3)	C4-diet (12)
		KBS (1.87 -1.61)	Browser (8)	Mixed-feeder (8)	C4-diet (11)
	Nachukui	**All**	**Mixed-feeder**	**Fruit-browser**	**C4-diet**
		Lomekwi (3.44 -2.53)	Mixed-feeder (6)	Mixed-feeder/ Fruit-browser (14)	C4-diet (18)
		Kalochoro (2.33 - 1.9)	Browser (1)	Mixed-feeder (3)	C4-diet (7)
		Kaitio (1.9 -1.61)	Browser (2)	Fruit-browser (3)	C4-diet (5)
	Shungura	**All**	**Mixed-feeder**	**Leaf-browser**	**C4-diet / C3-C4-diet**
		B (3.44 - 2.91)	Mixed-feeder (5)	Mixed-feeder/Browsing ()	C4-diet / C3-C4-diet (21)
		C (2.91 - 2.52)	Browser/Mixed (7)	Browsing ()	C3-C4-diet (23)
		D (2.52 - 2.4)	Mixed-feeder (5)	Mixed-feeder ()	C4-diet (24)
		E (2.4 - 2.32)	Browser/Mixed (5)	Mixed-feeder ()	C4-diet (13)
		F (2.32 - 2.27)	Mixed-feeder (10)	Mixed-feeder ()	C4-diet (24)
		G (2.27 - 1.9)	Mixed-feeder (8)	Mixed-feeder/ Grazer (15)	C4-diet (23)
	Modern	**All**	**Mixed-feeder (33)**	**Mixed-feeder (86)**	**C3-C4-diet (59)**

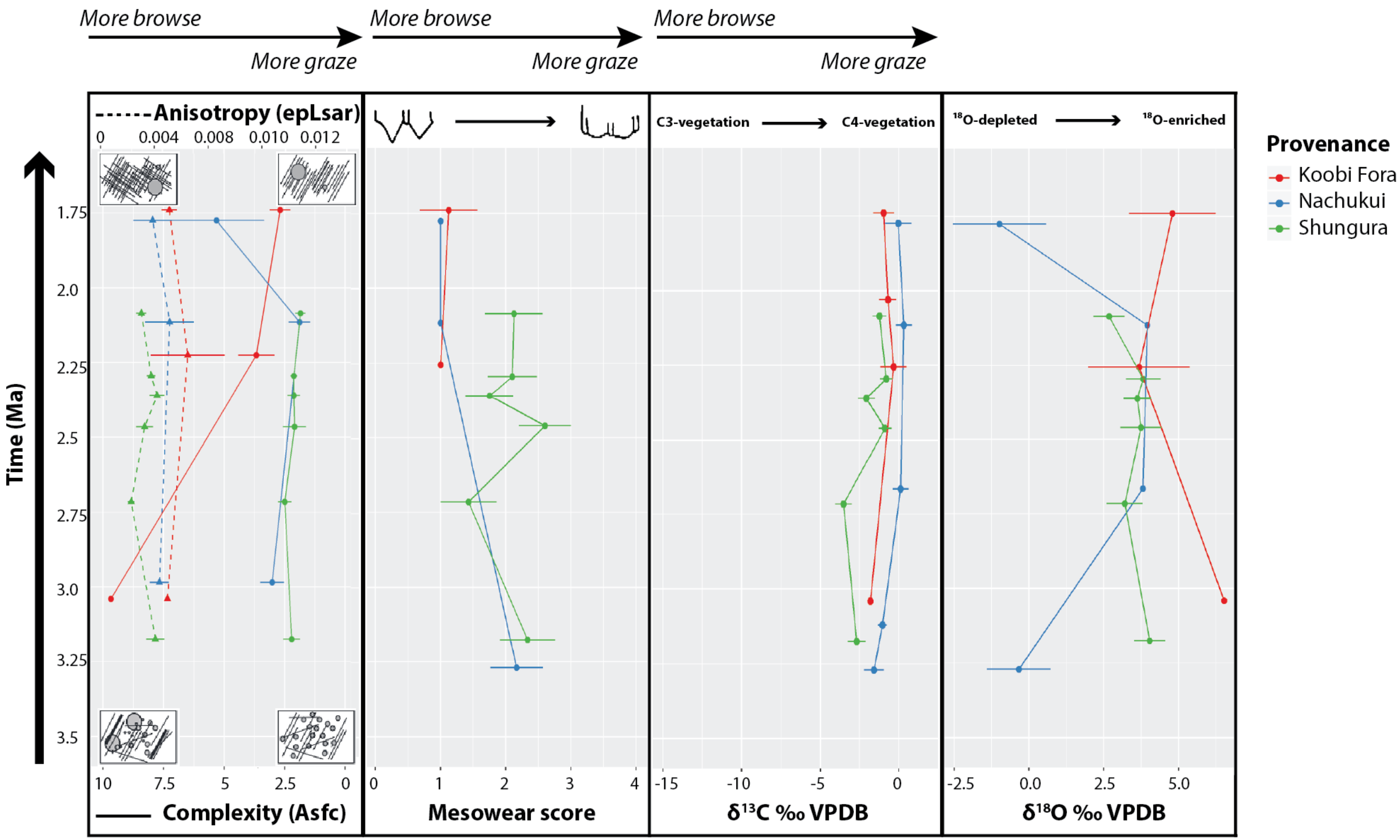

Figure 89: *Aepyceros* dietary variability though time, as assessed by (from left to right) dental microwear textural analysis (anisotropy and complexity), mesowear analysis (mesowear score), carbon stable isotope analysis ($\delta^{13}C$) and oxygen stable isotope analysis ($\delta^{18}O$).

At Koobi Fora, across all members, while mesowear analysis suggested browsing habits, dental microwear textural analysis (DMTA) suggested mixed-feedings behaviours, and carbon stable isotopes indicated a dominance of C_4-plants in the diet of fossil impalas. Out of the nine *Aepyceros* individuals analysed in this formation with two or more methods, only two individuals yielded dietary signals suggesting diets dominated by abrasive C_4-vegetation through life and before death, both in KBS member (appendix A.14 Table-A 32). All other specimens presented differences between use-wear and isotopic signatures, suggesting varying dietary behaviours throughout their lives. The mixed-feeding behaviours indicated by the results from DMTA could indicate a more varied diet during the few weeks before the death of the individuals. Little variation through time was observed in the dietary patterns of fossil impalas for the Koobi Fora formation, apart from a gradual decrease in complexity through time that could reflect a gradual increase in the consumption of tough and abrasive food items (such as monocots) before death (Figure 89).

Discrepancies between dietary proxies arose as well within the Nachukui impala assemblage, with some degree of variation across members. Impalas from the Lomekwi member (~3.44-2.53 Ma) appear to have had a moderately abrasive diet through life with a high proportion of C_4 -plants during early years and mixed-feeding/fruit-browsing habits before death. Impala specimens from the Kalochoro (~2.33-1.9 Ma) and Kaitio (~1.9-1.61 Ma) members also had a diet dominated by C_4-plants during their growth but with a lifetime diet dominated by soft food-items, and mixed-feeding or fruit-browsing habits just before death. Potential variations through time were therefore suggested by the results from each sample from the Nachukui formation, with a slight increase in the amount of C_4-vegetation consumed after ~2.8 Ma (i.e. between the Lower/Middle Lomekwi and the Upper Lomekwi members), and a reduction of the abrasiveness of the food items consumed after ~2.33 Ma (i.e. in the Kalochoro and Kaitio members) (Figure 89). Although results from DMTA suggest mixed-feeding to fruit-browsing practices before death for most specimens, an increase in mean complexity values between the Kalochoro and Kaitio members could reflect an increase in the consumption of hard food items such as browse after ~1.9 Ma. This is consistent with the results suggested by mesowear analysis for these two members. However, it must be noted that samples from this locality and this taxon are relatively small, especially for Kalochoro and Kaitio members (i.e. $n<5$), for which interpretations must remain cautious.

At Shungura, differences in dietary behaviours were observed through time among *Aepyceros* specimens when considering all proxies (Figure 89). Based on the low mesowear scores, low anisotropy values and the relatively low $\delta^{13}C$ values observed among specimens from members C (2.91-2.52 Ma) and E (3.32-2.27 Ma), it appears that impalas from these members had, overall, mixed-feeding diets with a preference for browse, dominated by mixed C_3 - C_4 plants in member C, and by C_4-plants in member E. Of the specimens studied through intra-tooth isotopic analysis, the specimens from these two members yielded a range of $\delta^{13}C$ values indicative of varied diets alternating between C_4-dominated diets and mixed C_3 - C_4 diets. A stronger reliance on graze was suggested from both mean mesowear score and $\delta^{13}C$ values for specimens from members B (3.44-2.91 Ma), D (2.52-2.4 Ma), F (2.32-2.27 Ma) and G (2.27-1.9 Ma). Similar patterns were observed through microwear analysis with higher epLsar values in members B and F, indicative of more abrasive diets before death. These results suggest lifetime diets dominated by moderately abrasive dietary behaviours among fossil impalas in these Shungura members (although more abrasive in member D), comprising mostly C_4-resources. This pattern of rather high mesowear score combined to high $\delta^{13}C$ values was observed for most of the individuals analysed with these two methods from members D, F and G, while most individuals from member B demonstrated mesowear and $\delta^{13}C$ values more typical of mixed-feeders, with a varied dietary intake through life. Of the specimens studied through intra-tooth isotopic analysis, although all specimens showed evidence of dietary variability during their early years, the specimens from members B, D and F yielded a smaller range of values than the specimens analysed from other members, indicative of less variable diets in which C_4-vegetation was predominant. On the contrary, a very large range of carbon and isotope values was observed for two of the specimens analysed for intra-tooth variation in diet in member G, suggesting significant seasonal shifts between mixed and C_4-dominated vegetation. Overall, mean $\delta^{13}C$ values, although showing slight fluctuations through time from a member to the next, appear to have increased gradually through time after member C (i.e. after ~2.52 Ma), suggesting diets increasingly dominated by C_4-vegetation among fossil *Aepyceros* specimens from Shungura.

7.3.2.3 Genus *Antidorcas*

Similarly to the *Aepyceros* assemblage, discrepancies appeared when comparing dietary analyses from each method for *Antidorcas* specimens (Figure 90 and Table 70).

In Koobi Fora, *Antidorcas* individuals appear to have had, overall, a diet dominated by C_4-plants during their growth, as suggested by carbon isotope analyses, although mean $\delta^{13}C$ values suggested an increase in the amount of C_4-plants included in the diet of springbok specimens in KBS member compared to specimens from Tulu Bor and Burgi. According to dental microwear analyses, their diets were more varied just before death, with mixed-feeding to fruit-browsing behaviours. While anisotropy did not appear to vary through time, an increase in complexity could be observed in the Burgi and KBS members, suggesting diets that included more browse for these specimens than for individuals from Tulu Bor. Very few specimens could be analysed for mesowear score. When specimens that were studied with two or more methods were assessed individually, most of the specimens from Tulu Bor and Burgi presented $\delta^{13}C$ values more typical of mixed C_3 - C_4 diets, combined with varying dietary signals before death (i.e. DMTA) covering the entire dietary spectrum from grazing to browsing (appendix A.14 Table-A 32). Specimens from KBS all yielded $\delta^{13}C$ values typical of C_4-dominated diets, combined with mixed-feeding or browsing signals before death. The differences observed between results for isotopic analyses and DMTA could reflect seasonal variation in dietary practices, particularly in the KBS member (1.87-1.61 Ma). Springbok specimens from Tulu Bor (~3.44-2.64 Ma) and Burgi (~2.64-1.87 Ma) appear to have had a mixed C_3 - C_4 diet through life, as suggested by both carbon stable isotopes and DMTA. $\delta^{18}O$

values in the Burgi and KBS members suggest relatively ^{18}O-enriched diets for the studied specimens. δ^{18}O values were much lower for the Tulu Bor member, but because of small sizes (n=1), it remains difficult to assess whether these values could reflect shifts in habitat conditions.

Table 70: Summary table of multiproxy dietary interpretations for genus *Antidorcas* (samples per provenance and per member: mesowear scores (MS), dental microwear textural analysis (DMTA), stable carbon isotopes (δ^{13}C).

Genus	Subset	Member (Ma)	MS score (n)	DMTA (n)	δ13C (n)
Antidorcas	**Koobi Fora**	**All**	**Mixed-feeder**	**Fruit-browser**	**C4-diet**
		Tulu Bor (3.44- 2.64)	/	Mixed-feeder (2)	C4-diet / C3-C4-diet (1)
		Burgi (2.64- 1.87)	Browser (1)	Mixed-feeder/ Fruit-browser (6)	C4-diet / C3-C4-diet (8)
		KBS (1.87 -1.61)	Grazer (1)	Mixed-feeder/ Fruit-browser (15)	C4-diet (9)
	Nachukui	**All**	/	**Fruit-browser**	**C3-C4-diet**
		Lomekwi (3.44 -2.53)	/	Mixed-feeder (3)	C4-diet (1)
		Lokalalei (2.53 - 2.33)	/	Browser (1)	C3-diet (1)
		Kalochoro (2.33 - 1.9)	/	/	C3-C4-diet (1)
	Modern	**/**	**Mixed-feeder (10)**	**Mixed-feeder (10)**	**/**

In Nachukui, carbon and oxygen stable isotope ratios showed a large range of values, from grazing to browsing. Because of sample size (i.e. n=3), potential changes in dietary practices through time could not be explored for this locality. Temporal variation in microwear patterns could not be assessed either due to sample size but results from DMTA suggested mixed-feeding behaviours. Overall, it appears that in West Turkana, the studied springbok individuals had a varied diet during their growth as well as just before their death.

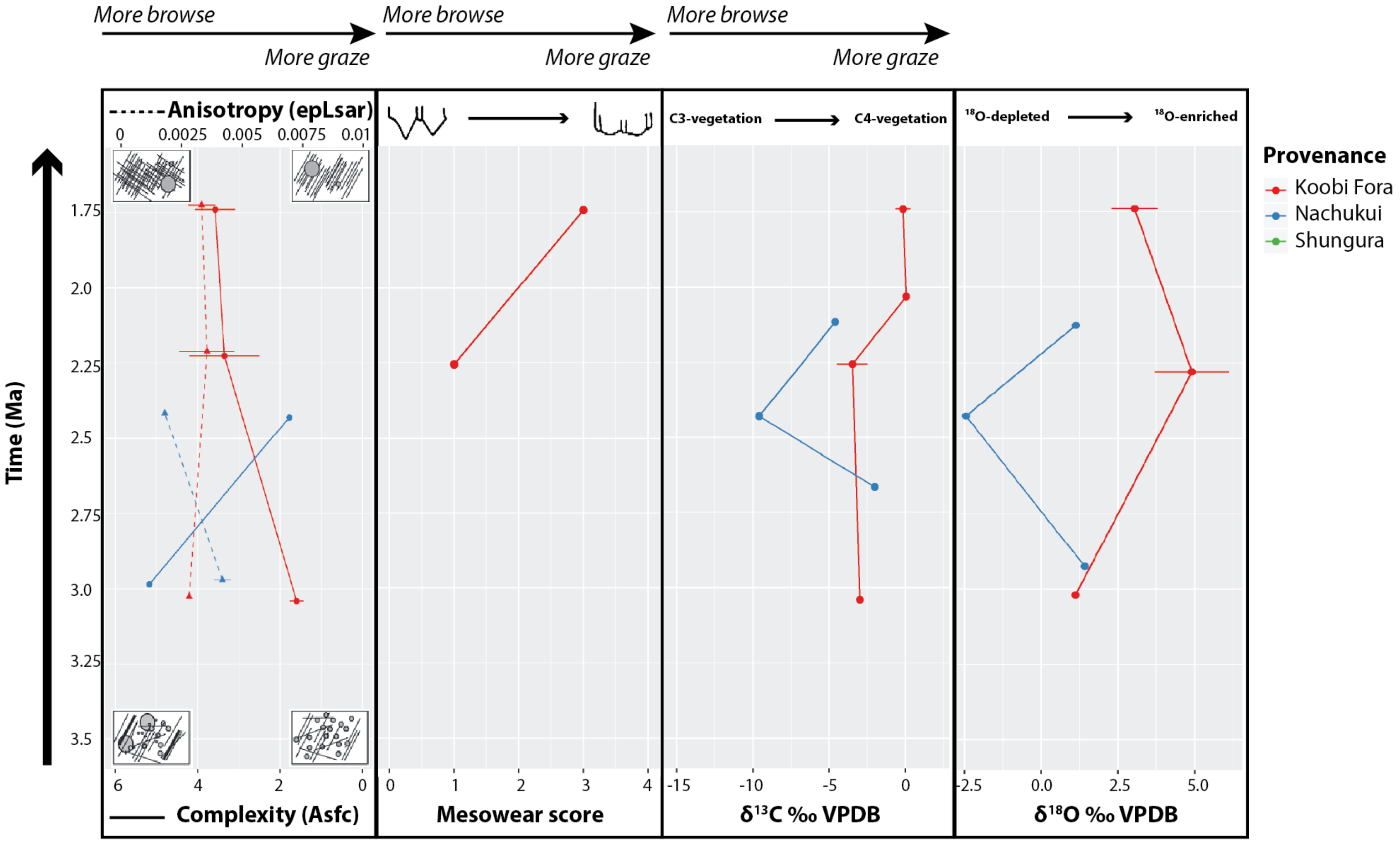

Figure 90: *Antidorcas* dietary variability though time, as assessed by (from left to right) dental microwear textural analysis (anisotropy and complexity), mesowear analysis (mesowear score), carbon stable isotope analysis ($\delta^{13}C$) and oxygen stable isotope analysis ($\delta^{18}O$).

7.4 Discussion

7.4.1 Palaeo-ecology of the studied taxa

7.4.1.1. Obligate-grazers and obligate browsers

Samples from one dedicated-browser taxon (genus *Giraffa*) and one dedicated-grazer taxon (genus *Equus*) were analysed in this study to help calibrate the overall dietary spectrum of ancient herbivores through time and investigate the diet composition of species that are usually assumed to rely mainly on graze or on browse. While a clear dichotomy between browsing and grazing species was highlighted in the present study, some degree of dietary variability was observed among fossil equid specimens.

