2 Approaches to the Study of Past Environments

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Introduction

In a book on African paleoecology and human evolution, it is important to define several key themes, including biomes, vegetation formations and associations, as well as plant physiognomy. We first define these terms, before examining the sources of data employed in paleoenvironmental reconstructions. Finally, we provide an overview of the approaches used to understand past habitats, which underpin the chapters on the specific sites which make use of these approaches to refine our understanding of African paleoenvironments and the place of hominins within them.

Biome – A major regional ecological community of plants and animals extending over large natural areas, for example, tropical forest, or subtropical grassland (Figure 2.1). The plants of terrestrial biomes consist of Formations. We are concerned here with the forest, savanna, grassland, and desert biomes, particularly with the first two, which are key habitats associated with early hominin activity.

Vegetation Formation – A climax community of plants extending over large areas and their nature determined by climate, for example, tropical rainforest. Plant formations form the main natural vegetation types of the world.

Vegetation Association – These are the natural units of vegetation within a Vegetation Formation. There might be many plant associations in a single forest, savanna, or grassland, the variations resulting from variations in soil, topography, and altitude. Soil catenas have a succession of plant associations dependent on the different soils.

Plant physiognomy – This term covers all aspects of the structure of vegetation, for example, height, density, thorniness, evergreen, or deciduous plants.

Catena – A grouping of soil–vegetation types in relation to topography (Milne, 1935). Catenas form when soils change along a gradient, usually down a slope, and this relationship is repeated wherever the same topographic and geological conditions occur. They form within single rainfall, temperature, and altitudinal zones and the nature of the vegetation associations is affected by the combination of soil types and topography (Milne, 1935). Several catenas have been described for Laetoli (Tanzania) environments (Andrews and Bamford, 2008; see also Harrison et al., Chapter 34), e.g., downslope from broad-leaved woodland association on hill slopes with shallow soil → low

Acacia woodland association on lower slopes with deep clay soils and impeded drainage → riverine woodland association where erosion has cut through the deep soils. Milne (1947) gives another example from the Uyansi plateau, Tanzania: upper slopes, deciduous thicket → middle to lower slopes, open woodland → lowest slopes, transition open woodland → bottom flats, hard pan vegetation of low trees and grass.

Mosaic vegetation – A soil–vegetation patchwork following topography and relief (modified from Morison et al., 1948). Landscape heterogeneity leading to heterogeneous habitats promotes the coexistence of a wide range of species and greater biodiversity (Reynolds et al., 2015). Fossil faunal assemblages may accumulate over enough time for climate changes between wetter and drier habitats to give the appearance of mosaic habitats. Mosaic vegetation associations follow topography within a single climatic zone, in which case it is based on catenas, or it may be related to altitude, with precipitation and temperature varying with altitude. Variations in climate occur over a minimum distance of 100 km (Griffiths, 1976), i.e., within areas of at least 10,000 km², and mosaic vegetation would normally occur within these distances. It is, therefore, a local effect at the landscape level, rather than a regional effect.

Habitat heterogeneity is assumed to be the major driving force behind continental and global biodiversity (Kerr and Packer, 1997), but within Africa the correlation between mammal species richness and variations in topography has low significance. Multiple regression models of 17 climate and topography variables in southern Africa showed that the one-variable and two-variable models most highly correlated with mammal species richness were measures of seasonality (temperature and precipitation), and only with the three-variable model did topography play a part (Andrews and O'Brien, 2000). Habitat heterogeneity is important at the local and landscape level and therefore also for fossil faunas.

