THE ROLE OF LANDSCAPES IN SHAPING HOMININ HABITATS IN AFRICA

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Abstract *Here I briefly review palaeoenvironmental evidence from sites repeatedly used by hominins in eastern and southern Africa, such as Sterkfontein (Cradle of Humankind, Gauteng, South Africa). Common 'mosaic' habitat reconstructions involve the presence of a lake or river setting, with a combination of forest or woodland with savannah grasslands in close spatial proximity. The Tectonic Landscape Model [Bailey et al. pp. 257-280 & Reynolds, et al., pp. 281-298 (JHE 60, 2011)], is a new hominin habitat model which explains why certain sites appeared to have been repeatedly used by our ancestors over millions of years. Specific geomorphological processes, such as tectonic faulting, would have created complex topography and thereby encouraged heterogeneous habitats to form, and sustained such features through time. The Plio-Pleistocene is characterised by several key climatic transitions that would have presented unique challenges for hominins and other fauna. Therefore, a more complete appreciation of how geomorphological processes affect landscapes, surface water and vegetation is critical to the characterisation of the hominin niche and also of the strategies employed by our ancestors to adapt to past climatic changes. Furthermore, the use of complex topography by hominins may explain aspects of their postcranial anatomy, diets and possible routes that they may have used to disperse to other regions.*
Keywords: *geomorphology, endemism, speciation, human evolution, Africa, Plio-Pleistocene.*

INTRODUCTION

Faunas are affected by landscapes in various ways and on a number of spatial and temporal scales. This is true also of human beings and their ancestors. Studies examining the role of landscape processes in shaping floral and faunal habitats and influencing evolutionary patterns over time are becoming more commonplace (Sepulchre et al., 2006; Trauth et al, 2010 Ashley et al., 2010; Bailey et al., 2011; Reynolds et al., 2011). Examining the role played by landscapes enables us to consider the following questions: How did habitats favoured by hominins promote their evolution of specific traits such as bipedality, tool use and larger brains? And to what extent did large-scale geomorphological processes influence the creation of the habitats sought out by hominins? And finally, do landscape processes create landscapes that modern man finds attractive?

This contribution focuses on the role played by landscape processes at different scales in shaping hominin habitats, and also creating opportunities for faunal populations to become separated and for speciation to occur over time. The first aspect is the role of geomorphological processes in creating 'mosaic' habitats, which are loosely defined as a lake, pan or river setting with gallery forest and patches of open savannah in close proximity. The Tectonic Landscape Model (Reynolds et al., 2011; Bailey et al., 2011) explains how specific geomorphological processes in the presence of ground water will create and maintain mosaic habitats for as long as the faults remain active (Reynolds et al., 2011). Here I discuss tectonic and faunal features from the site of Makapansgat (South Africa) to illustrate how the geomophololog and re-assessments of the faunal lists can be explained by the Tectonic Landscape Model, and how these types of data can be applied to other fossil sites.

The second aspect, which acts on far longer timescales (i.e. thousands and millions of years), is the role of landscape features in promoting speciation by acting as a vicariant agent, separating populations and allowing genetic divergence to occur. For this aspect, I use the example of the Eastern Arc Mountains in Kenya and Tanzania as a case study (Burgess, et al., 2007). A third aspect must be noted, that is the deliberate utilisation of landscape features for hunting purposes, specifically during the Later Stone Age. Evidence from Greece and Kenya show how humans successfully incorporated landscape features into their hunting strategies and patterns of land-use (Bailey et al., 1993; Marean, 1997). While the discussion of deliberate and tactical use of the landscape is well-known in military and hunting contexts, this use falls outside of the scope of the present paper.