Overall, results from the analyses conducted using several dietary proxies showed, as expected, dietary behaviours typical of browsing herbivores for all of the *Giraffa* species studied. Dietary patterns dominated by soft-leaf-browsing were observed for the modern and fossil *Giraffa* samples, although fossil *G. stillei* specimens were suggested to have included more seeds and pods in their diet than their modern counterparts. The results highlighted by stable oxygen isotope analyses suggested as well that fossil giraffids, like their extant relatives, were likely water-independent and that potential variations in $\delta^{18}O$ values across the Omo-Turkana basin would therefore likely reflect variations in local aridity conditions. Results from the analyses performed on fossil giraffid specimens for this project are therefore in agreement with previous studies on extinct giraffids (Merceron *et al.,* 2018). Indeed, although *Giraffa stillei* and *Giraffa jumae* differed morphologically in some aspects (Dietrich, 1942), they both have been described as a dedicated-browsers based on isotopic studies (Cerling *et al.,* 2015).

Similarly, analyses of fossil equid specimens suggested diets typical of grazing species throughout most of their life. This agrees with previously published isotopic data on equids from the Koobi Fora and Nachukui formation, which indicated a C_4 -based diet for fossil equids, reflecting grazing feeding habits (Cerling, Dearing and Ehleringer, 2005; Cerling *et al.*, 2015). However, mixed-feeding behaviours just before death were identified for a significant number of studied fossil equid specimens based on dental microwear textural analysis. This suggests slightly more variable dietary behaviours among fossil equids than initially predicted, although their overall lifetime dietary signals remain indicative of a strong reliance on graze. In contrast with fossil giraffids, results from stable oxygen isotope analyses suggested that fossil equids were likely water-dependent, hence suggesting that potential variations in $\delta^{18}O$ values across the Omo-Turkana basin would likely reflect variations in the isotopic composition of local groundwater.

Following these results, fossil giraffids and equids can therefore be used as indicators of the browsing-grazing end-members of the dietary spectrum, and as evaporation-sensitive (ES) and evaporation-insensitive (EI) baseline taxa, to which the studied mixed-feeding antelope species can be compared.

7.4.1.2 Mixed-feeding taxa

While the modern antelope species *Antidorcas marsupialis* and *Aepyceros melampus* demonstrated mixed-feeding behaviours throughout all proxies as predicted, more variability in feeding practices was suggested for their extinct relatives.

Results from analyses of the *Antidorcas recki* assemblage suggested variable dietary behaviours throughout their life, with early-life diets dominated by C_4-vegetation, last meals before death dominated by mixed-diets, and a mildly abrasive lifetime diet suggesting a predominance of mixed-feeding behaviours throughout their life and likely seasonal variation in diet. These results contrast with previous observations made on fossil *A. recki* specimens from the South African fossil record, where mixed-feeding habits with a preference for browse were identified (Luyt, 2001; Lee-Thorp, Sponheimer and Luyt, 2007; Sewell *et al.*, 2019). However, the high dietary plasticity of this fossil springbok species with an important C_4 -component in the diet, as well as feeding behaviours influenced by seasonality, have been suggested previously for Pleistocene *cf. A. recki* specimens from Olduvai (Tanzania) at ~1.7 Ma, based on multiproxy paleo-dietary analysis (Rivals *et al.*, 2018). These differences in palaeo-ecological reconstructions of *Antidorcas recki* dietary behaviours between the eastern and the southern African fossil records could potentially highlight different palaeo-environmental conditions between the two regions. However, these differences could also be due to species mis-identification, as previous studies have pointed out the difficulty to identify *Antidorcas* specimens at the species-level based on dental remains only, with previous attributions of South African specimens to *A. recki* having been called into question (Vrba, 1976; De Ruiter, 2001; Adams *et al.*, 2016). The marked difference in inferred dietary signals between *A. recki* specimens from eastern Africa and South Africa could indicate that these assemblages actually contained different *Antidorcas* species, raising once more the question whether *A. recki* truly occurred as one species in both eastern and southern Africa.

Results from the analysis of the fossil *Aepyceros melampus* assemblage suggested lifetime variability in dietary behaviours, with early-life diets dominated by C_4 -vegetation, last meals before death dominated by mixed-diets containing a significant amount of fruits and/or seeds, and a poorly abrasive lifetime diet suggesting a predominance of browsing behaviours throughout their life. This likely highlighted strong seasonal variation in diet for this fossil species. Evidence for seasonal variation was also highlighted by results from intra-tooth isotopic analyses of fossil impala specimens from the Shungura formation, although the stable carbon isotope ratios observed indicated, overall, a predominance of grazing behaviours throughout the year in the diet of these specimens (see 7.4.3 for further discussion on seasonal variability). These results contrast with previous studies that have suggested that Plio-Pleistocene impalas may have relied more heavily on browsing (Sponheimer, Reed and Lee-Thorp, 1999), but remain in agreement with published isotopic analyses that showed that *Aepyceros* specimens from fossil deposits younger than ~4.0 Ma had a strong grazing component in their diet (Cerling *et al.,* 2015). Based on their morphology (straighter, less lyrated and more gracile horn cores, shorter and thicker limb bones), previous studies suggested that *A. shungurae* might have inhabited preferentially more closed woodland habitats than *A. melampus* (Harris, 1991; Bobe and Eck, 2001). This is in relation to the palaeo-environmental reconstructions that were proposed for the Shungura formation, where this impala species was abundant during the Plio-Pleistocene. The varied diets suggested for *A. shungurae* in the present study, across all proxies, are consistent with such hypothesis, especially when considering the stronger C_4-component that was suggested for the diet of fossil *A. melampus* specimens in comparison to *A. shungurae*.

Results from stable oxygen isotope analyses suggested that fossil *Aepyceros* species were, similarly to modern *Aepyceros melampus* (Faith, 2018), likely water-dependent (i.e. evaporation-insensitive), with lower $\delta^{18}O$ values than those observed in fossil giraffes. Indeed, obligate drinkers are usually expected to have $\delta^{18}O$ values depleted in ^{18}O compared to mammals that derive most of their water from fruits or leaves (Cerling, Hart and Hart, 2004). Consequently, potential variations in $\delta^{18}O$ values for *Aepyceros* specimens across the Omo-Turkana basin likely reflect variations in the composition of local groundwater and could potentially be used alongside data from evaporation-sensitive taxa such as giraffids to evaluate aridity conditions in the fossil record.

7.4.2 Spatial and temporal variability in feeding patterns: palaeo-environmental interpretations per fossil locality

This section discusses the palaeo-environmental implications of the various paleo-dietary patterns observed across the studied taxa for each fossil locality, comparing results from this study with previous work on palaeo-environmental reconstructions for the Plio-Pleistocene deposits of the Omo-Turkana basin.

7.4.2.1 Koobi Fora formation, East Turkana

While *Giraffa* individuals from Koobi Fora formation consistently classified as a leaf-browsers/ C_3-browsers across all dietary proxies, a wider dietary variability was suggested for the other three taxa studied, with evidence for grazing, browsing and mixed-feeding practices (Table 71). Although the year-round dietary patterns of *Equus* specimens appear dominated by C_4-grazing signals in all members, occasional mixed-feeding behaviours were also highlighted for this taxon via dental microwear analysis (DMTA).

The palaeo-dietary analysis of the impala specimens from Burgi (2.64- 1.87 Ma) and KBS (1.87 -1.61 Ma) and from the springbok specimens from the Burgi member suggested for both taxa a poorly abrasive diet through life with high proportion of C_4-plants during early years and mixed-feeding habits before death, in association to open-canopy habitat. These similarities could relate to similar environments and similar foraging strategies from both *Aepyceros* and *Antidorcas* individuals in east Turkana at the time. The analyses of the springbok specimens suggest an increase in C_4-plants after 1.87 Ma (in KBS member) combined with rather high oxygen isotope ratios. For both antelope taxa, dental DMTA suggested mixed-feeding and/or fruit-browsing behaviours before death. These results could suggest, because of the high dietary plasticity of these mixed-feeding antelopes, high seasonal variation in food availability and climatic conditions in eastern Turkana, or alternatively high vegetation heterogeneity in the area, which allowed these antelope species to adapt their diet depending on seasonal food availability, or when facing potential niche competition in food resources.

When specimens from the genera *Aepyceros*, *Antidorcas* and *Equus* are considered all together, a variety of dietary patterns are suggested through DMTA, suggesting individuals with varying diets before death, covering the entire dietary spectrum. This could be interpreted as further evidence for seasonal variations in vegetation availability or high vegetation heterogeneity in the area. Carbon isotope values also showed a large range of food items consumed by individuals from these three taxa, with individuals with C_4-dominated diets, but also individuals with mixed C_3 - C_4 diets. The assemblage is dominated by C_4-diets in the Tulu Bor (~3.44-2.64 Ma) and KBS (1.87-1.61 Ma) members, while individuals with C_3 - C_4 diets are found in Burgi member (~2.64-1.87 Ma), mostly for genus *Antidorcas*. A wide range of oxygen stable isotope ratios was also observed in this locality suggesting varied aridity conditions, potentially in relation to a mixture of closed- and open-canopy habitats. This wide range of dietary practices observed across methods for three of the studied taxa in the Koobi Fora formation could reflect, once more, high vegetation heterogeneity in the area or high seasonality in dietary patterns, related to seasonal plant availability, and/or to seasonal niche competition.

Table 71: Summary table of multiproxy dietary interpretations for all studied taxa, for each member of the Koobi Fora formation.

Subset	Member (Ma)	*Aepyceros*	*Antidorcas*	*Equus*	*Giraffa*
Koobi Fora	**All**	**Poorly abrasive diet through life but high proportion of C4-plants during early years and fruit-browsing-feeding habits before death**	**Moderately abrasive diet through life with high proportion of C4-plants during early years and fruit-browsing habits before death**	**Grazing habits dominated by C4-plants through life and mixed-feeding behaviours before death**	**Poorly abrasive diet through life with leaf-browsing/browsing habits dominated by C3-plants though life and before death**
	Tulu Bor (3.44- 2.64)	High proportion of C4-plants during early years and browsing habits before death (n=1)	Relatively high proportion of C4-plants during early years and mixed-feeding habits before death	Grazing habits dominated by C4-plants during early years	Leaf-browsing/browsing habits dominated by C3-plants though life and before death
	Burgi (2.64- 1.87)	Poorly abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	Poorly abrasive diet through life with relatively high proportion of C4-plants during early years in some specimens, and mixed-feeding/fruit-browsing habits before death	Grazing habits dominated by C4-plants through life and during early years, and mixed-feeding behaviours before death	Poorly abrasive diet through life with leaf-browsing/browsing habits dominated by C3-plants though life and before death
	KBS (1.87 -1.61)	Poorly abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	Abrasive diet and high proportion of C4-plants through life but mixed-feeding/fruit-browsing habits before death	Grazing habits dominated by C4-plants through life and during early years, and mixed-feeding behaviours before death	Poorly abrasive diet through life with leaf-browsing/browsing habits dominated by C3-plants though life and before death

Interestingly, previous studies of faunal composition have shown that, while each member of the Koobi Fora formation was dominated by the Reduncini tribe (potentially indicative of C_4 -mesic environments), the second most abundant tribe differs across members, with Tragelaphini being well-represented in Tulu Bor and Burgi members, but outnumbered by Alcelaphini specimens in KBS member. This could suggest a shift from habitats with a wide change of C_4 and C_3 resources (as preferred by tragelaphins) to habitats dominated by C_4 -dominated environments (as preferred by alcelaphins), at ~1.87 Ma. This is in agreement with the increase in $\delta^{13}C$ values observed for the *Antidorcas recki* specimens analysed in this study, and with the gradual increase in consumption of tough and abrasive food items before death observed for *Aepyceros* and *Giraffa* specimens via dental microwear textural analysis (i.e. decrease in complexity, Asfc).

The apparent increase in $\delta^{18}O$ values observed between the Burgi and KBS members for *Aepyceros* and *Equus* specimens could also reflect an increase in aridity conditions in this locality after ~ 1.87 Ma. A shift from C_3 -dominated to C_4 -dominated environments has been suggested in other studies, such as from paleosol carbonates and palaeontological studies (Cerling, Bowman and O'Neil, 1988; Harris, 1991; Reed, 1997; Bobe *et al.*, 2007; Quinn *et al.*, 2007; Levin *et al.*, 2011). Such changes in environmental conditions could relate to the transition from a river system in Tulu Bor and Burgi members to a lacustrine phase in KBS, as suggested by palaeo-geographic reconstructions (Brown and Feibel, 1991; McDougall and Brown, 2008). Furthermore, several studies suggested that environments were likely more heterogeneous in the Burgi member, with more closed woodlands in the north and more open habitats in the south, providing a mixture of woodland and grassland areas (Harris, 1991; Reed, Fleagle and Leakey, 2007). Such habitat conditions could explain the higher number of individuals demonstrating mixed C_3 - C_4 dietary signals in samples from Koobi Fora dating between 2.64 and 1.87 Ma and the wide range of $\delta^{18}O$ values observed in the Burgi and KBS members.

Overall, the dietary patterns observed across the studied taxa from the Koobi Fora formation likely suggest rather heterogeneous habitats in this locality during the Plio-Pleistocene, with a gradual increase in the proportions of C_4-resources in the landscape, which could relate to an increase in aridity conditions, especially after ~1.87 Ma. Similarly to the stable carbon isotope ratios observed across the Koobi Fora sequence, isotopic studies of fossil hippotamids, suids and elephantids have suggested an increase in C_4-vegetation included in the diet of these taxa in the Upper Burgi member, compared to the Tulu Bor member (Cerling *et al.*, 2010; Souron, Balasse and Boisserie, 2012).

The highly variable dietary signals observed among *Aepyceros*, *Antidorcas* and *Equus* specimens via dental microwear textural analysis suggest variable dietary behaviours during the few weeks before the death of the individuals, which could reflect the presence of a large range of resources, either all year round or seasonally, which allowed the individuals to vary their diet if necessary when facing a shortage of their "preferred" food resources due to seasonal variation in vegetation availability, or to niche competition. Indeed, seasonal variation in food availability could explain the high dietary variability observed in these specimens, especially when discrepancies were observed at the individual-scale between life-time dietary patterns (assessed via mesowear and/or stable isotope analyses) and short-term dietary signals (assessed via DMTA, i.e. last supper effect).

7.4.2.2 Nachukui formation, West Turkana

Similarly to specimens from Koobi Fora, *Giraffa* specimens from the Nachukui formation were classified as browsers across all methods (Table 72). Results for *Equus* specimens were also consistent across methods, suggesting a prevalence of grazing habits.

Results for *Aepyceros* individuals in this locality suggested varied dietary patterns through time, potentially suggesting seasonal variations in diet, with evidence for grazing, browsing and mixed-feeding to fruit-browsing practices. Results for *Antidorcas* individuals suggested some degree of dietary variation as well, with grazing, browsing and mixed-feeding signals, although results remain difficult to interpret with confidence due to very small sample sizes for this taxon in this locality (i.e. $n<4$). Both mixed-feeding antelope taxa demonstrated a prevalence of fruit-browsing behaviours during the few weeks before their death (i.e. via DMTA), associated to either C_4-dominated or mixed C_3 - C_4 early years diets (i.e. via stable carbon isotopes). Such results could reflect seasonal variation in food availability, either due to seasonal changes in land cover, local habitat heterogeneity, and/or to niche competition with other species.

Table 72: Summary table of multiproxy dietary interpretations for all studied taxa, for each member of the Nachukui formation.

Subset	Member (Ma)	*Aepyceros*	*Antidorcas*	*Equus*	*Giraffa*
Nachukui	**All**	**Moderately abrasive diet through life with high proportion of C4-plants during early years and fruit-browsing habits before death**	**Mixed-feeding habits with mixed C3-C4 plants during early years and fruit-browsing habits before death**	**Moderately abrasive diet through life but high proportion of C4-plants during early years and abrasive diet before death**	**Leaf-browsing habits dominated by C3-plants during early years and before death**
	Lomekwi (3.44 -2.53)	Moderately abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding/fruit-browsing habits before death	High proportion of C4-plants during early years and mixed-feeding habits before death	/	Leaf-browsing habits dominated by C3-plants during early years and before death
	Lokalalei (2.53 - 2.33)	Poorly abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	C3-diet during early years and browsing behaviour before death (n=1)	/	/
	Kalochoro (2.33 - 1.9)	/	Mixed-feeding habits with mixed C3-C4 plants during early years (n=1)	Moderately abrasive diet through life with high proportion of C4-plants during early years and abrasive diet before death	Browsing habits dominated by C3-plants during early years (n=1)
	Kaitio (1.9 -1.61)	Poorly abrasive diet through life with high proportion of C4-plants during early years and fruit-browsing habits before death	/	Poorly abrasive diet through life with high proportion of C4-plants during early years and abrasive diet before death (n=1)	/

Potential evidence for dietary variation through time was found for impala samples from the Nachukui formation, with stable carbon isotopes suggesting a slight increase in the amount of C_4-vegetation included in their diet after ~2.8 Ma, and use-wear analyses pointing to a reduction of the abrasiveness of the food items consumed after ~2.33 Ma and an increase in the consumption of hard food items such as fruits and seeds after ~1.9 Ma. This could relate to changing vegetation conditions in West Turkana throughout the Plio-Pleistocene, with a gradual increase in the presence of open-grassland habitat from ~2.8 Ma onwards but with varied habitats that retain a significant proportion of woody vegetation available to the impalas, especially after ~2.33 Ma. The large range of complexity values (Asfc) observed for impala specimens from the Kaitio member could reflect an increased temporal variability of vegetation composition (either seasonal or in relation to longer-scale climatic variations within the member) after ~1.9 Ma, with individuals feeding on a varying amount of browse before death depending on the season/period in which they died.

According to previous studies focusing on the faunal composition of the Nachukui fossil deposits, the faunal assemblage was dominated, overall, by the Alcelaphini and Reduncini tribes, usually both considered as dedicated-grazers. Alcelaphines were the most abundant specimens in the Lower-Middle Lomekwi member, while reduncins were most abundant in the upper Lomekwi, Lokalalei and Kalochoro members. Although alcelaphins were well-represented as well in Kaitio member, the Tragelaphini tribe dominates the assemblage from this member. These patterns of faunal abundance suggest a rather high competition for C_4-monocot resources between ~3.44 and 1.9 Ma, when both Alcelaphines and reduncins dominated the assemblage.

