Hominin Dietary Niche Breadth Expansion During Pliocene Environmental Change in Eastern Africa

by

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A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved March 2020 by the
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ARIZONA STATE UNIVERSITY

May 2020

ABSTRACT

Stable carbon isotope data for early Pliocene hominins *Ardipithecus ramidus* and *Australopithecus anamensis* show narrow, C_3-dominated isotopic signatures. Conversely, mid-Pliocene *Au. afarensis* has a wider isotopic distribution and consumed both C_3 and C_4 plants, indicating a transition to a broader dietary niche by ~ 3.5 million years ago (Ma). Dietary breadth is an important aspect of the modern human adaptive suite, but why hominins expanded their dietary niche ~ 3.5 Ma is poorly understood at present. Eastern Africa has produced a rich Pliocene record of hominin species and associated mammalian faunas that can be used to address this question. This dissertation hypothesizes that the shift in hominin dietary breadth was driven by a transition to more open and seasonal environments in which food resources were more patchily distributed both spatially and temporally. To this end, I use a multiproxy approach that combines hypsodonty, mesowear, faunal abundance, and stable isotope data for temporally well-constrained early and mid-Pliocene mammal assemblages (5.3-2.95 Ma) from Ethiopia, Kenya, and Tanzania to infer patterns of environmental change through time. Hypsodonty analyses revealed that early Pliocene sites had higher annual precipitation, lower precipitation seasonality, and lower temperature seasonality than mid-Pliocene sites. Mesowear analyses, however, did not show from attrition- to abrasion- dominated wear through time. Abundance data suggest that there was a trend towards aridity, as Tragelaphini (woodland antelope) decline while Alcelaphini (grassland antelope) increased in abundance through time. Carbon isotope data indicate that most taxa shifted to diets focusing on C_4 grasses through time, which closely follows paleosol carbon isotope data documenting the expansion of grassland ecosystems in eastern Africa. Overall, the results suggest *Ar. ramidus* and *Au. anamensis* preferentially exploited habitats in which preferred food resources were likely available year-round, whereas *Au. afarensis* lived in more variable, seasonal environments in which preferred foods were available seasonally. *Au. afarensis* and *K. platyops* likely expanded their dietary niche in less stable environments, as reflected in their wider isotopic niche breadth.

This dissertation is dedicated to
my mom Segenet, my wife Kidist and
our children Yosef and Matewos

ACKNOWLEDGMENTS

My graduate study would not have been possible without the support of many individuals. I would like to thank my committee members Drs. William Kimbel, Kaye Reed, Christopher Campisano and Zeresenay Alemseged for their unreserved support and guidance, particularly Bill for his patience and his famous amharic saying “ enkulal kesbekes begru yihedal” which means slowly, but surely, the egg will walk on its legs, Kaye for her tireless, careful reading and extremely positive feedback throughout this project, Zeray for supporting, inspiring and having faith in me throughout this research project and my graduate education over the years. I would also like to thank Dr. John Rowan and Ellis Locke who helped me design this project in its very early stages. In particular John for his guidance throughout this project and his availability to discuss and share his thoughts every step of this project. I also want to thank, my ex-committee member, Dr. Gary Schwartz for his continued support.

I would like to thank Tomas Getachew, Yared Assefa, Dawit Tibebu, Getahun Tekle, Sahel Melaku, Metasebia Endalamew, Demerew Dagne and Yonas Desta from National Museum of Ethiopia and Dr. Fredrick Manthi, Jimmy Yatich and Cecilia Kanya from National Museum of Kenya for the help they provided me over the course of my work in their respective museums. I am also thankful to Dr. Yohannes Haile-Selassie and Dr. Tim D. White for their permission to access the Woranso Mille and Middle Awash collections for my study. I am indebted to thank Institue of Human Origins, Elizabeth C. Harmon Research Endowment, Donald C. Johanson Paleoanthropological Research Endowment, The Leakey Foundation and Wenner-Gren Foundation for their financial support. I am thankful to the Authority for Research and Conservation of Cultural Heritage and the staffs for their continued support for my graduate education.

I also want to thank the members of Dr. Kaye Reed’s Reading Group that includes John, Ellis, Ignacio, Irene and Morayse that gave me the opportunity to develop and structure my dissertation. My special thanks to Susanne Daly and Krista Hicks for their companionship throughout the years of my graduate study and being my best friends who brought unwavering love and happiness to my family and myself. I would like to thank the many friends who supported me over the years, which includes but not limited to Tomas Getachew, Dr. Enqu Wondimu, Dr. Kierstin Catlette, Belay Zelalem, Dr. Anne Titlebaum, Dr. Halszka Glowacka, Dr. Terrence Ritzman, Mesfin Mekonnen, Dr. Amy Shapiro, Dr. Thiera Neily, Dr. Amelia Villaseñor, Dr. Jeremiah Scott, Dr. Emily Hallett, Dr. Alejandra Ortiz , Dr. Julie Lawrence, Dr. Maria Nieves Colon, Dr. Genevieve Housman, Dr. Hallie Edmonds, Belay Gebresenbet, Zenebe Gebremeskel, Milu Tefera, Mesfin Haile, Amanda Slotter, Amanda McGrosky and Narry Savage. I am also thankful for the IHO administrative staff Lindsay Mullen, Aubree Morrissey, Bethany Baker and Julie Russ for their unreserved support throughout my years in Arizona.

Finally, I am thankful to my mom, Segenet Mengesha who is my motivation and inspiration. My wife, Kidist and our boys Yosef and Matewos have been very supportive of me throughout the many ups and downs, without complaining being away from home all these years. Thank you for your love and support.

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CHAPTER 1
Introduction

1.1 Introduction

Over the course of their evolution hominins exhibited morphological and behavioral changes. Some of the key hominin adaptations include, for example, large brain size (Kimbel and Delezene, 2009), megadontia (White et al., 2009), habitual terrestrial bipedality (Ward et al., 2011), and use and manufacture of stone tools (Semaw et al., 2005; McPherron et al., 2010; Harmand et al., 2015). These adaptations have at some point been linked to climatic and environmental changes, as hominins are thought to have responded to their changing environment and climate via locomotor, foraging and dietary adaptations (e.g., deMenocal, 2004; Behrensmeyer, 2006; Maslin et al., 2015; Potts, 2007, 2013).

One key hominin adaptation that is less well-studied is dietary niche breadth and its tempo and mode. Dietary niche breadth refers to the range of food resources that a species exploits and/or depends on. Generally, species can be grouped in to two broad dietary categories, generalists and specialists. Species that depend on a wide variety of food items are usually considered to be generalists (dietarily flexible), while those with narrower dietary niches are considered specialists. Specialists may have gone through morphological and physiological adaptations that affect their flexibility, limiting them from expanding their diet under changing environmental conditions (Feranec, 2003; Bearhop et al., 2004; Shipley et al., 2009; Slatyer et al., 2013).

Consuming a wide variety of food resources (i.e., dietary generalization) is a key component of hominin evolution and is linked with morphological adaptations (Levin et al., 2008; Wynn et al., 2013; Sponheimer et al., 2013). More recently, a wide dietary niche has allowed modern humans to colonize extensive habitable environments on earth than any other terrestrial mammal (Marean et al., 2007). Furthermore, dietary flexibility has been linked to important events in human evolution, such as the dispersals of *Homo erectus* and *H. sapiens* out of Africa and the persistence of modern humans through glacial phases of the Pleistocene (Scholz et al., 2007; Marean et al., 2007). Using new methods, including stable carbon isotopes (Levin et al., 2008; Wynn et al., 2013; Sponheimer et al., 2013; Cerling et al., 2011a; 2013) and microwear analyses (Ungar et al., 2008; Ungar and Sponheimer, 2011), our understanding of the dietary ecology of early hominins has improved in recent decades. However, it is still unclear why a wider dietary niche emerged during the early phases of hominin evolution.

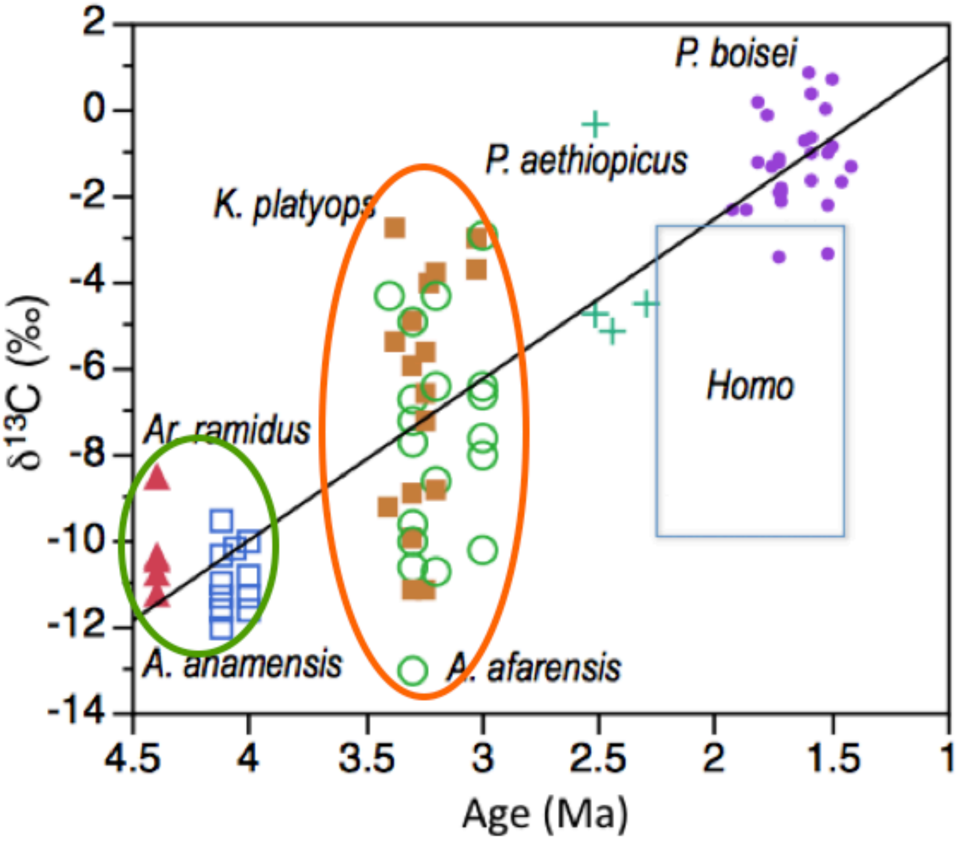

Figure 1.1. Temporal change in carbon isotope value of eastern African hominin lineages (adapted from Sponheimer et al., 2013).

Among Pliocene hominin species from eastern Africa, *Ardipithecus ramidus* and *Australopithecus anamensis* exhibit a narrow diet characterized by C_3 plants, whereas *Au. afarensis* and *Kenyanthropus platyops* consumed both C_3 and C_4 plants (Wynn et al., 2013; Sponheimer et al., 2013; Cerling et al., 2013) (Fig. 1.1). C_3 plants are trees, bushes, forbs, and shrubs, while C_4 plants are grasses and sedges. Both plant types are found in most environments in Africa today, though there is evidence for changes in their relative abundance through time (Cerling et al., 2013). Research on non-human primates also points to a potential role for climatic and environmental factors in mediating changes in hominin dietary niche breadth. For example, a species can become a generalist in resource-limited environments, and a specialist in resource-abundant environments (Shipley et al., 2009; Slatyer et al., 2013). For instance, some species of gibbons (e.g., *Hylobates mulleri* and *Hylobates agilis*) consume only a few fruit species during high rainfall periods when fruit is abundant, and therefore have low dietary niche breadth at this time (McConkey et al., 2003). When fruit is scarce these species consume a greater diversity of plant species, and therefore become generalists. Hanya et al. (2011) demonstrated that in deciduous forests, where fruits are not available for several months of the year, the density of frugivorous mammals is negatively correlated with the degree of seasonality. This suggests that change in climate and habitats (vegetation and water source) change may have been important drivers of hominin dietary niche breadth and its evolution in the Pliocene. In this work, I will investigate the issue of dietary breadth among Pliocene hominin species using different proxies in order to elucidate the interplay between dietary shift, niche breadth, morphological novelties and potential links to environmental and climatic changes.

1.2 Study Area

The East African Rift Valley holds a special place in palaeoanthropology because of its rich and well-dated Plio-Pleistocene faunal and hominin fossils (MacLatchy et al., 2010). The Rift Valley is a vast area that encompasses many major hominin-bearing sites. The East African Rift System transects the high-elevation of the Ethiopian and East African plateaus, spanning north to south from Eritrea through Ethiopia, Kenya, Tanzania, and Uganda to Malawi and Mozambique (Taieb et al, 1976; Leakey et al., 1995; WoldeGabriel et al., 2000; Harrison, 2011). Many research groups have visited the region since the early 20th century, but it was in1967 that the International Omo Research Expedition was established by American, French and Kenyan teams and systematically collected thousands of vertebrate fossils, including hominin remains (Eck and Jablonsky, 1987). Continued work in the 1970s and 1980s across the rift valley led to systematic and well-organized multidisciplinary field expeditions that amassed a chronologically constrained contextual framework for the hominins, and assembled large huge fossil mammalian collection (Harris et al., 1988; Howell et al., 1987; Leakey and Harris, 2003; Taieb et al, 1976; Wynn et al, 2006; Campisano, 2007; Campisano & Feibel, 2007; Wynn et al, 2008). Fossil mammals from these sites have played an important role in the understanding of the changing environments and climate in eastern Africa through analyses of species diversity (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004), FADs and LADs (Vrba, 1993, 2005; Behrensmeyer et al., 1997), community structure (Reed, 1997; Andrews and Hixson, 2014), and stable isotopes (Cerling et al., 2013, 2015; Wynn, 2000; Wynn et al., 2013; Sponheimer et al., 2013). Results of these studies, in turn, have been used as proxies to reconstruct hominin environments and climate.

Most of these sites, situated in Ethiopia, Kenya and Tanzania, have yielded a large number of hominin specimens. *Ar. ramidus*, between 4.52 and 4.4 Ma year ago, was discovered from Middle Awash (White et al., 1994; White et al., 2009) and Gona (Semaw et al., 2005), in Ethiopia. *Au. anamensis* (4.2 – 3.9 Ma), which is considered a phyletic ancestor of *Au. afarensis,* is best known from the sites of Kanapoi (Leakey et al., 1995, 1998; Kimbel et al., 2006; Ward et al., 1999, 2016) and Allia Bay (Coffing et al., 1994; Leakey et al., 1995, 1998; Ward et al., 1999) in Kenya, and Asa Issie and Aramis (White et al., 2006), Woranso Mille (Haile-Selassie et al., 2010a; Haile-Selassie, 2010), Fejej (Kappelman et al, 1997; Ward, 2014), and Galili (Haile-Selassie and Asfaw, 2000) in Ethiopia. *Au. afarensis,* one of the better known and the longest-lived species (3.8 – 2.95 Ma), has been found at Laetoli in Tanzania (Johanson et al., 1978), Kantis (Mbua et al., 2016), Lothagam (Leakey and Walker, 2003; Brown et al., 2013), and Koobi Fora (Kimbel, 1988; Brown et al., 2013) in Kenya and Hadar (Johanson et al., 1978; Kimbel and Delezene, 2009), Dikika (Alemseged et al., 2006), Maka (White et al., 1993, 2000), Belohedelie (Clark et al., 1984; Asfaw, 1987), Woranso Mille (Haile-Selassie et al., 2007; Haile Selassie et al., 2010b) and Omo (Suwa et al., 1996) in Ethiopia. *Kenyanthropus platyops* overlapped with *Au. afarensis* (3.5 Ma) and is only known from Lomekwi and Kataboi members of the Nachukui Formation in Kenya (Leakey et al., 2001; Wood and Leakey, 2011; Brown et al., 2013).

While the *Au. anamensis* site of Kanapoi has often been considered to be environmentally similar to that of *Ar. ramidus* at Aramis, recent work by Louchart et al. (2009), White et al. (2009), Woldegabriel et al. (2009), Van Bocxlaer (2017), and Field (2017) suggests that *Ar. ramidus* lived in a mesic woodland environment while *Au. anamensis* occupied more arid mixed savanna vegetation (Dumounchel and Bobe, 2019). Moreover, recent work by Quinn (2019) suggests that *Au. anamenesis* consumed more C_4 foods than previously thought, aligning with its dentognathic adaptations though previous isotopic work had indicated a more C_3 based diet (Cerling et al., 2013). The paleoenvironments of *Au. afarensis* at Laetoli and Hadar and *K. platyops* at Lomekwi were reconstructed as mosaic and included closed woodland, patchy riverine forests, bushland, and open grassland (Reed, 1997, 2008; Kingston and Harrison, 2007) falling within the range of those occupied by the older *Au. anamensis*. However, detailed analyses comparing the paleoenvironments and differences in resource availability are scarce and often based on general patterns of faunal similarity. Methods for interpreting ancient climates and environments have progressed significantly in the past few decades and can be brought to bear on this question.

1.3 Dissertation Goals

Isotopic studies suggest that *Ar. ramidus* and *Au. anamensis* consumed mainly C_3 plants (White et al., 2009; Sponheimer et al., 2013) though Quinn (2019) suggested that *Au. anamensis* did consume C_4 food items, while *Au. afarensis* and *Kenyanthropus platyops* are shown to have a diet that included both C_3 and C_4 resources (Cerling et al., 2013; Wynn et al., 2013; Sponheimer et al., 2013), but the underlying causes of this niche expansion has received little attention. In this dissertation I will explore potential climatic and environmental forces that drove dietary niche breadth expansion in the hominin lineage during the Pliocene. Many approaches have been used to track climatic and environmental dynamics in the Pliocene, most of which center on analyzing temporal changes in faunal and floral composition and structure. Here, I focus on fossil ungulates (orders Artiodactyla, Perissodactyla, and Proboscidea) because they are often abundant and well-preserved taxa in hominin-bearing sites (Behrensmeyer, 1991; Reed, 1997).

Similarly, as primary consumers, ungulates are closely tied to climatic and vegetational aspects of present-day communities (e.g., Greenacre and Vrba, 1984; Fortelius et al., 2002), meaning that they could provide reliable information for inferring ancient environments in which hominins lived. In this dissertation I will employ a multi-proxy approach to further our understanding of the environmental and ecological context of hominin dietary niche breadth expansion in eastern Africa focusing on the earliest hominins.

This dissertation has five chapters: Chapter one introduces the study area and the objectives of the study. Chapter two (the first paper) ('Paleoclimates and environments of Pliocene hominin evolution in eastern Africa: implications for the origins of hominin dietary niche breadth') uses hypsodonty- and diet- based ecometric analyses to reconstruct climate and vegetation variables in the hominin fossil record (e.g., Eronen et al., 2010a and 2010b; Polly et al., 2011). Ecometric analyses quantify the link between functional traits of organisms (e.g., dietary adaptations) and their environments in the present, whose results are then used to infer paleoenvironments in the fossil record. Traits such as hypsodonty and diet are considered 'functional' because they mediate interactions between an organism and its environment, resulting in a tight relationship between the two (Janis, 1988; Polly et al., 2011) and allowing them to be used to infer ancient environments and vegetation. The goal of this first paper is reconstructing mean annual precipitation, mean annual temperature, and seasonality at the hominin bearing sites to understand a possible shift in the length of wet and dry seasons. This will allow to explore if seasonality had played a role in dietary niche expansion.

Chapter three (the second paper) ('Hominin paleoenvironments in the eastern African Plio-Pleistocene: evidence from bovid community mesowear') uses mesowear analyses to quantify the dietary structure of fossil bovid communities from Pliocene hominin-bearing sites in eastern Africa. Mesowear analyses involve scoring the lateral profile of ungulate teeth in terms of cusp relief and sharpness to determine whether an individual had attrition- or abrasion- dominated tooth wear (Fortelius and Solounias, 2000). The combination of cusp relief and sharpness permits classification of ungulates into dietary groups as browsers, mixed-feeders, or grazers on an attrition- to abrasion-dominated tooth wear gradient (Kaiser and Solounias, 2003; Kaiser and Schulz, 2006). Mesowear also sheds light on paleoenvironments in terms of climate, as extant species existing in habitats with low precipitation and greater seasonality have higher rates of abrasive wear overall due to exogenous dust and grit in their habitats (Kaiser and Solounias, 2003). I will combine mesowear analyses of fossil bovid communities with tooth crown height and stable isotope data to better understand the average diet of a particular species from hominin bearing sites in time and space. This is important because species existing in habitats with low precipitation rates or more seasonality are expected to have higher abrasion and may shed light on paleoecology of hominin species which they are associated with.

Chapter four (the third paper) ('Multiproxy evidence for Plio-Pleistocene environmental change during hominin evolution in eastern Africa') will combine findings from the first two dissertation papers (ecometrics and mesowear) with new mammalian community analyses (Reed, 1995, 1997, 1998) and previously published stable carbon isotope ($\delta^{13}C$) data to synthesize the environmental framework in which hominin dietary breadth expanded ~ 3.5 Ma in eastern Africa. This paper will bring different methods to bear on a question that is at the core of human evolutionary research and this dissertation: How did ancient climate and environmental change shape the adaptive evolution of our ancestors? While documenting morphological and dietary shifts in early hominins is crucial, the cause of these changes must be tested using multiproxy approaches in terms of paleoecology. The third paper is designed to combine multiple proxies and evaluates the proposed dietary breadth expansion that occur in the hominin lineage around 3.5 Ma. This is important because it will test whether dietary expansion occurred in conjunction with climatically-mediated environmental change.

Finally, the findings of all three papers are synthesized in the discussion and conclusion chapter (chapter five).

CHAPTER 2
Paleoclimate and environments of Pliocene hominins in eastern Africa: implications for the origins of hominin dietary niche breadth

1. Introduction

Recent studies have demonstrated an expansion of hominin dietary niche breadth from C_3 dominated to including a range of C_3 and C_4 resources ~3.5 Ma in association with *Australopithecus afarensis* and later. However, the cause(s) for this expansion remains poorly understood (Sponheimer et al., 2013; Levin et al., 2015). Some researchers posit that this dietary shift may have been linked to the expansion of open grassland habitats (Leakey and Harris, 1987; Wynn, 2004; Codron et al., 2008; Levin et al., 2015). However, chimpanzees (*Pan troglodytes verus*) that frequently dwell in open habitats show little evidence for consuming C_4 grasses and sedges, or arid adapted succulents (Crassulacean acid metabolism, CAM) in their diet (Schoeninger et al., 1999). Moreover, baboons in Waterberg, South Africa, consume relatively high amounts of C_4 foods, where grass productivity is far lower (Tainton, 1999), implying that increased C_4 food intake does not necessarily reflect availability. Likewise, increases in the consumption of C_4 foods in hominins during mid-Pliocene may not necessarily be associated with open grassland habitats. This suggests that there could be factors other than simple grassland expansion driving hominin niche breadth increase, such as mean annual rainfall and rainfall seasonality. Reduced rainfall and/or increased dry season months may have also been proximate factors in this dietary shift. Therefore, to explore food availability for early hominins, it is important to understand both the amount of rainfall and the approximate number of dry season months in a given year. Fruits, flowers, seeds, and other parts of C_3 plants are highly dependent on these two factors, whereas tropical grasses with their corms and rhizomes can exist with less rainfall and more dry season months (Parr et al., 2014; Veldman et al., 2015).

Reconstructing paleoclimate is possible using chemical, biological, and physical proxies that respond to environmental conditions. Pliocene climatic and vegetation changes at hominin-bearing sites were traditionally reconstructed by analyzing proxies such as pollen (Bonnefille, 1995, 2010), soil stable isotopes (Cerling et al., 1997; Ambrose and Sikes, 1991), fauna (Reed, 1997; 2008; Kappleman et al., 1997), depositional environments (Brown and Feibel, 1991; Potts, 1994), marine oxygen isotopes (deMenocal et al., 1993) or ocean dust records (deMenocal, 1995). Hernandez-Fernandez and Vrba (2006), in particular, attempted to reconstruct precipitation in the Turkana Basin using analyses of mammalian community composition. Following this and other studies, several researchers now use ecometrics, which assesses the relationship between species' functional traits and the environments they occupy, to reconstruct climate and environments in the past (Janis, 1988; Eronen et al., 2010a, 2010b; Polly et al., 2011; Fortelius et al., 2014). Though individual variation may mask the relationship in populations, when ecometric data are averaged and examined at the community-level, the relationship becomes clearer and links between community-average traits and their environments can be reliably established (Polly et al., 2016).

1.1 Ecometrics and Hypsodonty

Proxies used for paleoclimate reconstruction need to be based on reliable functional trait-environment relationships. High crowned (=hypsodont) teeth are one such functional trait that can be used in ecometric studies. Janis (1988) hypothesized that the tooth crown height of mammalian herbivores—their hypsodonty—is an adaptation to both the mechanical properties of plant foods (e.g., silicates in grass) and exogenous wear (e.g., dust or grit). This hypothesis was supported by Janis, (1988, 1989), Janis and Thomason (1995), and Damuth and Janis (2011). These studies showed that the crown height of ungulate teeth is correlated with diet, and is also related to the aridity or wetness of the particular environment they occupy (see also Eronen et al., 2010a and 2010b). Therefore, the mean hypsodonty of ungulate communities in various localities have been used to reconstruct rainfall in both modern and fossil communities (Fortelius et al., 2014; Fortelius et al., 2016). Generally, areas predominated by grazers, which have the greatest hypsodonty are often associated with drier, more open grassland environments, where silica and other abrasive materials are commonly found, while browser dominated areas, which have the lowest crowned teeth, are associated with wetter and wooded environments.

