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Landscapes and their relation to hominin habitats: Case studies from *Australopithecus* sites in eastern and southern Africa

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ABSTRACT

We examine the links between geomorphological processes, specific landscape features, surface water drainage, and the creation of suitable habitats for hominins. The existence of mosaic (i.e., heterogeneous) habitats within hominin site landscape reconstructions is typically explained using models of the riverine and gallery forest settings, or the pan or lake setting. We propose a different model: the Tectonic Landscape Model (TLM), where tectonic faulting and volcanism disrupts existing pan or river settings at small-scales (~10–25 km). Our model encompasses the interpretation of the landscape features, the role of tectonics in creating these landscapes, and the implications for hominins. In particular, the model explains the underlying mechanism for the creation and maintenance of heterogeneous habitats in regions of active tectonics. We illustrate how areas with faulting and disturbed drainage patterns would have been attractive habitats for hominins, such as *Australopithecus*, and other fauna. Wetland areas are an important characteristic of surface water disturbance by fault activity; therefore we examine the tectonically-controlled Okavango Delta (Botswana) and the Nylsvley wetland (South Africa) as modern examples of how tectonics in a riverine setting significantly enhance the faunal and floral biodiversity. While tectonic landscapes may not have been the only type of attractive habitats to hominins, we propose a suite of landscape, faunal, and floral indicators, which when recovered together suggest that site environments may have been influenced by tectonic and/or volcanic activity while hominins were present. For the fossil sites, we interpret the faulting and landscapes around australopithecine-bearing sites of the Middle Awash (Ethiopia) and Makapansgat, Taung, and Sterkfontein (South Africa) to illustrate these relationships between landscape features and surface water bodies. Exploitation of tectonically active landscapes may explain why the paleoenvironmental signals, anatomy, diets, as well as the fauna associated with *Australopithecus* appear largely heterogeneous through time and space. This hypothesis is discussed in light of potential preservation and time-averaging effects which may affect patterns visible in the fossil record. The model, however, offers insight into the landscape processes of how such habitats are formed. The landscape features and range of habitat conditions, specifically the wetter, down-dropped plains and drier, uplifted flanks persist in close proximity for as long as the fault motion continues. The Tectonic Landscape Model provides an alternative explanation of why mixed habitats may be represented at certain sites over longer timescales.

Introduction

The effect of large-scale Pliocene climate shifts on vegetation changes and mammalian evolution has been used to construct a framework within which hominin evolutionary changes have been interpreted (deMenocal, 1995, 2004; deMenocal and Bloemendal, 1995; Vrba, 1995; Campisano and Feibel, 2007; Kingston et al., 2007;). A key part of this framework is the reconstruction of habitats at hominin sites, using both faunal and floral indicators (e.g., Vrba, 1982; Reed, 1997; Spencer, 1997; Bamford, 1999; Avery, 2001; Bobe and Eck, 2001; Bonnefille et al., 2004; Hernández-Fernández and Vrba, 2006; Reynolds, 2007). Reconstructions for hominin sites typically identify 'habitat mosaic' environments: lakeside or riverside gallery forest, with a close proximity to open grassland or woodland habitats. These features are used to reconstruct the likely landscape use by the hominins

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across their foraging range (e.g., Peters and Blumenschine, 1995; Blumenschine et al., 2003). Habitat reconstructions often mention the presence of certain physical landscape features, such as lakes and rivers, which are important determinants of the surrounding vegetation (e.g., Peters and O'Brien, 2001). We examine the landscape processes which create specific landscape features and habitats at the sites; in particular, we present illustrations of how geomorphological processes can create certain combinations of landscape and surface features. This in turn provides new perspectives on how habitats exploited by hominins may have originated and been sustained in specific regions.

Volcanism and tectonic faulting are two processes that act on landscapes in specific and predictable ways (Bailey et al., 2011) and can also indirectly enhance the habitat diversity of a region (Ramberg et al., 2006; Havenga et al., 2007). We use the wealth of site, habitat, and dietary reconstructions for the genus *Australopithecus* as a case-study to evaluate the possible impact of small-scale tectonics on landscapes and human evolution. *Australopithecus* is suitable for several reasons: 1) it is known from geographically and temporally widespread localities, which differ quite substantially in depositional contexts, geology, and the degrees of volcanism and tectonism (e.g., Partridge et al., 1995a, b), 2) *Australopithecus* paleoenvironmental reconstructions range from wooded, forested conditions to more open, grassland-dominated conditions, and also varying combinations of these habitat categories (e.g., Clarke and Tobias, 1995; Brunet et al., 1995; Reed, 1997; Bamford, 1999; Avery, 2001; Bonnefille et al., 2004), and finally 3) it is a relatively long-lived genus by hominin standards, spanning approximately two million years. The earliest occurrence is from Asa Issie, Ethiopia, dating to around 4.1. Ma (White et al., 2006), while the youngest *Australopithecus* dates to approximately 2.1 Ma from the upper Sterkfontein Member 4 of South African deposits (Partridge, 2005).