Developments in remote sensing and satellite imagery during the 1970's and 1980's facilitated the recording and interpretation of landscape features. This, together with several landmark studies of how earthquakes deform the Earth's crust (e.g. King and Vita-Finzi, 1981) allowed scientists to understand how geomorphological changes affect landscapes at various scales. From there, this understanding of the dynamic interplay between faulting and human habitats could be extrapolated back into the past, as was done for Palaeolithic sites in Greece, such as Klithi (Bailey et al., 1993). Later, this essential understanding was reinterpreted for the australopithecine sites of eastern and southern Africa (Reynolds, et al., 2011). As well as creating attractive habitats for hominins, the use of tectonically altered landscapes may also explain the routes followed by hominins as they dispersed from Africa (Bailey et al., 2011).

METHODS

The theory underlying the landscape reconstruction in eastern and southern Africa follows different methodological rationales, and is discussed in depth in Bailey et al. (2011). The landscape features of South African sites are preserved by hard rocks and relatively low levels of tectonic activity and thus can be reconstructed within the present site locations, but the eastern African sites are in regions were erosion, faulting and volcanism destroy evidence of older landscapes. Landscapes in eastern Africa (such as sites in Ethiopia) are therefore reconstructed by the use of analogy with areas presently closer to the active Rift margin, which is where the ancient sites were located at the time of hominin habitation (Bailey, et al., 2011; Reynolds et al., 2011).

From a practical perspective, a combination of satellite images and digital elevation models are used to examine the landscape and interpret the salient features (e.g. Bailey et al., 2011). For example, images deriving from Landsat ETM (Enhanced Thematic Mapper) in different spectral colour bands which correspond to different features (such as different rocks or vegetation types) can be used. These images may be overlain with digital elevation models (DEMs), thereby creating composite images of the landscapes, the salient features of which are then interpreted (as in Figure 2a). Field work and visual inspection are used to validate these interpretations (Fig. 7. 2 b & c).

Examining the landscape uses combinations of satellite imaging methods and old-fashioned ground truthing to examine and understand the landscape on several spatial scales. Examining changes in the landscape over temporal scales partly involves the reinterpretation of faunal data recovered from previous excavations as a means to identify the types of landscape features (such as rocky cliffs and marshy areas) present at the sites during deposition (e.g. Reynolds et al., 2011).

Tectonically modified landscapes & creation of hominin habitats

Early publications on human evolution inferred that our ancestors left the forest and became bipedal in the African savannah. But from the 1970's onwards, palaeoenvironmental reconstructions pointed to the mosaic environment as an important habitat associated with hominins (Kingston, et al., 1994), and indicative of specific adaptations to mixed habitats and variable environments (e.g. Potts, 1998). 'Mosaic habitats' are loosely defined as a lake, pan or river setting with gallery forest and patches of open savannah in close proximity. The faunal assemblages of the majority of hominin sites in central, eastern and southern Africa show a combination of arboreal species, browsing and grazing species, along with certain aquatic animals, such as hippopotamus, crocodiles and otters, which are suggestive of these mixed habitats (e.g. Reynolds et al., 2011). A possible explanation could be time-averaging in the fossil record means that either fossils from wet, forested, climate phases are being mixed with species from separate, temporally distinct drier, more open grassland climatic episodes, making the habitats appear more mixed (heterogeneous) then they really were in the past. This explanation would imply that hominins were not adapted to live in variable habitats (sensu Potts, 1998).

An alternative explanation is the Tectonic Landscape Model, which explains how specific geomorphological processes in the presence of ground water will create and maintain mosaic habitats (Reynolds et al., 2011). Faulting can be of several different types, but in the cases of reverse and normal faulting, they create similar landscape features (Fig. 7.1a & b). Even in environments where there is no lake or river to begin with, tectonic activity can alter the drainage of the area to create surface water features where there were none before. Seeps and springs can form when faults intersect with the water-table (Reynolds, et al., 2011; Fig. 7.1a & b). A secondary effect of faulting is also the formation of grabens (a valley created by two parallel faults, such as the East African Rift Valley) and fault-bounded basins, which can then collect water that drains down from higher elevations, examples of which are the Olduvai Basin (Tanzania) and the Okavango Delta (Botswana). Fault-bounded basins can often host large, but shallow, seasonal lakes, such as the present-day lakes of Eyasi and Manyara (Tanzania). Shallow lakes with large surface areas are subject to high levels of evaporation, and are therefore often highly alkaline and saline. They do, however, create important and attractive habitats for bird and mammal faunas, such as flamingos.