Previous palaeo-environmental reconstruction for the Nachukui formation have suggested the presence of diverse habitats with a mosaic pattern of vegetation cover across the area, relatively wet with the presence of a perennial water source, and dominated by woodland and wooded-grassland (Reed, 1997; Brugal, Roche and Kibunjia, 2003; Tiercelin *et al.*, 2010;

Quinn *et al.*, 2013). These studies suggest as well an overall increase in grassland after 1.61 Ma, although C_3-woodlands remained an important vegetation component. Similar patterns were observed in the present study, first through the wide range of $\delta^{18}O$ values found in this locality, potentially reflecting a wide range of aridity conditions with open- to close-canopy habitats, dominated by lower $\delta^{18}O$ values suggesting a dominance of relatively closed-canopy habitats, especially after ~1.9 Ma (i.e. Kaitio member). A gradual increase in C_4-resources in the environment of the Nachukui formation is also suggested from the present study, with a slight increase in $\delta^{13}C$ values for *Aepyceros* specimens from ~2.8 Ma (i.e. upper Lomekwi). High vegetation heterogeneity was also suggested from the mixed-feeding behaviours of the studied antelope species before death (i.e. DMTA), which could reflect the presence of various food resources in the area able to sustain a wide range of dietary requirements.

All of these results suggest the presence, in west Turkana, of a rather heterogeneous environment able to provide a sufficient amount of graze for fossil equid, springbok and impala populations (and other grazers such as reduncins and alcelaphins), as well as browse for fossil giraffids and mixed-feeding species such as impalas, springboks and other competitors such as tragelaphins.

7.4.2.3 Shungura formation, Lower Omo river valley

The palaeo-dietary analyses performed on *Aepyceros* and *Giraffa* specimens from the Shungura formation highlighted, overall, typical C_3-browsing behaviours through life for fossil giraffids, and moderately abrasive yearly diets typical of mixed-feeders among most impala specimens, with proportions of C_3 and C_4 resources in their diet that varied depending on the member studied (Table 73). The mean $\delta^{13}C$ values recorded for *Giraffa* specimens were slightly lower in the Shungura formation compared to the Koobi Fora formation, likely reflecting the presence of denser closed-canopy habitats in the Lower Omo river valley compared to East Turkana, as expected from previous studies. Similarly, the $\delta^{18}O$ values measured from *Giraffa* specimens from this locality showed a large range of variation through time, with a gradual decrease in values through time, but peaks of ^{18}O-enriched values in members B (~3.44-2.91 Ma) and D (~2.52-2.4 Ma), which might relate to peaks in aridity in the region during these periods.

Table 73: Summary table of multiproxy dietary interpretations for all studied taxa, for each member of the Shungura formation.

Subset	Member (Ma)	*Aepyceros*	*Giraffa*
Shungura	**All**	**Moderately abrasive diet through life with relatively high proportion of C4-plants during early years and leaf-browsing habits before death**	**Poorly abrasive diet through life, dominated by C3-plants during early years**
	B (3.44 - 2.91)	Moderately abrasive diet through life with high proportion of C4-plants tduring early years in some specimens (as well as individuals with mixed C3-C4 diets) and mixed-feeding/browsing habits before death	Moderately abrasive diets through life dominated by C3-plants during early years
	C (2.91 - 2.52)	Poorly or moderately abrasive diets through life with with mixed C3-C4 plants during early years and browsing habits before death	Moderately abrasive diets through life dominated by C3-plants during early years
	D (2.52 - 2.4)	Moderately abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	Poorly abrasive diets through life dominated by C3-plants during early years
	E (2.4 - 2.32)	Moderately abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	C3-dominated diets during early years
	F (2.32 - 2.27)	Moderately abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding habits before death	C3-dominated diets during early years
	G (2.27 - 1.9)	Moderately abrasive diet through life with high proportion of C4-plants during early years and mixed-feeding/grazing habits before death	C3-dominated diets during early years

Evidence for dietary variation through time was observed more distinctly for impalas from the Shungura formation across all dietary proxies, with alternating shifts between mixed diets and diets dominated by C_4-graze. A predominance of mixed diets was highlighted for specimens from members B and C (3.44-2.52 Ma), with most individuals from member B demonstrating mesowear patterns and $\delta^{13}C$ values more typical of mixed-feeders, and individuals from member C yielding the lowest values recorded in the assemblage for all proxies, indicating a significantly higher proportion of browse included in the diet compared to other members. Both *Giraffa* and *Aepyceros* presented a decrease in mean mesowear scores between member B and C, potentially suggesting a less abrasive life-time diet between ~2.91-2.52 Ma, compared to individuals living between ~3.44-2.91 Ma, which could reflect habitats with higher proportions of soft-food items such as leaves. Similarly, both taxa have lower $\delta^{18}O$ values in member C, which could indicate wetter, less arid environments during that time period.

A significant shift towards diets dominated by more abrasive C_4-food items was observed for impala specimens from members post-dating ~2.52 Ma, suggesting a stronger reliance on graze for these specimens, although a shift back to slightly less abrasive/ C_4-dominated diets was suggested for individuals from member E (2.4-2.32 Ma). Results from stable oxygen isotope analyses also suggested a shift towards slightly more mesic habitats in member E, when compared to geologically older members (i.e. prior 2.4 Ma). The gradual increase in grazing practices observed through time from ~2.52 Ma (i.e. member D) for impalas from the Lower Omo-river valley could relate to a gradual increase in graze availability in the region as a result of seasonal change, climate change or niche competition.

This is consistent with previous studies of bovid abundance and palaeo-diet which suggested that a change occurred at ~2.52 Ma onwards (from member D) from palaeo-environments dominated by woodlands, riverine forests and mesic grasslands in members B and C to an environments with an increased presence of C_4-vegetation (Bobe and Eck, 2001; Negash *et* *al.*, 2015). Similarly, previous studies of faunal abundance in the Shungura formation highlighted a gradual decline in representation of tragelaphins in the fossil deposits after ~2.32 Ma, suggesting a gradual increase in C_4-dominated environments from that period. This trend suggested in previous studies is in agreement with the shift in dietary practices observed in this study for *Aepyceros* specimens when using carbon stable isotopes.

Despite the gradual increase in C_4-environments observed across the fossil record, it is interesting to note that the mean $\delta^{13}C$ values observed for *Aepyceros* specimens from member E are slightly lower than the values observed in members D, F and G, suggesting the inclusion of slightly more C_3-vegetation in the impalas' diet between ~2.4-2.32 Na. Similarly, mesowear scores from *Aepyceros* specimens from member E are slightly lower than for specimens from members D, F and G, suggesting a poorly abrasive diet, likely dominated by soft browse. The environment of member E has been described previously as likely characterised by well-watered woodland–bushland with a riparian woodland or forest (Reed, 1997; Alemseged, 2003). Such conditions could explain the lower mesowear scores and $\delta^{13}C$ values observed for fossil impalas in this member, compared to members F and G, and point to shifting environmental conditions in the lower Omo river valley during the Plio-Pleistocene, with a gradual increase in C_4-dominated habitats, but with a persisting presence of woodland and closed-canopy habitats, more or less developed depending on the time period.

Overall, mesowear and microwear analyses of the *Aepyceros* assemblage indicated, overall, lifetime diets dominated by mixed-feeding patterns throughout most of the sequence after ~2.52 Ma, suggesting a high variation in diet (either seasonally and all-year round) and associated habitats with a large range of food resources available to impala populations in the region. In line with this hypothesis, previous palaeo-environmental reconstructions for the Shungura formation have suggested the presence of mosaic habitats ranging from forests to open woodlands between ~3.4 and 2.0 Ma (Jaeger and Wesselman, 1976; Bonnefille and

Dechamps, 1983; Wesselman, 1984; Bobe and Eck, 2001; Alemseged, 2003; Levin *et al.*, 2011; Bibi *et al.*, 2013; Barr, 2015; Plummer *et al.*, 2015; Negash *et al.*, 2015; Blondel *et al.*, 2018; Martin *et al.*, 2018). For instance, studies of faunal abundance showed that the Shungura formation was inhabited during the Plio-Pleistocene by large number of bovids, among which the Reduncini, Tragelaphini and Aepycerotini tribes dominate. The dominance in the habitat of grazing, browsing and mixed-feeding species suggests the presence of a wide range of resources in the area, able to sustain various species with different dietary requirements.

7.4.3 Stable oxygen isotopes and aridity

In addition to the other proxies studied to reconstruct the palaeo-dietary behaviours of fossil *Aepyceros* specimens, stable oxygen isotope data were sought to analyse climate changes as experienced by local species, since $\delta^{18}O$ values in mammalian tissues are believed to vary due to changes in air temperature, humidity and precipitation/evaporation balance within an ecosystem (McCrea, 1950; Dansgaard, 1964; Schmidt, LeGrande and Hoffmann, 2007). This section discusses varying aridity conditions in the Plio-Pleistocene Omo-Turkana basin as assessed through stable oxygen isotope analyses of fossil impala specimens (genus *Aepyceros*). Variations in aridity conditions are first considered on a longer time-scale (i.e. across members), before being assessed at seasonal scale (i.e. intra-tooth analyses).

7.4.3.1 Habitat types and long-term aridity conditions: data from bulk analysis

As suggested when $\delta^{18}O$ values were compared between fossil and modern species previously in this chapter, a dichotomy was observed between *Giraffa* specimens and specimens from the other three taxa, which could be related to differing biological processes between taxa (i.e. evaporation sensitive (ES) vs. evaporation-insensitive (EI) species). If this previous hypothesis is correct, the spatial and temporal patterns observed in $\delta^{18}O$ values likely reflect patterns of local aridity conditions when observing values from ES species (here *Giraffa*), and patterns of meteoric water ^{18}O composition when observing values from EI species (here *Equus*, *Antidorcas* and *Aepyceros*). The fact that specimens from *Equus*, *Antidorcas* and *Aepyceros* assemblages appear to follow a similar pattern of $\delta^{18}O$ values across localities (i.e. high values in Koobi Fora, low values in Nachukui, and mid-range values in modern specimens; see Figure 76) suggest that these three taxa likely shared similar biologics and water-requirements and, hence, might all reflect the same aspect of their palaeo-environments: the $\delta^{18}O$ composition of meteoric water. If this was the case, the results presented for oxygen isotopes suggest local meteoric waters that were relatively depleted in

^{18}O in Nachukui and, in comparison, local meteoric waters that were relatively enriched in ^{18}O in Koobi Fora. Because previous studies have suggested that species foraging in open landscapes tend to have ^{18}O-enriched isotopic signals compared to species feeding in forested/closed-canopy habitats due to higher evaporation rates in open-canopy landscapes (Quade *et al.*, 1995; Ehleringer, 2005; Merceron *et al.*, 2013), these results could suggest more open habitats in the Koobi Fora formation and more closed habitats in the Nachukui formation during the Plio-Pleistocene.

However, when oxygen isotope patterns were observed through time (see Figure 77) the patterns of variation in δ^{18}O values differed between *Equus*, *Antidorcas* and *Aepyceros*, especially when comparing the *Antidorcas* assemblage with the *Aepyceros* and *Equus* assemblages. This could suggest differing drinking patterns between *Antidorcas* and *Aepyceros*/*Equus* fossil specimens. If fossil *Antidorcas* species had a similar dietary ecology than their extant relatives, this taxon is unlikely to be a faithful proxy for local meteoric water, as it is not water-dependant and might obtain most of its body water from plant-water. On the contrary, modern zebras and impalas are water-dependant, which could suggest that the ancestral species belonging to these genera could have been similarly highly water-dependant and therefore have obtained most of their body water from meteoric water. Genera *Aepyceros* and *Equus* might therefore be better indicators of variation in local meteoric water composition through time.

7.4.3.2 Seasonal variation in aridity conditions: data from intra-tooth analysis

As suggested by previous studies (e.g. deMenocal, 2004; Potts, 2013; Maslin *et al.,* 2014; Quinn, 2015), changes in species δ^{18}O mean values and increased intra-tooth variance in δ^{18}O values through time may correspond to climatic shifts due to heightened aridity or humidity and to changes in climatic variability, respectively. Higher δ^{18}O values would be expected under arid conditions, as increased aridity produces more evaporative conditions impacting both surface and leaf waters. Lower δ^{18}O values would be expected under more humid conditions, either seasonally or on the longer term (i.e. humid climatic pulses). Subsequently, intra-tooth $\delta^{18}O$ variance in the studied impala specimens may reflect periods of relatively high and low climatic variability, with larger ranges of $\delta^{18}O$ values observed in specimens living at a time of relatively high climatic instability.

The analysis of intra-tooth sequences showed, overall, a strong positive correlation between $\delta^{13}C$ and $\delta^{18}O$ values with synchronous peaks and decreases in both carbon and oxygen isotopic ratios throughout the intra-tooth sequences studied. These observations contrast with the results obtained from the modern impala specimens sampled by Copeland *et al.* (2009) in the Akagera National Park (Rwanda), where decreases in $\delta^{13}C$ values appear to have been, for most specimens, synchronous with increases in $\delta^{18}O$ values. This could potentially be explained by the dietary patterns observed in this impala population in which individuals fed preferentially on graze during the wet season (i.e. higher $\delta^{13}C$ due to C_4 - dominated diets, associated to lower $\delta^{18}O$ due to lower evaporation rates) and on browse during the dry season (i.e. lower $\delta^{13}C$ due to mixed C_3 - C_4 diets, associated to higher $\delta^{18}O$ due to higher evaporation rates). In contrast, the strong correlations observed between $\delta^{13}C$ and $\delta^{18}O$ values in fossil *Aepyceros shungura*e specimens could suggest that fossil impala specimens did adapt their diet with seasonally changing conditions, feeding preferentially on graze during the dry season (i.e. higher $\delta^{13}C$ due to C_4-dominated diets, associated to higher $\delta^{18}O$ due to high evaporation rates) and on mixed C_3 - C_4 diets during the wet season (i.e. lower $\delta^{13}C$ due to mixed C_3 - C_4 diets, associated to lower $\delta^{18}O$ due to lower evaporation rates). Such dietary patterns would then suggest that fossil mixed-feeding species such as fossil impalas could indeed be good environmental proxies, as they tend to adapt their diet to changing aridity and local vegetation conditions.

However, seasonal variation in local environmental conditions are not the only possible explanation for the variations in stable oxygen isotope ratios observed among fossil impala specimens. For instance, because meteoric water $\delta^{18}O$ values vary geographically due to different climates and source rains (e.g., Dutton *et al.*, 2005), the high variability of $\delta^{18}O$ values observed within the intra-tooth sequence could potentially reflect as well migratory behaviours that led to changing drinking water sources throughout the lives of the individuals. Although modern impala populations do not migrate over long distances and remain sedentary (Estes, 1991), it cannot be ruled out that fossil impala populations did migrate seasonally. Another potential explanation for intra-tooth variation in $\delta^{18}O$ values could be the inclusion, seasonally, of wetland sedges, fruits, and/or underground storage organs, which tend to yield relatively low $\delta^{18}O$ values (Lee-Thorp, 2011; Grine *et al.*, 2012). The strong correlations observed between $\delta^{18}O$ and $\delta^{13}C$ values across the intra-tooth sequences studied for fossil *Aepyceros shungurae* specimens could suggest a strong relationship between diet and body water content, hence arguing for the seasonal inclusion of a significant amount of moisture rich food-materials, such as fruits, leaves, sedges, and perhaps succulents.

Overall, the wide range of intra-tooth $\delta^{18}O$ values observed for *Aepyceros shungurae* specimens from the Shungura formation suggest seasonal shifts in the isotopic content of the ingested water. These variations of the impala body water-$\delta^{18}O$ values likely resulted from seasonal environmental changes that modified the isotopic composition of the local meteoric water from which the specimens were acquiring most of their body water, or to seasonal dietary shifts that lead to a seasonal increase in the amount of body water acquired from moisture rich food-materials (e.g. fruits, leaves, sedges, succulents).

Similarly to previously published results from intra-tooth analysis of hippopotamid remains from the Shungura formation (Souron, Balasse and Boisserie, 2012), an increase in the amplitude of variation of $\delta^{18}O$ values was observed between impala specimens from member B and member C (from 5.23‰ to 7.71‰, respectively). This could suggest an increased seasonality of rainfall amount in the lower Omo-river valley between 3.44 and 2.52 Ma, as suggested as well from the results of Souron *et al.* (2012). The smaller amplitudes of $\delta^{18}O$

values observed in the specimens studied from members D and F (~4‰) could therefore imply a reduced seasonality in rainfall amount between 2.52 and 2.27 Ma. In turn, the significantly larger ranges of $\delta^{18}O$ values observed in specimens from members G could suggest that these individuals lived at a time of relatively high climatic variability associated with high seasonal variations in rainfall amount between 2.27 and 1.9 Ma. This hypothesis would agree with previous research that hypothesized that seasonal and interannual rainfall variability in eastern Africa increased at ~2.0 Ma in response to the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.*, 2004; Blumenthal *et al.*, 2017; Hopley *et al.*, 2018). However, future analysis of additional impala specimens for these members will be required to confirm such trend.

7.4.4 Dietary plasticity of mixed-feeding antelope taxa as a proxy for palaeo-environmental change

7.4.4.1 Spatial and temporal variability in feeding patterns of fossil *Aepyceros*

As illustrated by the results from this study summarised in 3.5.2, highly variable dietary patterns could be observed for fossil impala specimens (genus *Aepyceros*), as predicted based on previous studies of their extant relatives. While little difference in feeding behaviours could be observed for the obligate-grazing (genus *Equus*) and obligate-browsing (genus *Giraffa*) taxa, significant differences could be observed between *Aepyceros* samples across the three Omo-Turkana formations considered when assessing intra-generic variation in dietary patterns. The main differences that arose, when considering the dietary patterns of fossil impala specimens across the Omo-Turkana basin, were between specimens from the Shungura formation, in the Lower Omo river valley, and specimens from the Koobi Fora and Nachukui formations, more particularly (Figure 92). Indeed, stable carbon isotope analyses suggested diets with a stronger C_4-component for *Aepyceros* specimens from the Koobi Fora and Nachukui formations compared to specimens from the Shungura formation, which could potentially relate to drier, more open environments East and West of the basin in comparison to wetter, more varied environments in the Lower Omo-river valley. Similarly, results from dental microwear textural analysis suggested, for fossil impala specimens, poorly abrasive diets before death in Shungura, similar to the diets of leaf-browsing species, in contrast with the mixed/fruit-browsing feeding behaviours observed in most specimens from Koobi Fora and Nachukui. This could indicate the availability, in the Lower Omo-river valley, of softer food items, such as leaves, than in the other two studied localities.