Conventionally, tooth crown height is categorized into three groups 1) brachydont (low crowned, usually reflecting species that consume C_3 resources (browsers)), 2) mesodont (intermediate crowned, usually reflecting species that eat both C_3 and C_4 resources (mixed feeders)), and 3) hypsodont (high crowned, mainly reflecting species that specialize on C_4 resources (grazers)). In general taxa consuming >90% of grasses in their diet are referred to as grazers and hypsodont, those consuming >90% of leaves of plants are referred to as browsers and brachydont, while mixed feeders are known as mesodont (Janis, 1988; Janis et al., 2004). It is generally thought that grass is a more abrasive food item than browse due to the silica in the blades. Species that consume abrasive foods usually have high-crowned teeth that last a longer time to compensate for the high rate of wear (Pfretzschner, 1992).

In a hypsodont tooth, part of the crown is buried within the jaw and will erupt later when the exposed portion wears down, whereas in a brachydont tooth the entire crown of the tooth is sitting above the level of the alveolar margin (Janis, 1988). Species eating greater proportions of grass in any given habitat have, on average, a higher hypsodonty index and species living in more open habitats have higher hypsodonty indices than those in closed habitats (Williams & Kay, 2001; Mendoza and Palmqvist, 2008).

Damuth and Janis (2011) confirmed that hypsodonty can be used to predict the dietary ecology of past and current species. Using a variety of different statistical and comparative techniques several researchers (Codron et al., 2008; Clauss et al., 2008; Mendoza et al., 2002; Mendoza and Palmqvist, 2008; Williams & Kay, 2001) have shown a strong correlation of hypsodonty with diet and habitat both in extinct and extant species.

Moreover, as mentioned above, some studies have used known mean annual rainfall at modern sites and regressed it against the mean hypsodonty index from the ungulates at each site to reconstruct rainfall at localities across the Miocene of Eurasia

(Eronen et al., 2010a, 2010b; Polly et al., 2011; Fortelius et al., 2016). Establishing ecometric relationships between functional traits and environments therefore allows the use of multiple fossil species' traits to assess the environments and climates in the past. Polly and colleagues (2011) showed that the average hypsodonty index of mammal communities is highly correlated with rainfall across the globe, especially in the tropics. Eronen et al. (2010b) used regression trees and found that 65.8 percent of the geographical variance in mean tooth crown height can be explained by precipitation. Higher-crowned species are abundant in drier and more seasonal environments and have teeth that can resist higher abrasion (tougher foods, dust, and grit) (Janis, 1988; Eronen et al., 2010b; Kaiser et al., 2013). The opposite is true of wet and weakly seasonal environments, where lower-crowned species preferably live and consume soft foods, such as fruits (Janis, 1988, 1995; Eronen et al., 2010b). These studies have enhanced our understanding of modern habitats and suggest that mean hypsodonty values of ungulates in fossil sites can be used to estimate rainfall and other climate variables in the past.

Although ecometric analysis is a valuable approach to understanding the relationship between species' functional traits and rainfall, its application thus far has primarily been limited to the analysis of fossil materials from Eurasia and North America (Eronen et al., 2010a; Fortelius et al., 2014, 2016). Recently, however, Fortelius and colleagues (2016) used this method to identify a decreasing trend in precipitation from 7 Ma to 1 Ma years ago in the Turkana Basin, Kenya. Building on these efforts the application of this approach in the east African mid-Pliocene at hominin sites is important in order to better understand Pliocene environmental and climatic condition and their influence on dietary niche expansion in the hominin lineage.

1.2 Vegetation Structure

Vegetation structure refers to the ground cover provided by the plant assemblage, which often comprises a dominant taxon that forms a relatively uniform patch, making it distinguishable from neighboring patches of different vegetation types. Similar vegetation types tend to co-occur within landscapes with similar ecological processes, substrates, and/or environmental gradients (Omernik, 2004; Diamond and Elliott, 2017). Though vegetation structure is something defined at the habitat-level, it can also be aggregated to the level of ecoregions – a scale intermediate between habitat and biome. According to the World Wildlife Fund (WWF), an ecoregion is a large area of land containing a distinct assemblage of species, natural communities, and environmental conditions, where each ecoregion is bounded based on the patterns and composition of biotic and abiotic factors (Olson et al, 2001).

Following past studies, I used a simplified version of the WWF's ecoregion classification for vegetation (Olson and colleagues, 2001). Eronen et al. (2010b) used WWF ecoregion classification for faunal community structure to estimate the annual precipitation and showed the usefulness of using mammalian communities to reconstruct the vegetational type and in turn the vegetational type to reconstruct the precipitation. Liu et al. (2012) also used the WWF ecoregion data to examine the dental traits of herbivorous large mammal species to the observed spatial patterns in climate variables and vegetation and found strong correlations between them.

1.3 Goals of this Study

Here, I evaluate the importance of rainfall and vegetation structure as factors driving dietary niche breadth expansion in the hominin lineage at ~3.5 Ma based on mean hypsodonty of the ungulate taxa at each locality to reconstruct the mean annual precipitation (MAP), precipitation seasonality, and temperature seasonality of the hominin-bearing sites (Figure 2.1). In addition, I use vegetation data from WWF's Ecoregions classification (Olson et al., 2001) on modern data to estimate vegetation structure for the hominin localities based on the structure of their ungulate faunas.

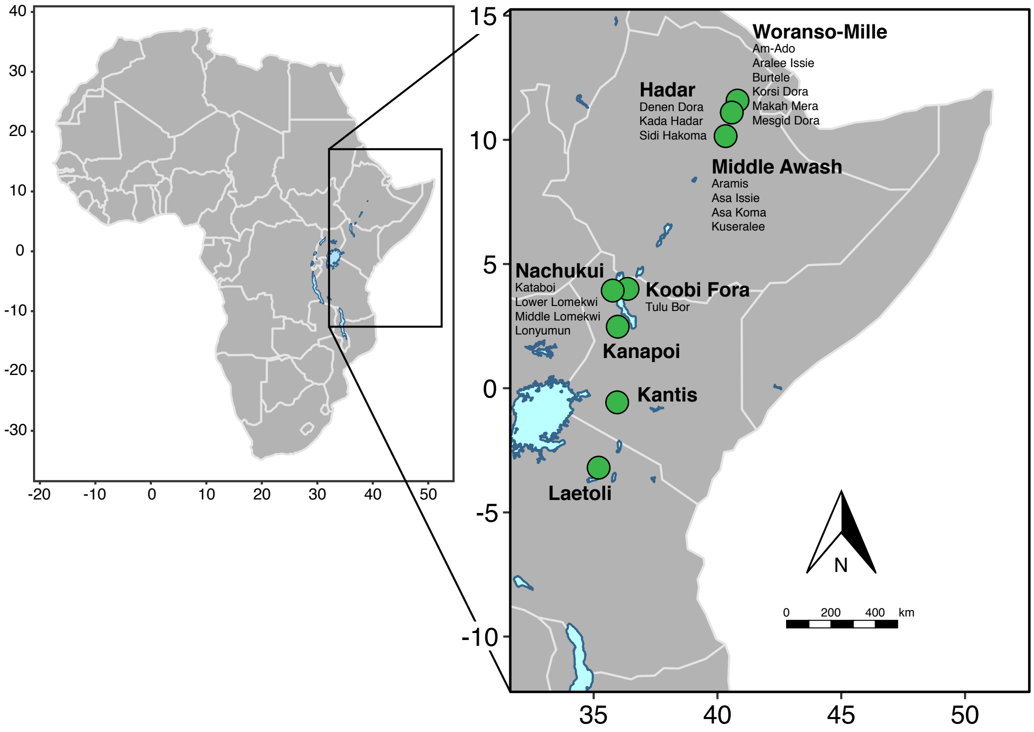

Figure 2.1. Overview of hominin (*Ardipithecus*, *Au. anamensis*, *Au. deyiremeda*, *Au. afarensis* and *Kenyanthropus*) bearing areas in eastern Africa showing sites, localities and stratigraphic units.

2. Materials and Methods

2.1 Modern Community Data

An African modern mammal community database (Rowan et al. 2016) allowed me to identify ungulate species at each locality for which I collected tooth crown height data. Rowan and colleagues collected data from 203 species (weighing more than 500g) of terrestrial mammals from Africa. Due to recent human-driven extinctions and range contractions in North Africa, only ungulates (orders Artiodactyla, Perissodactyla, Proboscidea – encompassing the majority of large herbivorous land mammal species) from 170 sub-Saharan African communities were considered.

Climate data for modern sites were collected from the WorldClim database (Hijmans et al., 2005; http://worldclim.org/version2), which contains high-resolution climate data commonly used in ecological analyses. Wordclim's bioclimatic variables are annual measures averaged from the monthly temperature and rainfall values in order to generate more biologically meaningful variables (Hijmans et al., 2005). The bioclimatic variables used in this study are mean annual precipitation (MAP) (BIO12), precipitation seasonality (BIO15), and temperature seasonality (BIO4), as shown in Table 1. Each of these variables is measured at 2.5 arc min resolution within cell ranges. I used the central latitude and longitude of each mammal community within the range to obtain MAP, precipitation seasonality, and temperature seasonality values used in this study.

Finally, I gathered vegetation data from WWF Ecoregions classification (Olson, 2001) using the central latitude and longitude of each community. Each modern community was assigned to one of seven simplified WWF Ecoregion vegetation type: montane, forest, forest mosaic, woodland, savanna, grassland, desert and semi-desert, to examine broad differences in vegetation communities (Olson et al., 2001). This broad classification will serve as the basis for reconstructing the paleovegetation of the Pliocene (Table 2.1):

- Montane vegetation is found at very high altitudes (like the Ethiopia highlands) and contains a mixture of groundsels (*Dendrosenecio*), lobelias (*Lobelia*), and temperate C_3 grasses, as well as shrubland and bushland (e.g., *Erica* heaths); bamboo can also be an important part of montane vegetation.

- Forests are areas of dense tree stands, with trees > 10 m on average, having interlocking crowns, and sparse ground cover; rainforests can consist of very tall trees (60-100 m), though average canopy heights are ~ 30-40 m.
- Forest mosaics are regions bordering the Central African rainforest that mix with adjacent woodlands; sometimes (such as in eastern Africa) these areas can be dominated by > 5 m stands of elephant grass (*Pennisetum purpureum*).
- Woodlands are areas of tree stands, but ones not dense enough to be considered forest; they often have a grassy understory and in southeast Africa are dominated by *Brachystegia* (Miombo).
- Grasslands are areas with virtually no woody cover, such as the Serengeti Plains. Though grasslands and woodlands are the ends of the savanna spectrum (grassy to woody savannas), I separate the spectrum here and reserve the use of savanna for regions containing more or less even mixes of grasses and trees (Shorrocks, 2015).
- Finally, desert and semi-desert regions are those largely barren of plant life but may contain low arid-adapted shrubs and trees (e.g., dwarf *Acacia*).

Ecoregion boundaries are not precise, where environmental conditions across ecoregion boundaries may change very gradually and mosaic habitats typically occur in transitional areas between ecoregions (Olson et al., 2001). Most of the vegetation types comprised similar plant communities but the classification referred here are based only in the identity of dominant species.

Table 2. 1. Ecoregions of modern sites with the lowest and highest precipitation.

WWF Biome	**Annual Precip. Range (mm)**
Woodland	476-1283
Savanna	417-1096
Desert and Semi-Desert	34-428
Grassland	466-1268
Montane	805-2437
Forest Mosaic	770-1910
Forest	1571-3330

To infer patterns of vegetation in the fossil record, I analyzed the number of ungulate grazers, mixed-feeders, and browsers across modern sub-Saharan African mammal communities in relation to their vegetation, then plotted the fossil communities on top of them to see which modern communities they resembled. Raw counts of dietary group numbers were not used because species richness varies in the fossil record as a result of both time averaging and sampling effort (Behrensmeyer et al., 2000), and therefore comparing raw counts of species will probably introduce biases into analyses that compare fossil and modern communities. To account for differences in community species richness, I corrected dietary group counts by overall community richness using regression (Faith et al., 2018). The residual from the regression line between grazer, mixed-feeder, or browser richness and overall ungulate community richness was used to measure the proportions of these dietary groups in both modern and fossil communities.

2.2 Fossil community data

To analyze fossil materials, I collected presence-absence data for ungulates from over 21 hominin-bearing early Pliocene and mid-Pliocene sites in eastern Africa (Fig. 2.1), housed in the National Museum of Ethiopia (Addis Ababa) and the National Museum of Kenya (Nairobi). Data from Laetoli were obtained from the literature (Kaiser, 2011). For each of the fossil ungulate taxon, I collected tooth crown height, length, and width. The data were collected from specimens which were identifiable at least at the tribal level. Broken specimens and subadult individuals were excluded from the analysis and only accessible/measurable isolated teeth were used. When possible, sites were analyzed as stratigraphically-defined units, bringing the number of localities/units to 18 from Ethiopia and 14 from Kenya. For example, Hadar is a site, but its various members, Basal, Sidi Hakoma, Denen Dora and Kada Hadar, are treated as different analytical units. These sites considered here span roughly ~ 6 Ma to 2.95 Ma. Each site was analyzed as separate analytical unit, but also aggregated into groups based on the hominin taxa they are associated with (e.g., *Ar. ramidus* and *Au. anamensis*, in one hand and mid-Pliocene hominins, *Au. afarensis* and *K. platyops* in the other hand).

2.3 Ecometric trait data

Crown height and length were collected to determine a hypsodonty index (HI, height to width ratio) for each tooth measured. Then each ungulate species was assigned to a tooth crown height group: hypsodont, or high crowned (HI > 1.2), brachydont, or low crowned (HI < 0.8), and mesodont, which is intermediate (0.8 <HI <1.2), based on Janis (1988) and others (Eronen, et al., 2010b; Fortelius et al., 2002, 2014. Species assignment to these classes was based on both upper and lower molars that are relatively unworn and represent the greatest height and width for each tooth (Feranec, 2003; Eronen et al., 2010a). These measurements are expected to show the level of hypsodonty for any particular species at any particular time. Finally, I calculated the mean crown height for each locality/unit by averaging the assigned molar crown height to estimate precipitation.

2.4 Ecometric analytical methods

Predictive models for annual precipitation were built using mean community hypsodonty across the 170 present-day ungulate communities using linear regression models in R (R Core Team). These models were then used to generate annual precipitation estimates for fossil communities using the predict() function in R. To infer vegetation for fossil communities, I analyzed species richness patterns in browsers, grazers, and mixed-feeders across the present-day ungulate communities in relation to vegetation groups based on WWF Ecoregions. Because time-averaging can artificially inflate richness in fossil communities–and therefore confound comparisons between past and present communities–I followed the method of Faith et al. (2018) and corrected functional type richness (i.e., number of grazers) by overall ungulate community richness. Faith and colleagues generated an ordinary least-squares regression and modeled the relationship between the richness of megaherbivores as a function of overall community richness in the modern data, and the middle 95% of variation in residuals was used as a modern baseline. Then functional type richness of fossil assemblage was regressed against overall ungulate community richness, with the residuals of this relationship being corrected functional type diversity measures. Functional type diversity measures the extent to which individual species trait characteristics differ between all species within an assemblage (Hooper et al., 2005).

3. Results

3.1 Modern hypsodonty-annual precipitation and precipitation and temperature seasonality relationships

A total of 170 recent day ungulate communities from sub-Saharan Africa were used to establish a baseline for modern mean ungulate community hypsodonty (Fig. 2.2). Table 2.2 and Figure 2.2 summarize the relationship between average ungulate community hypsodonty and mean annual precipitation (Fig. 2.2A), precipitation seasonality (Fig. 2.2B), and temperature seasonality (Fig. 2.2C). The correlation for mean annual precipitation, precipitation seasonality and temperature seasonality using linear regression are $R^2 = 0.57$ ($p < 0.001$), $R^2 = 0.35$ ($p < 0.001$) and $R^2 = 0.32$ ($p < 0.001$) respectively. Although statistically significant, the precipitation seasonality and temperature seasonality have only a weak correlation. Previous research (Eronen et al., 2010b, 2010c; Liu et al., 2012; Fortelius et al., 2016) shows a strong correlation between mean annual hypsodonty and mean annual precipitation and this is supported here by the highest correlation ($R^2 = 0.57$) between mean hypsodonty and mean annual precipitation. The precipitation regression indicates that tooth crown height, or hypsodonty, in modern mammalian communities is highly correlated with rainfall across Sub-Saharan Africa. Therefore, the mean hypsodonty index has the potential to predict the amount mean annual precipitation in the fossil sites. However, there is an outlier site, the Namaqua Park (located in the succulent Karoo), which only has two ungulates species, *Raphicerus campestris* and *Sylvicapra grimmia*. The community has a low hypsodonty value (1.5) but also low rainfall indicating an arid region. This is part of the fynbos regime and the succulent plants retain water, and are thus softer to eat than expected. It is also important that this area only supports two ungulate species. Namaqua has a mean hypsodonty of 1.5, this is because I scored the hypsodonty data on a rank scale (hypsodont = 3, mesodont = 2, brachydont = 1). *Raphicerus* in my dataset is scored as 2 (mesodont) and *Sylvicapra* is scored as 1 (brachydont). The mean hypsodonty value was calculated for each locality by averaging these ordinated scores, and the mean values were plotted on maps using interpolated colors to indicate regional differences.

Table 2.2. Summary of regression models predicting three climate variables (mean annual precipitation, precipitation seasonality, and temperature seasonality) across 170 modern sub-Saharan African ungulate communities.

Mean Annual Precipitation (bio12)			
Estimate	Std. Error	t-value	p-value
-1032.39	69.38	-14.88	<0.001
			***R2*=0.57**
Precipitation Seasonality (bio15)			
Estimate	Std. Error	t-value	p-value
46.584	4.881	9.544	<0.001
			***R2*=0.35**
Temperature Seasonality (bio4)			
Estimate	Std. Error	t-value	p-value
1619	179.1	9.042	<0.001
			***R2*=0.32**

In general, mean ungulate community hypsodonty increases with decreasing mean annual precipitation. In other words, species living in high rainfall areas have, on average, lower crowned teeth than species living in regions with less rainfall. Higher-crowned species that can resist tooth abrasion (tougher foods, dust and grit), generally consume grasses and are abundant in drier, more open environments.

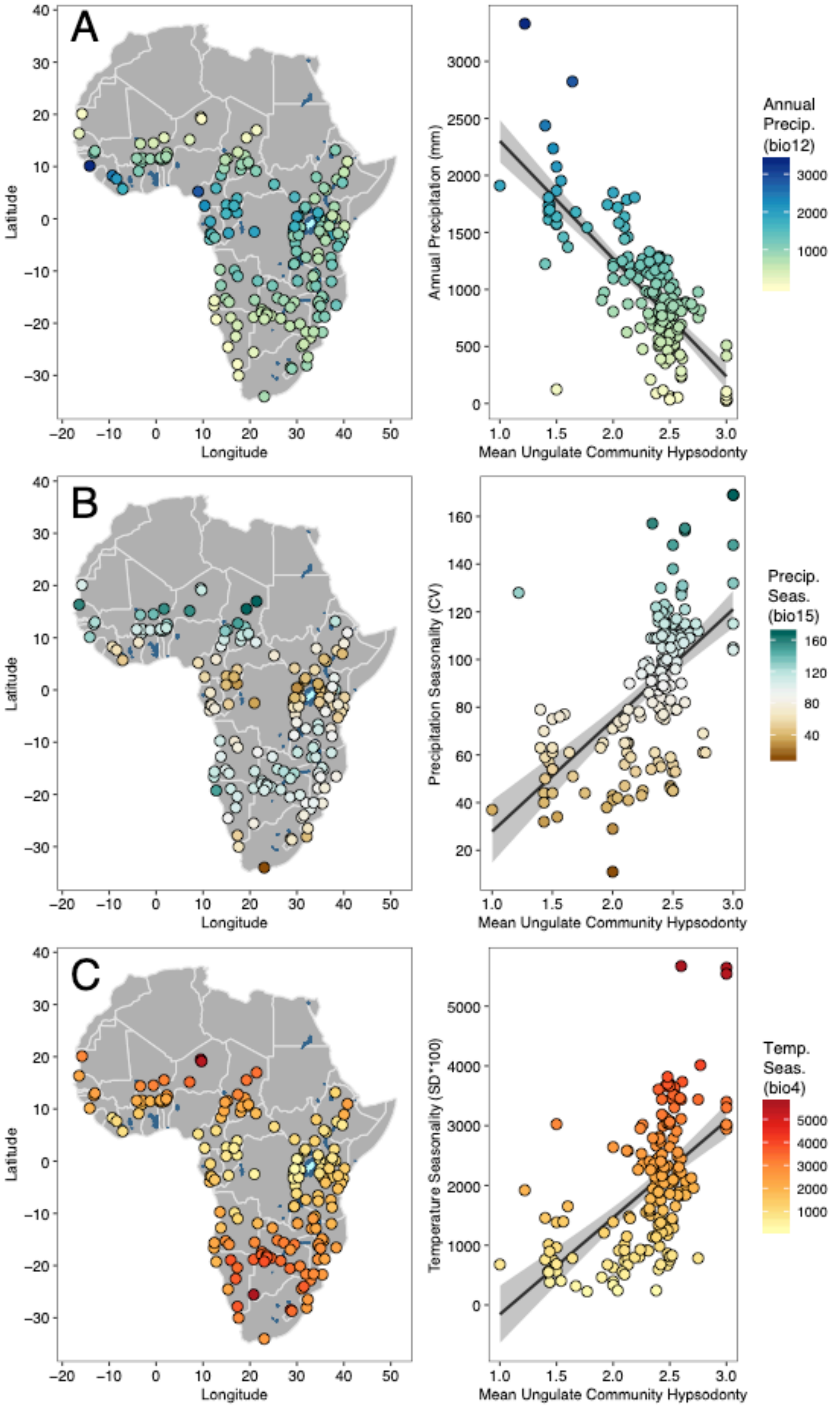
A
B
C
Latitude
Longitude
40
30
20
10
0
−10
−20
−30
−20
−10
0
10
20
30
40
50
Annual Precipitation (mm)
Mean Ungulate Community Hypsodonty
1.0
1.5
2.0
2.5
3.0
0
500
1000
1500
2000
2500
3000
Annual Precip. (bio12)
3000
2000
1000
Precipitation Seasonality (CV)
20
40
60
80
100
120
140
160
Precip. Seas. (bio15)
160
120
80
40
Temperature Seasonality (SD*100)
0
1000
2000
3000
4000
5000
Temp. Seas. (bio4)
5000
4000
3000
2000
1000

Figure 2.2. Maps and scatterplots of the relationship between mean ungulate community hypsodonty and annual precipitation, precipitation seasonality, and temperature seasonality across 170-present day ungulate communities from sub-Saharan Africa. The x-axis shows mean ungulate hypsodonty, and the y-axis shows mean annual precipitation, precipitation seasonality and temperature seasonality.

3.2 Estimated annual precipitation and precipitation and temperature seasonality for fossil sites

Annual precipitation is one of the determinant climatic factors of tree cover: grassland being relatively low precipitation and dry habitat, while forest environments have high annual precipitation and wet habitats (Janis et al., 2004). Reed (1997) also confirmed that tree coverage declines as precipitation decreases in a given area, indicating that precipitation is a determinant factor for habitat type. Figure 2.3A shows reconstructed mean annual precipitation across eastern Africa from 5.5 to 3 million years ago that indicates a correlation between annual precipitation and hypsodonty, and this represents a steady and long-term regional decrease in mean annual precipitation through time in eastern Africa. Generally, Figure 2.3A and 2.3B indicates the relationship between Pliocene hominin habitats and estimated annual precipitation—there is a significant difference between early and mid-Pliocene hominin bearing sites: the *Ardipithecus* and *Au. anamensis* sites on one side and the *Au. afarensis, Au. deyiremeda* and *Kenyanthropus* sites on the other hand. According to the ecometric analysis early Pliocene hominins lived in an environment where annual precipitation was higher compare to mid-Pliocene hominins. As predicted, early Pliocene hominins occupied relatively wet environments – roughly ranging from 900 - 1100 mm a year on average. Interestingly, *Au. anamensis* is suggested to have occupied a wetter environment than did

Ar. ramidus, although the latter species existed earlier in time. On the other hand, as predicted, mid-Pliocene hominins occupied drier environments that mostly received 870 mm of rainfall or less a year. In general, early Pliocene hominins lived in an environment where mean annual precipitation was fairly high, while mid-Pliocene hominins lived in an environment with lower mean annual precipitation.