In this way, faulting has the potential to transform a flat, relatively featureless landscape into one with cliffs and river gorges, water features, fertile sedimentary plains and uplifted, drier flank areas (Figure 1). This will increase the types of vegetation and fauna in a given region, and this effect can be seen in the high levels of biodiversity observed in the tectonically-controlled Okavango Delta (Botswana), or the Nylsvlei wetland (South Africa) for instance. This suite of landscape features will persist for as long as the fault motions continue. This effect will occur whether the tectonics are small, frequent motions, or large magnitude events which occur only very rarely (e.g. Bailey, et al., 2011).

Of particular interest is the creation of swampy, or marsh areas, a sign of disturbed drainage that signals tectonic alteration of the landscape. Swampy areas host high levels of biodiversity (for example, the Okavango Delta in Botswana) and are indicated in the fossil record by types of fauna unique to marshy habitats (discussed in Reynolds, et al., 2011). In sum, the tectonic alteration to a landscape creates zones of drier, uplifted savannah areas, with downdropped sedimented plains, steep cliffs and swampy areas; in short – habitat heterogeneity, or mosaic habitats. This type of habitat would meet the three essential habitat requirements of hominins, which are: 1) drinking water, 2) a range of vegetation zones for foraging and 3) places of refuge from predation, such as steep cliffs (Reynolds et al., 2011). Here I will summarise features from the South African site of Makapansgat to illustrate the geomopholology and re-assessments of the fauna and palaeoenvironmental reconstructions from these sites. Figure 2 shows the geomorphology of the Makapan Valley region and the cave sites, with the tectonically controlled Nylsvlei wetland indicated in Figure 2b). The river Nyl runs close to the fault location, which may indicate that tectonic activity is ongoing or that sediment from the east (left), is pushing the river course westwards (Bailey et al., 2011). There is a close agreement between present habitat heterogeneous conditions and those inferred from the fauna of Member 3 and 4 (Reynolds et al., 2011, and references therein).