Spatial mosaics are common wherever there are variations in soil, topographic relief, or water availability. Several recent soil/vegetation catenas have been described for the Laetoli region (Andrews et al., 2011) and their presence has been inferred for the Pliocene deposits based on the geomorphology of the region (Hay, 1987). Modern vegetation mosaics are typically transient stages in a vegetation succession, both spatial and temporal. For example, there is evidence for temporal mosaic variation
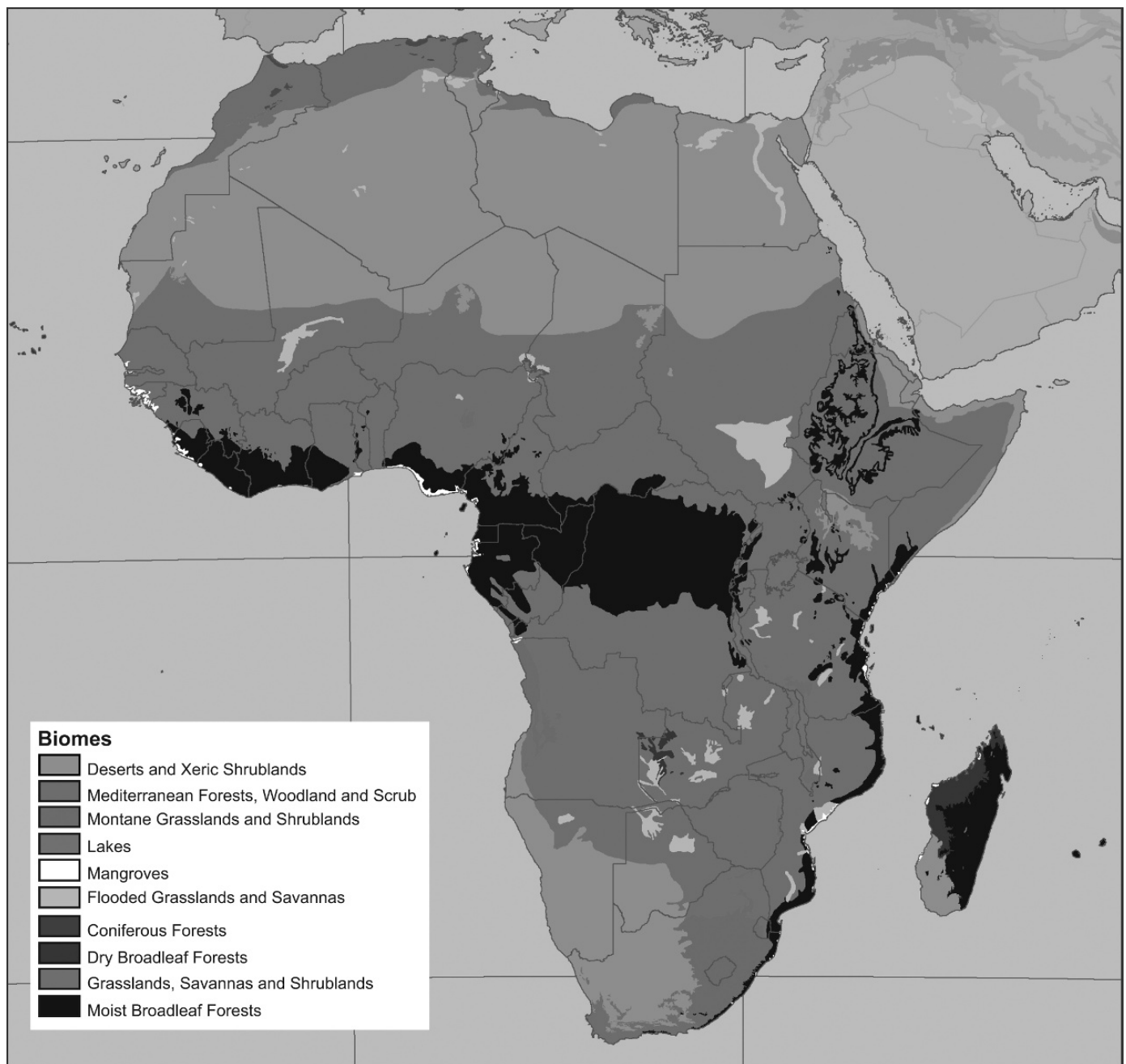
Figure 2.1 Simplified biome map of Africa, with emphasis on the major biomes of interest in the fossil record, namely forest, savanna, grassland, and desert. (*Source*: Modified from https://sedac.ciesin.columbia.edu/data/set/nagdc-population-landscape-climate-estimates-v3/maps based on WWF (2006) World Biomes Data set, www.worldwildlife.org/biome-categories/terrestrial-ecoregions). (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

for the Masai Mara: it was observed to be open grassland in the nineteenth century (White, 1915) and was heavily grazed by wild and domestic livestock, but it reverted to dense woodland thicket during the rinderpest outbreak in the late nineteeth century when there was ~95 percent mortality of large mammals, including almost all domestic stock (Sinclair, 1979a, 1979b). With European expansion into the region, much of the area was mechanically cleared to eradicate the tsetse fly, and bush-clearing was facilitated by the reintroduction of elephants in the 1970s, so that the area is now once again open grassland.

Sources of Evidence

In this section we describe several sources of evidence and analytical methods to infer past environments.

Sediments and Soils

Soils may be formed in the past and preserved as paleosols, and may be regarded as trace fossils representing past ecosystems (Retallack, 1991; Retallack et al., 1995). The different stages of soil formation can often be identified in preserved paleosols,

indicating how mature the soil was, and soil horizons may still be identifiable. In exceptional cases, the uppermost layer, the humus horizon may still be preserved. Paleosols are a key feature found at many hominin-bearing sites in Africa, such as Taung, South Africa (Parker et al., 2016; Hopley and Kuhn, Chapter 13). Fossil sand dunes, for example, are key ancient features associated with the other southern African sites of Langebaanweg, Elandsfontein, and Still Bay (Reynolds, Chapter 6). There is a close relationship between aeolian processes and climatic aridity, and at its most extreme this may be seen in the formation of fossil sand dunes. The presence of tropical forest in Central Africa growing on old sand dunes shows the existence of a former arid period affecting the region, and the structure of the aeolian deposits may indicate wind strength and direction. The formation of soil calcretes is another indicator of aridity, coupled with highly seasonal rainfall, for both are requisites for the formation of calcareous nodules in soil and calcretes.