LOESS (locally estimated scatterplot smoothing) regression with 95% confidence limits show annual precipitation was stable between 5.5 Ma and ~4.0 Ma, but thereafter abruptly declined around 3 Ma, which is coincident with the expansion of the hominin dietary niche.

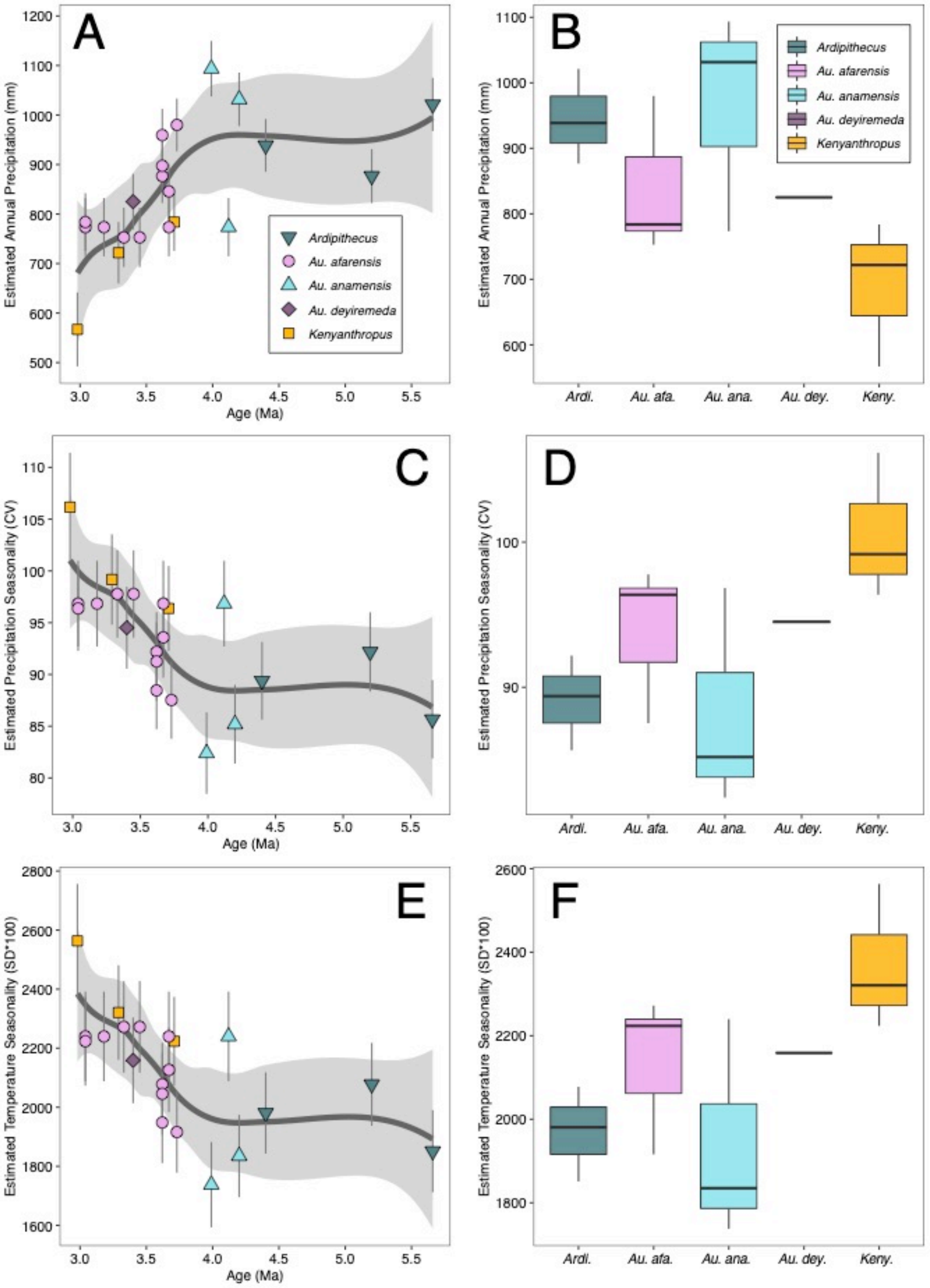

Figure 2.3. Ecometric reconstructions of annual precipitation, precipitation seasonality, and temperature seasonality based on mean ungulate community hypsodonty for Pliocene hominin-bearing fossil sites. LOESS curves show average trends through time, whereas

boxplots show site-to-site differences aggregated by the hominin taxon present (whiskers indicate range, boxes represent two standard deviations, and the horizontal lines are the means).

Although there is a general trend of increasing rainfall and temperature seasonality through time across eastern Africa (Fig. 2.3C and 2.3E), this trend is not statistically supported. The grouped seasonality plots (Fig. 2.3D and 2.3F) shows the existence of a significant difference between the *Ardipithecus* and *Au. anamensis* sites and the *Au. afarensis, Au. deyiremeda* and *Kenyanthropus* sites, where early Pliocene hominin taxa lived in environments with relatively low seasonality, while Mid-Pliocene hominins occupied more seasonal environments. One very interesting pattern is that the *Kenyanthropus* sites west of Lake Turkana are by far the most arid and seasonal, even compared to contemporaneous *Australopithecus afarensis* sites. This intriguing because these sediments are the only place where *Kenyanthropus* has so far been found, and they have also yielded the world's oldest stone tools 3.3 million years old (Harmand et al., 2015). This suggests *Kenyanthropus* and the Lomekwian toolmakers lived in very different environments compared to other contemporaneous hominins, which may suggest a niche difference between these taxa.

3.3 Modern and fossil diet-vegetation relationships

Modern dietary category-vegetation relationships are shown in Figure 2.4. Each plot (Fig. 2.4A-C) shows one dietary category plotted against another, after correcting for differences in sampling (so the axes say Grazer Richness (Residuals) after Faith et al., 2018). The closer a fossil point is to a particular modern vegetation cluster, the more similar in vegetation it likely is. This indicates that variation in ungulate community tooth crown height can discriminate major vegetation types in Africa. In general, the PCA (Fig. 2.4) of the diet group residuals separates browsers from grazers in the first axis, whereas the second axis separates mixed-feeders from browsers plus grazers. Fig. 2.4A shows the richness of browsers (y-axis) vs the number of grazers (x-axis) across both modern and fossil communities. Most of the fossil sites in Fig. 2.4A fall towards vegetation types of woodland, savanna, grassland, and desert on the x-axis (grazers). All of the fossil sites have far fewer browsers (y-axis) than communities today, because they fall below the scatter of modern points.

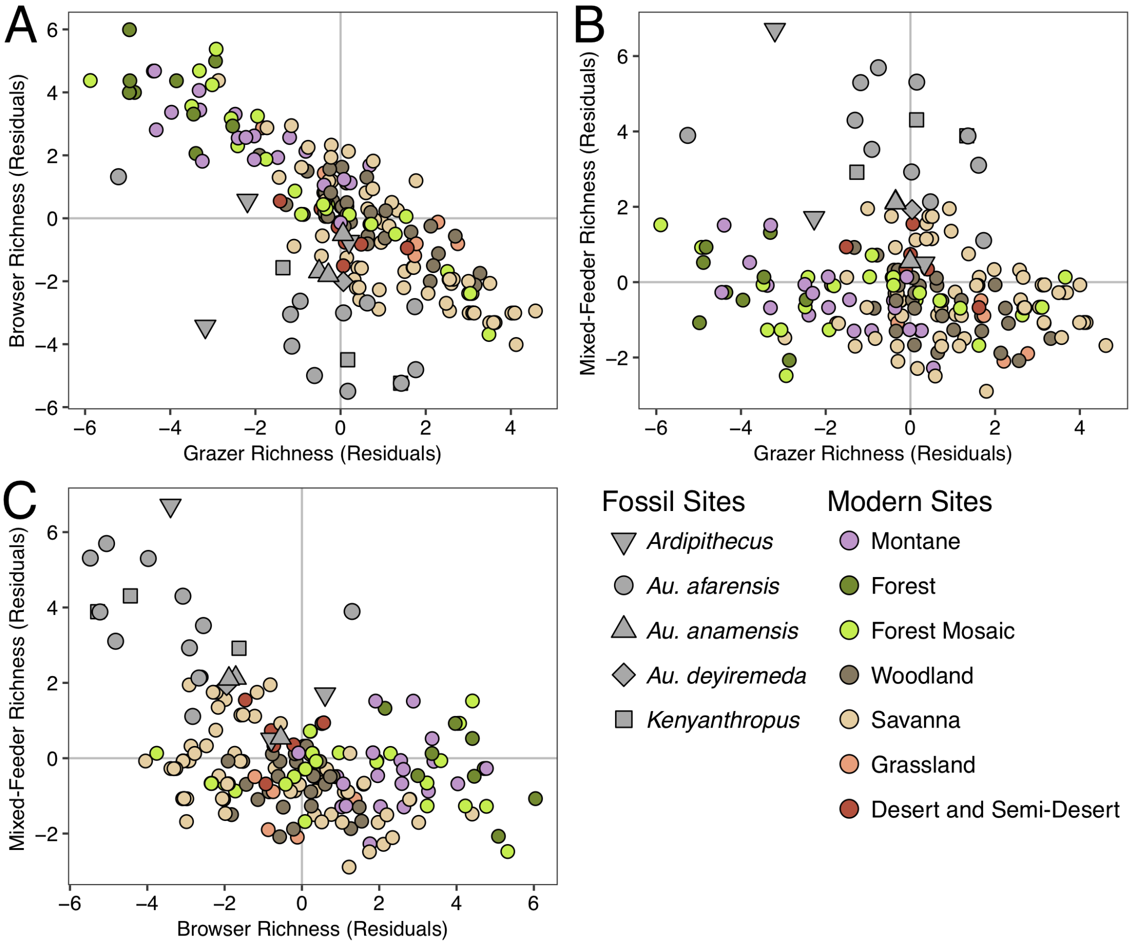

Figure 2.4. Scatterplots of corrected (residual) species richness in browsers, grazers, and mixed-feeders across present-day and fossil ungulate communities (A-C). The modern communities are shown in color and are colored by their vegetation type (e.g., red = desert, dark green = forest). The fossil communities are shown in gray, with the shapes indicating which hominin species is found at the site.

Fig. 2.4B shows the number of mixed-feeder (y-axis) vs the number of grazers (x-axis) across both modern and fossil communities. Some of the fossil sites in Fig. 2.4B are overlapping with savanna, and desert and semi-desert on the y-axis (mixed feeders). Most of the fossil sites have more mixed feeders than communities today and they fall above the scatter of modern points. Fig. 2.4C shows the number of mixed-feeder (y-axis) vs the number of browsers (x-axis) across both modern and fossil communities. Several of the fossil sites in Fig. 2.4C fall mainly with savanna and desert and semi-desert but with some overlap to forest mosaic on the y-axis (mixed feeders). All of the fossil sites have fewer browsers (x-axis) than communities today and they fall above the scatter of modern points. Generally, there is a consistent pattern where the fossil sites are much richer in mixed-feeders and have fewer browsers compared to the modern ungulate communities.

4. Discussion

Cerling et al. (1993, 1997) and Polissar et al. (2019) found that the expansion of C_4 grasses was associated with the declining of atmospheric carbon dioxide and further suggested that C_4 photosynthesis is favored over C_3 photosynthesis when the atmospheric carbon dioxide is low. Seasonality is also suggested as one of the major underlying factors for the evolution of C_4 grasses and grazer dominated biomes (Blumenthal et al., 2017). The opposite is true of wet and weakly seasonal environments, which have lower-crowned species adapted to consuming soft foods, such as fruits. Blumenthal and colleagues (2017) showed that community hypsodonty of fossil sites can be used to estimate their rainfall and other climate variables including precipitation seasonality and temperature seasonality.

The composition of communities of large herbivorous mammals reflects their local habitat: generally, grazers are associated with grasslands/open environments and browsers with forests. However, some browsers may prefer habitats within drier environments, such as gazelle species. Depending on their species-specific dietary and habitat preferences individuals of different species may experience different levels of dental abrasion during their lifetimes, and this different degree of hypsodonty may affect the contemporary ecology of individuals (Janis et al., 2004; Eronen et al., 2010b; Polly et al., 2011). For example, while those browser species feeding above ground level have low crowned teeth, browser species feeding at ground level may have higher crowned teeth (Janis, 1988). Mammals have only a single adult dentition and those herbivores consume abrasive food items should increase their tooth crown height. High-crowned (hypsodont) species can sustain themselves on extremely abrasive diets, and are likely to compete successfully with intermediate and low-crowned (mesodont and brachydont) species for such resources. Therefore, it is reasonable to assume that hypsodonty index will have some predictive power for the ecology of both past and present species.

The relationship between hypsodonty and annual precipitation is illustrated in Fig. 2.3. The mean value of hypsodonty in each hominin locality increases consistently across hominin localities of decreasing precipitation. Thus, it is clear from the figure that the mean hypsodonty index is able to predict the amount of precipitation. It also predicts precipitation seasonality and temperature seasonality but not strong like precipitation. The association between hypsodonty and diet is the result of vegetation structure being sensitive to levels of annual precipitation. The early Pliocene hypsodonty pattern shows faunas dominated by brachydont ungulates in localities that indicate wet environments, and the localities with ungulates having increased hypsodonty are all from the middle Pliocene, with a sharp decline in precipitation around 3.5 Ma. While the fossil localities may be closer to certain modern environments than others (like savannas and woodlands in Fig 2.4), they are mainly dissimilar from environments today. This is almost certainly because Pliocene environments have no modern analogs (i.e., no environment today replicates what Pliocene vegetation might have looked like) (Faith et al., 2019). The best we can say is that the fossil sites are most similar to savannas and woodlands, but the ungulate community structure, differed greatly and they fall outside the modern range of variation.

The hypsodonty data of this study indicate that the early Pliocene sites are predicted to have had higher precipitation and were dominated by browsing ungulate species, suggesting that early Pliocene hominins occupied wetter habitats compared to those of the mid-Pliocene. It is well understood that plant productivity and quality are influenced primarily by precipitation. In turn herbivore community structure, distributions and species richness are affected by plant quality and productivity (du Toit and Owen-Smith, 1989; Maurer, 1996; Danell et al., 1996; Belovsky, 1997; McConkey et al., 2003; Hanya et al., 2011). The mid-Pliocene environments likely had patchier food distributions in both space and time, and therefore hominins had to broaden their dietary niches to survive. The results agree with mesowear, isotope and microwear studies, which say latter hominins lived in a more open habitat (Cerling et al., 2013, 2015; Curren and Haileselassie, 2016). However, the results indicate significant variability across sites. One very interesting pattern is that the *Kenyanthropus* sites (Fig. 2.3A and B) west of Lake Turkana are by far the most arid and seasonal, even compared to contemporaneous *Australopithecus afarensis* sites, reflecting the development of regionally diversified climate systems and perhaps reflecting the spread of C_4 grasses in eastern Africa. I note that this is a result found by other authors using various proxy data and methods, including Bobe and Behrensmeyer (2004) and most recently Fortelius et al. (2016).

The paleoenvironment of *Ardipithecus* is a contentious issue, with some researchers suggesting it was a closed woodland or forest mosaic (White et al., 2009), while others suggest it was more of a woody savanna with abundant grass cover (Gani and Gani, 2011). The reconstructed rainfall here suggests the former, i.e., closed woodland or forest mosaic. This research, thus, shows that hypsodonty levels in the ungulate communities do indeed carry a strong signal about diet and habitat aspects of the environment as well as precipitation both in extant and extinct herbivores mammals.

5. Conclusion

In this study I have been able to show a relationship between mean tooth crown height (hypsodonty) in an herbivore community and the precipitation level of the community's local habitat in the hominin bearing localities in East Africa. This study also shows early Pliocene hominins lived in environments where annual precipitation was higher than was at mid-Pliocene hominin sites, supporting the usefulness of hypsodonty approach used here as a good predictor of past climate variables (including precipitation). This has been previously shown by several studies (Fortelius, 1985; Janis and Fortelius, 1988; Janis, 1988, 1995; Fortelius and Solounias, 2000; Fortelius et al., 2002, 2014, 2016; Eronen et al, 2010b; Damuth and Janis, 2011; Polly et al, 2011) strengthening the finding on the relationship between hypsodonty and climate variables. I conclude, therefore, hypsodonty is fundamentally an adaptive response to increasing demands for wear tolerance and functional durability of the dentition as precipitation decreases and more open conditions prevail.

CHAPTER 3

Hominin paleoenvironments in the eastern African Pliocene: evidence from bovid community mesowear

1. Introduction

1.1. Mesowear and Diet

Reconstructing hominin evolutionary adaptation requires a detailed understanding of the paleoecological setting in which they evolved. Among factors that make our effort to understand the interplay between paleoecology and hominin adaptation very difficult are small sample size in the fossil record and possible lack of modern analogues to past environments. Despite this, researchers have been able to draw some conclusions about eastern African Pliocene hominin adaptations based on various paleoenvironmental proxies. Many studies suggest that hominins occupied a variety of habitats ranging from woodland to open woodland and shrubland habitats (Reed, 1997, 1998; Behrensmeyer and Reed, 2013) and exploited different dietary resources. Stable isotope signatures show that early-Pliocene hominins consumed C_3 dominated diets while mid-Pliocene hominins incorporated both C_3 and C_4 food items in their diet (Cerling et al., 2013; Wynn et al., 2013; Sponhemeir et al., 2013). Most studies show that both regional and local climatic and paleoenvironmental changes were important factors for hominin dietary change (Cohen et al., 2009; Potts, 1996, 2013; Potts and Faith, 2015). In order to understand the interaction between adaptations and the environment we need to work at finer scales that are relevant to understand human and mammal evolutionary trajectories. Mesowear analysis is one such approach. East Africa, particularly Ethiopia and Kenya, where most of these Plio-Pleistocene hominin specimens were discovered, is an excellent place to investigate the underlying factors for possible cause of hominin dietary adaptations. Since fossil hominins were relatively rare on the paleolandscape, the goal of this project is to shed light on the habitat and environments hominins preferred by studying the remains of more abundant and ecologically diverse contemporaneous ungulates in eastern Africa.

The hypsodonty index is a measure of how high the crown of a molar is relative to its width. It is used to assign the categories of grazing, browsing and mixed feeding to ungulates and are also considered to be good predictors of diet and thus habitats (Janis, 1988; Fortelius et al., 2002). Some researchers (Mihlbachler and Solounias, 2006; Kaiser et al., 2013), however, have suggested that this index should not be used alone to determine dietary categories, since some taxa have been shown to deviate from these categories. For example, grazers such as hippos (*Hippopotamus amphibius*) that eat grasses near water have lower crowned teeth than would be predicted, while pronghorn antelope (*Antilocapra americana*) have high-crowned teeth but are browsers (Janis, 1988, Janis and Thomason, 1995; Mendoza et al., 2002). Carbon isotope values from tooth enamel also sometimes deviate from what is predicted by hypsodonty index. Carbon isotope values of llamas, *Lama angustimaxilla* and *Vicugna provicugna*, suggest that these species predominantly consumed C_4 plants and are therefore interpreted as grazers, but the hypsodonty index for both taxa is remarkably low (Mendoza et al., 2002). Moreover, since habitat (closed vs open) and diet (tall vs short grasses) have an independent effect on species' hypsodonty indices (Damuth and Janis, 2011), it is crucial to use additional supplementary methods, such as mesowear analysis, to evaluate factors affecting tooth wear.

Mesowear (middle-range tooth wear) is a paleo-dietary proxy that allows documentation of the relative amount of attrition (a result of tooth-to-tooth contact) and abrasion (a result of food-to-tooth contact) on ungulate molars (Kaiser et al., 2000). Attrition is mostly associated with browsing species where the upper and lower occlusal surfaces of the teeth come in contact during the feeding process, whereas abrasion is associated with grazing species in which facets develop due to tooth contact with plant materials which have high proportions of silica, dirt and grit (Fortelius and Solounias, 2000; Kaiser et al., 2013). Because of this, abrasion results in molars that have high and sharp cusps, while attrition results in molars exhibiting low and blunt cusps. Fraser et al. (2014) using mandibular dental analysis conclude that mesowear can provide an estimation of 60-80% of ungulate diets of grass (grazers), leaves and shrubs (browsers) and those that eat both (mixed feeders). Fortelius and Solounias (2000) were the first to introduce the mesowear method as a tool to describe the effect of diet on tooth wear, which then became an important way of reconstructing paleodiet and by extension paleoecology in the fossil record.

Since the shape and the relief of the facets of ungulates molars differ between grazing, browsing and mixed-feeding taxa (Kaiser et al., 2013) due to differences in the properties of the food types and the relative amount of grit they contain (Janis, 1988, 1995; Eronen et al., 2010b; Kaiser et al., 2013), mesowear facets can be used to reconstruct not only the diets, but the vegetation structure in which these animal communities lived. Depending on the relative values within each fossil assemblage (community), an estimation of the habitat type can be made.

At eastern African fossil bearing localities, bovids are abundant and frequently associated with hominins. Bovid paleoecology has proven particularly useful for understanding hominin paleoecology (Reed, 1998). Mesowear analysis has been applied to some hominin sites in Ethiopia, Kenya, and Tanzania to shed light on the diets of ungulates and habitat from which they derived. This includes, Gona (Semaw et al., 2005), Middle Awash (White et al., 2009), and Woranso Mille (Curran and Haile-Selassie, 2016) from Ethiopia, Allia Bay and Kanapoi (Dumouchel and Bobe, 2019) from Kenay and Laetoli from Tanzania (Kaiser, 2011).

Here, I focus on regional-level mesowear analysis of eastern African fossil localities to investigate the underlying factors in other animals that may shed light on hominin dietary niche variation in the mid-Pliocene. Thus, this chapter examines ungulate mesowear from localities where *A. ramidus*, *Au. anamensis*, *Au. deyiremeda*, *Au. afarensis* and *K. platyops* were found to better understand the paleoenvironments of these sites.

1.2. Goal of the Study

The East African Rift Valley (Figure 3.1) has produced the richest Plio-Pleistocene records of hominin fossils and associated mammalian faunas. Bovidae (antelopes and kin) numerically dominate most East African fossil assemblages in terms of both species' richness and absolute abundance (Faith et al., 2019). As primary consumers tightly tied to vegetation structure and other physical environmental features (e.g., climate), fossil bovids therefore serve as a good proxy for inferring aspects of hominin paleoenvironments in East Africa. The goal of my study is to use mesowear to reconstruct diets of fossil bovid species, and then use diet to make vegetation inferences for 16 eastern African, Plio-Pleistocene fossil sites.

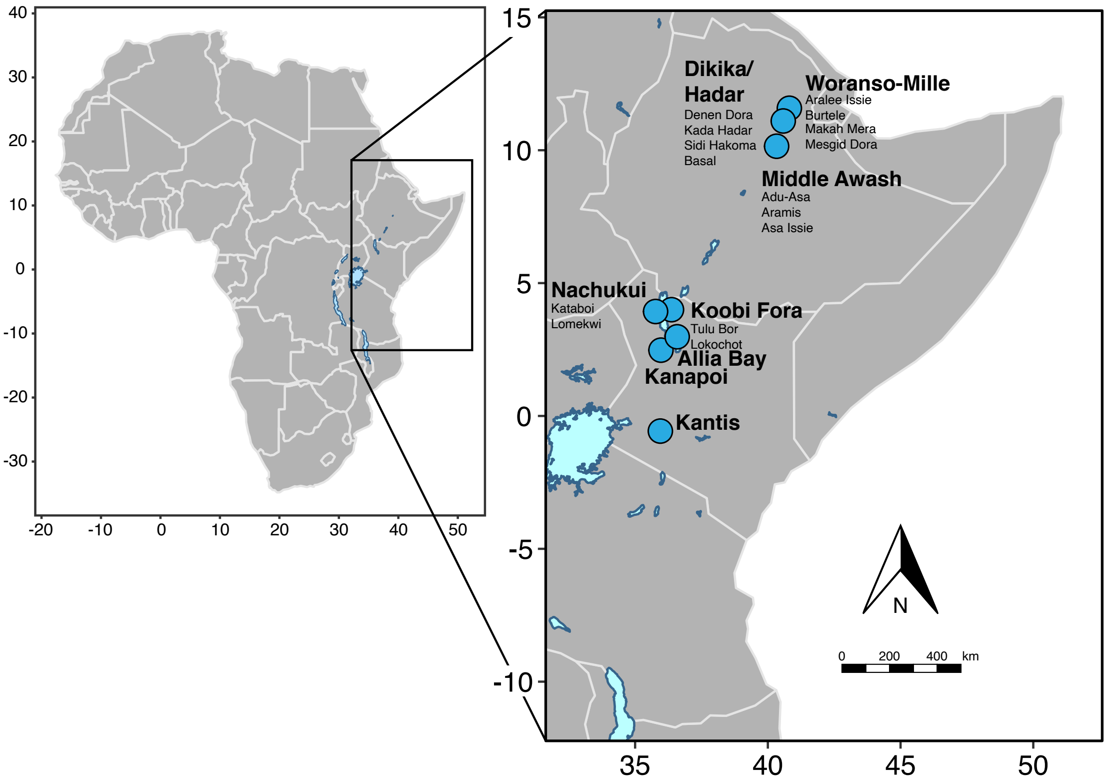

Figure 3.1. Hominin bearing areas in eastern Africa showing sites, localities and stratigraphic units used for mesowear analysis.