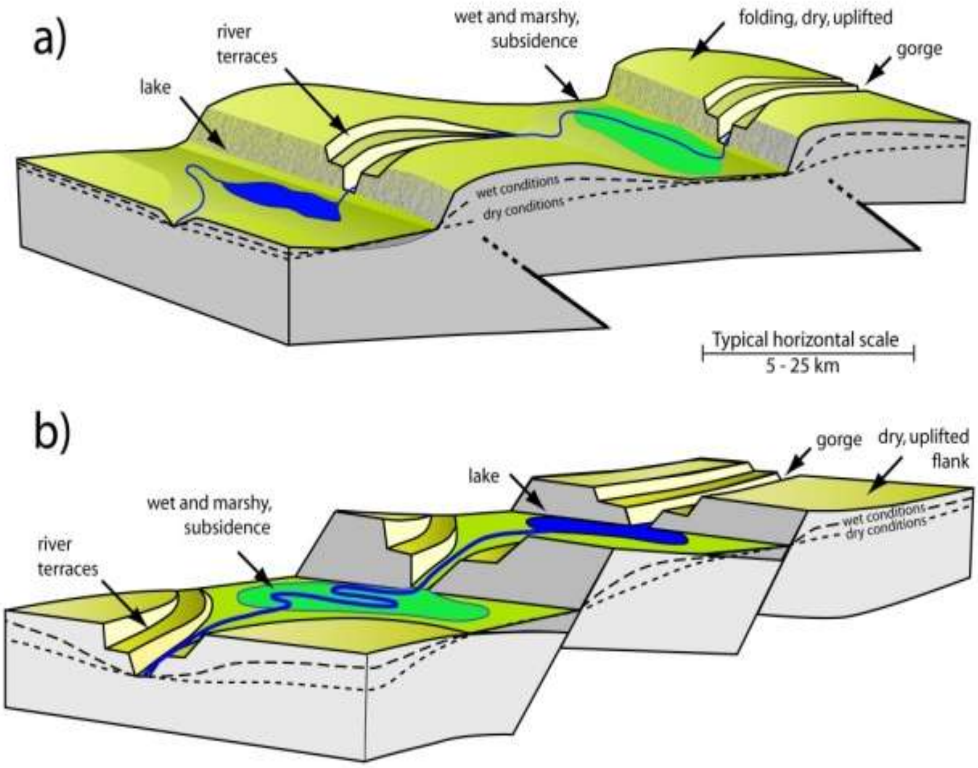


Fig. 7.1a & b. Tectonic Landscape Model (after Bailey et al., 2011; Reynolds et al., 2011) illustrating the range of landscape features and vegetation types that occur within a relatively restricted spatial area as a result of reverse (shown in 1a) and normal faulting (shown in 1b) in the presence of surface water

The high biodiversity of present and past species suggests that the wetland and rocky cliff areas were present during the time of hominin occupation, while studies of stable isotope of australopithecines from Limeworks Cave reveal a significant C4 (grass and sedge) signal, suggesting these vegetations were spatially accessible (Sponheimer and Lee-Thorp, 1999). The landscape evidence from Makapansgat shows the combination of features, such as the river and the sedimentary plains, which would have offered foraging areas close to the relative safety of the river gorges, caves, and the characteristic cliffs of the Makapan Valley (Fig7.2c).

Within the site region, there are also plains of varying sizes and wetlands within ranging distance of the valley itself. Presence of species such as the klipspringer (Oreotragus oreotragus) as well as several primate species indicates the presence of rocky outcrops and trees for these animals (Reynolds et al., 2011 and references therein). Similar landscape geomorphology and tectonic activity is also identified at the fossil sites of Taung and the Sterkfontein Valley (South Africa), suggesting that tectonic motions created attractive, heterogeneous habitats which Australopithecus most likely exploited preferentially (Bailey et al., 2001; Reynolds et al., 2011).

It is very likely that sites repeatedly occupied over longer timescales (such as Sterkfontein) were tectonically-altered, and that this maintained the suite of attractive features. Over longer timescales, other types of landscape changes have the potential to influence the genetic structure of populations, and this is dealt with in the next section.