The presence of lakes and their expansion and contraction is shown by past shorelines and the formation of shoreline terraces, providing information on changes in past rainfall. The chemical composition of the sediments themselves may indicate if the lakes had drainage outlets or were closed systems with consequent build-up of minerals. The taxonomic distribution of aquatic organisms such as diatoms or ostracods can indicate water temperature or salinity. Many key hominin sites were based around paleo-lakes, such as Olduvai Gorge, Tanzania (see Peters et al., Chapter 33; Farrugia and Njau, Chapter 32), Hadar, Ethiopia (Campisano et al., Chapter 18), Konso, Ethiopia (Suwa et al., Chapter 22), Olorgesailie, Kenya (Potts and Faith, Chapter 30), and the Chad Basin, Chad (Vignaud et al., 2002; Bobe and Reynolds, Chapter 15).

Structures in the immediate vicinity of fossil sites provide evidence on the local environment. For example, evidence of rivers or channels may be present, or there may be drainage features in the sediments, outflow or spring deposits. Both the soil formation processes and the nature of weathering processes in the soils provide evidence on past climates. Well-aerated soils may have a reddish color indicating the presence of oxidized iron compounds, or waterlogged soils may be deprived of oxygen and be gleyed, giving a gray color. Lignites and black clays may form in waterlogged soils, and calcareous horizons in the soil profiles may form under conditions of seasonal drying of the soil. As the rain penetrates the soil, it carries down dissolved minerals from the upper part of the soil, and if the rain is heavy and prolonged, these minerals may be carried to great depths through the soil, but when it is sparse and seasonal, the minerals may only be carried down a few tens of centimeters. When the rain stops and no more water is passing down the soil, the soil dries out and the minerals in the water are deposited at the lowest point the water has reached. Repetitions of this process over hundreds or thousands of years result in calcretes or hard pans in the soil, sometimes so thick that they impede further drainage of water through them, resulting in local flooding.

The integration of local and regional sedimentary features is therefore a primary source of evidence on past environments. Landscape reconstruction at Olduvai Gorge showed that the sediments at FLK 22 accumulated as a 100 m wide and half-meter high peninsula between a river to the south and a freshwater marsh to the north (Blumenschine et al., 2012b). Recent minor uplift of the FLK Fault appears to have played a role in deflecting the river channel and containing the wetland's flood basin. Good drainage on the peninsula permitted the establishment of woody vegetation. Short mixed sedge/grassland occurred in open areas on the peninsula and lower-lying channel (Bamford et al., 2006, 2008; Peters et al., Chapter 33), while mixed-species marshland occurred in the wetland. The trees on the peninsula within this landscape mosaic provided repeated activity foci for hominins and carnivores, and arboreal refuge in the vicinity that allowed hominins to acquire resources at the more open ecotone between the peninsula and wetland. In this way, the dense and diverse paleoanthropological assemblages from FLK 22 and elsewhere on and immediately north of the peninsula are predicted by a model of Oldowan hominin land use (Blumenschine et al., 2012b). This example shows just how valuable the landscape approach is and how much it adds to interpretations based on single sites.

Geomorphology on the landscape level may also provide insights into habitat variability (Bailey et al., 2011; Reynolds et al., 2011). This is a function of variations in geology, soils, and topography rather than climate, and if these features can be reconstructed for a fossil site it may then be possible to reconstruct the structure of plant communities that were present in the past. For example, the geomorphology of the Laetoli area in northern Tanzania (Hay, 1987) showed that the Pliocene sediments at Laetoli were deposited on an uplifted peneplain of basement rocks that had an uneven surface with low relief, dissected by shallow valleys for the most part and with drainage to the west and southwest. Compared with today, there was less topographic relief over most of the area during the Pliocene. The development of paleosols on the surfaces of the sediment and the presence of fossilized termite nests, which have been found in some abundance in some levels, indicate stable land surfaces with good drainage and well-established vegetation over several thousands of years (Leakey and Harris, 1987; Harrison et al., Chapter 34).

Relating present-day vegetation to existing geomorphological structures showed great variability of woodland types related to different topographical and edaphic features (Andrews and Bamford, 2008; Andrews et al., 2011): several types of riverine woodlands and gallery forest, broad-leaved deciduous woodlands on thin, well-drained soils, *Acacia* woodlands on valley bottoms with impeded drainage; limited areas of grassland on soils with well-developed calcretes; and increasing forest elements in the flora to the east with increasing altitude (and rainfall). All these associations exist today under one climatic regime, semi-arid with rainfall 500–700 mm. Comparing this distribution of existing vegetation to geomorphology and then extending this comparison to the Pliocene geomorphology of the Laetoli area, it was possible to reconstruct the distributions of past mixed woodlands at the site. For some levels it was possible to check predictions against fossil plant remains; for example, fossil wood, grass and sedges, and pollen (Bamford, 2011a, 2011b).