2. Materials and Methods

2.1 Fossil sample

A total of 920 mesowear samples (Table 3.1) were collected from specimens housed in the National Museum of Ethiopia (NME) and the National Museum of Kenya (NMK). I focused on both upper and lower molars in mid-wear (slightly worn teeth) that were free of taphonomic artifacts (e.g., enamel chipping) representing seven bovid tribes (see Table 3.1). This includes 662 individuals from Ethiopia (Hadar = 241, Dikika = 34, Woranso-Mille = 151 and Middle Awash = 235) and 258 individuals from Kenya (Allia Bay = 59, Kanapoi = 28, Tulu-Bor/Lokochot = 20, Kataboi/Lomekwi = 139 and Kantis = 12). I only used teeth that were taxonomically identified to at least the tribal level mentioned above. Only adult molars were used and both isolated and teeth intact in the jaw were scored for the mesowear analysis. Teeth which are heavily worn (old individuals) or still emerging from the jaw (young individuals) were excluded from this analysis. This technique minimized the effect of age on my scoring.

Table 3.1. Bovid tribes used for this analysis.

Order	Family	Tribe
Artiodactyla	Bovidae	Aepycerotini
Artiodactyla	Bovidae	Alcelaphini
Artiodactyla	Bovidae	Antilopini
Artiodactyla	Bovidae	Bovini
Artiodactyla	Bovidae	Hippotragini
Artiodactyla	Bovidae	Reduncini
Artiodactyla	Bovidae	Tragelaphini

2.2 Mesowear methods

Both upper and lower molar teeth were considered to expand the sample size. I followed Fortelius and Solounias (2000) in overall mesowear scoring methodology. I scored the mesowear value based on two variables: cusp shape (sharp, round, blunt) and cusp relief (high, low) to generated an ordinal (1-5) score for each tooth. The buccal edges of upper molars and lingual edges of lower molars were scored based on two modes of tooth wear: first, the occlusal relief of the tooth– the height between the cusp tips and intercusp valleys – as high or low, and second, the shape of molar cusps as sharp, round or blunt based on the degree of facet development. Scores were collected using a modified version of Kaiser's (2011) mesowear score scale: a high and sharp mesowear score was assigned to MS-1, a high and round mesowear score was assigned to MS-2, a low and sharp mesowear score was assigned to MS-3, a low and round mesowear score was assigned to MS-4, a low and blunt mesowear score was assigned to MS-5. For each tribe the respective cusp shapes were summarized as percentages and were given as three variables: percentage sharp, percentage round, and percentage blunt, which add to 100%. Although the factors governing tooth wear are complex, the combined scoring and percentages of the mesowear analysis permits grouping ungulates into dietary groups: grazers, browsers and mixed feeders (Kaiser and Solounias, 2003; Kaiser and Schulz, 2006). Grazers have a high degree of abrasion, browsers have low degree of abrasion, and mixed feeders are intermediate.

The shapes of the facets differ between grazing (grass-eating) and browsing (leaf-eating) taxa depending on the properties of the foods they ingested (abrasion) and the tooth-on-tooth wear during mastication (Fortelius and Solounias 2000). Animals that feed on leaves possess teeth with higher and sharper cusps than those that feed on grass. This is because grazers consume plants with greater structural defenses (e.g., silica) and because their feeding environments are laden with abrasive grit and dust. Thus, scores indicate the level of abrasiveness of the diet a species had to cope with. In this convention, a combined score of 1 represents the most attrition-dominated mesowear signature, while a score of 5 would represent the most abrasion-dominated signature.

Cusp relief was scored as high or low depending on how high is the relief from the bottom of the valley (Fig. 3.2). The first few hundreds of the teeth were measured after the buccal (upper) and lingual (lower) profile of cusp relief were traced on to a paper and a vertical distance between a line connecting two adjacent cusp tips was projected. All of the specimens were photographed and used to double check some of the teeth during data analysis. Cusp shape was scored as sharp, rounded and blunt, using handheld magnifier when necessary. A sharp cusp has no rounded area between the mesial and distal wear facets, a rounded cusp has a rounded tip with facets on the lower slopes, while a blunt cusp is defined as those in which the wear facets had been worn away (Fortelius and Solounias, 2000).

I followed the convention and used a mean mesowear score to obtain conservative bovid population values. That is, individual species or tribal scores were averaged, and a mean score was calculated for each fossil species or tribe. Species existing in habitats with comparably low precipitation rates or more seasonality are expected to have higher abrasion, for example, and thus reflect the habitat from which they derived (Kaiser and Solounias, 2003). When all bovid species in a site's faunal assemblage are considered together, they should reflect the habitat. Most of the time, many species with low relief and rounded or blunt cusps suggest grassland habitats with high seasonality and low precipitation. Mesowear scores were aggregated into analytical units, these being primarily stratigraphic members (e.g., the Denen Dora Member of Hadar) or spatiotemporally constrained collections areas (e.g., Aramis from the Middle Awash).

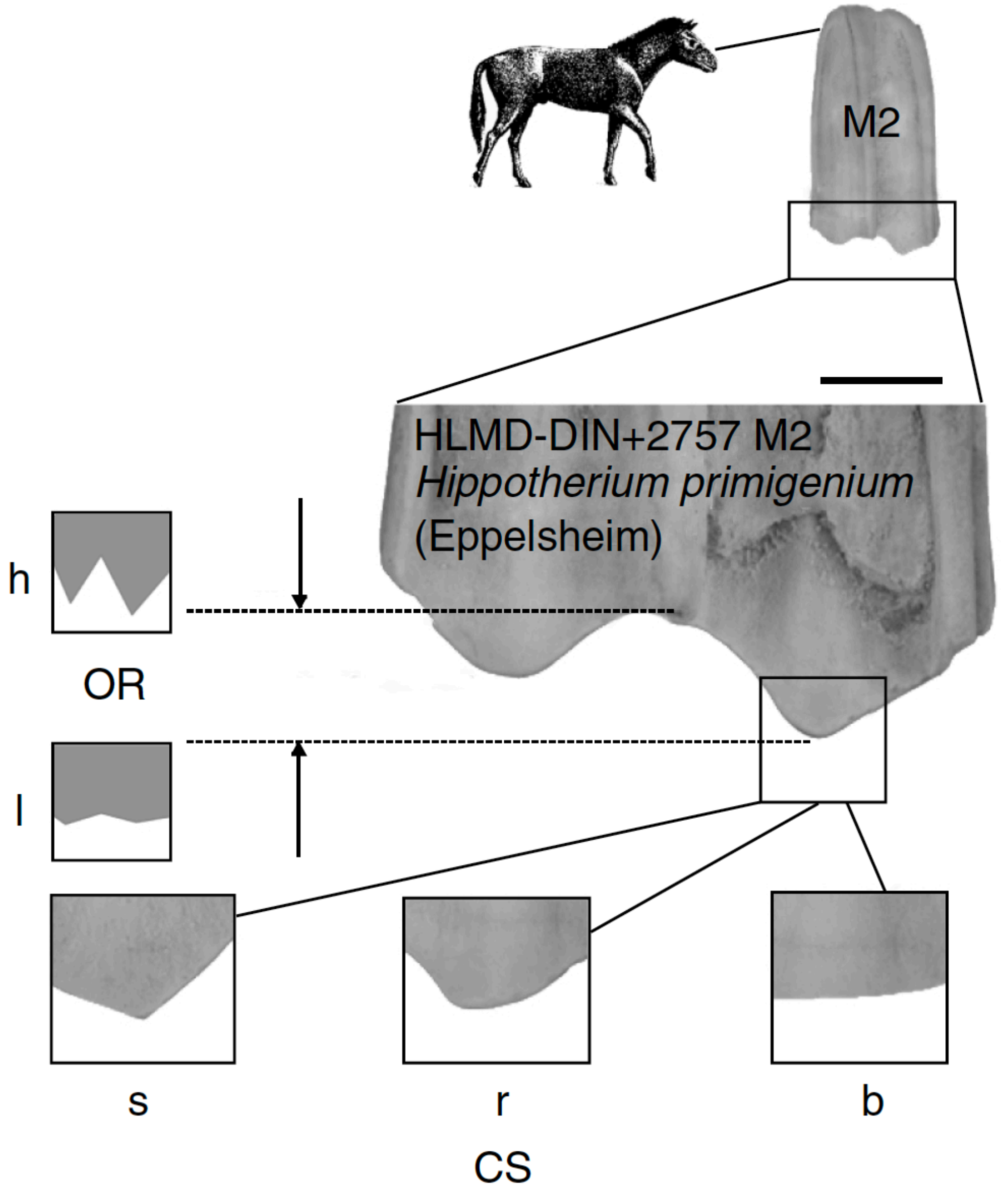

Figure 3.2. Typical mesowear variables (occlusal relief and cusp shape) of ungulates. Occlusal Relief (OR) can be scored as high (h) and low (l). Cusp Shape (CS) can be scored as sharp (s), round (r), and blunt (b). The dotted lines indicate the height of the occlusal relief, from the bottom of intercusp valley to the apex of the highest cusp. (Adapted from Kaiser and Fortelius, 2003)

2.3 Analytical methods

Mean and standard deviations of mesowear scores were tallied and plotted across sites. Tukey's HSD post-hoc tests from an ANOVA were used to test for significant differences in mesowear scores between sites aggregated by hominin taxon present. The sites are plotted individually in the boxplot figure (Table 3.2 and Fig. 3.3) but for statistical analyses I based the analysis on hominin taxon. A combined mesowear score was computed (see Table 3.5). The scores are essentially an ordinal scale, ranging from the most abrasion-dominated signature (i.e., 1), to the most attrition dominated signature (i.e., 5).

A Correspondence Analysis (Figure 4) was used to examine the proportion of the percentages of bovid tribes at various sites. The rainfall of the modern localities was displayed so that relative precipitation could be assessed for the fossil localities.

3. Results

Table 3.2 presents the mesowear data of ungulates in the hominin bearing sites in eastern Africa. The mesowear data includes the number of specimens (n), the number of bovid tribes represented in the sample (Tribes), and the mean (Mean), mode (Mode), and standard deviation (SD) of mesowear scores for each site. In all sites analyzed here, a mesowear score of 4 is the highest proportion documented. Of these Alcelaphini (Table 3.3) was the most dominant taxon in eastern Africa. There is very rare scoring for 5, which is low relief and blunt cup shape, while the remaining MS (1,2,3 and 4) are present in varying distributions. In general, mixed feeders were the dominant taxa in all sites.

Bovid fossils from all sites except Allia Bay, Kantis, Lokochot/Tulu-Bor, Kataboi/Lomekwi had an abrasion-dominated diet ranging from 3.05 to 3.61. However, Kada Hadar member from Hadar, Aramis and Asa Issie from Middle Awash, Aralee Issie, Burtele, Makah Mera from Woranso Mille and Kanapoi from West Turkana show the strongest grazing signal in the assemblage. Among the fossil assemblages included in this analysis, Kanapoi bovids stand out as having a much more dominant grazing signal.

Table 3.2. Summary of site, hominin, and mesowear data analyzed in this study (ordered by mean value from highest to lowest).

Country	Subregion	Site	Hominin	n	Tribes	Mean	Mode	SD
Kenya	West Turkana	Kanapoi	*Au. anamensis*	28	6	3.61	4	1.26
Ethiopia	Woranso-Mille	Burtele	*Au. deyiremeda*	39	7	3.54	4	0.79
Ethiopia	Hadar	Kada Hadar	*Au. afarensis*	71	7	3.46	4	0.92
Ethiopia	Middle Awash	Aramis	*Ardipithecus*	134	1	3.38	3	0.67
Ethiopia	Woranso-Mille	Aralee Issie	*Australopithecus* sp.	39	5	3.38	4	0.85
Ethiopia	Middle Awash	Asa Issie	*Au. anamensis*	25	2	3.32	4	0.90
Ethiopia	Woranso-Mille	Makah Mera	*Au. afarensis*	13	4	3.31	4	1.18
Ethiopia	Dikika	Basal/Sidi Hakoma	*Au. afarensis*	34	5	3.26	4	0.96
Ethiopia	Woranso-Mille	Mesgid Dora	*Australopithecus* sp.	61	7	3.21	3	0.80
Ethiopia	Middle Awash	Adu-Asa	*Ardipithecus*	76	7	3.08	4	0.95
Ethiopia	Hadar	Basal/Sidi Hakoma	*Au. afarensis*	63	7	3.05	4	1.08
Ethiopia	Hadar	Denen Dora	*Au. afarensis*	107	7	3.05	4	1.14
Kenya	West Turkana	Kataboi/Lomekwi	*Kenyanthropus*	139	7	2.91	3	1.07
Kenya	East Turkana	Allia Bay	*Au. anamensis*	59	4	2.56	3	1.13
Kenya	East Turkana	Lokochot/Tulu-Bor	*Au. afarensis*	20	3	2.35	1	1.31
Kenya	Kantis	Kantis	*Au. afarensis*	12	6	1.92	1	1.08

Table 3.4 shows the result of Tukey's HSD post-hoc test from the ANOVA comparing differences in mesowear scores aggregated by hominin taxon present. Since the sites used in this analysis vary in their sample sizes, an ANOVA and Tukey posthoc test were used between hominin taxa rather than by site. There was a statistically significant difference between tribes across some sites according to the ANOVA, F-value = 4.29 and p-value < 0.001. Pairwise comparisons of the means according to Tukey's HSD test showed significant differences between three pairs of hominin aggregates (bold values in Table 3.4): *Au. deyiremeda* and *Au. anamensis* (p=0.045), *Kenyanthropus* and *Ardipithecus* (p=0.017), and *Kenyanthropus* and *Au. deyiremeda* (p=0.009). The teeth of bovids from *Ardipithecus* sites (the Adu Asa and Aramis) collection show a diet containing abrasive elements indicating mixed feeding, as seen in the mesowear scores ranging from approximately 2-4 (Figure 3.3). Bovids in *Au. afarensis* sites (BM/SH/DD/KH from Hadar, BM/SH from Dikika and Makah Mera from Woranso Mille) also indicate mixed feeding but with higher range into greater amounts of abrasive diets. Interestingly, Kantis and Lokochot/Tulu Bor *Au. afarensis* localities from Kenya were dominated by bovids consuming more attrition dominated diets (browsing). This indicates that *Au. afarensis* in Hadar and Dikika likely existed in more open habitats compared to that of Kantis and Lokochot/Tulu Bor sites. Bovids from Allia Bay indicate greater amount of attrition, i.e., browsing compared to Asa Issie and Kanapoi, indicating that *Au. anamensis* from Allia Bay lived in more closed environments than Asa Issie and Kanapoi. I also compared the habitats among *Au. deyiremeda* from Burtele, *Australopithecus sp*. from Aralee Issie and Mesgid Dora and *Kenyanthropus* from

Kataboi/Lomekwi. While Kataboi/Lomekwi shows more browsing bovids indicating closed habitat, the Burtele site is dominated by taxa that indicate more grazing bovids representatives of open dry habitat. Aralee Issie and Mesgid Dora are intermediate. This comparison generally indicates that *Kenyanthropus* habitat was likely more closed compared with the Woranso Mille localities.

Table 3.3. Loadings from a principal component analysis (PCA) of mesowear scores across sites. Together, PC1 and PC2 account for 85.20% of overall variation in the mesowear data.

Variable	PC1 (59.14%)	PC2 (26.06%)	PC3 (10.87%)	PC4 (3.93%)	PC5 (< 1.00%)
MS-1	**0.58441**	**0.45404**	0.36875	-0.34096	0.4473
MS-2	-0.086444	0.33522	-0.82468	-0.0069525	0.44723
MS-3	0.28203	**-0.8249**	-0.12098	-0.15915	0.44726
MS-4	**-0.75555**	0.0039	0.32633	-0.35006	0.44733
MS-5	-0.024413	0.031735	0.25061	0.8578	0.44695

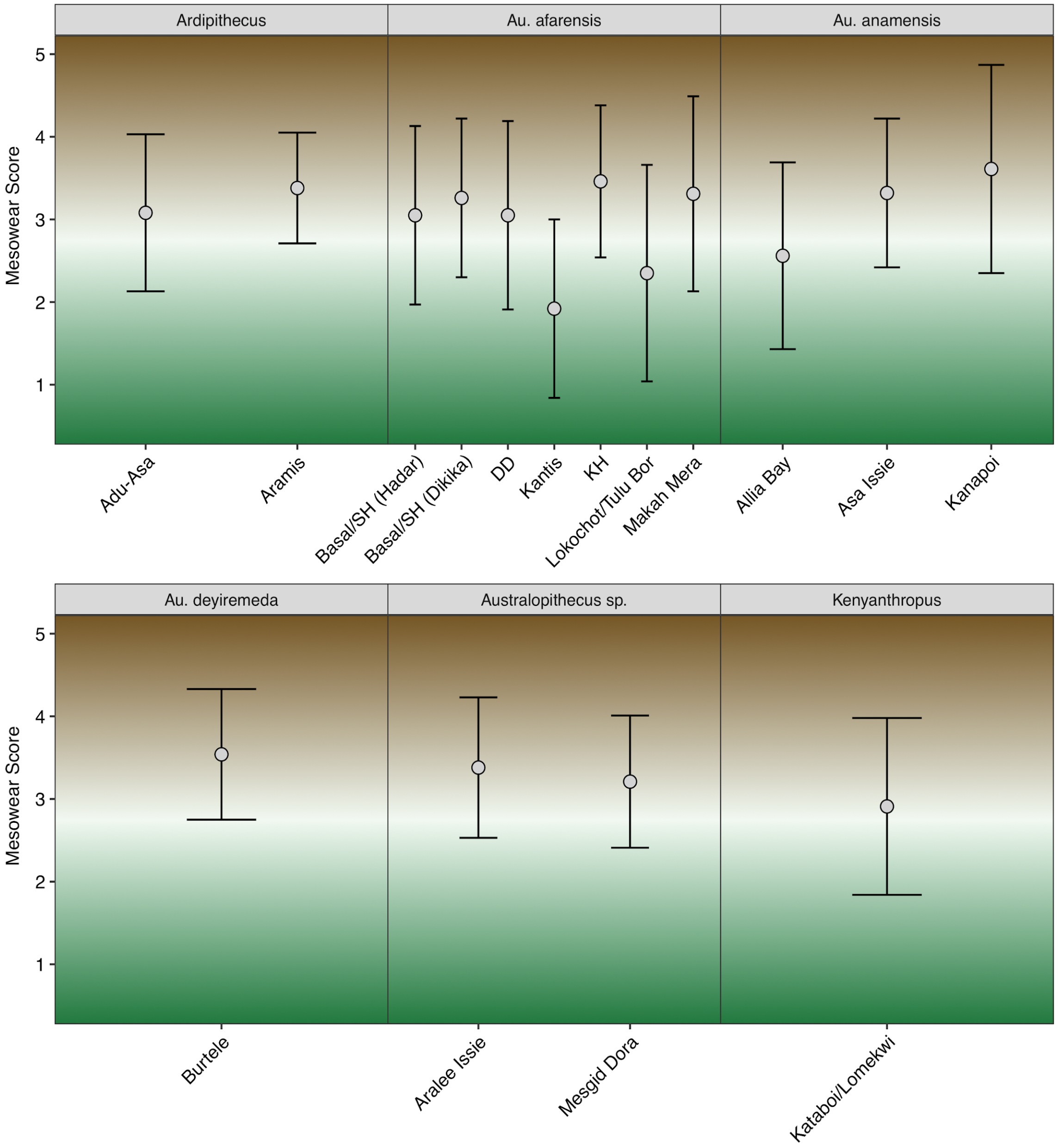

Figure 3.3. Mean (point) and standard deviations (bar) of mesowear scores across sites analyzed in this study, grouped by the hominin taxon present. The color gradient from dark green to brown indicates the spectrum of attrition-dominated tooth wear (low mesowear scores) to abrasion-dominated tooth wear (high mesowear scores).

Table 3.4. Tukey's HSD post-hoc results from the ANOVA comparing differences in bovid mesowear scores aggregated by the hominin taxon present. Only three comparisons are significantly different at α = 0.05 (bold values). The ANOVA score for the hominin taxon is F-value = 4.29 and p-value < 0.001.

Comparison	Difference	Lower	Upper	p-value
Au. afarensis – Ardipithecus	-0.184	-0.442	0.074	0.322
Au. sp. – *Ardipithecus*	0.009	-0.344	0.361	1.000
Au. sp. – *Au. afarensis*	0.193	-0.140	0.525	0.564
Au. anamensis – Ardipithecus	-0.280	-0.620	0.059	0.173
Au. anamensis – Au. afarensis	-0.096	-0.415	0.222	0.955
Au. anamensis – Au. sp.	-0.289	-0.688	0.111	0.306
Au. deyiremeda – Ardipithecus	0.267	-0.239	0.773	0.660
Au. deyiremeda – Au. afarensis	0.451	-0.042	0.943	0.095
Au. deyiremeda – Au. sp.	0.258	-0.290	0.807	0.759
Au. deyiremeda – Au. anamensis	0.547	0.008	1.087	**0.045**
Kenyanthropus – Ardipithecus	-0.358	-0.675	-0.040	**0.017**
Kenyanthropus – Au. afarensis	-0.174	-0.469	0.121	0.543
Kenyanthropus – Au. sp.	-0.366	-0.747	0.014	0.067
Kenyanthropus – Au. anamensis	-0.077	-0.446	0.291	0.991
Kenyanthropus – Au. deyiremeda	-0.625	-1.151	-0.099	**0.009**

Figure 3.4 is a correspondence analysis of bovid tribe abundance at fossil (Table 3.5) and modern localities. The correspondence analysis was converted to relative abundance of tribes rather than actual numbers of individuals because of major differences between modern communities and fossil assemblages. The modern abundance of bovids and the rainfall data come from Greenacre and Vrba (1984). The x-axis accounts for 30.37% of the differences in tribal representation among localities. Aepycerotini and Tragelaphini, an ecotone tribe and mostly woodland habitat tribe, respectively, align on the left of the graph, contrasted with Reduncini, an open wet

habitat group and Hippotragini and Alcelaphini, usually considered open and drier habitat groups. The y-axis shows 24.15% of the variation in tribes with Antilopini at the very bottom, usually representative of very dry, shrubland habitats, and Bovini and Reduncini at the top, both of which rely on more edaphic (wetland) grasslands than other taxa. Thus, this graph does not show differences in MAP, but in the habitats utilized by these bovid tribes, although the wetland taxa show evidence of higher rainfall than the Alcelaphini grouping. Most of the fossil assemblage group with the Tragelaphini, Aepycerotini, and Bovini. This is surprising considering, for example, the huge proportion of reduncins in the Denen Dora Member at Hadar. The tribal abundances—based on what is known of modern tribes—indicate that the fossil sites were all fairly wooded with patches of grasses (e.g., Aepycerotini). Most of the fossil localities lie close to the sites with MAP between 400mm-1000mm, which also indicates more wooded habitats. One exception is the Burtele locality from Woranso Mille site. The abundance data suggests the Burtele locality is Alcelaphini dominated and reconstructed as an open or mixed environment.

Table 3.5. The tribal abundance proportions across the sites (%).