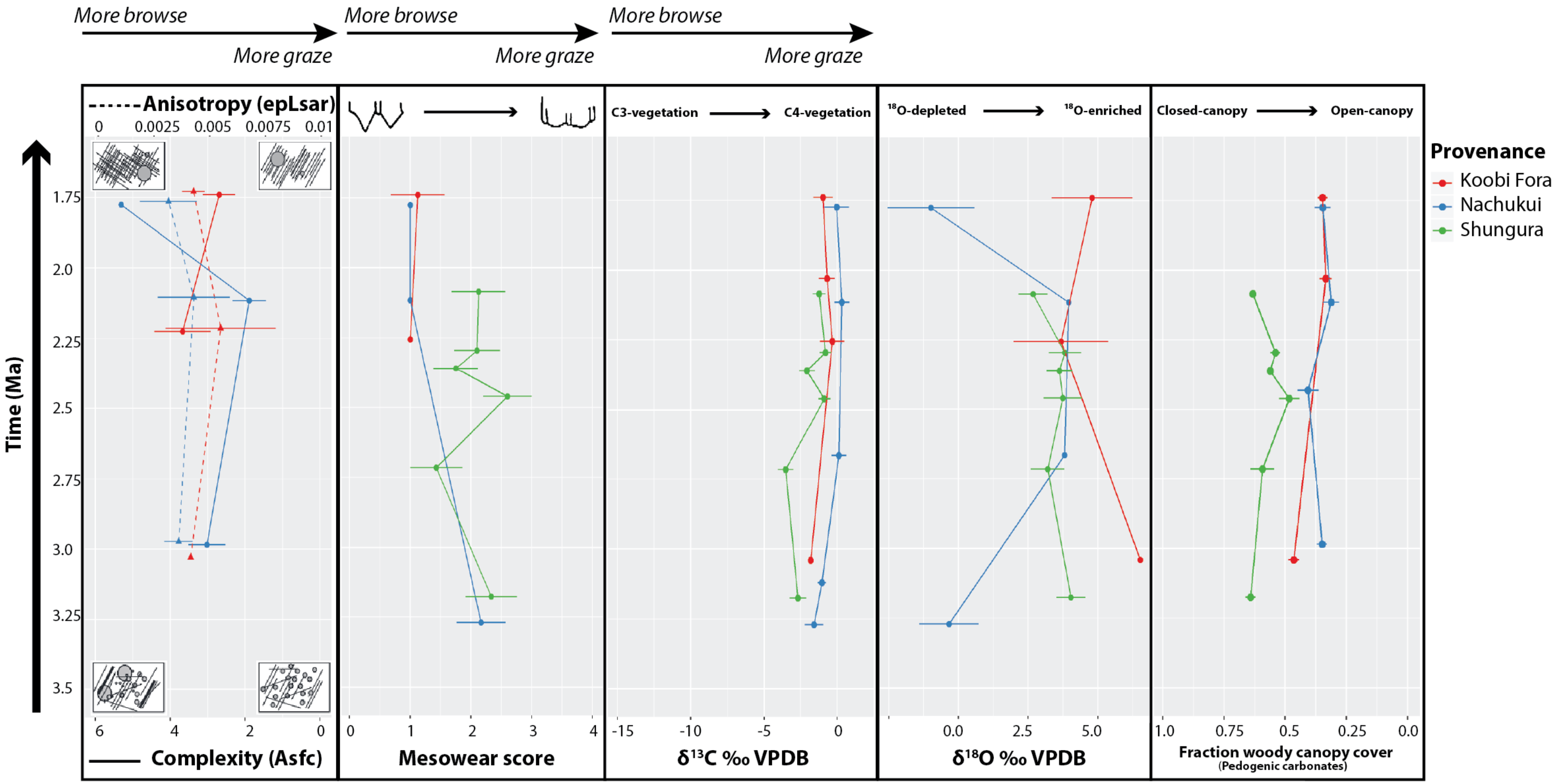

Figure 91: *Aepyceros* dietary variability though time, as assessed by (from left to right) dental microwear textural analysis (anisotropy and complexity), mesowear analysis (mesowear score), carbon stable isotope analysis ($\delta^{13}C$), oxygen stable isotope analysis ($\delta^{18}O$), and fraction of woody canopy cover (based on pedogenic carbonate data from Levin *et al.* 2011, converted following the equation developed by Cerling *et al.*, 2011).

These patterns of dietary variation among fossil *Aepyceros* populations, and the inferred palaeo-environmental conditions, are consistent with previous studies which have suggested, based on other proxies, that more arid open habitats characterised Plio-Pleistocene habitats in Koobi Fora and Nachukui, while more wet closed environments characterised habitats in the Shungura deposits (see 2.2.2). For instance, a similar pattern has been previously observed from paleosol carbonates data, which suggested a prevalence of closed-canopy habitats in the Lower Omo river valley, as opposed to prevailing open-canopy habitats in east and west Turkana (Levin *et al.*, 2011) (see also Figure 91).

While $\delta^{13}C$ values were very similar between Koobi Fora and Nachukui for *Aepyceros* specimens, $\delta^{13}C$ values were slightly higher for specimens from west Turkana, suggesting a stronger reliance on C_4 -vegetation in that locality compared to east Turkana. A similar pattern was observed, to a lesser extent, in the dental microwear textural patterns of this taxon which demonstrated, overall, lower complexity and higher anisotropy values in Nachukui compared to Koobi Fora, implying the consumption of more tough and abrasive food items (such as C_4 -monocots) before death among specimens from west Turkana. This could relate to environments more clearly dominated by more open C_4 -grassland habitats and more arid in the Nachukui formation, compared to Koobi Fora. These observations would agree with previous studies of faunal abundance and diversity which suggested that the Nachukui formation documents deposits from more open and drier habitats in the basin, as opposed to more complex habitats in the Koobi Fora formation (Bobe *et al.*, 2007). Such differing patterns between East and West Turkana could relate to the complex configuration of the Turkana basin highlighted by palaeo-geographical studies, with the environments sampled in the Nachukui formation likely located more marginally away from the course of the palaeo-Omo river than the environments sampled in the Koobi Fora formation (Feibel, Harris and Brown, 1991).

However, recent studies highlighted as well the complexity and spatial heterogeneity that likely characterised paleo-habitats in this region (e.g. Du and Alemseged, 2018), with fragmented habitats that differed depending on their proximity to the lake margins, especially in the Koobi Fora deposits (Quinn *et al.*, 2007; O'Brien *et al.*, 2020). Similarly, previous studies of the Nachukui deposits have suggested that the west Turkana area likely supported rather heterogeneous habitats during the Plio-Pleistocene, with varying proportions of grassland, bushland and woodland through time (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013). For both localities, regional landscapes were suggested to be highly fragmented, more particularly, after ~2.0 Ma. For the Shungura formation, most studies suggested the presence of mosaic habitats throughout the sequence (e.g. Bobe and Eck, 2001; Alemseged, 2003; Levin *et al.*, 2011; Negash *et al.*, 2015; Blondel *et al.*, 2018), which is consistent with the results obtained in this study from both mesowear and carbon isotope analyses of fossil *Aepyceros* specimens, for which the dietary signals observed were typical of species with mixed-feeding behaviours. The multi-scale dietary variability observed among the *Aepyceros* specimens studied for the Koobi Fora and Nachukui localities could relate to some degree of habitat heterogeneity in these two localities. However, it remains difficult to assess whether these varied diets were related to seasonal changes in local vegetation conditions, or to the presence of year-round mosaic habitats on the eastern and western margins of the basin.

When considering temporal variations in the dietary patterns of fossil impala populations throughout the Plio-Pleistocene sequence, interesting patterns could be observed, as described previously for each of the Omo-Turkana fossil localities (3.5.2) and as summarised in Figure 91. Overall, the differences in dietary patterns observed for fossil *Aepyceros* specimens when comparing assemblages from different members appeared to coincide with environmental shifts indicated by previous studies based on other types of fossil evidence. Most particularly, the suggested shifts in dietary behaviours observed through time for impala specimens from the Shungura formation were shown to be consistent throughout all of the dietary proxies used in this study, and to compare well with other paleo-environmental proxies such as paleosol carbonates (Levin *et al.*, 2011; see also Figure 91) or paleo-dietary analyses of other adaptable herbivore species (e.g. Blondel *et al.*, 2018).

The varied dietary behaviours observed for genus *Aepyceros* across the Omo-Turkana basin during the Plio-Pleistocene and the consistence with which these observations compare well with previous palaeo-environmental reconstructions demonstrate that abundant fossil herbivore species can potentially be useful indicators of palaeo-vegetation conditions in the past, most particularly when focusing on species of high dietary plasticity.

7.4.4.2 Seasonal variability in feeding patterns of fossil *Aepyceros*

In addition to the high spatial and temporal variability in feeding behaviours observed across the studied assemblage for fossil impala specimens (genus *Aepyceros*), results from this study showed, in the Plio-Pleistocene fossil record, a high degree of seasonal dietary variability for all of the *Aepyceros shungurae* specimens sampled for intra-tooth isotopic analysis. The stable carbon isotope ratios observed suggested, overall, diets dominated by C_4 -vegetation, with shifts to mixed C_3 - C_4 diets for some of the specimens. These results would suggest that fossil *Aepyceros shungurae* specimens did vary their diet seasonally, but favoured C_4 -vegetation, similarly to their extant relatives.

Evidence for seasonality in diet had been only assessed for impala, so far, in modern populations (Wronski, 2002; Sponheimer, Grant, *et al.*, 2003; Botha and Stock, 2005; Codron *et al.*, 2006; D. Codron *et al.*, 2007; Copeland *et al.*, 2009; Cerling *et al.*, 2015). Indeed, previous studies have suggested that modern impalas tend to select their food depending on protein content to maintain high levels of diet quality, favouring grass during the wet season when its quality is higher, and browse during the dry season due to decreasing protein content in grasses (Dunham, 1980; Wronski, 2003; Codron *et al.*, 2006). If fossil impalas, similarly to their modern counterparts, varied their diet seasonally to maximize forage quality, intra-tooth variation in stable carbon isotope ratios was expected, with lower $\delta^{13}C$ values corresponding to browsing/mixed-feeding intervals (likely during the dry season) and higher $\delta^{13}C$ values corresponding to grazing intervals (likely during the wet season).

As previously mentioned (3.5.1.2), the intra-tooth data collected for this study confirmed the likely seasonal variation in diet of fossil impala species but suggested a stronger reliance of C_4 -food resources in fossil *Aepyceros shungurae* individuals compared to modern impala populations. Indeed, intra-tooth isotopic evidence revealed seasonally varied diets for most specimens from the Shungura formation. *A. shungurae* specimens from members C (2.91-2.52 Ma), E (2.4-2.32 Ma), and G (2.27-1.9 Ma) were shown to yield large ranges of stable carbon isotope values (i.e. $\sim -6.5‰ < \delta^{13}C < \sim +2‰$), indicative of varied diets alternating between C_4 -material and mixed vegetation, although the isotopic data suggested an important C_4 -component in the year-round diet of all specimens.

Smaller ranges of $\delta^{13}C$ values were observed for the specimens analysed from members B (3.44-2.91 Ma), D (2.52-2.4 Ma), and F (2.32-2.27 Ma), indicative of less variable diets in which C_4 -vegetation was clearly predominant (i.e. $\sim -1‰ < \delta^{13}C < \sim +4‰$). The range of $\delta^{13}C$ values observed in these specimens remained within the range of $\delta^{13}C$ values usually observed in relation to pure grazing behaviours. Yet, despite diets clearly dominated by C_4 -vegetation, each of these specimens displayed an amplitude of $\delta^{13}C$ values of ~2-3‰. This could indicate the consumption of a wide range of C_4 -plant types of differing isotopic composition throughout the year, such as arid-adapted NAD-ME grasses typical of xeric savannah and bushland, mesic NADP-ME grasses more typical of humid environments, or even succulent CAM-plants which tend to mimic the $\delta^{13}C$ values yielded by C_4 -plants (Mooney *et al.*, 1977). Indeed, previous research reported, in the modern Turkana basin area, that the carbon isotope ratios of hyper-grazers feeding on arid-adapted grasses tend to yield more negative $\delta^{13}C$ values (i.e. +1 to +2 ‰) than grazers feeding in more mesic regions (i.e. +2 to +4 ‰) (Cerling *et al.*, 2003, 2010). The higher $\delta^{13}C$ values (i.e. >3‰) observed in the intra-tooth sequence of the specimens from members E to G could reflect the presence of mesic grasslands in the region after ~2.52 Ma. This would be in agreement with previous palaeo-environmental reconstructions for these members (e.g. Bobe and Eck, 2001; Alemseged, 2003; Negash *et al.*, 2015). These results suggest therefore the presence of a wide range of C_4 -resources in the Lower Omo-river valley, either all year-round in rather heterogeneous habitats, or in quantities varying seasonally due to climatic variations.

Overall, the intra-tooth data gathered in this study confirm the likely seasonal variation in diet of fossil impala species but suggest a stronger reliance of C_4 -food resources in fossil *Aepyceros* individuals compared to what was previously recorded among modern *Aepyceros melampus* populations. Such a strong reliance on C_4 - (and potential CAM) -vegetation could indicate a taxon-specific dietary preference for C_4 -vegetation among fossil *Aepyceros* species. However, it could also reflect associated habitats where C_4 -vegetation was the vegetation-type most available to impalas, either due to climatic conditions or to competition for C_3 -resources with other species within the niche. Similarly, the seasonal fluctuation in enamel carbon isotope values observed in most of the *Aepyceros shungurae* specimens studied could suggest, when high $\delta^{13}C$ values dominate the entire intra-tooth sequence, a seasonal alternance between arid-adapted and mesic grasses. This could reflect seasonally changing vegetation availability, or the availability of a large range of C_4 -resources all year-round from which impala populations could alternate seasonally to maximise nutritional content or to compensate for seasonal dietary niche competition.

The highly seasonally variable dietary behaviours observed for genus *Aepyceros* across the Shungura sequence illustrate once more the potential provided by detailed palaeo-dietary studies of highly adaptable herbivores species, as they can inform on the diversity of food resources that were available to extant species at a given time, not only on a large geological scale, but also in finer detail at the seasonal scale.

7.5 Conclusion

By assessing in detail the palaeo-dietary behaviours of mixed-feeding herbivores such as the impala (genus *Aepyceros*) and the springbok (genus *Antidorcas*), this study revealed interesting trends of varying feeding behaviours across the Omo-Turkana basin. Significant differences in dietary ecology could be observed for these taxa when comparing assemblages from different fossil localities, as well as when comparing assemblages between members, suggesting significant changes in dietary behaviours through time. This was more particularly the case for the fossil *Aepyceros* assemblage, which benefits from large sample sizes due to the abundance of this taxon in the East African fossil record. While the *Antidorcas recki* assemblage from the Omo-Turkana basin was less extensive than that of *Aepyceros*, interesting dietary trends were observed for this taxon, more particularly when compared with previous palaeo-ecological studies of *A. recki* specimens from the South African fossil record. Indeed, the predominance of grazing behaviours observed among *A. recki* specimens from eastern Africa contrast with the browsing behaviours suggested for this species in South Africa during the Plio-Pleistocene (Luyt, 2001; Lee-Thorp, Sponheimer and Luyt, 2007; Sewell *et al.*, 2019). This could relate to differing environmental conditions between these two regions, as can be expected due differing latitudinal position and varying degrees of volcanic and tectonic activity (King and Bailey, 2006; Reynolds, 2007; Bailey and King, 2011; Bailey, Reynolds and King, 2011). However, these differences could also be due to species mis-identification, as previous studies have pointed out the difficulty to identify *Antidorcas* specimens at the species-level based on dental remains only, with previous attributions of South African specimens to *A. recki* having been called into question (Vrba, 1976; De Ruiter, 2001; Adams *et al.*, 2016). The marked difference in inferred dietary signals between *A. recki* specimens from eastern Africa and South Africa could indicate that these assemblages actually contained different *Antidorcas* species, raising once more the question whether *A. recki* truly occurred as one species in both eastern and southern Africa.

Most of the palaeo-environmental interpretations drawn from the detailed assessment of these mixed-feeding antelope species were shown to be in agreement with previous palaeo-environmental proxies, highlighting the great dietary plasticity of fossil impala and springbok species. As predicted based on the ecology of their extant relatives, impalas and springbok were shown to have a great dietary plasticity and to have significantly varied their diet depending on the local habitats these species were inhabiting. Results from this study therefore suggest that fossil mixed-feeding herbivore species can be excellent indicators of past environments, most particularly when they can be studied in detail through various proxies.

The multi-scale approach used in this study allowed to investigate the dietary ecology of fossil herbivore to a great detail and to identify variations in dietary behaviours through the lifetime of the studied individuals. This allowed to make inferences on habitat heterogeneity and seasonal variation in diet in the past, which can seldom be achieved when using a single dietary proxy.