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Stable Isotopes

The analysis of stable isotopes in soil carbonates and organic matter measures proportions of C_3 to C_4 plants present. In tropical environments, C_3 plants include nearly all trees, shrubs, and herbs, together with grasses where there is a cool growing season, while C_4 grasses grow in open, unshaded places. The carbon isotope composition of carbonates in fossil soils shows that C_4 vegetation was present in Africa by about 9 Ma, but it began to expand only after about 7 Ma (Cerling, 1992). In other words, Miocene vegetation was mainly trees and shrubs, with little evidence of open grassland until the Pleistocene, after the emergence of *Homo*.

The paleogeographic reconstruction mentioned previously for landscape analysis of Olduvai Bed I has also been tested for carbon isotopes, and this confirms the existence of open wooded grassland for upper Bed I, the level associated with the earliest member of the genus *Homo*, *H. habilis*. Analyses of micromammals confirms this, and it contrasts with the results for middle Bed I, for which the small mammals indicate the presence of dense closed woodland (Fernandez-Jalvo et al., 1998; Harrison et al., Chapter 34).

The carbon isotope proportions can also be investigated in the enamel of herbivorous mammals, which provides an indication of the vegetation the animals were eating while the tooth enamel was forming. For example, 500 specimens from the Pliocene deposits at Laetoli had a mix of C_3 and C_4 signals on the teeth from 23 large mammal species (Kingston and Harrison, 2007; Kingston, 2011; Harrison et al., Chapter 34): suids had mixed and C_4 diets; giraffes had only C_3 diets; equids had mainly C_4 diets; different bovid tribes ranged from C_3 to C_4; and monkeys, proboscideans, and rhinos had mixed diets. Ostrich eggshells had an exclusively C_3 signal. The results indicate environmental variability at Laetoli, with vegetation varied enough to support both grazers and browsers. Oxygen isotopes were used to calculate an aridity index for the site derived from the water deficit (WD) calculated for different groups of mammals, and the range of values for WD at Laetoli indicated mean annual precipitation nearly the same as it is today.

Isotopic analysis of herbivore teeth from Dikika, Ethiopia (Bedaso et al., 2013; see also Bobe et al., Chapter 19) show that a range of wooded savanna habitats was present at the site, but there was no indication of forest or closed canopy woodland and C_4 grasses made up nearly 75% of herbivore diets. The relative proportions of wooded versus grassed habitats changed through time, and the oxygen isotope values suggest that the climate was wetter than earlier in the Pliocene and at present. In a similar vein, Wynn and colleagues (2020) have used hominin stable carbon isotope values to reconstruct changing diets of *Paranthropus* within the Shungura and Usno Formations (Ethiopia), which complements the findings of Negash and colleagues (2020; Chapter 24) on the herbivore isotopes of the same deposits.

The oxygen isotope composition of bone is largely determined by the $\delta^{18}O$ value of environmental water, although this is affected by the different species' metabolic processes. Plant foliage can be enriched in ^{18}O by evaporation from the leaves, so that an animal feeding on leaves exposed to the sun has enriched $\delta^{18}O$ values. This is the case with giraffes, which feed high up on the tree canopies, and for arboreal monkeys such as the seven arboreal monkeys living in closed canopy forest in the Taï Forest, Côte d'Ivoire (Krigbaum et al., 2013). Differences in $\delta^{18}O$ values between species correlated with the different canopy levels and suggest that it might be possible to identify the canopy levels occupied by fossil species.

Nitrogen isotopes are used to investigate differences in trophic level, which may indicate the presence of meat in the diets of fossil animals or the consumption by herbivores of aquatic plants (Palmqvist et al., 2008). The $\delta^{15}N$ levels distinguish meat-eaters and herbivores, but as many carnivorous species also eat vegetation, the evidence can be debatable, and meat-eating populations of chimpanzees show no difference in isotope values between males and females although males have been observed to eat six or seven times more meat (Smith et al., 2010). The explanation may be that the tooth enamel is formed during infancy, when infants and juveniles have little access to meat, or that adults do not eat enough meat to influence their isotopic signal.

Trace Fossils and Taphonomy

Trace fossils are the imprint left by living organisms in sediment where the organisms themselves have disappeared, such as footprints. Commonly found trace fossils are burrows in the sediment that have later been infilled with sediment of different colors or textures. Rarely, the organism is found in association with the burrow. Also trace fossils are the impressions made by plant roots, which form both in the sediment and on the surfaces of bones preserved in the sediment, which are visible as branching grooves with rounded profiles on the surfaces of the bones. Occasionally, whole trees are preserved as infilled cavities, for example the fossil ape site of Rusinga Island, Kenya (Walker and Teaford, 1988).

The presence of footprints preserved in the Footprint Tuff at Laetoli, described by Mary Leakey (Leakey and Harris, 1987), was the first and earliest unequivocal evidence for hominin bipedalism just over 3.6 Ma. Tracks, trails and footprints of many species of mammals and birds preserve evidence of the movements of animals across the Pliocene land surface (Bennett and Reynolds, 2021).

Traces of carnivore activity such as chew marks or digested bones and teeth may show the presence of a predator species even if body fossils are absent (Brain, 1981; Andrews, 1990; Su and Harrison, 2008). Other traces may be present, such as rodent gnawing, weathering, and rounding by water or wind abrasion. These traces are considered as the focus of taphonomic studies, but can also be environmental indicators.