	Age (Ma)	Aepycerotini	Alcelaphini	Antilopini	Bovini	Hippotragini	Reduncini	Tragelaphini	Total (%)
Kada Hadar	3.0	0.2	0.25	0.13	0.12	0.04	0.07	0.19	100
Denen Dora	3.2	0.19	0.16	0.01	0.09	0.01	0.38	0.17	100
Kataboi/ Lomekwi	3.3	0.24	0.3	0.12	0.03	0.04	0.15	0.12	100
Lokochot /TuluBor	3.3	0.09	0.09	0.05	0.14	0	0.4	0.24	100
Sidi Hakoma	3.3	0.3	0.18	0.04	0.15	0.04	0.1	0.19	100
Burtele	3.4	0.17	0.39	0.27	0.02	0.02	0.03	0.1	100
Kantis	3.45	0.21	0.39	0.08	0.17	0.12	0.01	0.02	100
Basal	3.5	0.26	0.12	0.02	0.35	0.03	0.02	0.21	100
Makah Mera	3.62	0.2	0.34	0.03	0.04	0.09	0.03	0.27	100
Aralee Issie	3.67	0.37	0.1	0.08	0.03	0.04	0.01	0.37	100
Mesgid Dora	3.67	0.36	0.12	0.11	0.14	0.06	0.02	0.2	100
Allia Bay	4.1	0.07	0.2	0	0	0	0.03	0.69	100
Kanapoi	4.12	0.16	0.21	0.02	0.04	0.04	0.07	0.47	100
Asa Issie	4.2	0.19	0	0	0	0.01	0	0.8	100
Aramis	4.4	0.07	0.01	0	0.02	0	0.03	0.86	100
Adu-Asa	5.43	0.01	0	0.03	0.22	0.04	0.37	0.33	100

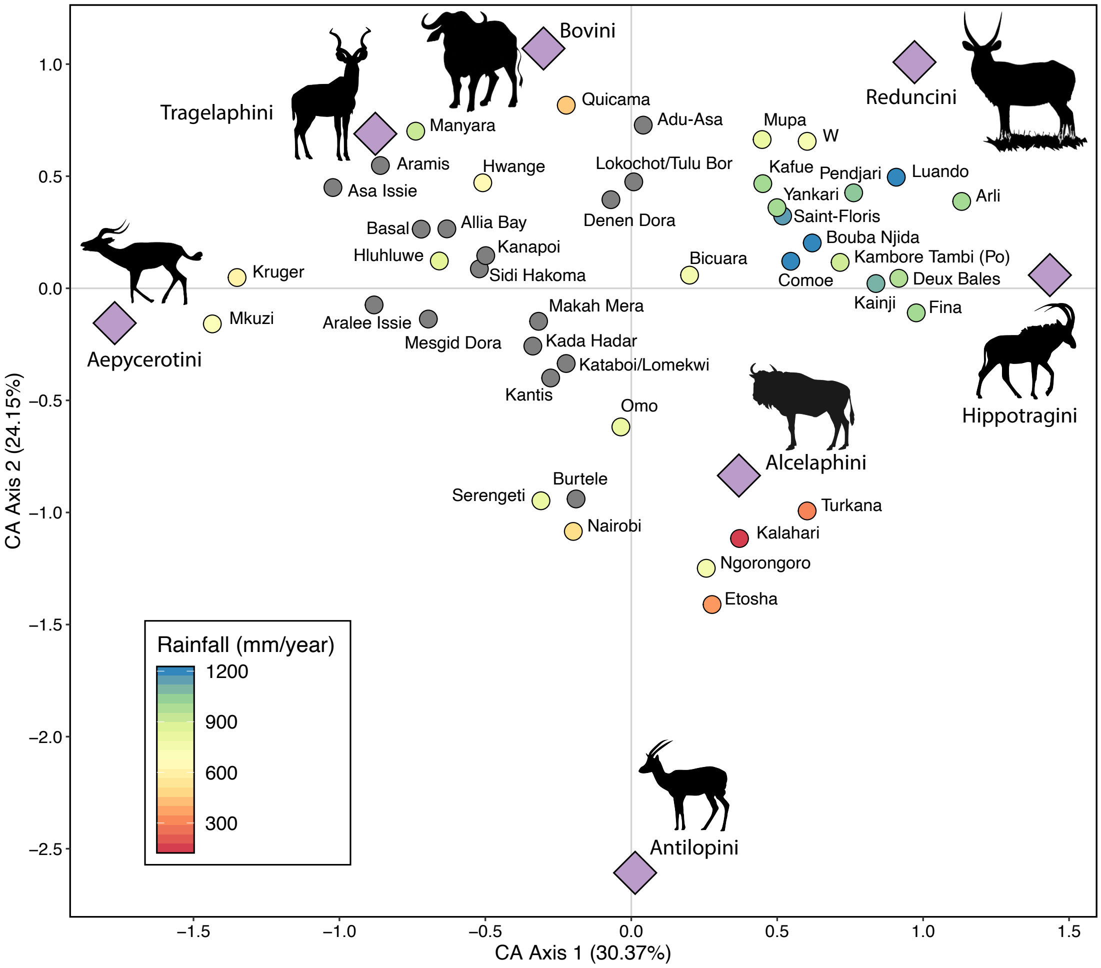

Figure 3.4. The correspondence analysis of bovid tribal abundance. The purple diamonds are the bovid tribes and the fossil sites are in gray; the modern sites are colored by the amount of mean annual rainfall. The rainfall ranges from 300mm to 1200mm per annum.

Percentages of mesowear scores across the sites were used for the principal component analysis (PCA). Table 3.6 shows the mesowear scores of the bovids from different sites in eastern Africa. The PCA reveals separation of hominin species based on bovid dietary groups in a dietary space as represented by mesowear scores defined by PC1 (59.14%) and PC2 (26.06%), which together explain 85.2% of the observed variance (Fig. 3.5). There is hardly any overlap in the bovid dietary space as represented by the hominin species in the assemblages. PC1 separates sites dominated by MS-4 (negative;

the percentage of more grazing taxa) from sites dominated by MS-1 (positive; the percentage of more browsing taxa). Thus, the x-axis separates sites that have more grazers (left) to more browsers (right). PC2 is driven by MS-1 (positive loadings) and MS-3 (negative loadings). PC2 separates sites dominated by MS-3 (mixed feeders likely with no preference) from those dominated by MS-2 and MS-1 (more browsing taxa).

As expected, at *Au. afarensis* sites bovid taxa range from browsing to grazing, consistent with the presence of C_3 and C_4 plants that this hominin also ate (Cerling et al., 2013; Wynn et al., 2013; Sponheimer et al., 2013). As noted above, however, the Kenyan localities appear to have different bovid communities with more browsing taxa, indicating that the Ethiopian sites were likely different in their food distribution. The Burtele locality habitat is suggestive of more open considering the mesowear. Preliminary evaluation of the paleoecology of suids from Burtele also suggests mixed habitats with a component of open grassy habitats that was at least as important or even more relevant than in other Woranso-Mille localities (I. Lazagabaster, personal communication). Other localities appear to be intermediate with mixed feeding taxa preferring leaves, grass, or are non-preferential.

Table 3.6. Summary of mesowear score frequency (%) across sites analyzed in this study. MS-1 indicates percentage of teeth with mesowear score 1, MS-2 indicates percentage of teeth with mesowear score 2, MS-3 indicates percentage of teeth with mesowear score 3, MS-4 indicates percentage of teeth with mesowear score 4, and MS-5 indicates percentage of teeth with mesowear score 5 for the given site.

Subregion	Site	MS-1	MS-2	MS-3	MS-4	MS-5
Dikika	Basal/Sidi Hakoma	2.94	26.47	11.76	58.82	0.00
Hadar	Basal/Sidi Hakoma	7.94	30.16	12.70	47.62	1.59
Hadar	Denen Dora	12.15	24.30	12.15	49.53	1.87
Hadar	Kada Hadar	4.23	12.68	19.72	59.15	4.23
Middle Awash	Adu-Asa	9.21	13.16	38.16	39.47	0.00
Middle Awash	Aramis	2.99	1.49	50.00	45.52	0.00
Middle Awash	Asa Issie	8.00	4.00	36.00	52.00	0.00
Woranso-Mille	Aralee Issie	5.13	5.13	38.46	48.72	2.56
Woranso-Mille	Burtele	2.56	10.26	17.95	69.23	0.00
Woranso-Mille	Makah Mera	15.38	7.69	7.69	69.23	0.00
Woranso-Mille	Mesgid Dora	3.28	13.11	42.62	40.98	0.00
East Turkana	Allia Bay	27.12	13.56	35.59	23.73	0.00
East Turkana	Lokochot/Tulu-Bor	45.00	0.00	30.00	25.00	0.00
Kantis	Kantis	50.00	16.67	25.00	8.33	0.00
West Turkana	Kanapoi	14.29	0.00	17.86	46.43	21.43
West Turkana	Kataboi/Lomekwi	16.55	10.07	41.01	30.22	2.16

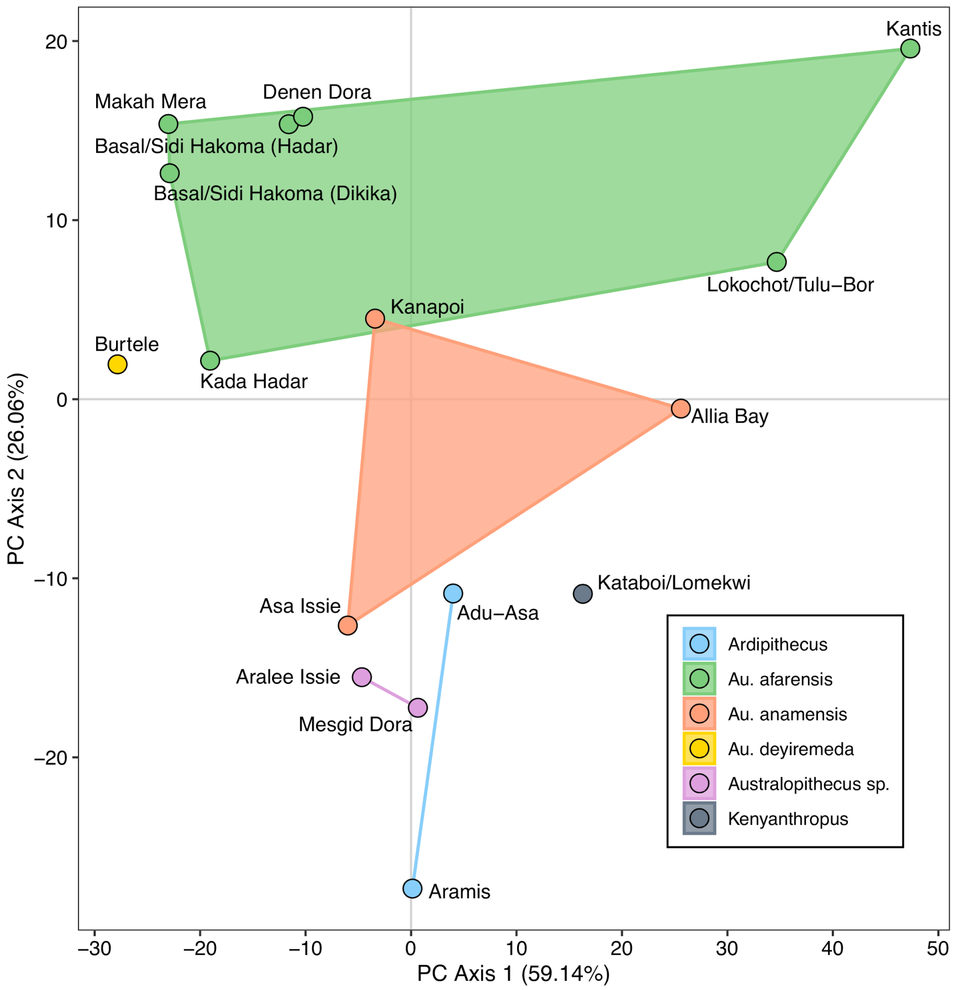

Figure 3.5. Principal components analysis of mesowear data, with convex hulls connecting sites that have produced records of particular hominin taxa. Collectively PC1 and PC2 account for 85.20% of overall variation.

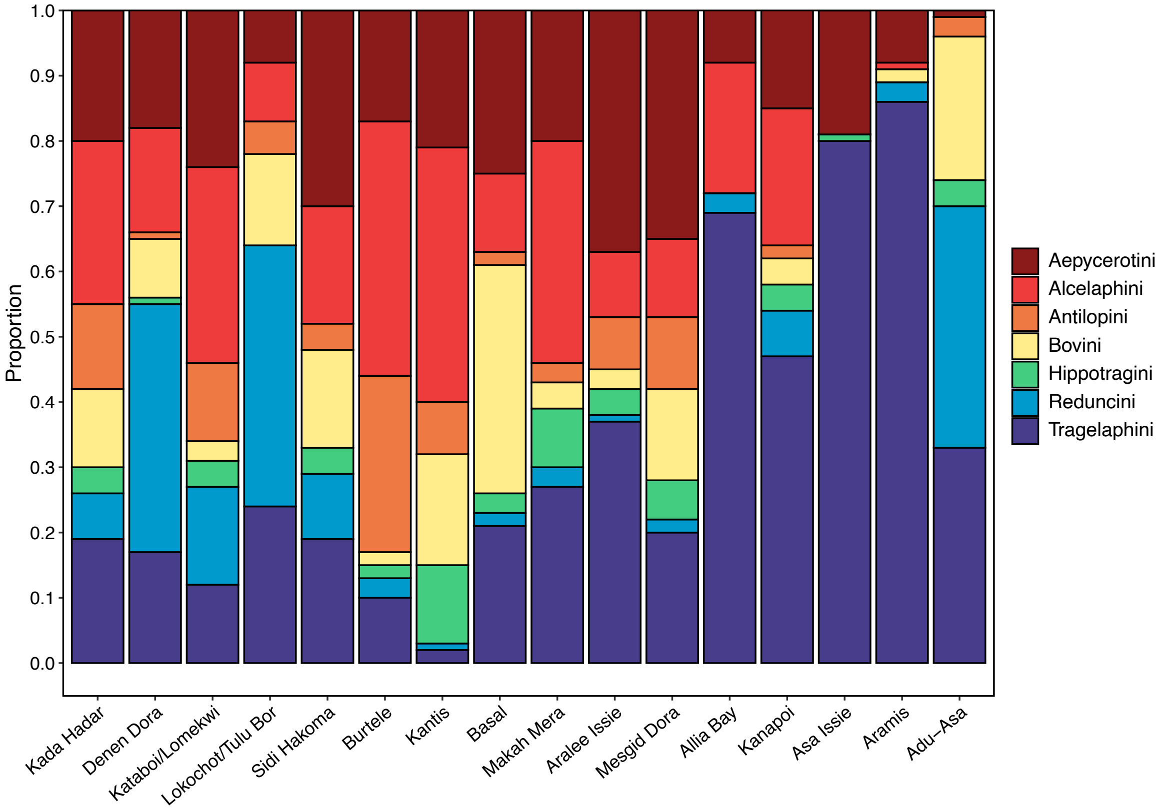

Figure 3.6. Stacked barplot of tribal abundances showing the proportion (relative abundance) of each tribe across sites. The sites are arranged on the x-axis from youngest (left) to oldest (right).

Alcelaphini and Reduncini are classified isotopically as grazers, Aepycerotini, Antilopini, Bovini and Hippotragini as mixed feeders and Tragelaphini as browsers (Cerling et al. 2013). In general, Tragelaphini, Aepycerotini and Alcelaphini dominate the bovid biodiversity in eastern Africa during the Pliocene time, except in Adu Asa, Asa Issie and Aramis (all in the Middle Awash research area) where Alcelaphini is very rare or absent (Table 3.5 and Fig. 3.6). Tragelaphini (2%) is very rare at Kantis, while Alcelaphini (39%) is the most dominant taxon (Fig. 3.6). Tragelaphini is more abundant at Aramis (85%), Asa Issie (80%), Kanapoi (47%), Allia Bay (69%) and Aralee Issie

(37%). Aepycerotini (37%) is also dominant in Aralee Issie along with Tragelaphini. The Asa Issie collection only comprises three bovid tribes, and is dominated by Tragelaphini. All members of Hadar, Kataboi/Lomekwi, Lokochot/Tulu Bor, Kantis and Woranso Mille, except Aralee Issie show decreased Tragelaphini abundance compared to Aramis, Asa Issie, Allia Bay and Kanapoi, indicating that the former sites most likely became more open habitat. In contrast, Aepycerotini and Alcelaphini became more dominant in the younger sites (Kada Hadar (20% and 25%), Sidi Hakoma (30% and 18%), Kataboi/Lomekwi (24% and 30%) and Mesgid Dora (36% and 12%) respectively) confirming the open habitat in these areas. However, in Sidi Hakoma, Tragelaphini (19%) is the second dominant taxon. Reduncini, fresh grass grazers, is proportionally much more abundant taxon at Adu-Asa (37%) and younger stratigraphic units at Denen Dora (38%) and Lokochot/Tulu Bor (40%). Moreover, whenever Reduncini is dominant, Tragelaphini become less abundant in those sites. This may imply the existence of wetland areas with edaphic grassland indicating more open environment which is not a typical habitat of Tragelaphini. The dietary category is also well represented in these sites (in the Adu-Asa, Denen Dora and Lokochot/Tulu Bor assemblage). The Burtele assemblage had the most mixed feeders (Antilopini being the second most abundant tribe after Alcelaphini), indicating mixed but tending towards open and dry environments. Aepycerotini is the most dominant tribe in Mesgid Dora and the second most common tribe at Aralee Issie, both from the Woranso Mille site. Aepycerotini is a mixed diet feeder. Despite substantial overlap in their tribal distribution there is a significant difference in the faunal abundance across sites. The most important trend is Tragelaphini abundance decreases and the abundance of Alcelaphini and Aepycerotini increases over time. In general, the tribal abundance data shows *Ar. ramidus* and *Au. anamensis* sites are proportionally more dominated by browsing taxa, suggesting that the individuals could have been incorporated larger proportions of browse in their diet. However, the mesowear data indicates that bovids from both *Ar. ramidus* and *Au. anamensis* sites had higher proportion of taxa dependent on more abrasive diet. *Au. afarensis* and *Kenyanthropus platyops* sites are characterized by grazer and mixed feeder taxa. Nevertheless, the *Au. afarensis* sites both at Hadar (Denon Dora) and West Turkana (Lokochot/Tulu Bor) are dominated by Reduncini, indicating wet environment.

4. Discussion

Based on the mesowear data from 920 fossil samples of ungulate taxa (Aepycerotini, Alcelaphini, Antilopini, Bovini, Hippotragini, Reduncini and Tragelaphini), I conclude that the best discrimination between tooth-wear traits is achieved by grouping taxa into grazer, mixed feeder and browser categories. Mesowear has been used to infer diet of extant and extinct species as well as their surrounding habitat and appears to resolve details within the main dietary classes and it can rank ungulates into grazers, mixed feeders and browsers by their relative degree of abrasion in the fossil record (Fortelius and Solounias, 2000). Ungulates adopt their diet based on the availability of vegetation types in their environment (Franz-Odendall and Solounias, 2004; Rivals and Semprebon, 2006; Rivals, 2012). More importantly, habitat is often known to influence species distribution and it is equally important to understand the influential variables that affect habitat diversity. Because habitat encompasses so many aspects of an organism's needs, including substrate use and, often, dietary sources, it is usually considered the main factor that influences a species distribution (Thorn et al., 2009). Therefore, it is crucial to understand the habitat of a species in order to reconstruct the species' diet.

Taxa from the older stratigraphic units were classified as browsers and taxa in the younger stratigraphic units were classified as mixed feeders and grazers, suggesting that shifts in diet occurred within the dietary range of these taxa. The correspondence analysis of bovid tribal abundance clearly indicates a gradient from browsers to grazers along correspondence analysis axis 1 (Fig. 3.4). Along this axis, fossil ungulates are generally positioned very close to the mixed feeders and some to the browsing end of the spectrum, indicating a higher proportion of browsing even within a mixed diet. The classification of these fauna as mixed feeders (rather than browsers) can be attributable to the classification of several bovids as mixed feeders, and difficulties assigning broad dietary categorizations to species with diets that vary greatly across their range (Fortelius and Solounias (2000). For example, *Tragelaphus eurycerus* and *Tragelaphus scriptus* have been categorized as browsers in Louys and Faith (2015), whereas, Fortelius and Solounias (2000) categorized them as mixed feeders based on mesowear. Future analysis may refine this distinction, but for this study I choose browser categorization for Tragelaphini as a tribe.

The mesowear data of ungulates from eastern Africa assemblages suggests highly heterogeneous environments, where open, intermediate and closed settings are represented in different proportions. In Kenya, a multi-proxy analysis that included mesowear suggested that *Au. anamensis* from Kanapoi lived in a mosaic, but relatively open environment, the results of which were similar to the Allia Bay site, but it was estimated that the habitat was more open at Kanapoi (Dumounchel and Bobe, 2019). Generally, closed environments are represented in the *Ar. ramidus* and *Au. anamensis* bearing sites. Open environments are overrepresented at *Au. afarensis* and *Kenyanthropus platyops* bearing sites. The mesowear analysis of fossil ungulate species suggest that, overall, the ungulates in early Pliocene had a higher percentage of browse in their diets compared to mid-Pliocene sites. Thus, the higher proportion of browse in the diet of early Pliocene taxa is indicative of a more closed and wooded environment compared to mid Pliocene sites. Better results may have been achievable using larger sample sizes for fossil taxa. Nevertheless, mesowear appears to resolve details within the main dietary classes and it can rank ungulates into grazers, mixed feeders and browsers by their relative degree of dental abrasion. Mesowear analysis coupled with other paleodietary studies, such as stable carbon and oxygen analysis and hypsodonty, each of the method represents a different temporal scale, would allow us to discuss changes in the paleoecology in a more detailed manner. Chapter 3 is fully devoted for comparative analysis of these different but complementary approaches.

5. Conclusion

Mesowear variables, occlusal relief and cusp shape, are found to be positively correlated with dietary classification and can successfully distinguish among extinct ungulate taxa with differing diets. My study shows moderate shifts in mesowear through eastern Africa from ~5.5 - 3.0 Ma: specimens from Adu-Asa, Aramis, Kanapoi and Allia Bay show (4.4 – 3.9 Ma) wear indicative of browsing, whereas the younger stratigraphic units (3.9 – 3.0 Ma) contain significantly more mixed-feeding and grazing. Despite being roughly contemporaneous in time, the Burtele assemblages from Woranso-Mille significantly differ from that of the Sidi Hakoma member at Hadar, with the latter having fewer grazers. However, the taxa from the Denen Dora member is most closely linked to the abrasion-dominated edge of the mesowear scale. Dene Dora is strikingly dominated by Reduncini. Reduncini prefer water-logged floodbank environments and their commonness at Hadar may reflect the persistent fluvio-lacustrine system associated with paleolake Hadar. Overall the mesowear score shows that Tragelaphini, categorized as browser, is the most dominant bovid tribe in the early Pliocene faunal assemblages in eastern African indicating early Pliocene was more closed habitat. Mid-Pliocene, however, is dominated by Aepycerotini (mixed feeder) and Alcelaphini (grazer) tribes indicating more open habitat.

CHAPTER 4

Multiproxy evidence for Pliocene environmental change during hominin evolution in eastern Africa

1. Introduction

Hominin morphological and behavioral adaptations are a result of the selection pressures that operate within each species' environment. To elucidate these pressures requires detailed reconstructions of the Plio-Pleistocene landscapes navigated by our ancestors. To understand the relationship between environmental change and hominin evolution it is necessary to understand the ecological parameters of the overall fauna as well as the physical setting of the fossil locality (Reed, 1997, 1998; Bobe et al., 2002; Uno et al., 2011). Hominins have shared their changing ecosystems with other taxa, many of which are represented by the family Bovidae. Paleohabitat reconstructions based on bovids are very common because bovids are adapted to exploit a wide array of dietary resources that occur within various habitats (Reed, 1998; Levin et al., 2015). Much of our dietary and habitat knowledge of fossil bovids comes from studies of their postcranial morphology (e.g., morphology associated with closed to open habitat types) that indicates possible vegetation structure and craniodental attributes (e.g., hypsodonty, mesowear, and microwear) that indicate diet types (Janis, 1988; Kappleman et al., 1997; Fortelius and Solounias, 2000; DeGusta and Vrba, 2003; Ungar and Sponheimer, 2011; Kaiser et al., 2013). Although, each of these approaches has been successful in inferring habitats and diets in the fossil record, they are inherently incomplete, and multiproxy data are needed to provide a better understanding of the proximate habitats. Isotopic data, providing a quantitative record of an animal's feeding ecology, can validate morphological measurements of dentition. The goal of this chapter is to synthesize findings from analyses of hypsodonty and mesowear of modern and fossil bovid taxa with stable carbon isotope data to explore the environmental framework for the expansion of the hominin dietary niche in eastern Africa around 3.5 Ma.

In the past two decades stable isotope studies have increasingly been used to explore feeding relationships in ancient ecosystems (Schwarcz and Schoeninger, 2012; Sandberg et al., 2012; Crowley, 2012; Sponheimer et al., 2013; Wynn et al., 2013; Cerling et al., 2013, 2015; Levin et al., 2015). Stable isotope analysis is a powerful tool for investigating animal ecology across time and space. It is a useful approach for enhancing our understanding of the dietary adaptation and possible habitat preferences of both extant and extinct species, including hominins (Sponheimer et al., 2009; Crowley, 2012), because teeth are the best-preserved elements in fossil assemblages and used for stable isotope analysis. Dental enamel bioapatite is the most applicable tissue in the organism's body for isotopic analysis because it is resistant to diagenetic changes during fossilization (Lee-Thorp and Van der Merwe, 1991; Sandberg et al., 2012). Tooth enamel records dietary and water intake information during its formation which covers the entire period of dental growth. Carbon isotope composition of the enamel which is the focus of this study reflects the diet that was consumed by individual organism and in turn reflects past environment and habitat. This is because tooth enamel, once formed and fully mineralized, does not undergo biological changes (Sandberg et al., 2012).