The use of intra-tooth stable isotope analysis in addition to use-wear and bulk isotopic analyses provided much needed insights into the seasonality of the dietary patterns observed from *Aepyceros* specimens from the Shungura formation, complementing previously published research using this method on other taxa from this fossil formation. More specifically, the ranges and patterns of $\delta^{18}O$ values observed in the studied assemblage suggested a time of relatively high climatic variability associated with high seasonal variations in rainfall amount between 2.27 and 1.9 Ma, which would agree with previous research that hypothesized that seasonal and interannual rainfall variability in eastern Africa increased at ~2.0 Ma in response to the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.*, 2004; Blumenthal *et al.*, 2017; Hopley *et al.*, 2018). However, future analysis of additional impala specimens for these members will be required to confirm such trend. In addition, seasonal variability in diet could not be assessed for the other two localities using this method. It could be interesting, in future work, to attempt comparing the degree of seasonality in diet observed through intra-tooth analysis for *Aepyceros* specimens from Shungura, Koobi Fora and Nachukui. This would allow to assess whether the high degree of seasonal dietary variation observed for impalas from the lower Omo-river valley was mirrored in impalas living further away from the river, closer to the lake margins, where palaeo-vegetation conditions differed drastically, as illustrated in this work and in previous studies.

Similarly, future work could focus on assessing the range of impala dietary patterns in more spatial detail within each of these fossil localities to tackle questions around within-sites habitat diversity. However, due to small sample sizes for most members and most sub-localities as well as time-averaging issues, it might remain difficult to observe trends in dietary behaviours that can be reliably interpreted.

While results from this study have shown the high potential of using palaeo-dietary data from fossil mixed-feeding antelopes to help assess palaeo-vegetation conditions, it remains difficult to evaluate, when observing evidence for dietary plasticity and mixed-feeding behaviours, whether such behaviours were likely associated to seasonal variation in vegetation composition or to year-round locally heterogeneous habitats. To attempt providing more tools to interpret fossil evidence, the relationship between land cover and dietary behaviours of modern impala populations is explored in the next chapter.

Chapter 8: Discussion and conclusion

The Plio-Pleistocene of eastern Africa saw the emergence and disappearance of several hominin species, such as *Australopithecus afarensis*, *Homo habilis*, *Paranthropus boisei*, and *Homo ergaster*. This period and region also saw the advent of stone tool technologies (e.g. Lomekwian, at ~3.3 Ma; Harmand *et al.*, 2015), as well as other associated behavioural advancements, such as the controlled use of fire (James *et al.*, 1989). Because of the abundance of fossil evidence preserved alongside these fossil hominid remains, the region and period have been extensively studied in the past to better understand the context of human evolution, and theorise about the factors that likely influenced speciation, extinction, dispersal events, as well as favoured the technological advancements observed throughout the human lineage. As previously mentioned in chapters 1 and 2, major Pliocene and Pleistocene climate transitions have been suggested to have led to cooling, drying trends that resulted in the spread of grasslands and the shrinking of forests (e.g. Demenocal, 1995; Spencer, 1995;, Lee-Thorp *et al.*, 2007), and which were hypothesized, in turn, to have led to major changes in the structure and composition of local floral and faunal communities (e.g. Vrba 1985). Such changes potentially triggered some of the major biological and behavioural changes observed within the hominin clade (e.g. tool use, increase in brain size, dispersal events… etc), particularly in relation to the emergence of the genus *Homo* (Dart, 1925; Hopley *et al.*, 2007).

The Omo-Turkana basin (Ethiopia/Kenya), in particular, has been the focus of many studies due to the discovery of several hominin species in relatively rich and well-dated fossil deposits. Distinct changes in palaeo-environmental condition in this region were indicated by several studies, suggesting a trend of gradual change towards more arid conditions in the region between ~4.0 and ~2.0 Ma (e.g. Sepulchre *et al.*, 2006; Feibel and Smith, 2011; Fortelius *et al.*, 2016), with increasingly warmer and drier conditions after 2.2 Ma (Cerling and Hay, 1986; Uno, Polissar, Jackson, *et al.*, 2016). However, if most studies agree on the general palaeo-environmental trends presented above, more detailed reconstructions of habitats within each of the Omo-Turkana basin fossil localities have proven more complex, with individual palaeo-environmental proxies sometimes disagreeing for some localities during specific time-intervals, more particularly regarding the degree of habitat heterogeneity and the amount of C_3-vegetation present at the time (e.g. Bobe and Eck, 2001; Alemseged, 2003; Brugal, Roche and Kibunjia, 2003; Bobe, 2011; Cerling, Mbua, *et al.*, 2011; Levin *et al.*, 2011; Quinn *et al.*, 2013; Domínguez-Rodrigo, 2014; Du and Alemseged, 2018). Diverging conclusions between studies could relate to the limitations of each method and of the fossil record, but could also highlight the complexity of palaeo-habitats, with each method and palaeo-environmental proxy contributing to refining the picture drawn of the landscapes inhabited by hominins.

This research project proposed to take advantage of the abundance of bovid dental remains in the Omo-Turkana fossil deposits, and of the multiplicity of methods available for dietary ecology studies, to test the relevance of detailed palaeo-dietary analyses of mixed-feeding herbivores for palaeo-environmental reconstructions. Ecological data from modern populations and their associated habitats were explored as well, to evaluate the strength of the relationship between the dietary behaviours of mixed-feeding herbivores, as inferred from the isotopic content of their teeth, and the vegetation conditions of their habitats.

Indeed, while herbivores, especially bovids, are often considered faithful reflectors of vegetation conditions in their habitat, and have often been a focus of research (e.g. Vrba, 1995, 1974, 1980; Harris, 1991; Brink and Lee-Thorp, 1992; Kappelman *et al.*, 1997; Bobe and Eck, 2001; Sponheimer, Lee-Thorp, *et al.*, 2003; Lee-Thorp, Sponheimer and Luyt, 2007; Lüdecke *et al.*, 2016; Blondel *et al.*, 2018), mixed-feeding species, which tend to have very variable diets, have seldom been the focal point of details studies (e.g. Sewell, 2019; Sewell *et al.*, 2019). Yet, flexible feeding behaviours could potentially provide interesting data regarding environmental conditions in a studied region, as mixed-feeding species are able to adapt their diet locally and/or seasonally according to the prevailing vegetation in the area. Because of the abundance of Aepycerotini remains (i.e. the impala, genus *Aepyceros*) in the fossil record of East Africa, and due to the reported dietary plasticity of their extant relatives, the impala was selected as the focal study taxon in this project. Similarly, because particular attention has been given in previous work, especially for the South African Plio-Pleistocene, to another mixed-feeding species, the springbok (genus *Antidorcas*), the dietary ecology of fossil springbok specimens from the Omo-Turkana basin was also studied, to compare with that of fossil impala specimens, but primarily to allow future comparisons with datasets from South Africa (e.g. Sewell, 2019; Sewell *et al.*, 2019).

The dietary ecology of these taxa was evaluated through stable carbon and oxygen isotope, mesowear and dental microwear textural analyses. The results obtained from these complementary methods were combined to evaluate the detailed dietary behaviours of the studied fossil species (i.e. early life, lifetime, last weeks prior to death), enabling the investigation of the structural properties of the food items consumed (toughness, abrasiveness, grain size) as well as their chemical properties (isotopic content). To provide more tools to interpret fossil evidence, the influence of local land cover patterns on the dietary behaviours of modern impalas was investigated using published stable carbon isotope data alongside land cover data from selected study areas in Africa. This data was then used to build predictive models designed to evaluate the degree to which some of the Omo-Turkana habitats (i.e. specific localities and members) might have resembled some of the studied modern-day African habitats, in terms of land cover composition and land cover structure.

This project therefore examined the dietary behaviours of selected extant and extinct mixed-feeding antelopes, using a combination of methods to assess whether detailed studies of the dietary ecology of mixed-feeding antelope species could be used to investigate hominin palaeo-environments in the Omo-Turkana basin during the Plio-Pleistocene. More particularly, this research aimed to assess whether abundant and adaptable herbivores such as the impala or the springbok could prove to be accurate local vegetation proxies, checking upon the assumption that their dietary behaviours are mainly influenced by the vegetation conditions in their habitats. This was to work towards the following research aims:

- Provide a new method to compare past and present habitats by testing the relationship between modern impala dietary variability and their habitats (i.e. predictive land cover models)
- Study the dietary ecology of mixed-feeding antelope species in the Omo-Turkana basin between 3.5-1.6 Ma
- Discuss the palaeo-environmental implications of the inferred dietary patterns, in relation to human evolutionary theories

This chapter discusses the results obtained throughout this study, and how these answer the initial research questions set out for this work. Firstly, the potential of combining dietary analyses with land cover studies of modern mixed-feeding populations to provide an additional tool for palaeo-environmental reconstruction is discussed, as well as the differences between fossil taxa and their extant relatives (8.1). Secondly, the dietary ecology of the studied mixed-feeding antelope species is examined for the Omo-Turkana basin fossil record, summarising the trends observed for the inferred feeding behaviours, and discussing their potential palaeo-environmental implications (8.2). Finally, the palaeo-environmental conditions in the Omo-Turkana during the Plio-Pleistocene suggested from this study are discussed in relation to previous theories linking palaeo-environmental conditions/major shifts in climate to mammalian evolutionary events, to evaluate the potential implications of results from this study when considering hominin habitats and hominin evolution (8.3).

8.1 Mixed-feeding herbivore diets as a palaeo-vegetation proxy

81.1 Initial research questions

With fossil mammals constituting a significant part of the fossil record in the field of palaeontological studies, palaeo-environmental reconstructions are often proposed based on in-depth studies of faunal assemblages. The composition of the faunal record as well as the relative abundance of specific taxa are often used, for instance, to assess the type of habitats that likely provided the optimal environmental conditions for the biodiversity observed from the fossil evidence (e.g. Harris, 1991; Vrba, 1995; Kappelman *et al.*, 1997; Bobe and Eck, 2001). Herbivores, more particularly, are often considered as faithful reflectors of prevailing vegetation types in a habitat because of the various dietary specialisations that are known from extant populations, and which can be deducted for extinct species based on specific traits such as dental morphology (Janis and Fortelius, 1988; Gagnon and Chew, 2000; Hillson, 2005).

Although faunal remains can provide valuable evidence to reconstruct palaeo-environments, palaeontological studies can suffer from various biases. For instance, analyses focusing on faunal abundance data can suffer from taphonomic and identification/collection biases (e.g. Maxwell *et al.*, 2018). These can cloud the palaeo-environmental signal as part of the ecological niche sampled might be missing or mis-represented in the assemblage. Another bias that can significantly impact palaeo-environmental reconstructions is the fact that reconstructions focusing on presence/absence of specific taxa strongly rely on knowledge of the behavioural ecology of modern mammals, assuming that ancestral species shared similar behaviours with their extant relatives. This bias can be reduced by complementing faunal composition studies with palaeo-dietary analyses to check, in addition to morphological studies, if the diet of extinct species compares well with that of their extant relatives.

In the case of mixed-feeding species such as the impala (genus *Aepyceros*), however, assuming association to a specific habitat type based on their presence in an assemblage may be only tentative, as their extant relatives have been described as highly adaptable. Detailed studies of modern impala populations, for instance, have shown that these antelopes are mixed-feeders with a varying seasonal diet, which can adapt their diet depending on local food availability by shifting between grazing and browsing (Wronski, 2002; Sponheimer, Grant, *et al.*, 2003; Cerling *et al.*, 2015). Regional variations in dietary content were observed in modern populations in several studies (Sponheimer, Grant, *et al.*, 2003; Wronski, 2003; Codron *et al.*, 2006; Copeland *et al.*, 2009), suggesting dietary behaviours strongly influenced by forage quality and availability.

Because forage quality and availability are strongly dependant on local vegetation, climate, and soil conditions, it was hypothesized for this research project that the detailed study of the diet of impalas might act as a good indicator of local vegetation conditions, in both the present and in the past. To test this hypothesis, the relationship between local land cover patterns and modern impala dietary behaviours was studied using land cover maps of selected modern African landscapes and published stable carbon isotope data. This was to test whether modern impala dietary variability could be positively correlated with specific habitats and climatic conditions, and assess if such relationship could be used to help interpret dietary patterns identified from the fossil record. In addition, the dietary patterns of fossil impala and springbok specimens from the Plio-Pleistocene were analysed and compared with modern dietary data. This was to evaluate how different the inferred feeding behaviours of the studied species were in the past, compared to modern days.

This section therefore explores the first main research question set out for this project: **What type of evidence can dietary studies of mixed-feeding herbivores provide to help make inferences about the prevailing vegetation conditions of their local habitats?**

8.1.2 Outcome of this research

What is the relationship between modern impala dietary variability and the composition/structure of their habitats (evaluated through land cover analysis of modern landscapes)?

It was hypothesized that, if modern *Aepyceros melampus* truly adapts its diet to prevailing vegetation conditions, the variation in diet observed for different modern populations should mirror differences in vegetation cover between their habitats. For instance, if modern impala does adapt its diet to prevailing vegetation conditions, impala populations associated with closed-wooded environments should yield dietary signals indicative of a preference for browse/C_3-vegetation, as opposed to populations associated with open-grassland habitats, which should yield dietary signals indicative of diets dominated by graze/C_4-vegetation. It was also hypothesized that the degree of habitat fragmentation might also have an influence on the diet of modern impala populations, with more varied diets observed where habitats are highly fragmented and diverse, when compared to more homogeneous habitats with less vegetation diversity. If such clear relationships could be established between modern impala diet and habitat vegetation-conditions, it would suggest that dietary analyses of mixed-feeding species such as the impala can be used faithfully as vegetation-proxies in further studies.

The high variability in stable carbon isotope ratios observed in this study among modern impala populations, and the wide range of habitats these were associated to according to land cover data, highlighted that modern impalas tend to rely heavily on palatable grasses and forbs, suggesting a preference for C_4-plants for their higher protein content. These results were in agreement with previous studies that observed that impala populations include C_3-vegetation in their diet where and when high quality C_4-vegetation is not available in sufficient quantities in their habitats, either all-year round or seasonally.

Results from the models testing the relationship between land cover and stable carbon isotopes were partly in agreement with the initial hypothesis that impala individuals with high $\delta^{13}C$ values would be more likely associated to C_4-habitats, while individuals with low $\delta^{13}C$ values will be more likely associated to C_3-habitats. This positive relationship between the amount of C_4-vegetation present in the landscape and the amount of C_4-vegetation included in the diet was clearly observed for four of the seven localities studied (i.e. Swara, El Karama, Mpala, and KNP-North), but not for the other three localities (Nakuru, Welgevonden and KNP-South). Because of this, the models computed tended to struggle to differentiate either mixed from C_4-dominated habitats, or heterogeneous C_3-habitats from heterogeneous mixed/C_4-habitats. This could suggest that the diet of modern impalas do not always reflect the vegetation types prevailing in their environments. Indeed, it can be hypothesized that if high quality C_4-vegetation is available all year-round in their habitat, impalas will only include a limited amount of C_3-plant material in their diet, even if that vegetation-type is available to them. Such case was illustrated by the impala populations from the South of Kruger National Park (KNP, South Africa) whose diets indicated a strong reliance on C_4-vegetation despite a predominance of C_3-vegetation in the area. In contrast, impalas from the north of the park were shown to include a larger amount of C_3-vegetation in their diet, which could be explained by the reduced availability of herbaceous forage in the north of the park compared to the south, as described in previous studies (Sponheimer, Grant, *et al.*, 2003). Such cases suggest that while impala diets dominated by C_4-plants indicate the presence of herbaceous monocots in the landscape, it does not necessarily indicate the absence of C_3-vegetation in their habitat.

Interestingly, results from the general landcover model (model 2) showed that individuals with the most negative $\delta^{13}C$ values tended to be associated to heterogeneous and highly fragmented C_3-habitats or heterogeneous mixed/C_4-habitats (i.e. habitats similar to those observed in KNP-North or Nakuru), while individuals with the least negative $\delta^{13}C$ values were associated to homogeneous C_4-habitats (i.e. habitats similar to those observed in Swara and El Karama). This could suggest that heterogeneous and fragmented habitats tend to be associated with more varied diets for impalas, as initially hypothesized, and that variations in $\delta^{13}C$ values can potentially reflect not only the relative proportion of C_3-C_4 vegetation included in the diet, but also the structure and diversity of the vegetation present in the landscape.

Based on these results, it appears that impala could serve as a vegetation proxy in future studies, although a more detailed study of the dietary behaviours of modern impalas could help improve our understanding of the relationship between diet and land cover, and improve the accuracy of this approach. More particularly, a study including a larger number of samples and populations from a larger variety of habitat types, as well as data on seasonal variation in diet and land cover, could provide a clearer picture of the diversity of habitats inhabited by modern *Aepyceros* and the dietary strategies employed by each population to thrive in these habitats.

Although the models built for this study revealed some limitations, the predictions generated for fossil *Aepyceros* samples for the Omo-Turkana basin based on modern land cover and stable isotope data were consistent with some of the previous palaeo-environmental studies published for this region. This showed the potential of this method, as well as the potential for dietary analyses of mixed-feeding taxa to be used as an additional tool for palaeo-environmental reconstructions, albeit with room for the method to be developed further to test and improve accuracy.

How do the studied taxa's dietary patterns in the past compare to the dietary signals of their extant relatives?

Because Plio-Pleistocene environmental conditions likely differed greatly from modern African climatic conditions, differences in inferred dietary patterns were expected when comparing modern and fossil mixed-feeding populations. While the dietary analyses performed on the obligate grazing (genus *Equus*) and obligate browsing (genus *Giraffa*) taxa indicated similar dietary ecology between modern populations and their extinct relatives, more differences were observed when comparing extant and extinct species for genera *Aepyceros* (impala) and *Antidorcas* (springbok), as expected.