Trace fossils also include pellets and scats left by all types of animals, which are referred to as coprolites if preserved (Andrews, 1990). In some cases, it is possible to infer the presence of a specific predator in a fossil assemblage even without body fossils. If the actual pellet or scat is present, this may be informative, but even in their absence the degrees of breakage and digestion of the prey remains is often enough to identify the predator. At Laetoli, many coprolites retain enough of their original shape for them to be identified at least to family (Harrison, 2011i).

Taxonomic Evidence of Paleoecology

Paleoenvironmental reconstructions relying on indicator species (and their inferred ecologies) employ either a few "significant" species or larger sections of the faunal assemblage (Avery, 1987a, 1987b, 1990, 1991). This approach assumes ecological equivalence between fossil organisms and their living relatives, and the same representation of habitats between past and present. This may be justified for plants or for recent fossil faunas, since the species may still be alive today, in which case there is direct evidence as to their ecological attributes. Bamford and colleagues (2008; see also Peters et al., Chapter 33) documented an area of grassland at Olduvai dated to 1.8 Ma, with similar fossil species and floral composition to the present day.

Ecological assessments using mammal species can be more problematic and are based on intuitive knowledge of the adaptations of the species concerned. Previous assessments of the specialist grazing diet of *Antidorcas bondi*, using dental morphology (specifically hypsodonty) and isotopic studies for example, have been shown to underestimate the degree of dietary variability observed using other dietary proxies (Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018; Sewell et al., 2019). This method has some application along a continuous stratigraphic sequence, for example of small mammals in the study by Van der Meulen and Daams (1992) on the Miocene small mammal faunas from Spain.

Pollen is widely used for habitat reconstruction, but it is rarely preserved in association with mammal fauna. While the floral species composition may be well-documented by pollen analysis, the structure of the vegetation may still be ambiguous, especially if there is some indication that the pollen (which is wind-dispersed) comes from many different locations and has been time-averaged, as has been shown for Olduvai Gorge floral fossils (Bonnefille, 1984a).

Fossil leaf morphology may provide rainfall estimates, for in tropical Africa the physiognomy of leaves (independent of plant species identification) is related linearly to moisture variables, providing evidence both of seasonality and total rainfall. Regression models of the relationship between leaf area and annual precipitation as calculated for living floras have been applied to sites in the Tugen Hills (Kenya) generating rainfall predictions for comparison with independent identifications of fossil vegetation (Jacobs, 1999, 2001).

Invertebrates and lower vertebrates, where preserved, are a valuable source of paleoenvironmental evidence. Land gastropods are ecologically conservative and many have highly specific habitat requirements, and because they are small and not very mobile they can be found in microenvironments which are informative of edaphic or topographic features. A high diversity of carnivorous snails in East African fossil faunal assemblages may indicate forest environments, for example (Verdcourt, 1963).

Taxonomic analysis is still generally used for small mammal Pleistocene faunas. Taxonomic composition of successive faunas in a sedimentary sequence may be due to differences in vegetation and climate, but also indicates the predator behavior of the accumulating agents (owls, versus hyaenas). The taxonomic composition of large rodent assemblages from the Miocene of Spain has been used to make inferences about climatic change during the mid- to late Miocene (Van der Meulen and Daams, 1992). The strength of this technique is that it is based on a consistent approach to large faunal assemblages, where the pattern of the taxonomic change in the rodent faunas over a 10-million-year period appears to coincide with temperature curves from other environmental sources, indicating temperature increase during the first part of the middle Miocene followed by a sharp decrease about 15 Ma.

A similar approach has been used for the species abundances and species numbers of the large mammals in the long Omo sequence by Bobe and colleagues (2002) spanning the end of the Pliocene and into the early Pleistocene (from 4 to 2 Ma). Changes in abundances in suids, monkeys, and bovids were related to vegetation changes from more forested environments to more open woodland environments and have been shown to be coincident with marine isotope evidence of climate change.

Vrba (1980) developed a taxonomic index based on the proportions of bovid tribes in fossil faunas: alcelaphines and antilopines (grazers such as wildebeest and gazelles) compared with tragelaphines and reduncines (mainly browsers such as bushbuck and waterbuck). The index of one to the other, known as the alcelaphini and antilopini criterion, or AAC, shows the relative proportions of grazers to browsers, leading to inferences about vegetation cover and climate and habitats. The link with vegetation and climate is tenuous at best, for grass is the dominant ground vegetation in all phases of savanna, and closed woodland and open grassland can exist side by side within the same climatic regime based on differences in soil, topography and altitude. Many studies use alcelaphines as indicators of open grassland, as in the open plains of Serengeti, but modern ecology shows that alcelaphines live equally in wooded or bushed environments.