The isotopic composition of enamel is expressed as parts per thousand (per mil, ‰) in reference to an international standard using a standardized δ notation, e.g., $\delta^{13}C$, where $\delta = ((R\ sample/R\ standard) -1) * 1000$, and R is the ratio of heavy to light isotope ($^{13}C/^{12}C$). Positive and negative δ values indicate that the sample has more or less of the heavy isotope relative to the standard, respectively (Cerling et al., 2015; Levin, 2015). If enamel has relatively less of the heavy isotope (less ^{13}C), then its δ value is lower. Conversely, if enamel has relatively more of the heavy isotope (more ^{13}C), its δ value is higher. This variation most likely results from differences in digestive physiology and the dietary source (e.g., C_3- versus C_4-derived foods). Stable isotope ratios in animal tissues are informative because they provide a record of the food or water actually ingested and assimilated into an animal's body. These ratios are predicted to vary as a function of habitat, physiology, and dietary proclivity (Koch, 2007; Schoeninger, 2010). Accordingly, stable isotopes have been used to investigate foraging ecology and niche partitioning among both living and extinct taxa (Codron et al. 2006; Dammhahn and Kappeler 2010; Lee-Thorp et al. 2003).

Enamel carbon isotope values have been used to discriminate between diets dominated by C_3 and C_4 plants. These values mainly reflect plant physiology and photosynthetic pathways. Terrestrial plants use three different photosynthetic pathways. These are: C_4, C_3 and Crassulacean Acid Metabolism (CAM). Trees, shrubs and cold growing grasses use the C_3 photosynthetic pathway, whereas temperate and tropical warm growing season grasses use the C_4 photosynthetic pathway (Koch 1998; Lee-Thorp et al. 1989; Kohn and Cerling, 2002; Koch, 2007; Cerling et al. 2015). Desert environment succulents use CAM (O’Leary, 1988; Keeley and Rundel, 2003; Lüttge 2004). These three plant types can be differentiated based on their isotope values. The $\delta^{13}C$ in tooth enamel differentiates the relative contribution of certain plant types (e.g., grasses, succulents, trees) to reconstruct dietary information about extinct fauna (Spoheimer and Lee-Thorp, 1999; Crowley, 2012). Based on this, herbivores can be classified into grazer, browser and mixed feeders. Herbivores that consume C_4 tropical grasses are grazers and have $\delta^{13}C$ value -1‰ or higher; those who consume both are mixed feeders and have $\delta^{13}C$ value between -1 and -8‰; herbivores that consume C_3 plants are browses and have $\delta^{13}C$ value -8‰ or lower (Cerling et al., 2015).

Soil carbonate nodules preserved in the fossil record formed in isotopic equilibrium with the surrounding soil and proxy for surface vegetation have been widely used for deep-time vegetation reconstructions (Levin et al., 2011). Soil carbonates allows a direct comparison between the $\delta^{13}C$ values of enamel and paleosol carbonates (Cerling et al., 1997; Wynn, 2004; Quade and Levin, 2013; Du et al., 2019). The study of the vegetation patterns and structure is important for estimating paleoclimatic factors, such as precipitation and temperature. In combination with data from the fauna, these factors allow a better understanding of the ecosystems in which hominins lived and the ecological context for shift observed in Plio-Pleistocene hominin diet. To date, stable isotope analysis has been carried out on an array of geographically and taxonomically diverse fossil and extant taxa, as well as on soil carbonates recovered from fossil sites (Sponheimer et al., 2006; Quade and Levin, 2013). Soil carbonate isotope is one of the best tools to distinguish C_3 and C_4 dominated ecosystems (Cerling et al., 1993). In conjunction with data on dental mesowear and hypsodonty, carbon isotope information both from dental enamel and paleosol contributes to assessing the factors driving mid-Pliocene hominins dietary niche expansion.

2. Materials and Methods

2.1 Isotope Data

This study analyzes 1,126 published isotopic values derived from fossil ungulates and primates. Ungulate and primate remains in East Africa have been the subject of a long-term research program that has generated a wealth of isotopic data (Cerling et al., 1993, 1997, 2015; Wynn, 2000, 2004; Wynn et al., 2013; Levin el al., 2015; Sponheimer et al., 2013). My focus is on carbon isotopes, which constitutes the largest available data sets and the most useful dietary proxies. The dataset used for this study is mostly obtained from Du et al. (2019), a compilation of published herbivore enamel carbon isotope and paleosol isotopic data from East Africa. Additional data were gathered from other published sources (White et al., 2009; Bedaso et al., 2013; Cerling et al., 2015; Levin et al., 2015; Wynn et al., 2016). All available enamel data for early and mid-Pliocene hominin bearing sites, spanning from 4.4 – 3.0 Ma, from Hadar, Dikika, Woranso Mille and Aramis (Ethiopia), Kanapoi, Lomekwi, Kataboi, Lokochot and Tulu Bor (Kenya) and Laetoli (Tanzania) were considered in this study. The taxa include: *Anancus*, *Elephas*, *Loxodonta*, *Theropithecus*, Aepycerotini, Alcelaphini, Antilopini, Bovini, Hippotragini, Reduncini, Tragelaphini, *Deinotherium*, *Diceros*, *Ceratotherium*, *Eurygnathohippus*, *Giraffa*, *Sivatherium*, Hippopotamidae, *Kolpochoerus*, *Nyanzachoerus*, *Notochoerus*. For detailed information of the sites/stratigraphic units and sample sizes see Table 4.1.

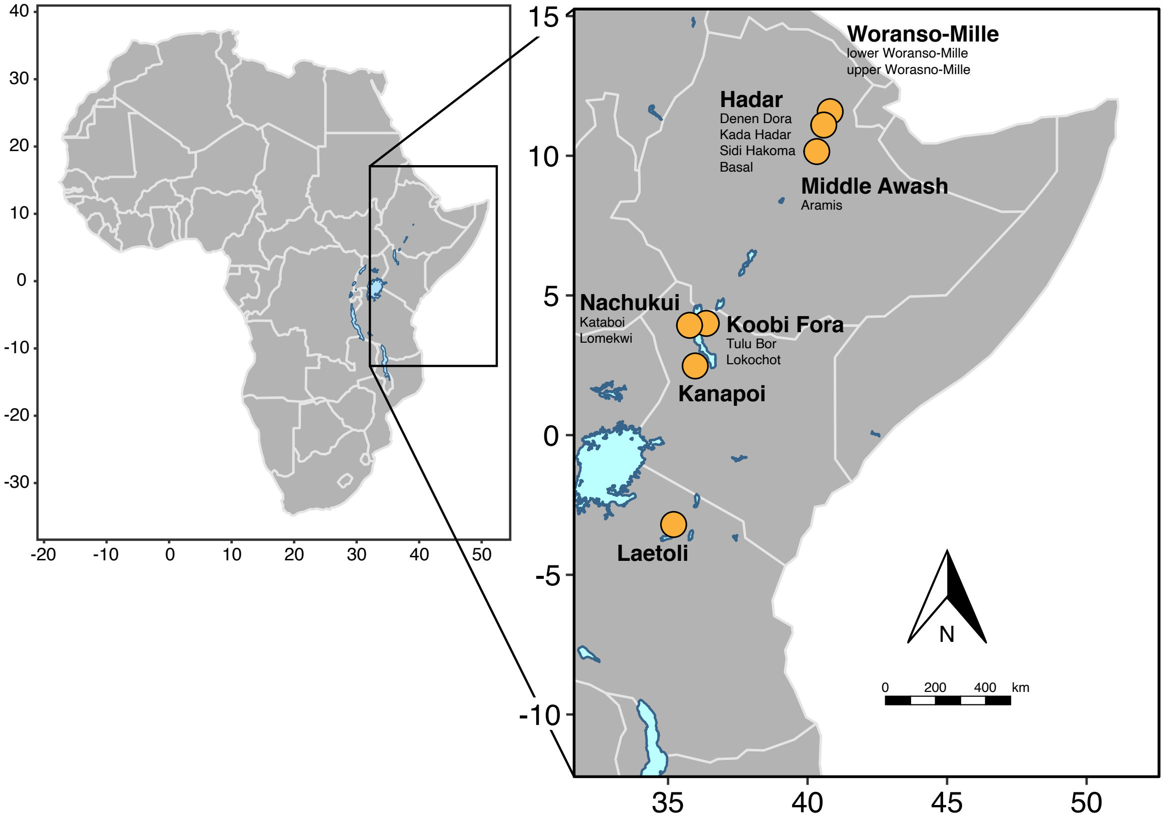

Figure 4.1. Hominin bearing areas in eastern Africa showing sites, localities and stratigraphic units used for stable carbon isotope analysis.

Similarly, paleosol $\delta^{13}C$ were obtained from the published literature (Wynn, 2004; Cerling et al., 2011b; Levin et al., 2011). These available paleosol $\delta^{13}C$ data for the sites were converted into fraction of woody cover following Cerling et al. (2011b). Cerling et al. developed a quantitative relationship between the percentage of woody cover and the $\delta^{13}C$ signal of the soil based on soil organic matter. This new model allows us to examine vegetation cover change through time on a global scale. The Plio-Pleistocene of eastern Africa, which encompasses well-dated and temporally continuous hominin and mammalian fossil-bearing sites, is an ideal place for investigating hominin behavioral and biological evolution using combined pedogenic carbonate and herbivore tooth enamel $\delta^{13}C$ signals.

2.2 Analytical Methods

Enamel isotope values were grouped into the taxonomic units mentioned above. Each taxon's enamel isotope values were visualized across sites using boxplots. Overall mammalian community enamel values were then visualized by aggregating all taxa and plotting $\delta^{13}C$ across sites using probability density functions. To visualize differences in dietary composition, all plots with enamel $\delta^{13}C$ data were color-coded using the isotopic breakdowns of Cerling et al. (2015) for browsers (< -8 per mil), mixed-feeders (-8 to -1 per mil), and grazers (> -1 per mil).

Paleosol $\delta^{13}C$ values were converted to percentage of woody cover (0%-100%) following Cerling et al. (2011b), grouped by site, and visualized using probability densities through time. These fraction of woody cover plots were color-coded based on the vegetation habitat breakdown of Cerling et al. (2011b): grassland (< 10% woody cover), wooded grassland (10%-40% woody cover), woodland (40%-80% woody cover), forest (> 80% woody cover).

Table 4.1. Specimen counts for all sites and/or stratigraphic units in eastern Africa used for enamel carbon isotope analysis. The Hadar and Dikika sites are the two sites with stratigraphic units (Basal, Sidi Hakoma, Denon Dora and Kada Hadar members) and they are treated as stratigraphic units and compared with other sites. Abbreviations as follows: KH=Kada Hadar, TB=Tulu Bor, UWM = Burtele and Waytaleyta of Upper Woranso-Mille, SH=Sidi Hakoma, BS=Basal, LOK=Lokochot, KAT=Kataboi, LWM = Amado, Aralee Issie, Korsi Dora, Makah Mera and Mesgid Dora of Lower Woranso-Mille, LAET=Laetoli, KAN=Kanapoi, ARA=Aramis.

	KH	TB	DD	LO	UW	SH	BS	LOK	KA	LWM	LAE	KA	AR
Aepycerotini	12		10	10		16	6		3	2		8	7
Alcelaphini	1		13	20		20	3		3	1	33	5	3
Antilopini	5			5					1		16		
Bovini	1	2	6	1		25	3	1		1			7
Hippotragini				6		3					18		2
Reduncini		1	23	2		3							
Tragelaphini	7	1	3	2	3	7	1	1		19	10	3	14
Anancus										1		2	5
Elephas	11	2	5	9		4						7	
Loxodonta				2					1	1	21	9	
Deinotherium	7		7	4		5	1	3	2		2	2	4
Theropithecus	4		9		12	13				25		2	
Diceros				3							2	7	
Ceratotherium				3			2			1	30	1	
Hippopotamidae	3	3	1	7		12	7	4	2	8		7	9
Eurygnathohippu	13	4	24	8		40	15	4			18	1	11
Giraffa	6		6	7	7	3		2		5	39	5	4
Sivatherium	4	1		2	3	1				3	3	3	4
Kolpochoerus	14		5			15	5				5		7
Nyanzachoerus						7	4	1				8	15
Notochoerus	13	2	26		14	14	6	3		7	36	4	

3. Results

3.1 Enamel Carbon Isotope Analysis

Figure 4.2 shows herbivore enamel carbon isotope values of Hippopotamidae, *Kolpochoerus*, *Notochoerus* and *Nyanzachoerus*. Overall, the carbon isotopic values for Hippopotamidae indicate that they consumed a mixed diet across sites. However, the $\delta^{13}C$ mean values of Hippopotamidae from Aramis, Kanapoi, Kataboi, Lower Woranso Mille, Denen Dora and Tulu Bor are more positive than they are at Lokochot, Basal Member, Sidi Hakoma, Lomekwi and Kada Hadar, although not statistically significant. In general, Hippopotamidae individuals have higher carbon isotope variation within each site rather than between sites, indicating that Hippopotamidae had flexible diets in the Pliocene.

Kolpochoerus has mean $\delta^{13}C$ values that plot between -6 and -2, which are all in the range for mixed C_3/C_4 feeders. Slight variation occurs because the means of *Kolpochoerus* from Upper Laetoli and Kada Hadar are more positive than Aramis, Basal Member, Sidi Hakoma, and Denen Dora. Individuals from Aramis have more negative values than those from the other sites suggesting that these suids incorporated larger proportions of C_3 plants in their diet.

The mean $\delta^{13}C$ value of *Notochoerus* from Lower and Upper Woranso-Mille and Lokochot is in the range of grazing only, although some were mixed feeders preferring grasses. *Notochoerus* from Kanapoi, Upper Laetoli, Basal Member, Sidi Hakoma, Denen Dora, Tulu Bor and Kada Hadar show more negative values suggesting grazing dominated C_3-C_4 mixed feeders.

The mean enamel carbon isotope value for *Nyanzachoerus* indicates that it was a C_3-C_4 mixed feeder across eastern Africa. Individuals from Aramis, and Lokochot have more positive values, indicating that this taxon consumed more C_4 food items than at other sites.

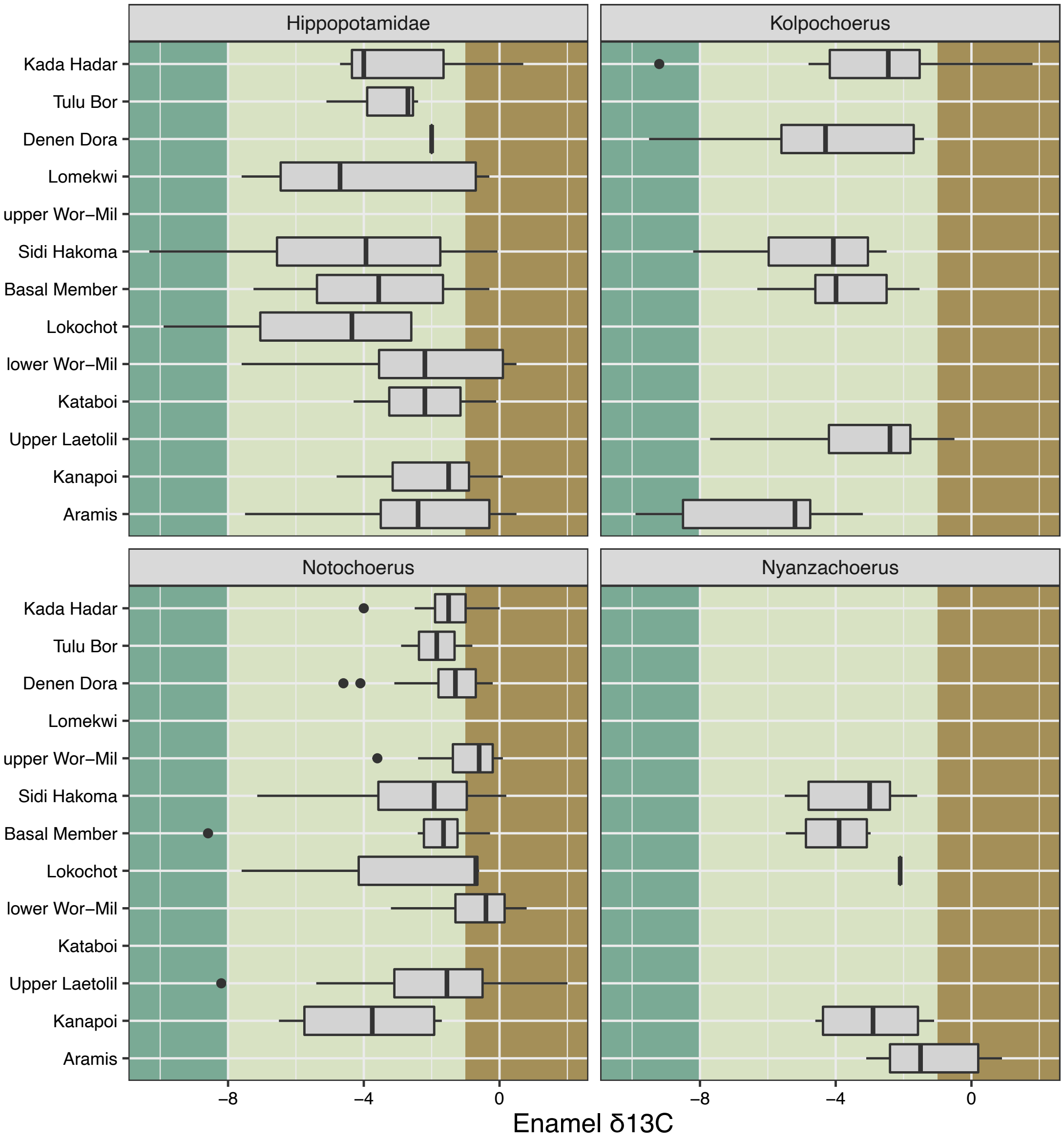

Figure 4.2. Enamel carbon isotope value of Hippopotamidae, *Kolpochoerus*, *Notochoerus* and *Nyanzachoerus* from East African Plio-Pleistocene hominin bearing sites. The colors indicate the designation of the C_3/C_4 distribution. Dark green is C_3 plants

(<-8 per mil), light green is mixed C_3/C_4 plants (-8 to -1 per mil), and brown is C_4 grass > -1 per mil). The sites are presented oldest to youngest stratigraphic units from bottom to up. Vegetation classifications are followed after Cerling et al., 2011b.

Figure 4.3 presents enamel carbon isotope value of the Proboscideans: *Anancus*, *Deinotherium*, *Elephas* and *Loxodonta*. *Anancus* was sampled only from three sites (Aramis, Kanapoi and Lower Woranso-Mille). The mean carbon isotope values of *Anancus* from Aramis and Lower Woranso-Mille indicates that they were grazing, whereas individuals from Kanapoi were mixed feeders. *Deinotherium* values from all localities are in the browsing range, although there is some variation. The mean enamel carbon isotope values of *Elephas* from Lomekwi, Denen Dora and Tulu Bor shows that they were clearly dependent on grasses. Individuals from Kanapoi, Sidi Hakoma and Kada Hadar were mixed feeders. The average enamel carbon isotope value of *Loxodonta* from Kataboi and Lower Woranso-Mille indicate that they were grazers and individuals from Kanapoi, Upper Laetoli and Lomekwi consumed grass dominated C_3-C_4 diet. However, Loxodonta from Upper Laetoli has a broader range than found at the other sites.

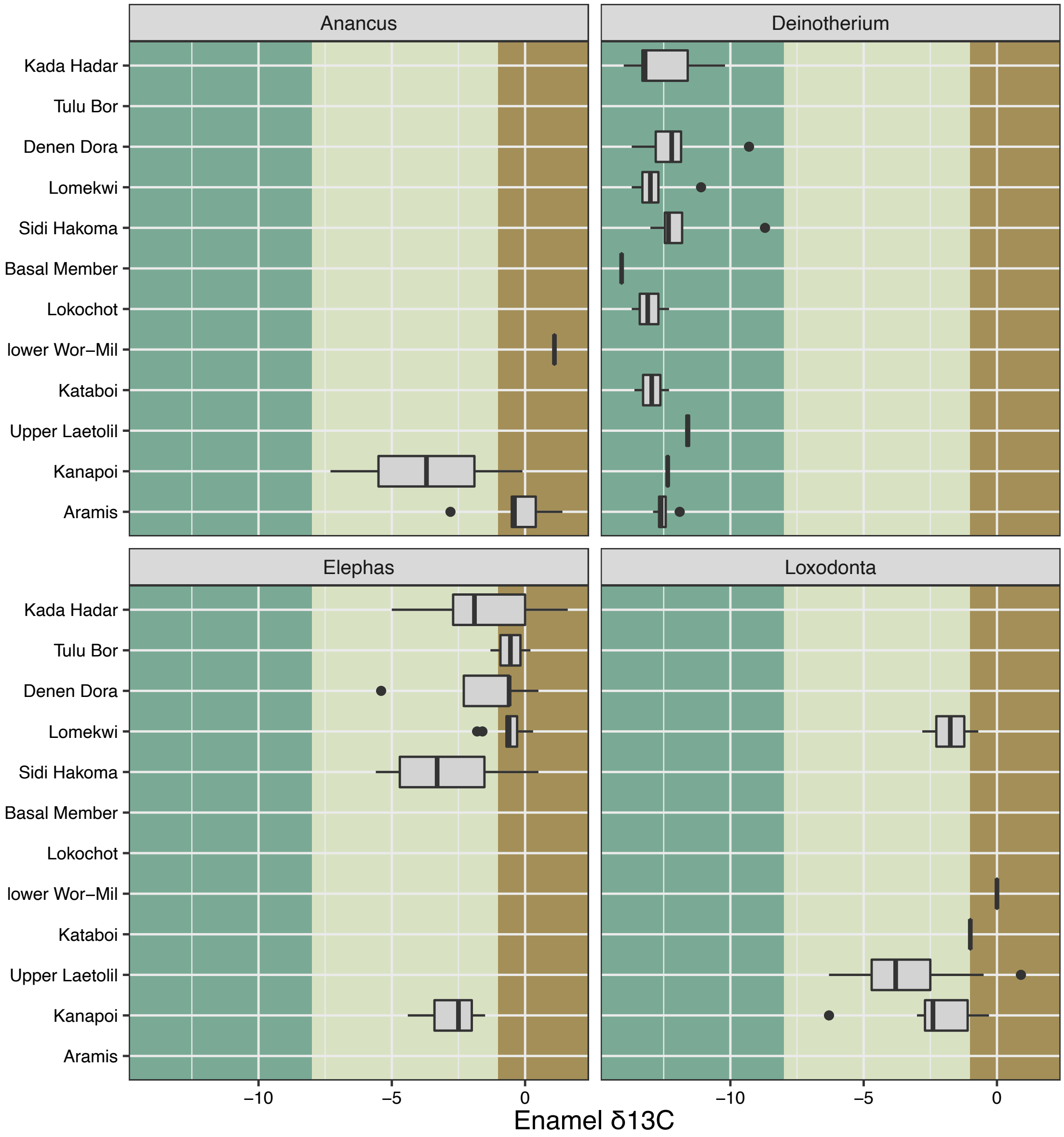

Figure 4.3. Enamel carbon isotope value of *Anancus*, *Deinotherium*, *Elephas* and *Loxodonta* from East African Plio-Pleistocene hominin bearing sites. The colors indicate the designation of the C_3/C_4 distribution. Dark green is C_3 plants (<-8 per mil), light green is mixed C_3/C_4 plants (-8 to -1 per mil), and brown is C_4 grass > -1 per mil). The sites are presented oldest to youngest stratigraphic units from bottom to up. Vegetation classifications are followed after Cerling et al., 2011b.

Figure 4.4 reports enamel carbon isotope values of *Ceratotherium*, *Diceros*, *Eurygnathohippus* and *Theropithecus*. *Ceratotherium* individuals from Kanapoi, Lower Woranso Mille, Basal Member, and Lomekwi have means and ranges indicating mostly grazing. *Ceratotherium* from Upper Laetoli have lower $\delta^{13}C$ values and were browse dominated mixed feeders. *Diceros* were sampled from only three sites and from Kanapoi and Lomekwi were browsers. However, individuals from Upper Laetoli were mixed C_3-C_4 diet consumers. This indicates that both Ceratotherium and Diceros have basically the same mean value from Upper Laetoli (although different range) while they are very distinct from each other at all the other sites. The mean enamel carbon isotope values of *Eurygnathohippus* from Aramis, Kanapoi, Upper Laetoli, Lokochot, Lomekwi and Kada Hadar fall within C_4 grasses. Individuals from Basal Member, Sidi Hakoma, Denen Dora and Tulu Bor were grass dominated mixed feeders.

Theropithecus enamel carbon isotope values fall within the mixed dietary category. The variation within the lower Woranso-Mille is higher, suggesting *Theropithecus* was capable of exploiting a broader range of plant foods.