Results from analyses of the *Antidorcas recki* assemblage suggested diets that differed greatly from extant *Antidorcas marsupialis*, with, overall, mixed-diets with a preference for graze in the fossil assemblage, contrasting with the mixed-diets with a preference for browse described for modern springbok (Bigalke, 1972; Estes, 1991; Sponheimer, Lee-Thorp, *et al.*, 2003). These results are consistent with previous studies that highlighted the wide range of dietary behaviours that existed in the fossil record across the different fossil *Antidorcas* species (Brink and Lee-Thorp, 1992; Luyt, 2001; Lee-Thorp, Sponheimer and Luyt, 2007; Ecker and Lee-Thorp, 2018; Sewell *et al.*, 2019). Most interestingly, the dietary patterns observed for the Omo-Turkana basin *A. recki* assemblage were in contrast with the patterns observed in previous studies of *A. recki* assemblages from the South African fossil record, which indicated mixed-feeding habits with a preference for browse for this species (Luyt, 2001; Lee-Thorp, Sponheimer and Luyt, 2007; Sewell *et al.*, 2019). However, the high dietary plasticity of this fossil springbok species and the importance of C_4-plant resources to its diet highlighted in the present study were suggested as well for Pleistocene *cf. A. recki* specimens from Olduvai (Tanzania) (Rivals *et al.*, 2018). These differences in palaeo-ecological reconstructions of *Antidorcas recki* dietary behaviours between the eastern and the southern African fossil records could potentially highlight different palaeo-vegetation conditions between the two regions. Such differences would be expected due to the difference in latitudinal position between these regions, which results in climatic conditions favouring C_3-vegetation at higher latitudes, as opposed to landscapes closer to the Equator where C_4-vegetation is often dominant. However, these differences could also be due to species mis-identification and to the difficulty if identifying Antidorcas specimens at the species-level based on dental remains only. Indeed, some South African specimens previously attributed to A. recki, have since been questioned (Vrba, 1976; De Ruiter, 2001; Adams *et al.*, 2016; Sewell, 2019). The marked difference in inferred dietary signals between *A. recki* specimens from eastern Africa and South Africa could indicate that these assemblages actually contained different *Antidorcas* species, raising once more the question whether *A. recki* truly occurred as one species in both eastern and southern Africa.

Analyses of the impala assemblage suggested that extant and extinct *Aepyceros* species might have differed in their dietary ecology. *Aepyceros shungurae* yielded similar dietary patterns than modern *Aepyceros melampus,* but the diet of fossil *Aepyceros melampus* specimens differed by a stronger grazing/C_4-component in their diet. Predictions from the different models built for this study suggest that, in the studied assemblage, most fossil *Aepyceros melampus* specimens were associated to either mixed habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2). Most *Aepyceros shungurae* specimens were predicted to be associated to a wider variety of habitats, either to a mixture of C_3- or mixed habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2), suggesting more heterogeneous habitats and/or a stronger reliance on C_3 -vegetation for species *Aepyceros shungurae*. The difference in dietary signals observed between these *Aepyceros* species was interpreted as possible evidence for differing local habitats, as *Aepyceros shungurae* was found in the Shungura formation and in the Nachukui formation member Lomekwi, while *A. melampus* specimens were represented in samples from the Koobi Fora and Nachukui formations. These results were in agreement with previous studies which suggested, based on its morphology (straighter, less lyrated and more gracile horn cores, shorter and thicker limb bones), that *A. shungurae* might have inhabited preferentially more closed woodland habitats than *A. melampus* (Harris, 1991; Bobe and Eck, 2001).

Overall, the results obtained from the analysis of mixed-feeding antelope species showed that the dietary ecology of fossil herbivore species do not always mirror that of their extant relatives, especially when studying bovid taxa that are known today to be able to survive on various types of food resources. These results are in line with those of the palaeo-dietary study undertaken by Blondel *et al.* (2018) which highlighted the significant intra-tribal dietary variability of tragelaphines in the fossil record (i.e. from predominantly C_3 browsing to C_4 grazing) (Bedaso *et al.*, 2013; Bibi *et al.*, 2013; Negash *et al.*, 2015), which contrasted with the diet of their extant relatives, known to subsist mainly on browse. This demonstrates the importance of palaeo-dietary studies to assess the likely dietary behaviours of extinct species, as a way to improve the accuracy of palaeo-environmental reconstructions based faunal association data.

Can data from modern impala populations' dietary behaviours and habitats be used to identify modern African environments that might be similar to those experienced by impala populations in the past, and if so, what are the main characteristics of these modern habitats?

It was hypothesised that, if similar dietary patterns can be identified between selected fossil impala assemblages and specific modern impala populations, it might indicate that these populations were associated to similar habitats.

The predictions from the land cover models presented in chapter 3 suggested that vegetation conditions in the Koobi Fora and Nachukui formations during the Plio-Pleistocene resembled mixed- or C_4 -vegetation dominated habitats, likely reflecting local environments similar to most of the modern localities studied where open-grassland conditions prevailed (e.g. Swara, El Karama, Mpala) or where high quality C_4 -vegetation was available in sufficient quantities all year-round in either mixed or C_3 -dominated habitats (e.g. Nakuru and KNP-South) (see Figure 92 for illustrations).

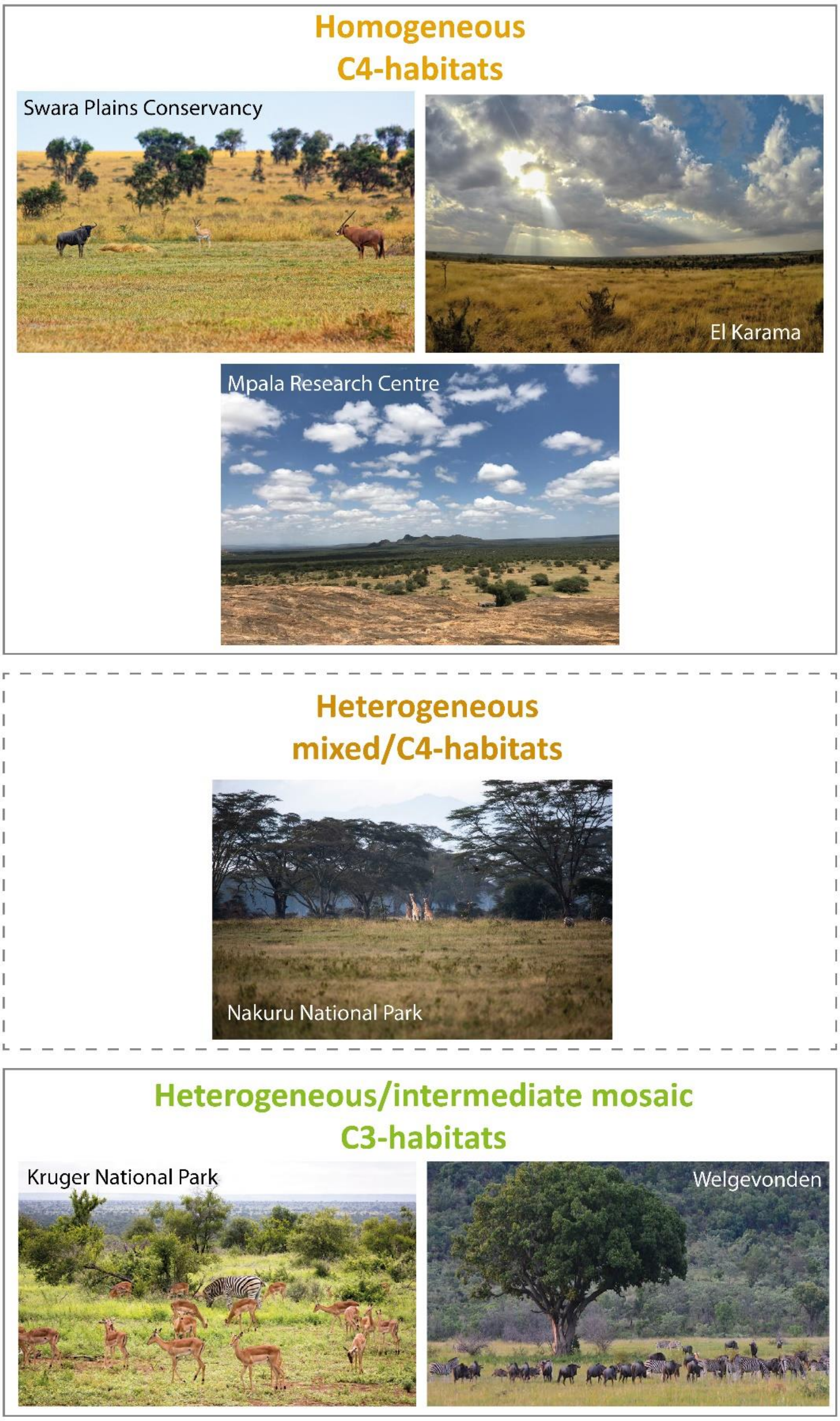

Figure 92: Examples of land cover types associated with the modern impala populations studied. Photo credits: ©Ross Donihue (for Nakuru National Park), © Steppes Travel 2021(for El Karama), Copyright © 2021 African Safari Group (for Welgevonden), © 2021 The Mawazo Institute (for Mpala Research Centre),photo by Allison McCarthy @2019 Intrepid Travel (for Kruger National Park), ©Kjersti Holmang, https://iallverden.no/ (for Swara Plains).

The range of $\delta^{13}C$ values observed for impala specimens from the Shungura formation suggested more varied vegetation conditions throughout the sequence. Vegetation conditions between 3.44 and 2.52 Ma and between 2.4 and 2.32 Ma were suggested to be similar to the land cover conditions observed in Welgevonden and in the north of Kruger National Park (KNP), where vegetation is relatively heterogeneous but dominated by woodland-type habitats (i.e. C_3 -vegetation). In contrast, the local habitats suggested for the Lower Omo-river valley between 2.52 and 2.4 Ma and between 3.32 and 1.9 Ma were similar to those experienced by impalas from Koobi Fora and Nachukui.

5.1.3 Perspectives for future research

Future work using a modelling approach to reconstructing palaeo-environments from palaeo-dietary data could improve the precision and relevance of the predictions by including in the model additional variables that can help identify patterns of dietary plasticity in extinct species. More particularly, future work could focus on building a strong and detailed modern dataset to record the dietary variability of extant impalas in carefully selected localities, ideally using dietary proxies that can easily be compared with data from the fossil record (i.e. stable isotopes, or dental use-wear). By also recording detailed information on their habitats and the local conditions experienced by the studied populations (climate, seasonal changes, niche competition, etc), the models tested in this study could be improved and provide more accurate predictions to help evaluate in more detail what types of habitats and land cover patterns once characterised the landscapes of eastern Africa during the Plio-Pleistocene.

In addition, improved models could be used on other mammal taxa for which isotope data is available for both extant and extinct population. This would allow to explore how different faunal communities directly relate to their environments and how dietary studies can inform on their habitats depending on their feeding ecology. Building a strong modern baseline for various mammals to compare with the fossil record could help explore local Plio-Pleistocene environments from a different angle by testing if models calibrated for various groups would converge in similar environmental reconstructions when fitted to a same fossil depositional context.

8.2 Dietary ecology of mixed-feeding antelopes in the Omo-Turkana basin between 3.5 Ma and 1.6 Ma

8.2.1 Initial research questions

Various palaeo-environmental proxies have been previously used to reconstruct Plio-Pleistocene habitats in the Omo-Turkana basin. These reported, overall, a general trend of increasing open grasslands in the environment, with a significant shift from C_3 - to C_4-dominated landscapes occurring more particularly at ~1.8-1.9 Ma at the time of the transgression/regression of Lake Lorenyang in the basin. While more arid open habitats have been suggested in Koobi Fora and Nachukui, more wet closed environments were described for the Shungura deposits. However, more recent studies focusing on habitat diversity within each of the Omo-Turkana basin formations proposed more complex land cover patterns than those described in previous studies, suggesting that a high degree of spatial heterogeneity likely characterised the palaeo-habitats of this region (e.g. Du and Alemseged, 2018). Such results led to hypothesize that habitat heterogeneity may have influenced hominin presence and evolution through complex biotic interactions that necessarily impacted human foraging strategies and selective pressures.

This study proposed to examine the dietary behaviours of selected extinct mixed-feeding antelopes, using a combination of methods to produce a comprehensive picture of the environments experienced by these species during the Omo-Turkana basin fossil deposition. It was hypothesized that if, across all dietary proxies, a predominance of diets dominated by a main vegetation-type (browse/C_3 or graze/C_4) was observed across taxa, this could indicate a rather homogeneous vegetation cover in that area during the time span examined, forcing a majority of the studied specimens to feed primarily on the type of resources that was available to them in larger proportions. A wider range of isotopic ratios and dental microwear textures, indicative of a large range of resources, would likely indicate the presence of more heterogeneous environments and more variable aridity levels, with habitats able to support a greater range of species.

The results obtained from both palaeo-dietary analyses and predictive models are summarised in this section and are discussed to evaluate the potential palaeo-environmental implications of these observations, and propose inferences about vegetation cover conditions in the Omo-Turkana basin between 3.5 and 1.6 Ma. Basin-wide habitat composition is discussed as well as smaller-scale habitat heterogeneity (East, West and North of Lake Turkana) and variations through time. Results from this study are compared with previous research to assess whether impala and springbok dietary proxies agreed with other datasets for climate and vegetation from the area, and to answer the following research question: **what additional insights into palaeo-environmental conditions in the Omo-Turkana basin do the inferred dietary patterns of mixed-feeding species provide, and how do these help to resolve apparent contradictions between other environmental proxies?**

8.2.2 Outcome of this research

Do the inferred dietary patterns of mixed-feeding antelope differ from one locality to the other across the Omo-Turkana basin (e.g. Lower Omo river valley vs East/West Turkana), and what do these differences (if any) could imply in terms of local vegetation conditions?

For the dietary results of this study to confirm differences in local vegetation conditions across the Omo-Turkana basin suggested by previous studies (e.g. Bobe *et al.*, 2007; Cerling, Levin and Passey, 2011; Levin *et al.*, 2011), differences in inferred dietary behaviours were expected between the assemblages, with a higher variability in diet through time and a stronger browsing/C_3-dominated diet signal in individuals from the Shungura formation, when compared to individuals from the Koobi Fora and Nachukui Formations. The presence of mosaic habitats (Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Patterson *et al.*, 2017) in the Omo-Turkana basin were hypothesized to be potentially reflected in the dietary results of this study if mixed-feeding signals could be shown to dominate the assemblages in some localities/members, with no distinct preference for either graze or browse, suggesting that a wide range of food resources were available to these herbivores throughout the sequence and the region.

When assessing the palaeo-dietary behaviours of the impala (genus *Aepyceros*), significant differences in dietary ecology were observed when comparing assemblages from different fossil localities. The patterns of dietary variation among fossil *Aepyceros* populations were (if reflective of local vegetation conditions as initially hypothesized) consistent with previous studies which suggested more arid open habitats in Koobi Fora and Nachukui, while more wet closed habitats prevailed in the Shungura deposits (e.g. pedogenic carbonates data, Levin *et al.*, 2011). Indeed, although stable carbon isotopes indicated a prevalence of C_4-vegetation in the diet of most impala specimens, multi-proxy analyses highlighted clear differences between fossil impala specimens from these regions.

Specimens from the Lower Omo-river valley were suggested to have diets that included a larger amount of softer food items and C_3-vegetation, compared to the diet of specimens from the other two fossil localities. The predictions that were generated from the land cover models suggested a stronger C_3-vegetation component in the habitats associated with impalas from the Shungura formation as well as a greater land cover diversity, compared to habitats in the rest of the Turkana basin. The strong C_4-component that was identified in the diet of impalas from the Shungura formation could potentially be explained if fossil impalas had a preference for C_4-vegetation similar to that of their extant relatives, as suggested from the present analyses of modern impala populations. This would suggest that environments in the Shungura formation were indeed more mesic and wooded than environments in the Koobi Fora and Nachukui formation, but that vegetation in the lower Omo-river valley included a significant amount of C_4-resources that fossil impalas could rely on preferentially, at least seasonally. Results from intra-tooth stable isotope analyses confirmed that most of the impala specimens studied varied their diet throughout the year, switching from C_4-dominated to mixed-diets seasonally.

In contrast, results from stable carbon isotope analysis suggested drier habitats with a stronger C_4-grassland component in Koobi Fora and Nachukui, compared to habitats in Shungura. However, the mixed/fruit-browsing feeding behaviours observed through use-wear analyses for most specimens from these two localities likely indicated the presence of a wide range of resources within these two regions during the Plio-Pleistocene. Similarly, results from multi-scale dietary analysis of *Aepyceros* specimens from East and West Turkana highlighted varied dietary patterns through life for most individuals, suggesting seasonal variation in food availability, either due to seasonal changes in land cover or local habitat heterogeneity. In line with these observations, predictions suggested that most *Aepyceros* specimens from Koobi Fora and Nachukui were likely associated to either mixed-habitats (model 1), or to heterogeneous mixed/C_3 habitats (model 2).

These interpretations of the dietary patterns inferred from a multi-method analysis of mixed-feeding antelope taxa from the Omo-Turkana basin therefore align with studies which argued for high spatial heterogeneity and the presence of highly fragmented habitats across the basin, with varying degrees of vegetation heterogeneity depending on proximity to the lake margins (e.g. Quinn *et al.* 2007, O'Brien *et al.* 2020). For instance, previous studies of the Nachukui deposits suggested that the west Turkana area likely supported rather heterogeneous habitats during the Plio-Pleistocene, with varying proportions of grassland, bushland and woodland through time (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013), while most studies of the Shungura Fm suggested the presence of mosaic habitats throughout the sequence (e.g. Bobe and Eck, 2001; Alemseged, 2003; Levin *et al.*, 2011; Negash *et al.*, 2015; Blondel *et al.*, 2018). Interpretations from the present study are therefore consistent with these previous analyses using other palaeo-environmental proxies, the multi-scale dietary variability observed among the *Aepyceros* specimens studied for the Koobi Fora and Nachukui localities potentially reflecting some degree of habitat heterogeneity in these two localities, although it remains difficult to assess whether these varied diets were related to seasonal changes in local vegetation conditions, or to the presence of year-round mosaic habitats on the eastern and western margins of the basin.

How much variation in inferred dietary behaviours can be observed throughout the Omo-Turkana sequences, and what type of trends do these variations suggest (i.e. no variation through time, gradual/pulsed changes, increased variability in diet, browsing/grazing alternance…etc).

For the dietary results of this study to confirm the long-term trend of regional aridification suggested by previous studies (e.g. Sepulchre *et al.*, 2006; Feibel and Smith, 2011; Fortelius *et al.*, 2016)(Sepulchre *et al.*, 2006; Feibel and Smith, 2011; Fortelius *et al.*, 2016), general dietary trends for the studied mixed-feeding taxa were expected to demonstrate an increase in grazing signals through time. In addition, for the results of the present study to agree with previous studies, dietary behaviours of fossil impalas and springbok were expected to display an increased dietary variability through time, which might relate to varying degrees of habitat heterogeneity and to a gradual increase in climatic variability through time, as suggested by other studies (e.g. Potts, 2007).