Small and large-bodied bovids may coexist because their feeding strategies are so different. The dominant bovids in the later Pliocene deposits at Laetoli were alcelaphines, which are grass-eaters like wildebeest, and neotragines, which browse on leaves (Su and Harrison, 2008): the latter is a small antelope, like dik-diks today, and they frequent and feed in dense thickets, hence their browsing diet, but the thickets are often found scattered in more open wooded areas occupied by the alcelaphines.

Carnivore diversity during the late African Miocene (Werdelin and Lewis, 2013) showed major changes through time: between 7 and 8 Ma, there were sabre-toothed cats, long-limbed hyaenas, giant bear dogs with many smaller carnivores as well. Three million years later there were members of the cat family (modern lions and leopards), modern-looking hyaenas, several dog species, and a giant civet present. Carnivore diversity peaked between 3 and 4 Ma, but after 2 Ma numbers of species declined steeply, with the loss of the sabre-toothed species and other giant forms and the modern carnivoran guild emerged. Functional adaptations of the carnivores at these different stages indicate that hypercarnivores decline, while modern faunas fill fewer ecological niches than their Miocene counterparts. Climate cooling during this period may explain

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this, but carnivore biodiversity in southern Africa appears not to correlate with climatic factors (Andrews and O'Brien, 2000), but may indicate the effects of the emergence of the genus *Homo*, with a greater reliance on hunting.

Numbers of species per unit area may provide climatic or habitat information, but also present several confounding issues. Different types of mammal have different relationships with climate and habitat variables, as suggested by Andrews and O'Brien (2000). Arboreal frugivore species richness is most highly correlated with presence of forests, whereas terrestrial herbivores are more highly correlated with habitat heterogeneity; similarly, small mammal species richness is correlated with rainfall, whereas large mammals are most highly correlated with minimum monthly temperature. Another issue is that the greatest species richness in Africa is found where topographic relief is greatest, in contrast to plant species richness, which is highest in high temperature/rainfall conditions, that is in tropical forests. In the absence of climatic and habitat context, the interpretation of paleoecology from species richness can be problematic.

Two attempts to reconstruct past communities through analysis of species lists were habitat spectra and the taxonomic habitat index by Van Couvering (1980) and Evans and colleagues (1981), respectively. These both weight fossil species according to their degree of relationship to living species. For habitat spectra, living species were given a weight of six, and their habitat preferences were weighted by this amount. Extinct species were given weights of five if their genus was still extant and four if it was not and decreasing still further to subfamily and family relationships. Habitat preferences modified by this weighting was calculated for all species in a fossil assemblage and a spectrum constructed for the sum of the habitat weightings (Van Couvering, 1980).

The taxonomic habitat index is based on weightings derived from habitat ranges for all living species in Africa, and the weighted averages for all species in recent faunal assemblages are added together and divided by the number of species to give an average ordination score for the fauna (Evans et al., 1981). For fossil faunas, further calculations consider degrees of relationship of the fossil species with living taxa: extant species in the fossil fauna keep their habitat ranges unchanged, but extinct species are given scores averaged for all species in the genus; extinct genera have scores averaged for all species and genera in a subfamily, and so on. For example, an extant monkey species such as the red-tailed monkey (*Cercopithecus ascanius*) is scored 1 for forest habitats; an extinct species of *Cercopithecus* is weighted for the genus, which averages 0.9 for forest and 0.1 for woodland; and an extinct cercopithecine genus has a score based on all extant cercopithecine genera.

Regarding all types of paleoecological reconstructions being attempted, there remains the issue that past environments, ecosystems, or habitats may have no modern counterparts. It may be possible to interpolate evidence within and between modern habitats to try and reconstruct what the nature of the habitats was like, for example the Olduvai Gorge woodland in middle Bed I (Fernandez-Jalvo et al., 1998). The structure of the woodland faunal community at three levels in middle Bed I had no match in any of the modern woodland communities compared with it, and it seemed to be intermediate between deciduous woodland and semideciduous forest.

The study by Andrews (2006) explores the mix of species found in fossil assemblages by creating artificially reconstructed faunal assemblages composed of different modern habitats. Mixed faunas produced greater variability in habitat representation, and when experimental habitat mixtures were compared with the Pliocene deposits at Laetoli, which did not resemble any single fauna, it showed a mixture of semideciduous forest and woodland faunas, while the Ndolanya Beds fauna was most like the three to one mixture of faunal assemblages from bushland and grassland sites (Andrews, 2006). This may suggest that dense woodland with patches of forest were present for the Laetoli Beds and bushland with patches of grassland for the Ndolanya Beds.

The effects of faunal impoverishment can be approached by deliberately introducing known biases into recent faunas representing different habitats (Andrews, 2006). These biased faunas can then be used for comparison with fossil faunas to see if they match better than unbiased assemblages. Removal of small species produced no change in the ecological signal of the faunas until over half of the species had been removed, so that tropical forest faunas retained their forest signal with only 40 percent of the species remaining. Removing large mammals progressively, starting from the largest, produced even less of a change in the habitat signal.