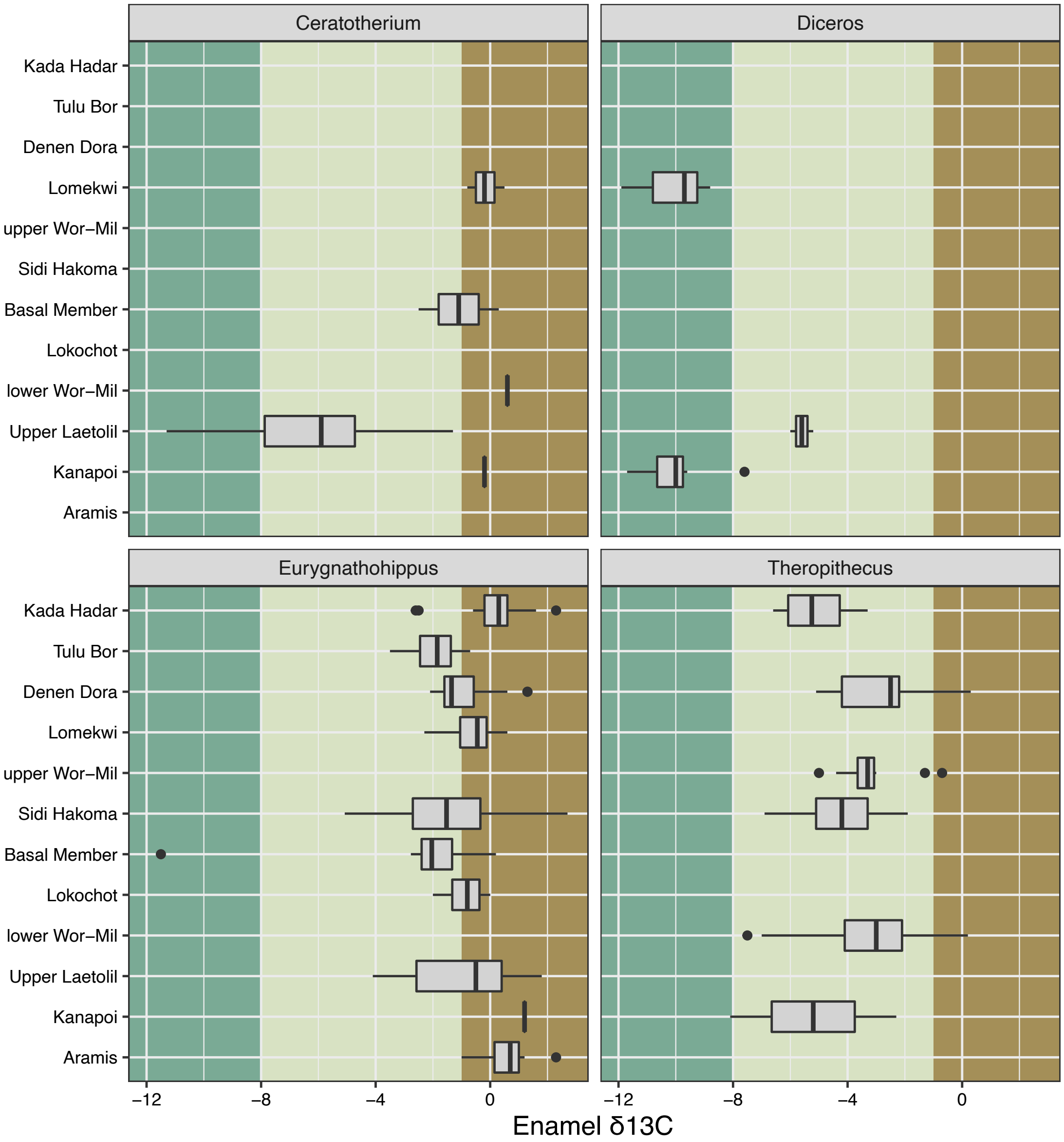

Figure 4.4. Enamel carbon isotope value of *Ceratotherium*, *Deciros*, *Eurygnathohippus* and *Theropithecus* from East African Plio-Pleistocene hominin bearing sites. The colors indicate the designation of the C_3/C_4 distribution. Dark green is C_3 plants (<-8 per mil), light green is mixed C_3/C_4 plants (-8 to -1 per mil), and brown is C_4 grass > -1 per mil). The sites are presented oldest to youngest stratigraphic units from bottom to up. Vegetation classifications are followed after Cerling et al., 2011b.

Figure 4.5 shows enamel carbon isotope value of bovids tribes, and the Giraffidae, *Giraffa* and *Sivatherium*. Overall, Aepycerotini has more positive enamel carbon isotope values, showing that it predominately consumed C_4 vegetation. Alcelaphini from Aramis, Kanapoi, Kataboi, Lower Woranso Mille, Sidi Hakoma, Lomekwi, Denen Dora and Kada Hadar have higher average enamel carbon isotope value, indicating a C_4 diet. However, individuals from Upper Laetoli and Basal Member have a grass dominated mixed diet. Antilopini were sampled from only four sites (Upper Laetoli, Kataboi, Lomekwi and Kada Hadar). Most Antilopini fall in the mixed feeder's range, however, individuals from Upper Laetoli have higher negative enamel carbon isotope values indicating more C_3 plants in the diet. The average carbon isotope values of Bovini from Aramis, Lomekwi, Denen Dora and Kada Hadar indicate they were consuming a component of C_4 vegetation, but from the other localities they were eating a mixed plant diet. The mean enamel carbon isotope values of Hippotragini from Upper Laetoli, Sidi Hakoma and Lomekwi indicates mixed diet. However, individuals from Aramis were grazers.

All Reduncini individuals sampled from Sidi Hakoma, Lomekwi, Denen Dora and Tulu Bor have high enamel carbon isotope values indicating grazing behavior. The average $\delta^{13}C$ value of Tragelaphini from Aramis, Kanapoi, Upper Laetoli, Lokochot, Basal Member, Upper Woranso-Mille and Kada Hadar is more negative than individuals from Lower Woranso-Mille, Sidi Hakoma, Lomekwi, Denen Dora and Tulu Bor indicating browsing diet for the former sites. Individuals from the later sites, however, have carbon isotope values showing likely browse dominated mixed C_3-C_4 diet. The individual variations within the Kada Hadar is much higher, suggesting Tragelaphini at Kada Hadar either had more flexible or seasonal diets or there are several species, which partitioned the resources. Generally, *Giraffa* consumed C_3 food items across sites in eastern Africa. *Sivatherium* values indicate that this taxon also consumed C_3 diets. Individual variation within the Kada Hadar Member is higher than at other places, showing that *Sivatherium* was shifting to some grass in the diet sometime during this time period.

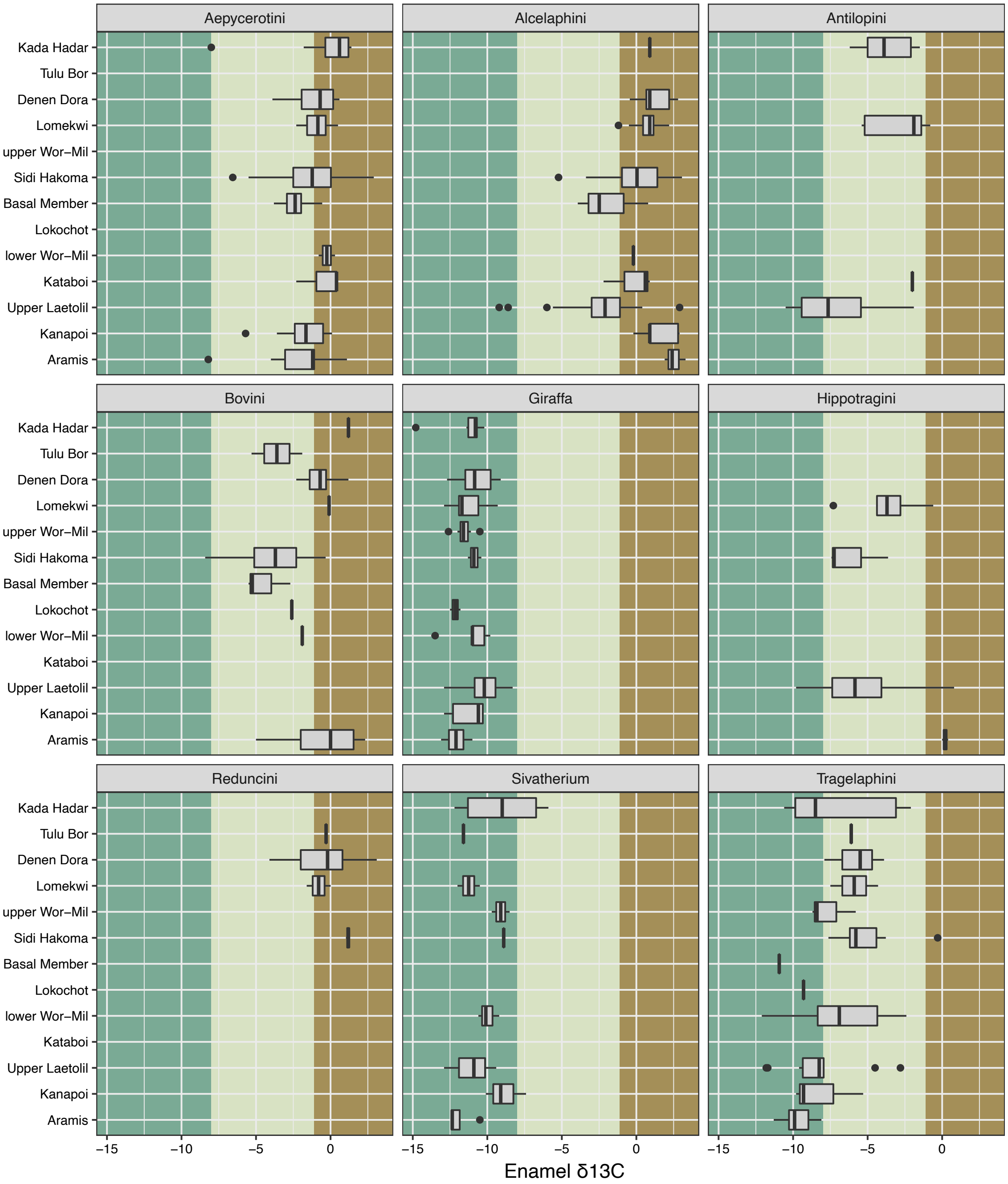

Figure 4.5. Enamel carbon isotope value of *Aepycerotini, Alcelaphini, Antilopini, Bovini, Hippotragini, Reduncini*, *Tragelaphini*, *Giraffa* and *Sivatherium* from East African Plio-Pleistocene hominin bearing sites. The colors indicate the designation of the C_3/C_4 distribution. Dark green is C_3 plants (<-8 per mil), light green is mixed C_3/C_4 plants (-8 to -1 per mil), and brown is C_4 grass > -1 per mil). The sites are presented oldest to youngest stratigraphic units from bottom to up. Vegetation classifications are followed after Cerling et al., 2011b.

Figure 4.6 shows a summary of herbivore enamel carbon isotope values for each site in eastern Africa. All of the localities possess taxa that are exploiting both C_3 and C_4 resources. None of the sites have a high density of taxa consuming C_3 resources. However, the highest peaks in this category are at Aramis, Kanapoi, Upper Laetolil, Kataboi, Lokochot, and Upper Woranso-Mille. These tend to be in the older localities, except for upper Woranso-Mille. All of the localities have an abundance of mixed feeders, but with most tending to peak between -5 and -1 per mil, suggesting many taxa that are preferring grass to other plant species—or must eat grass seasonally. The exceptions are Aramis, Kataboi, and Lomekwi, which have their peak around 0-1 per mil, suggesting an even higher proportion of grass. However, the Hadar site members treated as stratigraphic units, show mix of dietary adaptation.

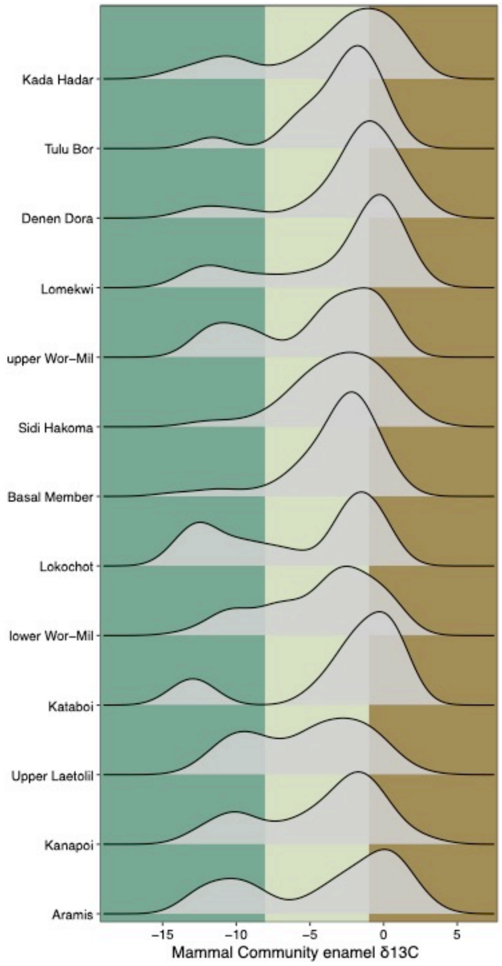

Figure 4.6. The isotopic density showing the distribution of δ^{13}C enamel values across the sites (all taxa together pooled together).

3.2 Paleosol Carbon Isotope Analysis

Figure 4.7 presents δ^{13}C values from paleosol carbonates of Plio-Pleistocene sites in East Africa, and provides a basin-scale record of the structure of paleo-vegetation during the period from 5.3–3.0 Ma. The δ^{13}C values in the soils reflect the amount of woody cover and help determine whether C_4-rich ecosystems or C_3-rich ecosystems predominated the depositional system (Cerling et al., 2011b). It is important to remember than the fraction of woody cover uses the paleosols from C_3 and C_4 plants found in carbonate nodules in the ancient soils, and that C_3 vegetation are not necessarily trees. They could be shrubs, bushes, or even forbs. Localities that have paleosols indicating 40-80% woody cover are indicated at Asa Koma, Aramis, Upper Laetoli, and Upper Woranso-Mille. The other localities have peaks in the 10-40% range of woody cover, except for Upper Woranso-Mille. Upper Woranso-Mille is unique in that it is bimodal, with peaks in both high woody and low woody cover, with few paleosols indicating mixed cover.

Most of these hominin sites have peaks of vegetation at 30-15% woody cover--the mixed wooded grassland habitats. They shift slightly back and forth through time with no overall trend from Kanapoi through the Kada Hadar Member at Hadar (except for Upper Woranso-Mille).

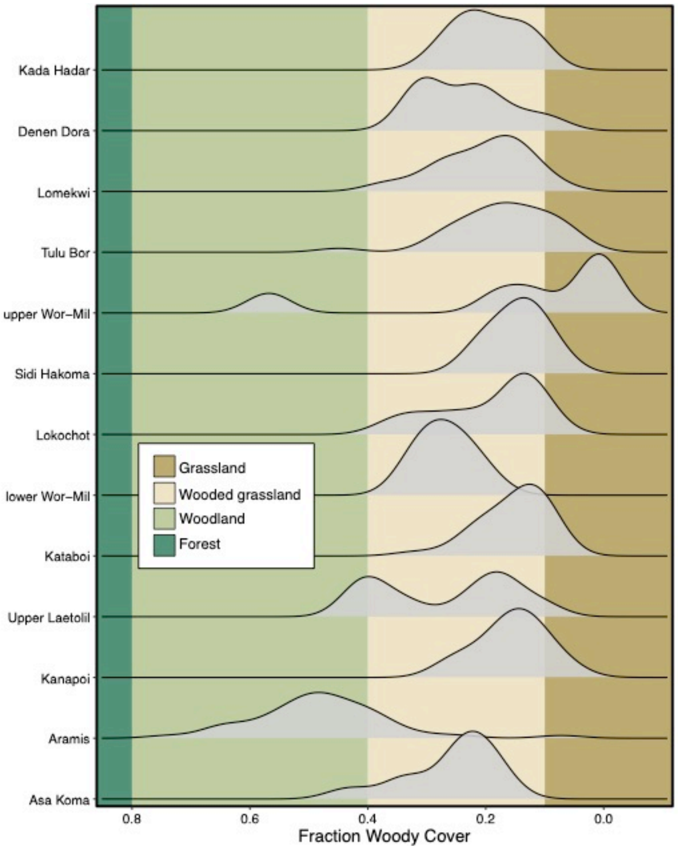

Figure 4.7. Stable carbon isotopic composition of pedogenic carbonate illustrating the change in woody cover through time at different sites of East Africa. The colors indicate the degree of woody cover: dark green representing > 80% woody cover, light green representing between 40%-80% woody cover, light brown representing woody cover of 20%-40%, and brown representing > 10% woody cover. The sites are presented oldest to youngest stratigraphic units from bottom to up. Vegetation classifications are followed after Cerling et al. (2011b).

4. Conclusion

When individual as well as combined proxies are considered, slight difference in the results are evident. However, the overall result of hypsodonty, mesowear and carbon isotope analysis complement each other and show that these approaches in the ungulate communities do indeed carry a strong signal about diet and habitat aspects of the environment as well as precipitation both in extant and extinct herbivores mammals. We know from faunal community analysis and paleosol carbonates that habitats were getting more open throughout the last 3.5 million years in East Africa. Hypsodonty, mesowear and the carbon isotope data reveal that the C_4 food items were predominat dietary components in most of hominin sites in eastern Africa during the mid-Pliocene. Hominins were responding to these habitat changes by modifying their diet to a certain extent. Therefore, the dietary niche expansion in the hominin lineage can be explained by their switch to consuming C_4 food items at some times. This could be related to seasonal changes in which rainy seasons were becoming shorter and the dry season hotter in later time periods. Understanding of paleosol carbonate as well as enamel $\delta^{13}C$ data is a useful tool to reconstruct C_4-dominated vs. C_3-dominated ecosystems, and in assessing the dietary niche expansion in the hominin lineage during Middle Pliocene.

CHAPTER 5
Discussion and conclusion

5.1 Discussion

5.1.1 *Comparing the Data*

In general, the hypsodonty data (Chapter 2) showed that early Pliocene sites predict higher annual precipitation, lower precipitation seasonality, and lower temperature seasonality than mid-Pliocene sites, thus there appears to be a trend of increasing aridity. Species richness data (Chapter 2) based on the fossil assemblages showed that the structure of these fossil communities also was different from modern localities. In browsing, mixed feeding and grazing taxa, there were different patterns among the localities containing different hominin species. These will be discussed individually below. The results from the mesowear analyses (Chapter 3) suggested that there was not a trend from higher crowned to lower crowned teeth through time. The abundance of the various bovid tribes (Chapter 3) through time did follow a trend toward aridity in some taxa with Tragelaphini declining through time and Alcelaphini tending to increase through time. In this chapter, carbon isotope data showed that some taxa remained the same through time (*Deinotherium*, *Giraffa*), while others added more grass to their diets through time (Aepycerotini, Antilopini). The paleosol carbon isotope data clearly showed that the early sites had higher woody cover than the later sites, but in general they also seemed to only vacillate slightly between 3.8 and 2.95 Ma. In the following section I will discuss the implications of these results for each hominin species.

5.1.2 *Ardipithecus ramidus*

Ardipithecus ramidus has been recovered from Adu-Asa and Aramis in the Middle Awash (the only sites used in this study). The hypsodonty ecometric regressions predicted that these sites had rainfall between 850 -1000 mm with lower precipitation and temperature seasonality in comparison to most of the later Pliocene fossil localities. The mesowear analysis of Adu-Asa and Aramis had mean scores between 3 and 3.5, but ranges from 2-4 indicating that mixed feeders predominated these assemblages. The correspondence analysis of bovid abundances at modern and fossil localities showed that Aramis grouped with Tragelaphini and closest to the modern site of Lake Manyara, Kenya while Adu-Asa was influenced by increased Reduncini and grouped near the Angolan site of Quicama. Tragelaphini, which is categorized as a browsing bovid taxon, is more abundant at Aramis (86%) than any other locality. The faunal isotope values at Aramis, surprisingly showed peaks in both browsing and grazing with few mixed feeding taxa. Finally, soil carbonate data indicate that Aramis had a peak in cover between 40-80%. The reconstruction of the paleoenvironment of *Ardipithecus* (especially at Aramis) is a contentious issue, with some researchers suggesting it was a closed woodland or forest mosaic (White et al., 2009). However, soil carbonate study carried by Gani and Gani (2011) demonstrated that *Ar. ramidus* had occupied wooded grassland habitat at Aramis.

If all of these proxies are compared, it would appear as if Aramis is either a mosaic habitat or a woodland in which the species partitioned the resources between C_3 and C_4 plants with peaks in both. The mesowear results do not match with some of the other proxy data, and indicate more grazing taxa.

5.1.3. *Australopithecus anamensis*

Australopithecus anamensis has been recovered from Kanapoi and Allia Bay from Kenya and Asa Issie, Galili, and Woranso-Mille from Ethiopia. This study, however, focused only on Kanapoi, Allia Bay and Asa Issie localities which were available for the study. The hypsodonty ecometric regressions predicted that *Au. anamensis* sites had mean annual rainfall of 1050 mm, and ranged from 750 to 1100 mm per annum. This is higher than *Ar. ramidus* sites. There is also low seasonality of precipitation and temperature with *Au. anamensis* sites being the wettest of all sites in the Pliocene. The mesowear analyses of bovids from these sites suggests a mosaic nature of the habitats at these sites. However, bovids from Allia Bay indicate greater amount of attrition in the diet, i.e., browsing compared to Asa Issie and Kanapoi, indicating that *Au. anamensis* from Allia Bay lived in more closed and wooded environments. Kanapoi bovids stand out as having a much higher grazing signal among *Au. anamensis* sites. As at Aramis, Tragelaphini is the most dominant taxon at Asa Issie (80%), Kanapoi (47%), and Allia Bay (69%) indicating some wooded habitat. The correspondence analysis of modern and fossil sites also showed that Kanapoi and Allia Bay localities grouped with modern Tragelaphini and closest to the modern site of Hluhluwe (850mm), South Africa and Hwange (640mm), Zimbabwe, while Asa Issie grouped with closest to the modern site of

Lake Manyara, Kenya. Only the Kanapoi site was examined in both enamel and paleosol carbon isotope analyses. The enamel isotope signals at Kanapoi showed peaks in both browsing and grazing with few mixed feeding taxa, but dominantly grazing taxa. The soil carbonate data indicate that Kanapoi had woody cover between 5-35%. The paleosol isotope study conducted by Wynn (2000) suggests that *Au. anamensis* was associated with relatively open semi-arid low tree-shrub savanna habitats at Kanapoi. His result agrees with the mesowear analysis of this study that Kanapoi bovids were more grazers. Overall, looking at all proxies *Au. anamensis* occupied a wetter environment than *Ar. ramidus*, and exploited C_3 dominated food items, except at Kanapoi.

5.1.4. *Australopithecus afarensis*

Australopithecus afarensis specimens were reported from several sites including Dikika, Hadar, Ledi Geraru, Woranso-Mille, Middle Awash, Galili and Fejej in Ethiopia, Lokochot, Tulu Bor, Kantis in Kenya and Laetoli in Tanzania (Behrensmeyer and Reed, 2013). Ledi Geraru, Galili and Fejej were not considered in this study. The hypsodonty ecometric regressions predicted that *Au. afarensis* sites had mean annual rainfall of 780 mm (ranging from 750–1000mm) and higher seasonality of precipitation and temperature than sites containing *Ardipithecus* and *Au. anamensis*.

The mesowear results of bovids from Ethiopian *Au. afarensis* sites (Hadar, Dikika, Makah Marah (Woranso-Mille)) showed tooth wear that indicates browsing through grazing but with the highest proportions of bovids in the MS-4 category indicating a large proportion of C_4 grasses in their diets. While these bovids utilized C_4 resources more, both C_3 and C_4 plants were available and *Au. afarensis* exploited these resources in different ways, i.e., some ate both C_3 and C_4, some ate one or the other (Cerling et al., 2013; Wynn et al., 2013; Sponhemeir et al., 2013). It is possible that the isotope data is picking up seasonal differences in the hominin diet in Ethiopia.

Au. afarensis sites in the East Turkana Basin (Lokochot and Tulu Bor members) included bovid taxa that were mixed feeders consuming more C_3 plants—only 25% of the taxa are MS-4. Therefore, the Kenyan sites were likely different from those in Ethiopia with more C_4 food resources available. Fortelius et al. (2016) also suggested that west side of Lake Turkana was more arid than the east side starting around 4 Ma. The *Au. afarensis* sites/stratigraphic units, Denen Dora Member (38%) from Hadar and Lokochot and Tulu Bor members (40%) from West Turkana are dominated by Reduncini, a fresh grass grazer. This implies the existence of wetland areas with edaphic grassland indicating more open environment which is not a typical habitat of Tragelaphini. Alcelaphini (39%) is the most dominant taxon at Kantis, suggesting more open habitat. Fossil enamel $\delta^{13}C$ value of Reduncini, plots with the region for C_4 diet and is consistent with the mesowear data, demonstrating that dental abrasion levels were higher.