When assessing the palaeo-dietary behaviours of the impala (genus *Aepyceros*), significant differences in dietary ecology could be inferred when comparing assemblages from different members within the studied fossil localities, suggesting significant changes in dietary behaviours through time.

Overall, the dietary patterns observed across the studied taxa from the Koobi Fora Fm likely suggested rather varied diets (potentially reflecting heterogeneous habitats in this locality during the Plio-Pleistocene), with a gradual increase in the proportions of C_4-resources in the diet (potentially reflecting an increase in the proportions of C_4 grasses and sedges in the landscape). This pattern could relate to an increase in aridity conditions, especially after ~1.87 Ma. Similar dietary patterns were inferred for the specimens from the Nachukui Fm, suggesting a high vegetation heterogeneity associated to a slight gradual increase in C_4 -resources in the environment from ~2.8 Ma was suggested for the Nachukui formation. However, if fossil impalas had a preference for C_4-vegetation similar to that of their extant relatives, an observed increase of their grazing signals through time might not necessarily reflect a decrease in woody vegetation but might relate, more simply, to a greater availability of high quality C_4-vegetation in landscapes that retained a significant amount of C_3-vegetation. This would agree with previous studies which suggested that C_3-woodlands remained an important component of the vegetation in the Nachukui formation despite a gradual grassland expansion, resulting in highly fragmented regional landscapes in the region, more particularly after ~2.0 Ma (Brugal, Roche and Kibunjia, 2003; Quinn *et al.*, 2013). A similar pattern of grassland expansion and increased habitat fragmentation from ~2.0 Ma was suggested as well for the Koobi Fora formation (Quinn *et al.*, 2007).

The range of $\delta^{13}C$ values observed for impala specimens from the Shungura formation in members B, C and E were similar to the range of values observed in modern specimens from Welgevonden and the north of Kruger National Park (KNP) where C_3 -vegetation dominated, and where less C_4 -plant material was likely available to impalas in the landscape. This suggested that local habitats were likely dominated by closed wooded C_3-environments between 3.44 and 2.52 Ma and between 2.4 and 2.32 Ma. These predictions were consistent with previous palaeo-environmental reconstructions which described environments dominated by C_3 -vegetation and closed-wooded habitats for a long part of the Shungura sequence (up to ~2.0 Ma), alongside mosaic habitats (Alemseged, 2003; Barr, 2015; Plummer *et al.*, 2015). In contrast, the local habitats suggested for the Lower Omo-river valley between 2.52 and 2.4 Ma and between 3.32 and 1.9 Ma were similar to those experienced by impalas from Koobi Fora and Nachukui, likely reflecting environments were C_4-grassland was dominant or represented in the landscape all year- round.

What additional information on the taxa's dietary ecology does combining dietary-proxies provide, as opposed to using each dietary-proxy in isolation?

As discussed in chapter 2, each of the dietary proxies used in this study suffer from limitations that are inherent to the method used and the part of the dental remains that is analysed. For instance, the mesowear method can only inform on the overall degree of toughness and abrasiveness of the consumed food items though life, which does not allow palaeo-environmental interpretations of greater detail than the open habitat vs closed habitat dichotomy based on the general grazing vs browsing dietary categories. On the contrary, while dental microwear textural analysis (DMTA) can provide information on individual feeding behaviours in relation to the physical properties of the food items in greater detail than mesowear analysis, this method can only identify dietary patterns on a short time scale (few days/weeks before death), due to the rapid turnover rate of the traces imprinted on the enamel surface (Kaiser and Brinkmann, 2006; Ungar, 2015; Calandra and Merceron, 2016). These limitations have led previous researchers to combine these two dental use-wear analysis methods, using microwear and mesowear analysis together to assess dietary behaviours in greater detail and on a different temporal scale, allowing to potentially detect seasonal changes in diet (Rivals, Solounias and Mihlbachler, 2007; Rivals *et al.*, 2015). Stable carbon and oxygen isotopes can also be combined to dental use-wear analyses to provide information on the diets recorded during the time of enamel-mineralisation. They can complement the data acquired from use-wear studies with information on the relative proportions of C_3-C_4 vegetation (i.e. browse vs graze) included in the diet of animals, and on aridity levels (Sewell *et al.*, 2019).

It was therefore hypothesized for this study that, combined, these dietary proxies could provide a thorough assessment of the dietary ecology of the studied species and mitigate for some of the limitations of each method, maximising the strengths of each proxy. More particularly, the combination of dietary proxies on the same assemblages was sought to allow a multi-scale dietary analysis in which diets were compared across several temporal scales to assess how much the diet of the studied individuals changed throughout their lifetime, and inform on their overall and seasonal dietary variability (Davis and Pineda Munoz, 2016). It was postulated that, if results from the various methods used for dietary analysis display similar patterns across the fossil assemblages, it would suggest that all methods are equally informative on dietary behaviours, and can be used in isolation without losing information or accuracy. Contrastingly, if results differed between methods, it was hypothesized that this would likely highlight how each of these methods can complement each other when used in combination, by informing on different aspects of the studied animals' feeding ecology (i.e. geochemical or structural food properties, seasonal variation in diet…etc).

The multi-scale approach used in this study allowed, as hypothesized, to identify variations in dietary behaviours through the lifetime of the studied individuals, more particularly when focusing on the mixed-feeding antelope species. As predicted, little variation in dietary signal was observed across dietary proxies for the obligate-grazing and obligate-browsing species (i.e. genus *Equus* and genus *Giraffa*, respectively), confirming consistent dietary behaviours through life for these taxa, from their early years to their death. It must be noted, however, that results from dental microwear analysis highlighted mixed-feeding behaviours just before death for most of the fossil *Equus* specimens, suggesting slightly more variation in diet than expected for this taxa. This pattern would not have been identifiable if the assemblage had been studied using only mesowear and/or stable isotopes.

In contrast, discrepancies were observed between results from stable isotopes, dental microwear textural analysis and mesowear analysis for all impala (genus *Aepyceros*) and springbok (genus *Antidorcas*) samples, indicative of mixed-feeding dietary behaviours that likely varied significantly through life. Seasonal variation in diet was also confirmed for the fossil impala species *Aepyceros shungurae* through intra-tooth stable isotope analysis. Multiproxy results therefore highlighted the clear dichotomy between the relatively homogenous lifetime dietary behaviours of browsing and grazing species and the dietary plasticity of mixed-feeding species such as impala and springbok, which tend to vary their diet throughout their life.

Despite the high lifetime dietary variability observed within the mixed-feeder assemblages, differences in overall dietary patterns could be identified between modern and fossil specimens, as well as when comparing fossil samples from different sites or from different time periods. This was hypothesized to likely relate to the habitats and climate conditions experienced by the studied individuals, allowing to make inferences about local habitat heterogeneity and seasonal variation in diet in the past. This can seldom be achieved when using a single dietary proxy.

Results from this study therefore confirmed that the combination of multiple dietary proxies can help investigate the dietary ecology of fossil species to a greater level of detail than when these proxies are used in isolation. However, several limitations remain when using such approach, more particularly when attempting to reconstruct the dietary ecology of adaptable mixed-feeding species to make inferences about local palaeo-vegetation conditions. These limitations are discussed in the following section.

8.2.3 Perspectives for future research

The accuracy of multi-scale interpretations could be improved by in-depth studies of the relationship between the different proxies, based on modern populations of known diet or on experimental designs. Alike previous feeding experiments that investigated the impact of different food properties on use-wear signals (e.g. Hoffman, Fraser and Clementz, 2015; Ackermans, 2016; Merceron, Blondel, *et al.*, 2016; Ramdarshan *et al.*, 2016; Ackermans, Winkler, *et al.*, 2020)(Hoffman, Fraser and Clementz, 2015; Ackermans, 2016; Merceron, Ramdarshan, *et al.*, 2016; Ramdarshan *et al.*, 2016; Ackermans, Martin, *et al.*, 2020), it would be beneficial to evaluate more precisely, at the individual-scale, how lifetime variation in diet is reflected differently across each of the proxies that can be used in palaeo-dietary reconstructions. This would ensure a better understanding of the complex relationships between food properties, feeding habits, and seasonal variation in diet.

In addition, future palaeo-environmental reconstructions could be refined by using multi-scale experimental dietary analyses to provide the scientific community with means to identify in greater detail the vegetation-types present in eastern Africa during the Plio-Pleistocene. For instance, future studies could focus on evaluating the contribution of succulent plants to the diet of herbivore species as a way to evaluate the relative aridity of local habitats, as these plants generally occur in very arid environments. The majority of succulents adopt the CAM photosynthetic pathway, and CAM plants are known to develop strong defences against herbivory (Sewell, 2019). Such defences could potentially yield dental microwear patterns similar to those of browsing species while mimicking carbon isotope ratios similar to those of herbaceous C_4-plants. However, because CAM-plants are typically restricted to arid conditions, high levels of dust/grit and related abrasion could also yield to highly abraded use-wear patterns. It would therefore be interesting to gauge as well the impact of the consumption of succulent/CAM-plants to the lifetime use-wear patterns observed through mesowear analysis, which in turn would refine palaeo-environmental reconstructions for the Omo-Turkana basin.

Similarly, testing if the consumption of a large amount of C_4-dicots would results in specific use-wear patterns could help evaluate, when use-wear analyses are used alongside stable carbon isotopes, the relative proportion of C_4-monocots/ C_4-dicots included in the diet of fossil animals. Previous studies have hypothesized that C_4-dicots thrive in conditions of extremely low atmospheric CO_2 values such as during full glacial conditions (Ehleringer, Cerling and Helliker, 1997; Cerling, 1999). The higher abundance of C_4-dicots in the Plio-Pleistocene eastern African record after ~2.6 Ma by palynological studies (i.e. Amaranthaceae family, Bonnefille and Dechamps 1983; Bonnefille 2010), could hence be related to the onset of the Northern Hemisphere glaciation (ONHG) between ~3.0 and 2.5 Ma suggested by marine-core records (Flesche Kleiven *et al.*, 2002; deMenocal. 2004; Behrensmeyer, 2006 and references therein), which could have favoured the development of C_4-dicots in the area. Finding a method to evaluate the contribution of C_4-dicots to the diets of fossil herbivore populations could provide further insights into Plio-Pleistocene palaeo-environmental conditions, and provide further evidence for the increased abundance of C_4-dicots in the Omo-Turkana basin landscapes after ~3.0 M. in relation to global climatic events such as the onset of the Northern Hemisphere glaciation.

Finally, it could be highly beneficial to assess, in the fossil record, if the studied species were migratory or sedentary. Indeed, while modern impalas are known to be sedentary (Estes, 1991), their extinct relatives might have exploited a wider range of habitats in the vicinity of the Omo-Turkana basin, by migrating during periods of food shortage. Such behaviours would likely lead to biased palaeo-environmental reconstructions relying on palaeo-dietary data, as most of the dietary proxies would then potentially record information from the various habitats exploited by migrating individuals throughout their life, and not solely information on the local habitats where the remains were found. To mitigate for this potential bias, it could be interesting to analyse the strontium ($^{87}Sr/^{86}Sr$) isotopic signatures in fossil impala enamel samples, as a way to reconstruct the mobility patterns of selected individuals from this taxon (Copeland *et al.*, 2011; Slovak and Paytan, 2011).

8.3 Inferred palaeo-diets and palaeo-vegetation conditions in the Omo-Turkana in the Plio-Pleistocene: potential implications for hominin evolution

8.3.1 Initial research questions

Previous studies have suggested that major climatic events triggered important changes in ecosystems through speciation, extinction and migratory events (e.g. Vrba, 1993; Behrensmeyer *et al.*, 1997; Bobe, Behrensmeyer and Chapman, 2002; Bonnefille *et al.*, 2004; Bobe, 2006; Potts, 2013; Cerling *et al.*, 2015)(Vrba, 1993; Behrensmeyer *et al.*, 1997; Bobe, Behrensmeyer and Chapman, 2002; Bonnefille *et al.*, 2004; Bobe, 2006; Potts, 2013; Cerling *et al.*, 2015) , and that these changes likely played a predominant part in human evolution. More particularly, some researchers hypothesized that an increase in aridity and grassland-dominated landscapes in Pliocene and Pleistocene Africa likely forced early hominin species to adapt from dense wooded habitats to more open environments, with periods of enhanced aridification which likely triggered speciation events in the hominin lineage (Dart, 1925; Coppens, 1985; Demenocal, 1995). Alternatively, other researchers argued that the presence of mosaic habitats in east Africa during the Plio-Pleistocene might have been a key environmental factor to the hominin lineage diversity (Hopley and Maslin, 2010; Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Du and Alemseged, 2018), with mosaic patterns of vegetation associated with grassland expansion suggested in hominin-bearing localities, particularly between 2.4 – 1.4 Ma (e.g. Quinn *et al.*, 2013). However, debate remained around the characteristics of these mosaic habitats, most particularly to identify whether these mosaic habitats suggested from palaeo-environmental studies actually reflected alternating woodland-dominated phases and grassland-dominated phases or if habitat heterogeneity was a real, long-lasting, feature of the fossil record.

Many theories have used the evidence available from the various palaeo-environmental proxies available to help pin-point the timings and main characteristics of climatic events and environmental features that characterised the African Plio-Pleistocene: from the savannah hypothesis (Dart, 1925), to Vrba's Pulse Turnover Hypothesis (1985), Potts' Variability Selection Hypothesis (1998), and the Pulsed Climate Variability Hypothesis (Maslin, Shultz and Trauth, 2015), the link between climate change and faunal evolution remains debated. Indeed, not all palaeo-environmental proxies agree on the timings of the environmental changes postulated to have triggered the main evolutionary events observed among mammals and hominins, nor do they fully agree on the main environmental features that characterised the fossil localities investigated (Maslin and Christensen, 2007; Trauth, Larrasoañ and Mudelsee, 2009; Potts, 2013) (see chapter 1.1.2, table 2, for details of these theories).

This section attempts to answer the following research question, postulated at the beginning of this thesis: **how do palaeo-vegetation and palaeo-climate inferences made from mixed-feeding antelope palaeo-dietary studies compare with the main evolutionary theories proposed to explain mammal/human evolution?**

It was hypothesized that, for the dietary behaviours inferred in this study to agree with the Savannah Hypothesis (Dart, 1925), a gradual increase in grazing/C_4-dominated behaviours through time should be observed across the mixed-feeding assemblages (see Table 6 chapter 1.6). If following the temporal patterns of global environmental change suggested by the Turnover Pulse Hypothesis (Vrba, 1985), marked changes in dietary behaviours were anticipated to be observed at specific points in time in relation to major climatic events (e.g. iNHG at 3.2-2.5 Ma; and oWC at 2.0- 1.7 Ma). If in agreement with the Variability Selection Hypothesis (Potts, 1998) or the Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009), the observed mixed-feeders' dietary signals were expected to display a gradual increase in grazing/C_4-dominated signals, combined with an increased intra- and inter-specific dietary variation as well as increased seasonal variation in diet, potentially indicative of increased environmental instability and increased seasonality. If mosaic habitats were a predominant feature of the Omo-Turkana basin during the Plio-Pleistocene, as suggested by Mosaic Habitat theories (e.g. Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Du and Alemseged, 2019), no clear directional change was expected to be visible in the dietary signals of the studied mixed-feeders, with a relatively high but constant intra- and inter-specific dietary variability.

8.3.2 Outcome of this research

What are the timings/rates of dietary variation observed for mixed-feeding species towards the sequence, and what type of vegetation/climate change do these suggest?

The general dietary trends observed for the studied mixed-feeding antelope taxa indicated an increase in grazing signals in all three Omo-Turkana fossil localities, although more pronounced in the Shungura formation, potentially reflecting a gradual grassland expansion in the region, as suggested in most theories (e.g. Savannah Hypothesis, Dart, 1925; Variability Selection Hypothesis, Potts, 1998) (Table 74). This trend of expanding grassland has been confirmed by many other proxies, such as soil carbonates (Levin *et al.*, 2004; Wynn, 2004; Segalen, Lee-Thorp and Cerling, 2007) and fossilised mammal teeth (Harris *et al.*, 2008; Brachert *et al.*, 2010), and is often accepted as the main climatic change experienced by terrestrial mammals throughout the Plio-Pleistocene. The trends observed from the multiple dietary-proxies used in the present study confirmed this suspected environmental background of increasingly arid and open vegetation conditions, especially after ~2.5 Ma.

However, results from this study also suggested the presence of highly diverse habitats with high vegetation heterogeneity in most deposits, reflected in a wider dietary breadth and more marked mixed-feeding behaviours in some localities, and in some members. Overall, the differences in dietary patterns observed for fossil *Aepyceros* specimens when comparing assemblages from different members appeared to coincide with environmental shifts indicated by previous studies based on other types of fossil evidence. Most particularly, the suggested shifts in dietary behaviours observed through time for impala specimens from the Shungura formation were shown to be consistent throughout all of the dietary proxies used in this study, and compare well with other paleo-environmental proxies such as paleosol carbonates (Levin *et al.*, 2011) or paleo-dietary analyses of other adaptable herbivore species (e.g. Blondel *et al.*, 2018). The timing of these changes appears to coincide with some of the major global climatic events suggested to have influenced mammalian evolution (i.e. Turnover Pulse Hypothesis, Vrba, 1985; Pulsed Climate Variability Hypothesis, Maslin and Trauth, 2009), namely the Intensification of Northern Hemisphere Glaciation (iNHG) (at ~ 2.75 Ma), which marked the installation of 'glacial-interglacial cycles', and the Onset of the Walker Circulation (oWC) (at ~2.0 Ma), which has been suggested to have triggered an increase in aridity and variability after ~1.9-1.5 Ma (Trauth *et al.*, 2009) (see chapter 1.1.2, table 2 for more detail on these climatic events). This could suggest that the palaeo-dietary trends inferred from the fossil *Aepyceros* dental material from the Plio-Pleistocene Omo-Turkana basin mirror the patterns initially expected under the Pulsed Climate Variability Hypothesis, which argued for heightened environmental instability and habitat heterogeneity as a driver of mammalian evolution, with short periods of extreme climate variability (i.e. pulses/punctuations) within the long-term drying trend in East Africa (Maslin and Trauth, 2009).