Ecomorphology

Mammal ecomorphology considers the functional morphology of species environmentally, rather than taxonomically. By comparing the pattern of morphologies obtained for fossil species with those of modern species of known habitats, inferences are drawn about the range of fossil adaptations. The basic assumption is that similar morphologies suggest similar habitats, and that this method is to some degree taxon-free, that is, independent of the taxonomic identification of the species used, in contrast to the use of indicator species, as discussed previously.

There are several qualifications that must be considered to these assumptions: (1) present-day species may occupy habitats that are less than optimal, making them less informative about previous habitat adaptations; (2) species do not always adapt in identical morphological patterns, even in response to the same environmental stimulus (e.g., Rein, 2010); and (3) animals with similar morphologies do not always use it in the same way. For example, hawks, shrikes, and Australian shrike tits have similar hooked beaks, but use these for different diets (Harvey and Pagel, 1991).

The strength of ecomorphology is that it is quantifiable and repeatable. Most studies target specific skeletal elements, such as skulls and teeth, or long bones and phalanges, and they generally are restricted to single taxonomic groups. For example, within the family Bovidae, the morphology of the femur differentiates bovids associated with grassland, forest, and mixed habitats (Kappelman, 1991). Likewise, Meike Köhler (1993) defined three ruminant morphological types based on analyses of body profile, horn types, upper and lower jaws, morphology of the limb extremities, and proportions of the limb bones, and

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these three types are related to a finely graduated habitat change from closed to open habitats. Habitat change has likewise been detected at Laetoli, using bovid ecomorphology (Kovarovic et al., 2002; Kovarovic and Andrews, 2011), which indicates continuous regional woodland cover in the older Laetolil beds and decreasing cover in the younger upper Ndolanya Beds deposits, although the area was still wooded.

Molar hypsodonty is an important ecomorphological character, with higher crowns facilitating the longer effective life of the tooth (Janis, 1988; Jernvall and Fortelius, 2002; Damuth and Janis, 2011). Grazing herbivores in open habitats have significantly more hypsodont teeth (regardless of food preference) compared with those living in closed habitats, due to the presence of abrasive foods and grit in their diets. The amount of soil ingested during feeding is likely greater for animals feeding close to the ground in open habitats, but this does not necessarily imply grass. Browsing herbivores, by contrast, feed on leaves of trees or bushes well above ground level (Madden, 2014).

Measures of hypsodonty combined with stable isotopes from an early Pleistocene site at Venta Micena in Spain have been effective in reconstructing past diet and trophic patterns within large mammal communities (Palmqvist et al., 2008). Within the herbivore species, 7 had grazing adaptations, 2 were mixed feeders, and 2 were browsers, despite carbon isotopes indicating that all 11 species consumed exclusively C_3 vegetation. Oxygen and nitrogen isotopes revealed further differences in their uptake of water or consumption of aquatic plants and lichens, indicating different dietary niches.

Analysis of mesowear and microwear is highly useful and complementary for assessing dietary signals (Hunter and Fortelius, 1994; Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Sewell et al., 2019). Mesowear, specifically the relative heights of the cusps, indicates the lifetime dietary signals and can be used to distinguish between grazers and browsers, while microwear provides dietary information specific to the weeks prior to death.

Incisor morphology in primates is also related to diet, with frugivorous species having relatively larger incisors than leaf-eating species, particularly marked when colobine monkeys are compared with cercopithecines, or gorillas to chimpanzees and orangutans (Deane, 2009). Frugivores and hard-object fruit-eaters possess more strongly curved incisors, both side to side and from top to bottom, while soft-object fruit-eaters have less-curved incisors and leaf-eating primates have the flattest incisors. This spectrum observed in extant primates appears like that seen in Miocene apes (Deane, 2009).

The relationship between primate microwear and food is based on the jaw mechanics and the angle of the upper and lower teeth, although microwear patterns for primates with a known diet of large hard objects are not diagnostic (Butler, 1952; Grine, 1981; Walker, 1981; Gordon, 1982, 1988; Teaford, 1994; Ungar, 1994, 2005, 2007). Numerous pits and scratches may reflect the ingestion of grit with the food, which in the case of herbivores is easily explained because their food is at ground level, but primate diets (fruits and seeds) are unlikely to be contaminated with grit. The heavy wear, thick enamel and abundance of pits on the teeth of some Miocene apes have been explained by their feeding on

hard objects, but a study by Lucas and colleagues (2013) suggests primate enamel wear shows minimal input from plant remains, even hard shells and seeds. However, microscopic dust particles ingested with food could cause, and alter, existing microwear features on primate teeth.

Community Paleoecology

Community measures of paleoecology take all species in the fauna into account, and measure their functional attributes across size, diet, and locomotion. These have been invaluable in African hominin paleohabitat studies (Reed, 1997; Bobe and Eck, 2001; de Ruiter et al., 2008a; Negash et al., Chapter 24, and references therein).

Species richness for a specific assemblage is referred to as alpha diversity (α-diversity), which is simply the number of species in an assemblage for a given time and place, while beta diversity is specific to the differences between fauna or floral species between sites, and gamma diversity refers to the species differences that can be observed when looking across geographic regions (Whittaker, 1960, 1972; Peet, 1974; Sepkowski, 1988). These diversity measures are dependent on several specific factors, such as time, surface area, and sampling strategies.