The correspondence analysis of modern and fossil sites also showed that the Makah Mera (Woranso-Mille), Kada Hadar and Kantis localities grouped between modern Alcelaphini and Aepycerotini, closest to the modern site of Omo, Ethiopia, but in a group consisting of mostly other fossil sites. This suggests that these fossil sites have a different abundance distribution of fossil bovids than are found in modern localities. Aepycerotini and Alcelaphini became more dominant in the *Au. afarensis* sites confirming some open habitat in these areas. Aepycerotini today are an ecotone species, i.e., one that uses the boundary between grasslands and wood or bushlands, so their abundance also represents some woody cover. Generally, the overall faunal isotope values for *Au. afarensis* sites showed peaks in mixed feeding, but vary slightly across sites. Laetoli, Lokochot and Kada Hadar had peaks in both mixed feeding and browsing. The soil carbonate data indicate that *Au. afarensis* sites had a peak in cover between 5-55% woody cover, Laetoli has the highest woody cover, while Tulu Bor has the least woody cover—this is in contrast to the mesowear data that indicated Tulu Bor had many C_3 eating bovids. In summary, these multiple proxies suggest that *Au. afarensis* lived in a more mosaic habitat that consisted of bushland, open woodland and grassland environments (including wetlands) and exploited many of the resources across this landscape, as it was indicated by Sponheimer et al. (2013) in their hominin carbon isotope study. There are, however, regional differences in these sites as represented by the other taxa present at each.

5.1.5. *Kenyanthropus platyops*

Kenyanthropus platyops was recovered from Kataboi and Lomekwi in West Turkana, Kenya. The hypsodonty data indicate that the *K. platyops* sites west of Lake Turkana had ungulate taxa with high crowned teeth and are have the least mean annual rainfall at 700 mm (ranging from 550-800mm), which was more seasonal, even compared to contemporaneous *Au. afarensis* sites. This is very interesting because these sediments are the only place where *Kenyanthropus* has been found. This indicates that *Kenyanthropus* likely lived in more arid environments compared to other hominins, which may suggest some degree of niche divergence between *Kenyanthropus* and

Australopithecus taxa. This possibly reflects the development of regionally diversified climate systems, and perhaps indicates the spread of C_4 grasses in eastern Africa, that is, the *K. platyops* localities may have had grasslands before *Au. afarensis* sites. The mesowear analysis from Kataboi and Lomekwi had abrasion dominated diet representing mixed to grazing taxa, which agrees with the ecometric analysis. The vegetation tends to be rougher and more abrasive in drier environments and a tooth with a higher crown is therefore favorable in a drier environment because it will last longer. The correspondence analysis of modern and fossil sites showed that Kataboi and Lomekwi localities grouped between modern sites with Alcelaphini and Aepycerotini. Again, these sites are in the group of fossil localities between these two tribes, and not really close to any modern localities. The enamel carbon isotope results both from Kataboi and Lomekwi sites showed peaks in both browsing and grazing with few mixed feeding taxa like most other sites. The pedogenic carbonate isotope shows both Kataboi and Lomekwi had less than 40% woody cover. The hypsodonty and mesowear results correlate with the stable isotope and correspondence analyses, suggesting more grazing at these localities. Overall, the multi-proxy analysis of Kataboi and Lomekwi localities suggest that *K. platyops* lived in a drier and more open environment than *Au. afarensis*, but exploited a larger range of resources, similar to *Au. afarensis*.

5.1.6. *Australopithecus deyiremeda*

Australopithecus deyiremeda has been recovered only at Burtele from the Woranso-Mille research area in Ethiopia. The hypsodonty ecometric regressions predicted that *Au. deyiremeda* site had mean annual rainfall of 830 mm, slightly higher than *Au. afarensis* sites and high precipitation and temperature seasonality. The mesowear data from Burtele is suggestive of more open habitat at this locality. The faunal assemblage from this site had large proportions of Alcelaphini and Antilopini. Alcelaphini usually represent more grazing bovids representatives while Antilopini can be mixed feeders or even browsers in very arid environments. The correspondence analysis of modern and fossil sites also showed that the Burtele locality grouped with modern Alcelaphini and closest to the modern site of Serengeti National Park, Tanzania and Nairobi National Park, Kenya. The faunal isotope values at Burtele had both browsing and mixed feeding taxa. The carbon isotope analysis shows that this site had woody cover between 0-65%. All these data suggest that *Au. deyiremeda* lived in an open environment with grasses and some trees. Undergoing studies of suids are also suggesting mixed habitats with a component of open grassy habitats at Burtele (I. Lazagabaster, personal communication, November 21, 2019).

5.2. Conclusions

In general, the hypsodonty, mesowear and carbon isotope studies complement each other and provide a stronger basis for reconstructing hominin paleoecology during the Pliocene. This study suggests that precipitation and seasonality are the main factors driving taxa to switch their dietary sources regardless of their habitats in eastern Africa during the Pliocene and that hominin localities responded to these changes in differing degrees across time and space. There is also increased representation of C_4 diets in East Africa during Pliocene and this could have resulted from atmospheric CO_2 concentrations, fire, high level of seasonality and decreased mean annual precipitation (Wynn, 2004; Levin et al., 2011; Levin, 2015). This in turn might have changed the availability of preferred food resources and forced hominins to adapt a wider dietary niche. Seasonality is proposed as the underpinning selection pressure in the Pliocene fauna including our ancestors (Levin, 2015). Ecological instability in the Plio-Pleistocene has been consider as a determining factor for hominin behavioral and morphological evolution (Bond et al., 2003; Staver et al., 2011; Potts 2013; Antón et al., 2014; Levin, 2015). This instability coupled with the expansion of C_4 plants and the change in proportion availability of preferred C_3 food items could have caused hominin dietary niche expansion around 3.5 Ma.

For example, the gradual decrease of the browsing Tragelaphini and the subsequent increase of Alcelaphini, Antilopini, Aepycerotini and Hippotragini proportions in eastern Africa during the Plio-Pleistocene is an indicator of seasonally dry grasslands, bushlands, and woodland grassland mosaics. The abundance of Reduncini in the younger sites such as Denen Dora, Lokochot and Tulu Bor is indicative of moist, open habitats where there is fresh grass (Bobe et al., 2007; Levin, 2015). The association of these taxa with hominins is considered to be an indication of hominin habitat preference. In the *Ar. ramidus* site (at Aramis), and *Au. anamensis* sites (Asa Issie, Kanapoi and Allia Bay) Tragelaphini is the most dominant taxon suggesting closed environment, whereas in the *Au. afarensis* and *K. platyops* sites Tragelaphini was replaced by grazing and mixed feeding bovid taxa. The hypsodonty analysis also suggested that Aramis was a wet environment. Conversely, the mesowear result indicates the existence of wooded grassland environment at Aramis, suggesting open vegetation structure. *Nyanzachoerus*, from the Turkana Basin and modern *Syncerus caffer* lived in woodland and bushland habitats, but primarily consumed C_4 grasses (Harris and Cerling, 2002; Winnie et al., 2008).

The combined proxies also suggest that *Au. anamensis* from Kanapoi and Allia Bay, occupied wetter environments than *Ar. ramidus*, Allia Bay being the wettest site during the Pliocene. *Australopithecus afarensis* sites have a large proportion of open and mixed-habitat adapted bovid species, suggesting ecotone and shrub-land habitats. The combined analysis also suggested grassland or open woodland habitats. Nevertheless, *Au. afarensis* sites in the Turkana Basin were represented by bovid taxa consuming more C_3 diets, indicating that the Kenyan sites had likely wetter ecological conditions. The *K. platyops* sites are by far the most arid and seasonal, even compared to contemporaneous *Au. afarensis* sites, reflecting the development of regionally diversified climate systems. *Australopithecus deyiremeda* at Burtele is associated with large proportions of

Alcelaphini and Antilopini, indicating open and dry environments with a component of open grassy habitats.

The combined study of hypsodonty, mesowear, faunal abundance and stable carbon isotope analyses of herbivore enamel and paleosol have proven to be valuable proxies in assessing the dietary expansion during the Pliocene. However, the mesowear results are not consistent. In general, there is an overall trend in open environments through time during the Pliocene. For the future it will be important to involve more taxa with larger sample size, particularly for the mesowear analysis. Most of fossil specimens collected by various projects are not taxonomically identified to the lowest level which forced me to exclude many of the specimens from my analysis.

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APPENDIX A

SUPPLEMENTARY MATERIALS FOR CHAPTER 2

Supplementary Materials for:

Paleoclimate and environments of Pliocene hominins in eastern Africa: implications for the origins of hominin dietary niche breadth

The following table is the data of modern community with longitude, latitude, ecoregion, annual precipitation, precipitation seasonality and temperature seasonality information used as a reference for fossil analysis.

Raw data of modern community

Country	**Community Name**	**Long**	**Lat**	**WWF Biome**	**Temp. Seasonality (C)**	**Annual Precip. (mm)**	**Precip. Seasonality (mm)**
Angola	Bicuar National Park	14.81	-15.29	Woodland	27.85	773	99
Angola	Buffalo Partial Reserve	13.8	-12.77	Woodland	15.53	985	99
Angola	Cameia National Park	21.64	-11.91	Woodland	17.39	1266	89
Angola	Cangandala National Park	16.73	-9.87	Woodland	8.04	1195	76
Angola	Iona National Park	12.33	-16.64	Desert and Semi-Desert	20.65	89	116
Angola	Luando Integral Nature Reserve	17.38	-11.01	Woodland	11.4	1282	80
Angola	Luengue Luiana National Park	22.52	-17.4	Woodland	33.03	636	108
Angola	Mavinga National Park	20.99	-15.55	Woodland	29.11	830	110
Angola	Mocamedes Partial Reserve	12.42	-15.64	Desert and Semi-Desert	22.36	115	115
Angola	Mupa National Park	15.54	-15.96	Woodland	27.83	682	105
Angola	Quiçãma National Park	13.62	-9.75	Woodland	21.62	803	111
Botswana	Chobe National Park	24.51	-18.55	Woodland	35.49	506	110
Botswana	Okavango Delta World Heritage Site	23.04	-19.23	Grassland	38.17	466	105
Burkina Faso	Arly Partial Faunal Reserve	1.14	11.4	Savanna	18.33	872	110
Burkina Faso	Arly Total Faunal Reserve	1.44	11.55	Savanna	19.6	860	111
Burkina Faso	Bontioli Faunal Reserve	-3.12	10.85	Savanna	16.52	980	104
Burkina Faso	Deux Bales National Park	-2.94	11.6	Savanna	20.46	882	109
Burkina Faso	Kabore Tambi National Park	-1.26	11.47	Savanna	18.84	872	107

Burkina Faso	Kourtiagou Faunal Reserve	1.96	11.54	Savanna	20.73	889	111
Burkina Faso	Madjoari Faunal Reserve	1.28	11.35	Savanna	18.4	876	109
Burkina Faso	Mare aux Hippopotames	-4.15	11.59	Savanna	20.44	921	109
Burkina Faso	Pama Faunal Reserve	0.77	11.44	Savanna	18.38	863	109
Burkina Faso	Sahel Faunal Reserve	-0.58	14.5	Desert and Semi-Desert	30.64	390	138
Burkina Faso	Singou Faunal Reserve	0.96	11.68	Savanna	19.61	837	112
Burkina Faso	W National Park	2.16	11.9	Savanna	22.2	810	115
Burundi	Bururi Forest Nature Reserve	29.6	-3.93	Montane	6.71	1459	65
Burundi	Kibira National Park	29.5	-3	Montane	3.83	1744	59
Burundi	Rusizi National Park	29.26	-3.26	Montane	4.62	906	63
Burundi	Ruvubu National Park	30.37	-3.13	Woodland	5.1	1081	65
Cameroon	Benoue National Park	13.83	8.35	Forest Mosaic	17.47	1288	97
Cameroon	Boumba Bek National Park	14.99	2.66	Forest	5.62	1613	44
Cameroon	Campo Maan National Park	10.35	2.5	Forest	7.48	2236	57
Cameroon	Korup National Park	8.97	5.21	Forest	7.83	2823	61
Cameroon	Mbam et Djerem National Park	12.77	5.85	Forest Mosaic	9.11	1582	74
Cameroon	Waza National Park	14.7	11.29	Savanna	23.07	671	131
Central African Republic	Manovo Gounda Saint Floris National Park	21.26	9.14	Savanna	17.57	1060	99
Central African Republic	Ngotto Forest	17.24	3.88	Forest	5.66	1577	54
Central African Republic	Zemongo Faunal Reserve	25.16	6.6	Forest Mosaic	9.15	1441	75
Chad	Abou Telfane Faunal Reserve	18.89	12.08	Savanna	24.61	704	130

Chad	Bahr Salamat Faunal Reserve	19.43	10.56	Savanna	20.58	875	116
Chad	Binder Lere Faunal Reserve	14.46	9.66	Savanna	21.8	842	111
Chad	Fada Archei Faunal Reserve	21.4	16.97	Desert and Semi-Desert	33.98	72	169
Chad	Lac Fitri	17.43	12.77	Savanna	30.2	417	148
Chad	Manda National Park	18.02	9.41	Savanna	19.45	971	109
Chad	Mandelia Faunal Reserve	15.21	11.54	Savanna	24.85	592	129
Chad	Ouadi Rime Ouadi Achim Faunal Reserve	19.25	15.52	Desert and Semi-Desert	33.03	104	169
Chad	Siniaka Minia Faunal Reserve	18.2	10.44	Savanna	21.25	874	115
Chad	Zakouma National Park	19.67	10.82	Savanna	20.96	855	117
Congo	Conkouati Douli National Park	11.45	-3.93	Forest Mosaic	16.51	1371	77
Congo	Lac Tele Faunal Reserve	17.23	1.19	Forest Mosaic	5.55	1736	32
Congo	Lefini Faunal Reserve	15.43	-2.74	Forest Mosaic	6.71	1866	54
Congo	Mont Fouari Faunal Reserve	11.61	-2.8	Forest	13.84	1571	75
Congo	Nouabale Ndoki National Park	16.6	2.5	Forest	5.49	1685	40
Congo	Nyanga Nord Faunal Reserve	11.83	-2.96	Forest Mosaic	13.96	1459	76
Congo	Odzala Kokoua National Park	14.92	0.98	Forest	6.85	1637	44
Congo	Tsoulou Faunal Reserve	12.5	-3.58	Forest Mosaic	14.56	1223	79
Democratic Republic of the Congo	Garamba National Park	29.5	4.16	Forest Mosaic	10.14	1548	56

Democratic Republic of the Congo	Salonga National Park	20.94	-2.49	Forest	4.04	1953	34
Ethiopia	Abijatta Shalla Lakes National Park	38.53	7.55	Savanna	7.83	754	61
Ethiopia	Awash National Park	40.04	8.91	Savanna	20.54	565	79
Ethiopia	Bale Mountains National Park	39.68	6.93	Montane	6.26	1225	43
Ethiopia	Gambella National Park	34.13	7.96	Savanna	12.92	1046	79
Ethiopia	Mago National Park	36.25	5.54	Savanna	8.61	610	46
Ethiopia	Omo National Park	35.76	5.92	Savanna	8.1	873	45
Ethiopia	Simien Mountains National Park	38.18	13.16	Montane	11.35	1050	118
Ethiopia	Yangudi Rassa National Park	40.77	10.96	Desert and Semi-Desert	24.02	389	89
Gabon	Lope National Park	11.54	-0.53	Forest	10.14	1806	70
Guinea	Badiar National Park	-13.28	12.59	Forest Mosaic	22.98	1219	119
Guinea	Massif du Ziama Classified Forest	-9.34	8.28	Montane	7.59	2437	63
Guinea	Mount Nimba Strict Nature Reserve	-8.41	7.65	Montane	9.64	2076	61
Guinea	Rio Pongo Wetland of International Importance	-14.15	10.13	Forest	19.21	3330	128
Ivory Coast	Comoe National Park	-3.73	9.12	Savanna	13.89	1096	71
Ivory Coast	Tai Forest	-7.12	5.72	Forest Mosaic	8.95	1698	50
Kenya	Aberdare National Park	36.68	-0.38	Montane	7.35	1636	47
Kenya	Amboseli National Park	37.24	-2.64	Savanna	14.1	684	79
Kenya	Arabuko Sokoke Forest Reserve	39.89	-3.33	Forest Mosaic	12.09	974	65
Kenya	Arawale National Reserve	40.15	-1.41	Savanna	13.34	470	56

Kenya	Hells Gate National Park	36.32	-0.88	Savanna	11.4	686	61
Kenya	Kakamega National Reserve	34.86	0.33	Forest Mosaic	6.78	1910	37
Kenya	Lake Nakuru	36.1	-0.39	Savanna	6.67	859	47
Kenya	Lolldaiga Hills Conservation Area	37.13	0.122	Montane	5.94	806	55
Kenya	Marsabit National Park	37.96	2.27	Savanna	9.09	790	96
Kenya	Masai Mara National Reserve	35.11	-1.47	Savanna	7.48	1014	45
Kenya	Meru National Park	38.2	0.1	Savanna	9.81	516	120
Kenya	Mount Elgon National Park	34.51	1.19	Montane	6.76	1743	38
Kenya	Mount Kenya National Park	37.34	-0.12	Montane	7.96	1807	53
Kenya	Nairobi National Park	36.86	-1.38	Savanna	12.16	714	75
Kenya	Samburu National Reserve	37.54	0.61	Savanna	6.79	540	92
Kenya	Shimba Hills National Reserve	39.4	-4.26	Forest Mosaic	14.5	1137	59
Kenya	Tsavo National Park	38.77	-2.78	Savanna	13.79	841	77
Malawi	Kasungu National Park	33.13	-12.92	Woodland	23.57	837	119
Malawi	Lake Chilwa Wetland of International Importance	35.68	-15.25	Grassland	23.54	1268	98
Malawi	Lengwe National Park	34.57	-16.22	Woodland	28.18	788	100
Malawi	Liwonde National Park	35.34	-14.86	Woodland	24.05	970	109
Malawi	Majete Wildlife Reserve	34.62	-15.92	Savanna	27.28	867	97
Malawi	Mwabvi Wildlife Reserve	35.02	-16.71	Woodland	27.93	979	91
Malawi	Nkhotakota Wildlife Reserve	34.03	-12.87	Woodland	21.48	1169	109
Malawi	Nyika National Park	33.85	-10.57	Forest Mosaic	18.9	1274	95

Malawi	Vwaza Marsh Wildlife Reserve	33.45	-11.01	Forest Mosaic	25.19	770	115
Mali	Cliff of Bandiagara World Heritage Site	-3.37	14.37	Savanna	29.43	510	132
Mali	Reserve partielle de faune dAnsongo Menaka	1.7	15.53	Desert and Semi-Desert	31.12	231	154
Mauritania	Banc dArguin National Park	-15.79	20.1	Desert and Semi-Desert	30.02	38	104
Mauritania	Parc National du Diawling	-16.41	16.34	Desert and Semi-Desert	22.6	209	157
Mozambique	Banhine National Park	32.87	-22.81	Woodland	30.15	476	95
Mozambique	Bazaruto National Park	35.44	-21.73	Forest Mosaic	25.78	872	79
Mozambique	Gile National Reserve	38.38	-16.55	Woodland	23.45	1283	84
Mozambique	Gorongosa National Park	34.5	-18.82	Woodland	26.64	1064	87
Mozambique	Maputo Special Reserve	32.33	-26.5	Savanna	25.81	624	65
Mozambique	Marromeu Game Reserve	35.93	-18.75	Savanna	22.62	1095	78
Mozambique	Niassa Game Reserve	37.35	-12.01	Woodland	18.87	1235	110
Mozambique	Zinave National Park	33.56	-21.61	Woodland	29.54	663	94
Namibia	Ai Ais Hot Springs National Park	17.33	-27.85	Desert and Semi-Desert	37	61	53
Namibia	Daan Viljoen National Park	16.96	-22.53	Desert and Semi-Desert	36.59	352	107
Namibia	Etosha National Park	15.9	-18.95	Desert and Semi-Desert	37.33	395	112
Namibia	Khaudum National Park	20.78	-18.81	Savanna	36.42	519	109
Namibia	Mahango Game Reserve	22.46	-17.97	Woodland	35.22	565	106
Namibia	Mudumu National Park	23.57	-18.08	Woodland	36.62	574	110

Namibia	Namib Naukluft National Park	15.33	-24.55	Desert and Semi-Desert	22.69	53	90
Namibia	Nkasa Rupara National Park	23.66	-18.39	Grassland	36.99	534	109
Namibia	Skeleton Coast National Park	12.8	-19.27	Desert and Semi-Desert	18.6	34	148
Namibia	Waterberg Plateau National Park	17.29	-20.4	Desert and Semi-Desert	34.63	428	107
Niger	Addax Sanctuary	9.5	19.48	Desert and Semi-Desert	56.42	25	105
Niger	Air and Tenere Natural Reserves	9.67	19.12	Desert and Semi-Desert	55.41	26	115
Niger	Parc W Niger National Park	2.41	12.31	Savanna	24.47	692	121
Niger	Reserve de faune de Gadabedji	7.15	15.14	Desert and Semi-Desert	34.36	285	155
Niger	Reserve totale de faune de Tamou	2.3	12.6	Savanna	25.56	647	127
Rwanda	Akagera National Park	30.71	-1.64	Forest Mosaic	2.43	965	57
Rwanda	Gishwati Forest Reserve	29.38	-1.82	Montane	2.27	1543	44
Rwanda	Nyungwe National Park	29.29	-2.53	Montane	3.17	1678	51
Rwanda	Volcans National Park	29.52	-1.48	Montane	2.43	1721	42
Senegal	Mount Assirik	-13.03	13.01	Savanna	23.6	962	122
South Africa	Golden Gate Highlands National Park	28.67	-28.49	Forest Mosaic	40.13	818	61
South Africa	Hluhluwe Game Reserve	32.07	-28.09	Forest Mosaic	25.3	880	45
South Africa	Kapama Game Reserve	31.04	-24.45	Woodland	30.36	621	83
South Africa	Kgalagadi Transfrontier National Park	20.78	-25.56	Desert and Semi-Desert	56.7	243	82
South Africa	Knysna National Lake Area	23.04	-34.03	Montane	26.41	805	11

South Africa	Kruger National Park	31.48	-24.01	Woodland	36.06	502	79
South Africa	Namaqua National Park	17.57	-30.02	Desert and Semi-Desert	30.26	123	63
South Africa	Natal National Park	28.93	-28.7	Forest Mosaic	34.38	978	69
Tanzania	Arusha National Park	36.85	-3.25	Montane	14.83	1217	90
Tanzania	Gombe National Park	29.63	-4.69	Woodland	5.55	1250	72
Tanzania	Kilimanjaro National Park	37.33	-3.06	Montane	11.47	1787	61
Tanzania	Kizigo Game Reserve	34.52	-6.59	Savanna	13.93	591	113
Tanzania	Lake Manyara National Park	35.79	-3.49	Grassland	15	739	89
Tanzania	Lake Rukwa Game Reserve	31.92	-7.39	Woodland	14.47	924	96
Tanzania	Mahale Mountains National Park	29.92	-6.22	Montane	9.17	1145	86
Tanzania	Mikumi National Park	37.22	-7.44	Woodland	17.77	1128	82
Tanzania	Ngorongoro Conservation Area	35.38	-3.05	Savanna	13.43	562	76
Tanzania	Ruaha National Park	34.57	-7.65	Savanna	14.67	657	110
Tanzania	Selous Game Reserve	37.46	-8.84	Woodland	15.73	1245	91
Tanzania	Serengeti National Park	34.78	-2.33	Savanna	8.3	838	53
Tanzania	Tarangire National Park	36.1	-4.15	Savanna	15.85	721	88
Tanzania	Tongwe Forest Reserve	38.73	-5.3	Forest Mosaic	16.13	1331	54
Uganda	Budongo Forest Reserve	31.59	1.82	Forest Mosaic	7.77	1285	41
Uganda	Kibale National Park	30.38	0.42	Montane	3.94	1199	41
Uganda	Kidepo Valley National Park	33.8	3.86	Savanna	11.72	674	59
Uganda	Murchison Falls National Park	31.8	2.26	Forest Mosaic	9.26	1213	43

Uganda	Rwenzori Mountains National Park	29.98	0.39	Montane	3.34	1849	29
Zambia	Bangweulu Swamps Wetland of International Importance	30.15	-11.94	Grassland	23.29	1257	114
Zambia	Kafue Flats	27.23	-15.64	Grassland	31.37	843	121
Zambia	Kafue National Park	25.87	-15.15	Woodland	30.75	887	115
Zambia	Lake Mweru	29.42	-8.65	Woodland	12.54	1126	89
Zambia	Mweru Wantipa National Park	29.42	-8.65	Woodland	12.54	1126	89
Zambia	West Lunga National Park	24.78	-12.81	Forest Mosaic	23.14	1187	100
Zimbabwe	Gonarezhou National Park	31.88	-21.6	Savanna	29.92	573	91
Zimbabwe	Hwange National Park	26.56	-19.08	Woodland	34.52	547	110
Zimbabwe	Mana Pools National Park	29.46	-15.97	Woodland	31.86	705	123
Zimbabwe	Matobo National Park	28.52	-20.55	Savanna	34.41	578	99
Zimbabwe	Matusadona National Park	28.59	-16.96	Woodland	26.43	770	115
Zimbabwe	Mushandike Sanctuary	30.64	-20.11	Woodland	30.31	610	103