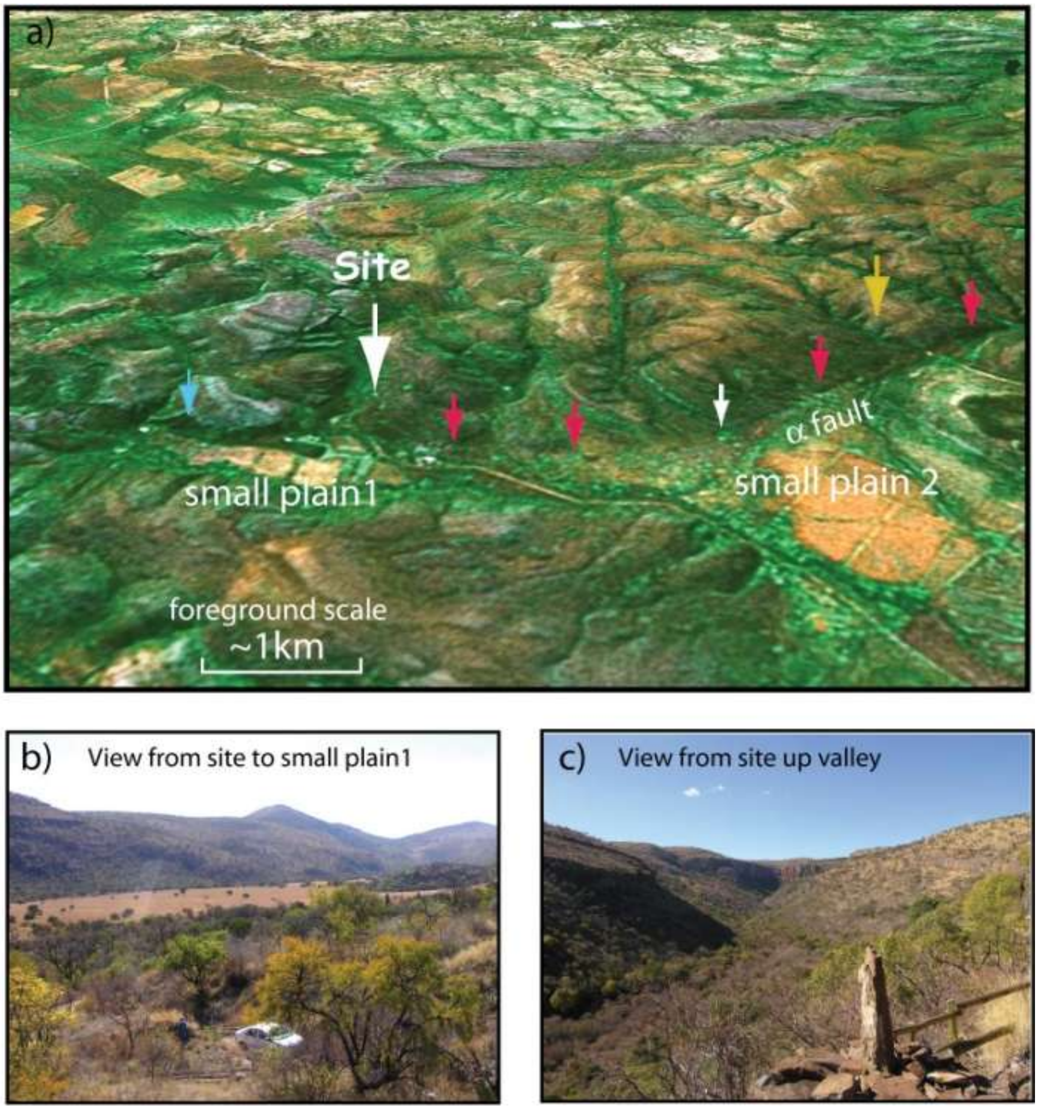
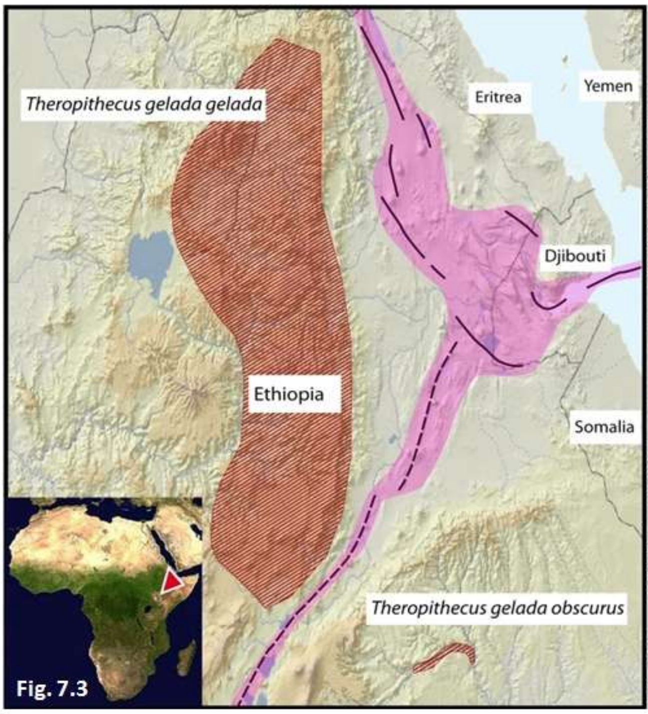


Fig.7. 2a-c). An interpreted landscape around the Makapansgat fossil site in South Africa illustrates how key landscape features attributed to tectonic activity can be identified within the site catchment area, specifically the sedimentary plains and rugged cliffs that are typically present in tectonically-altered landscapes. Observations of the key landscape features are made using Landsat enhanced thematic mapper (ETM) images overlain with digital elevation model (DEM) data (a) and visual inspection of key features on the ground (b, c) (after Bailey et al., 2011; Reynolds et al., 2011).