Beta diversity is important in fossil faunas that accumulate over time and from several disparate sources but is harder to measure. High turnover, which characterizes tropical savannas, could theoretically lead to disproportionately high diversity levels for time-averaged faunas. Fossil assemblages from sediments accumulating over thousands of years may be drawn from different parts of the environment, or the environment itself may have changed over time as a result of climatic or physical change. In all these cases, the level of species richness in a fossil assemblage may not be an accurate representation of any one environment in the past, and it may be difficult to compare with present-day richness figures, which are based on specific time and place data.

Levels of species richness are also directly related to area: for example, α-diversity scales to (area) 0.25 (Mares, 1992). South American present-day mammalian α-diversity appears to be lower in tropical lowland forests than in dryland habitats because they contain fewer species than dryland habitats (434 species against 509). However, the area occupied by the dryland habitats is almost double that of lowland forest, so that species richness per unit area is greater in the forest environments (Mares, 1992). For fossil faunas, however, there is often little information about the size of the area being sampled.

Fourth, the distribution of species within a fauna is another aspect of diversity, and is referred to as evenness (Tuomisto, 2012; Daly et al., 2018). This is a measure of equitability and it distinguishes between forest faunas, which have many mammal species all more or less abundant (more equable), and open grassland faunas, which are dominated by few species. The present-day mass herds of reindeer in the arctic tundra, bison in the American prairies, and wildebeest in the Serengeti plains are cases in point. Some living and fossil faunas are dominated by one or two species, while others have more or less equal numbers of individuals for most species.

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Finally, estimates of species richness are also affected by sampling problems, both for modern ecological communities and for fossil assemblages (e.g., Andrews, 1990). Ideally, the representation of animals or plants in a site is best shown both by the species present and by their abundances, but assessing abundances is affected by sample size, with larger samples showing higher numbers of species present. However, in fossil assemblages, sample size is often limited, and can affect how these patterns are interpreted within rare taxonomic groups, such as hominins (Hopley and Maxwell, Chapter 3; Maxwell et al., 2018).

Selective destruction of bones may occur both before and after fossilization. For example, at Laetoli, the rarity of hominin fossil remains has partly been attributed to taphonomic destruction by scavengers and slow accumulation rates of sediments, with bones left exposed on the ground surface (Harrison et al., Chapter 34; Su and Harrison, 2008). Bones from large-bodied species were exposed on the surface for longer and were therefore relatively rarely preserved in the sediments, while smaller mammal bones appear relatively more abundant due to quicker burial.

Most animal and plant taxa show diversity gradients, that is, changing numbers of species across space (and time in the case of fossil biota), and these have been interpreted in terms either of physico-chemical factors, such as latitude or climate, the heterogeneity of the habitat, or as a result of biological interactions such as competition or predation (Simpson, 1964; Kerr and Packer, 1997; Andrews and O'Brien, 2000, 2010; Willig et al., 2003).

Ecological diversity is based on convergence of adaptation in unrelated faunas and has been recognized since the time of Charles Darwin (1859). Convergent evolution results in the production of similar adaptations in phylogenetically distantly related organisms subject to similar agents of natural selection, although convergence is constrained by availability of genetic variability in the converging lineages and sufficient time for it to act (Harrison, 1962; Andrews et al., 1979; Dawkins, 1986). For example, in lowland tropical forests in Asia, America, and Africa, there are rodents with gliding (flying) adaptations belonging to different families, and anteaters in South America with similar adaptations to African anteaters (Myrmecophagidae and Tubulidentata, respectively) due to convergent evolution. Extending this to whole mammalian communities living in similar habitats, these tend to show similar adaptations despite having no species in common. Similarities in the fossil teeth morphology across communities can therefore be employed to reconstruct the community structure based on them, even if these groups are extinct, as in the case of Eocene adapiform primates (Seiffert et al., 2009). Interactions between flora and fauna can also be inferred, such as fruit production by plants and the radiations of rodents (hard fruits) and primates (soft fruits; Collinson and Hooker, 1991, 2003), or the relationships between spiny plants, and mammalian browsing (Charles-Dominique et al., 2016). Finally, Barr (2017) examined the relationship between bovid postcranial traits and vegetation in sub-Saharan Africa, which may be employed to infer environmental variables based on bovid fossils within an assemblage.

Some of the most informative studies have attempted to examine broader aspects of modern mammalian faunal communities and associate these to specific habitat types in the past (e.g., Reed, 1997, 1998, 2013; Faith, 2013; Andrews and Hixson, 2014 and references therein).

Conclusions

We have defined some key terms related to vegetation structure and presented a broad-brush review of approaches to past environments and paleoecology (e.g., Damuth et al., 1992; Bobe et al., 2007a; Reed, 2013). The chapters that follow make extensive use of these approaches and provide valuable examples of their application to our understanding of African paleoenvironments.

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