Table 74: Main evolutionary theories, hypothesized results of palaeo-dietary analysis of mixed-feeding antelopes, and outcomes of this research project (i.e. inferred dietary patterns).

Theory	Expected dietary behaviours for *Aepyceros/Antidorcas*	Inferred dietary behaviours for *Aepyceros/Antidorcas* from this study
Savannah hypothesis (Dart 1925)	• Increasing abundance of grazing signals observed through dental use-wear analyses, and of C_4-vegetation ($\delta^{13}C$) in the diet of the studied taxa throughout over the temporal range.	• Increasing abundance of grazing signals (dental use-wear analyses), and of C_4-vegetation ($\delta^{13}C$) observed in the diet of fossil *Aepyceros*

	- Increased aridity through time might be observable from the oxygen isotope content of the studied taxa ($\delta^{18}O$).	- Oxygen isotope content $\delta^{18}O$) fluctuating through time – no clear increasing trend.
Turnover Pulse Hypothesis (Vrba 1985)	- Habitat specialists are more likely to be affected by climate and habitat change (i.e. increased extinction rates) than generalists (Vrba 1988), although adaptable herbivores such as *Aepyceros* and *Antidorcas* might demonstrate variations in diet through time - Marked shifts in dietary behaviours at times of major climatic changes (i.e. iNHG at 3.2-2.5 Ma; and oWC at 2.0-1.7 Ma).	- Variations through time observed for *Aepyceros*, more particularly for the Shungura Fm (i.e. larger sample sizes, better time-resolution than Koobi Fora and Nachukui Fms). - *Aepyceros* intra-tooth stable isotope data (Shungura) point to periods of relatively high climatic variability associated with high seasonal variations in rainfall amount, more particularly between 2.27 and 1.9 Ma
Variability Selection Hypothesis (Potts 1998) & Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009)	- Environmental instability might be observable via temporarily increased intra- and inter-specific dietary variation (dental use-wear and stable carbon isotope analyses) within specific members, in addition to a gradual increase in grazing signals/C_4-diets across the sequence. - Increased seasonal variability in diet in some members (observed through intra-tooth isotopic analyses, and potentially through multi-method dietary analysis)	- Variations through time in the dietary breadth inferred from Aepyceros material (i.e. varying abundance of mixed-feeding signals depending in member/locality) - Abundance of grazing signals (dental use-wear analyses), and of C_4-vegetation ($\delta^{13}C$) observed in the diet of fossil *Aepyceros* - *Aepyceros* intra-tooth stable isotope data (Shungura) point to periods of relatively high climatic variability associated with high seasonal variations in rainfall amount, more particularly between 2.27 and 1.9 Ma
Mosaic Habitat Model (Domínguez-Rodrigo 2014, Reynolds *et al.* 2015a, Du and Alemseged 2018)	- No clear directional change would be apparent in dietary signals (dental use-wear and stable carbon isotope analyses), with a relatively high but constant intra- and inter-specific dietary variability. - Mixed-feeding signals should dominate the assemblage, suggesting the availability of varied food resources	- Varied diets suggested among impalas from the Koobi Fora and Nachukui Fms, with little evidence for significant temporal changes: regions of long-lived mosaic vegetation? - More variable dietary patterns suggested for impalas from the Shungura Fm, with variation through time: local mosaic habitats in the Lower Omo-river valley, with a more marked fluctuation through time between woodland-dominated and grassland-dominated phases?

In addition to the results from palaeo-dietary analysis and predictive models which suggested habitats of high vegetation heterogeneity throughout the Omo-Turkana basin during the Plio-Pleistocene, intra-tooth stable isotope data pointed to periods of relatively high climatic variability associated with high seasonal variations in rainfall amount, more particularly between 2.27 and 1.9 Ma. Similarly, recent findings based on intra-tooth isotopic records in equid teeth from early Pleistocene deposits in the Homa Peninsula (Kenya, ~2.0-1.0 Ma) suggested seasonally variable environments in the tropics, to an extent similar to present-day eastern African climates (Blumenthal *et al.*, 2019). This is in agreement with previous research that hypothesized that seasonal and interannual rainfall variability in eastern Africa increased at ~2.0 Ma in response to the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.*, 2004; Blumenthal *et al.*, 2017; Hopley *et al.*, 2018). The increasingly variable seasonal dietary patterns observed in the Shungura Fm would therefore be additional evidence in favour of the Plio-Pleistocene environmental dynamics proposed by the Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009), in which evolutionary events were triggered by increasingly variable climatic and vegetation conditions against a backdrop of increasingly arid conditions, with short periods of extreme climate variability (specific to East Africa) which potentially drove hominin evolution.

What types of local vegetation conditions do the inferred dietary behaviours suggest across the basin, and do they seem to have varied seasonally?

The varied diets observed among impalas from the Koobi Fora and Nachukui formations, along with little evidence for significant temporal changes in these dietary patterns, could suggest two regions of long-lived mosaic vegetation, where a wide range of food resources were available to these herbivores throughout the sequence and the region. In contrast, the more variable dietary patterns observed for impalas from the Shungura formation, which varied through time depending on the member studied, could suggest local mosaic habitats in the Lower Omo-river valley with a more marked fluctuation through time between woodland-dominated and grassland-dominated phases. While these differences in local patterns of vegetation heterogeneity could be artefacts of the fossil record due to the larger faunal sample sizes available for analysis and a better time-resolution of the Shungura deposits compared to those of Koobi Fora and Nachukui, these results could also highlight the presence of micro-habitats within the Omo-Turkana basin, and differing palaeo-vegetation dynamics between the Lower Omo-river valley and the rest of the basin.

Nonetheless, evidence from this research suggest the presence, across all three fossil localities of the Omo-Turkana basin, of long-lived mosaic habitats, which could have supported a high diversity of mammalian taxa with varying ecological requirements, including hominins, providing a wide range of habitats to species of differing morphological adaptations. In addition, the strong seasonality in rainfall patterns and vegetation availability suggested for the Shungura formation, and potentially mirrored in the rest of the Basin, would likely have influenced as well local vegetation and faunal biodiversity in the region, adding selective pressures associated with seasonal changes in resources abundance and distribution, acting as an additional driver of hominin evolution (Kingston *et al.*, 2007; Trauth *et al.*, 2007; Potts and Faith, 2015; Blumenthal *et al.*, 2019). This is consistent with previous research which proposed that climate variability and environmental stability/instability cycles were important features of past African environments, and therefore important drivers of human evolution, with seasonal cycles playing an important part in shaping local environments on a short-time scale, in relation and addition to longer-time scale global climatic changes related to suborbital and orbital insolation cycles (Milankovitch, 1941; Kingston and Harrison, 2007; Joordens *et al.*, 2011; Potts, 2013; Levin, 2015; Potts and Faith, 2015).

8.3.4 Perspectives for future research

To investigate further habitat heterogeneity during the Plio-Pleistocene and how habitat heterogeneity and/or increase in aridity conditions might have had a significant impact on hominin diversity and evolution, it would be interesting to compare the results from this study, focused on the Eastern African fossil record, with material from other key hominin-bearing regions in Africa, and more particularly in comparison with the Cradle of Humankind, in South Africa (Gauteng Province). Numerous hominin species have been discovered from South African fossil deposits (i.e. A*ustralopithecus sediba,* Berger *et al.*, 2010; *Australopithecus africanus,* Dart, 1925, Clarke, 2008; *Paranthropus robustus,* Broom, 1938; *Homo habilis* ,Hughes and Tobias, 1977; and *Homo ergaster,* Leakey, 1960, Kuman and Clarke, 2000, Anton *et al.*, 2014)*,* suggesting a potentially high diversity of that lineage in that region, alike East Africa and the Omo-Turkana basin for a similar time interval.

Similarly to East African fossil sites, reconstructions of palaeo-environmental contexts have been proposed for the Cradle of Humankind, using various methods such as macro- and micro-faunal associations, palaeo-botanical studies, and speleothem isotopic studies (e.g. Vrba, 1974, 1975; Avery, 2001; deMenocal, 2004; Hopley, Latham and Marshall, 2006; Hopley *et al.*, 2007). These studies have suggested a climatic trend similar to that of East Africa during the Plio-Pleistocene, with increasing aridity and grassland expansion. Furthermore, studies have highlighted fluctuating proportions of C_3 and C_4 vegetation through time, with increasing grassland-dominated habitats after ~1.7 Ma, potentially related to African aridity caused by the onset of the Walker Circulation in the Pacific Ocean at around that time (Hopley *et al.*, 2007).

Previous research pointed out differing environmental dynamics between East and South Africa, which might have been driven by differences in latitudinal position, and varying degrees of volcanic and tectonic activity, with East Africa being more affected by Earth dynamics than South Africa (King and Bailey, 2006; Reynolds, 2007; Bailey and King, 2011; Bailey, Reynolds and King, 2011). Tectonic uplifts in southern Africa are believed to have been less significant than in East Africa, resulting in a smaller impact on local environmental conditions, and less temporal variations (Partridge, Wood and DeMenocal, 1995).

To investigate further the differences and similarities in vegetation structure between East and South African hominin-bearing localities and test the hypothesis of differing landscape dynamics between the two regions, results from this study could be compared with the results produced for South African localities by Sewell and collaborators (Sewell, 2019; Sewell *et al.*, 2019) which used a similar methodological approach using fossil springbok remains (genus *Antidorcas*).

8.4 Conclusion of this study

As demonstrated throughout this thesis, and highlighted more particularly in the present discussion chapter, this research project examined the dietary behaviours of selected extant and extinct mixed-feeding antelopes, using a combination of complementary methods to assess whether detailed studies of the dietary ecology of mixed-feeding antelope species could be used to investigate hominin palaeo-environments in the Omo-Turkana basin during the Plio-Pleistocene. More particularly, this research aimed to assess whether abundant and adaptable herbivores such as the impala or the springbok could reliably be used as accurate local vegetation proxies, checking upon the assumption that their dietary behaviours are mainly influenced by the vegetation conditions in their habitats.

Firstly, this work evaluated what **type of evidence dietary studies of mixed-feeding herbivores can provide to help make inferences about the prevailing vegetation conditions of their local habitats.** This work demonstrated that, while the fossil record has been studied extensively to propose palaeo-environmental reconstructions of African regions key to the understanding of hominin evolution, new methods can be employed to gain further insights into palaeo-vegetation conditions. Indeed, this research proposed a novel approach to palaeo-environmental studies, which consisted of building models based on land cover and dietary data from modern populations. This was to test whether modern impala dietary variability could be positively correlated with specific habitats and climatic conditions, and assess if such relationship could be used to help interpret dietary patterns identified from the fossil record. Although the models built for this study revealed some limitations, the predictions generated for fossil *Aepyceros* samples for the Omo-Turkana basin based on modern land cover and stable isotope data were partly consistent with previous palaeo-environmental studies for this region. Improved models could be used on other mammal taxa for which isotope data is available for both extant and extinct populations, to explore how faunal communities directly relate to their environments and how dietary studies can inform on their habitats depending on their feeding ecology without prior assumptions of the similarity in ecology between fossil taxa and their extant relatives.

In addition, this study showed that detailed studies of the palaeo-diets of mixed-feeding herbivore species can provide useful information regarding palaeo-vegetation conditions, most particularly when evaluating differences between local habitats in one region, or potential changes in environmental conditions through time. Mixed-feeding species were shown to remain highly adaptable to changing vegetation conditions, although likely retaining dietary preferences when and where possible. While mixed-feeding taxa such as the impala (genus *Aepyceros*) are abundant in the fossil record, they had rarely been studied in such detail before. This study therefore demonstrated that mixed-feeding herbivores can be used as palaeo-vegetation proxies in future studies for fossil assemblages where they are abundant, and can be used alongside other palaeo-environmental proxies to investigate vegetation conditions in the past. This highlights the potential of this approach, as well as the potential for dietary analyses of mixed-feeding taxa to be used as an additional tool for palaeo-environmental reconstructions, although further studies could improve the accuracy of this approach with larger modern datasets for comparative studies, and with more experimental work to better understand the relationship between the various dietary-proxies (dental use-wear, stable isotopes), and specific plant-types/local environments.

Secondly, this project explored **what additional insights into palaeo-environmental conditions in the Omo-Turkana basin the inferred dietary patterns of mixed-feeding species could provide, and how these could potentially help resolve apparent contradictions between other environmental proxies.** The outcome of this study highlighted the great potential of multi-proxy dietary analyses, showing that the combination of multiple methods can help assess the dietary ecology of modern or fossil species to a greater level of detail than when these methods are used in isolation. More particularly, this approach allowed to perform a multi-scale dietary analysis in which diets were compared across several temporal scales to assess how much the diet of the studied individuals changed throughout their lifetime. This allowed to inform on the seasonal dietary variability of the studied taxa and, which might reflect seasonal variability of vegetation conditions in the past when studying flexible mixed-feeding taxa.

The interpretation of the dietary patterns inferred from mixed-feeder dental remains from the Omo-Turkana deposits aligned with previous studies which, using other paleo-environmental proxies, pointed to differences across the basin, with more arid open habitats in Koobi Fora and Nachukui, compared to more wet closed habitats described in the Lower Omo river valley (i.e. Shungura Fm). Similarly, the variations in inferred dietary behaviours observed through time for the mixed-feeding antelope studied, which suggested a gradual increase in the proportions of C_4-resources in the diet (potentially reflecting an increase in the proportions of C_4 grasses and sedges in the landscape), were consistent with observations made from other proxies which suggested an increase in aridity conditions and a gradual spread of open-grassland habitats. However, where previous studies have disagreed regarding the degree of habitat heterogeneity and the amount of C_3-vegetation present in the Omo-Turkana region during the Plio-Pleistocene, results from this study argued in favour of high spatial heterogeneity, suggesting the presence of highly fragmented habitats across the basin. This was based on the varied diets observed across the multiple dietary-proxies studied, potentially reflecting some degree of habitat heterogeneity and vegetation diversity in the region during the Plio-Pleistocene, although it remains difficult to assess whether these varied diets were related to seasonal changes in local vegetation conditions, or to the presence of consistently present mosaic habitats on the eastern and western margins of the basin.

Based on these observations and interpretations, and on comparisons with previous studies, this study then discussed **how the palaeo-vegetation and palaeo-climate inferences made from mixed-feeding antelope palaeo-dietary studies compared with the main evolutionary theories proposed to explain mammal/human evolution.** Indeed, **t**he inferred dietary patterns observed across the mixed-feeding assemblages from the Omo-Turkana basin, allowed the brief discussion of the palaeo-ecological and palaeo-climatic contexts that shaped the evolution of the human lineage, by comparing the trends observed in this study with previous hypotheses formulated based on other environmental-proxies. As mentioned above, results from this study indicated an increase in grazing signals in all three Omo-Turkana fossil localities, although more pronounced in the Shungura formation, potentially reflecting a gradual grassland expansion in the region throughout the Plio-Pleistocene, as suggested in most theories (e.g. Savannah Hypothesis, Dart, 1925; Variability Selection Hypothesis, Potts, 1998). Interestingly, the suggested shifts in dietary behaviours observed through time for impala specimens from the Shungura formation appear to compare well with other paleo-environmental proxies (such as paleosol carbonates or paleo-dietary analyses), the timing of these changes coinciding with some of the major global climatic events suggested to have influenced mammalian evolution (i.e. Turnover Pulse Hypothesis, Vrba, 1985; Pulsed Climate Variability Hypothesis, Maslin and Trauth, 2009), such as the Intensification of Northern Hemisphere Glaciation (iNHG) (at ~ 2.75 Ma) (which marked the installation of 'glacial-interglacial cycles'), and the Onset of the Walker Circulation (oWC) (at ~2.0 Ma) (which has been suggested to have triggered an increase in aridity and variability after ~1.9-1.5 Ma ; Trauth *et al.*, 2009).

The varied diets observed among impalas from the Koobi Fora and Nachukui formations, along with little evidence for significant temporal changes in these dietary patterns, could suggest two regions of long-lived mosaic vegetation, where a wide range of food resources were available to these herbivores (and to hominins) throughout the sequence and the region. In contrast, the more variable dietary patterns observed for impalas from the Shungura formation, which varied through time depending on the member studied, could suggest local mosaic habitats in the Lower Omo-river valley with a more marked fluctuation through time between woodland-dominated and grassland-dominated phases. In any case, the presence, across all three fossil localities of the Omo-Turkana basin, of long-lived mosaic habitats, could have supported a high diversity of mammalian taxa with varying ecological requirements, including hominins, providing a wide range of habitats to species of differing morphological adaptations, as suggested by 'Mosaic Habitat' theories, which argue for the importance of mosaic habitats in east Africa during the Plio-Pleistocene in promoting local biodiversity (Domínguez-Rodrigo, 2014; Reynolds *et al.*, 2015; Du and Alemseged, 2018).

In addition, intra-tooth stable isotope data pointed to periods of relatively high climatic variability associated with high seasonal variations in rainfall amount, more particularly between 2.27 and 1.9 Ma. This was in agreement with previous research that hypothesized that seasonal and interannual rainfall variability in eastern Africa increased at ~2.0 Ma in response to the Plio-Pleistocene intensification of the Walker Circulation (Ravelo *et al.*, 2004; Blumenthal *et al.*, 2017; Hopley *et al.*, 2018). The increasingly variable seasonal dietary patterns observed in the Shungura Fm would therefore be additional evidence in favour of the Plio-Pleistocene environmental dynamics proposed by the Pulsed Climate Variability Hypothesis (Maslin and Trauth, 2009).

Overall, the conclusions drawn from the present study of the paleo-dietary ecology of mixed-feeding antelopes from the Omo-Turkana basin appear to agree with the palaeo-environmental dynamics proposed by the Pulsed Climate Variability Hypothesis to explain patterns of faunal evolution in eastern Africa: heightened environmental instability and heightened habitat heterogeneity were suggested as one of the main drivers of mammalian evolution, with short periods of extreme climate variability (i.e. pulses/punctuations) within the long-term drying trend in East Africa (Maslin and Trauth, 2009). Such conditions have been previously hypothesized to have influenced local vegetation and faunal biodiversity in the region, adding selective pressures associated with seasonal changes in resources abundance and distribution, acting as an additional driver of hominin evolution.

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