Influence of landscape changes on populations

Eastern Africa experiences high levels of geomorphological processes such as rifting, faulting and volcanism due to the splitting of the Nubian and Somalian plates. The distribution of species is affected by altering topography, altitude, and surface drainage.



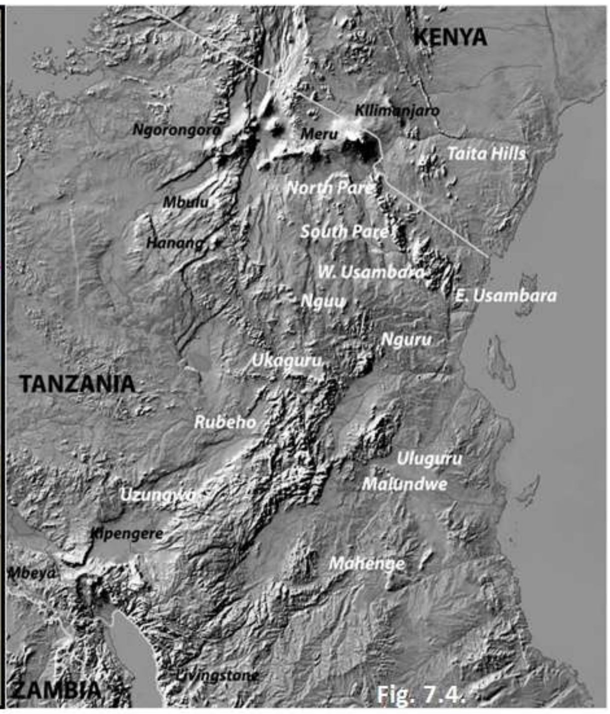


Fig.7.3. Influence of Rifting in Ethiopia. It has influenced the vicariance and genetic divergence within several species of vertebrates, including geladas (from Reynolds et al., 2011). Over time, the landscape geomorphological processes have significantly altered the genetic population structure of species living on the uplifted flanks of the Rift.
Fig.7.4. The Eastern Arc Mountains of Kenya and Tanzania illustrate the relationship between rough topography, climate change and endemism. The 13 mountain blocs which comprise the Eastern Arc range are labelled in white, while other important forested mountains are indicated in black

Tectonic activity can inhibit the movements of animals, by creating surface water features (such as rift and craterlakes) and landscape features such as steep fault scarps and lava flows. Large-scale climatic patterns can be mediated by these tectonically created lakes, as has been suggested for the so-called 'amplifier lakes' in eastern Africa (Trauth et al., 2010).

The overall effect of the geomorphological changes is that the physical location of habitats of plant and animal communities are altered, leading to habitat fragmentation, leading to population fragmentation. Populations subdivision is an important precursor to speciation, but when smaller, vulnerable species are further subdivided, the risks of inbreeding, disease and predation increase dramatically. Thus, areas where fragmentation and rates of endemicity are high are also at higher risks of extinction (e.g. Reynolds, 2007).

While changes in landscape geomorphology over time can have significant impacts on the populations, with long-term consequences for speciation and extinction, these effects have only recently become quantifiable by measuring levels of divergence across populations (e.g. chimpanzees; Eriksson et al., 2004; wildebeest; Arctander et al., 1999 and gelada baboons; Belay and Mori, 2006 among others).

Such studies clearly indicate that genetic structuring can be significantly altered by landscape factors, acting in concert with climatic changes. The most common effect of landscape changes on species is to separate populations, either completely or partially. This process, called vicariace, in turn can lead to speciation (e.g. Measey and Tolley, 2011). Obvious barriers to gene flow include deserts, mountain ranges and river courses. For example, the population genetic structure of the bonobo chimpanzees (Pan paniscus) in the Congo is affected by river flow, which separates populations from each other (Eriksson et al., 2004). In general, landscape vicariance can take several forms and act on widely differing spatial and temporal scales. Certain large-scale landscape changes dramatically alter almost every species living within the region. An excellent example of this is the uplift and spreading of the Rift, which has split populations of montane primates, bovids, and frogs with clearly identifiable genetic divergence in all cases (Fig. 7. 3).

Rift-splitting of populations have been documented in the gelada baboon subspecies (*Theropithecus gelada gelada* and *T. g. obscurus*), in the wildebeest (*Connochaetes taurinus*), and also in the African clawed frog (genus Xenopus, also known as the platanna), suggesting that this large-scale ecological pattern is likely to be identified from other species in future studies (Arctander et al., 1999; Belay and Mori, 2006; Evans et al., 2011; Reynolds et al., 2011). African clawed frog populations are estimated to have diverged approximately between 1-3.5 million years ago (Evans et al., 2011). Migration between flanks of the Rift appears to be limited because the floor of the Rift Valley is much drier and hotter than the prevalent conditions on the Ethiopian highlands, thus acting as a barrier between the two flanks (Evans et al., 2011).

In the contribution, I have outlined the Tectonic Landscape Model (Bailey, et al., 2011; Reynolds et al., 2011) and how this may explain why so many hominin sites appear to have been located in heterogeneous (i.e. mosaic) habitats. The Model explains how such habitats are created and sustained, and real-life examples of tectonically-controlled regions, such as the Okavango Delta illustrate that faulting can create areas of extremely high biodiversity (Ramberg, et al., 2006). These areas also offer a certain level of buffering against climatic aridification (Reynolds et al., 2011). The presence of sustained heterogeneous environments in specific areas may explain why certain archaeological sites are used only once, while others, such as Sterkfontein (South Africa) was repeatedly used by several species of hominins over millions of years (Reynolds, et al., 2011).

Finally, large-scale climatic changes act in concert with topography to fragment forest populations, such as the forest chameleons of the Eastern Arc Mountains of Kenya and Tanzania (genus Kinyongia; Measey and Tolley, 2011). Studies of the forest chameleon indicate that forested areas on the montane regions of the eastern Arc Mountains was stable over long timescales, but that Pleistocene drying fragmented these forest refugia. Forested mountaintops were isolated from each other by unforested, deep valleys which isolated the chameleon populations very effectively and leading to genetic divergence (Measey and Tolley, 2011).

The Eastern Arc Mountains are an excellent case study of an area with rough topography, high levels of endemism and also with high levels of endangered species. These are a chain of 13 mountain blocks in southern Kenya running into eastern Tanzania (Fig.7.4). This region has been highlighted as an important area of extremely high levels of endemism, i.e. containing species unique to this area (Burgess, et al., 2007, Measey and Tolley, 2011). So far, 96 endemic vertebrate species have been recorded, including four primate species. However, over 70 of these species are endangered, which underlines the close links between centres of endemism, fragmented populations and high risks of extinction (Burgess, et al., 2007; Reynolds, 2007).

DISCUSSION AND CONCLUSIONS

Military historians and hunters have always appreciated the tactical advantages of landscape features as lookout points or ambush locations. In human evolution studies, however, the role played by the landscape was largely overlooked in favour of the role played by vegetation and large-scale climate shifts as drivers of evolution and adaptation (e.g. de Menocal, 1995).

Therefore, a more complete appreciation of how geomorphological processes affect landscapes, surface water and vegetation is critical to the characterisation of the hominin niche and also of the strategies employed by our ancestors to adapt to past climatic changes. Over longer timescales, landscapes influence the fauna that inhibit them, causing vicariance and becoming centres of endemism, such as in the Eastern Arc Mountains of Tanzania and Kenya. However, the possibility of fragmenting populations also increases the risk of extinction. Thus, the study of the landscape can aid our understanding of how certain African regions have influenced the creation and preservation of biodiversity, both now, and in the past (Reynolds, 2007).

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