We assume that the site regions of Ethiopia and South Africa offered suitable habitats for *Australopithecus* at the time that they were present there, although the present-day landscapes of these regions differ from each other. Here we define 'suitable habitats' as comprising three basic elements, or resources: a range of C_4 and C_3 foods within foraging distance of the group, access to drinking water, and relatively safe sleeping and nesting areas or so-called 'predator refuge' opportunities (Durant, 1998). Even large modern primates such as gorillas and chimpanzees are vulnerable to predation by leopards (Hart, 2007), and hominins would have required strategies for avoiding predators. The use of cliffs for shelter and safety could have played an important role in reducing the risk of predation by large, cursorial predators. Several extant species utilize landscape features extensively for this reason (e.g., the gelada, *Theropithecus gelada*; Gippoliti and Hunter, 2008).

We investigate how geomorphological processes in eastern and southern Africa could have created homologous (or analogous) landscape features and habitats to accommodate hominins such as *Australopithecus*. To illustrate the models of the tectonically-altered landscape, we examine the site regions of Makapansgat, Taung, and the Sterkfontein Valley (South Africa) and compare these landscape features to our reconstructions of how Ethiopian fossil sites could have looked at the time of hominin occupation. We also discuss the advantages and disadvantages of using analogous sites closer to the Rift margin, rather than attempting to reconstruct the landscapes of the fossil sites in the Middle Awash in their present location and eroded condition (Bailey et al., 2011).

Australopithecus habitats and diets

Numerous studies have addressed the question of what types of habitats were preferred by hominins. A characteristic mix of environments is commonly identified from hominin sites across Africa and through time, from the site of Koro Toro, Chad (Brunet et al., 1995) to the latest site of upper Member 4 at Sterkfontein in South Africa (Bamford, 1999; Sponheimer and Lee-Thorp, 1999; Kuman and Clarke, 2000). Various paleoenvironmental proxies indicate a wide range of vegetation types, ranging from wooded, forested conditions to more open, grassland-dominated conditions at *Australopithecus*-bearing Members of Sterkfontein and Makapansgat (e.g., Wells and Cooke, 1956; Vrba, 1982; Cadman and Rayner, 1989; Rayner et al., 1993; Clarke and Tobias, 1995; Reed, 1997; Bamford, 1999; Avery, 2001). High resolution palynological studies from Hadar (Ethiopia) show that *Australopithecus afarensis* is associated with a range of habitats, including forest and grassland, between 3.4–2.9 million years ago (Bonnefille et al., 2004). Studies of *Australopithecus* microwear from a large geographic sample of *Australopithecus* (referred to *Praeanthropus afarensis*) in eastern Africa indicate a stable but varied diet through space and time (Grine et al., 2006), while stable carbon isotopes from *Australopithecus africanus* enamel at Sterkfontein Member 4 suggest that variable proportions of C_3 and C_4 foods were consumed (van der Merwe et al., 2003). The range of habitats have led authors to suggest that *Australopithecus* may have been a eurotypic genus capable of surviving in a range of different habitats (Potts, 1996, 1998) or that certain *Australopithecus* species were adapted to specific local niches. We approach the vegetation question from the known landscape processes of that region and the effect these would have had on habitat diversity.

Examining the landscapes around hominin sites

This study focuses on four *Australopithecus*-bearing sites and their surrounding regions, specifically Makapansgat, Taung, and Sterkfontein (South Africa) and the Middle Awash region (Ethiopia), as specific examples of how landscapes can be modified by tectonic activity, and the implications of these processes for habitat creation. But before this, we must address a series of potentially confounding issues:

1) What did these ancient sites look like at the time that hominins were present?
2) Are the distributions of *Australopithecus* sites in Africa a pattern created by preferential preservation and intensive prospection in certain regions for hominins and other fossils?
3) Did sites possess suitable habitats, or were australopithecines more prone to die there?
4) How would time-averaging and large-scale climate shifts affect our ability to see evidence of tectonically- controlled environments in the fossil record?
5) How does the Tectonic Landscape Model apply more broadly to other *Australopithecus* sites which we do not directly address here?

Hominin landscape site models

We consider three simple landscape models of the regions around *Australopithecus*-bearing sites and the abilities of each to meet the suitable habitat requirements of *Australopithecus* (Fig. 1). As general landscape models, however, they cannot represent all possible combinations of landscape features at every fossil locality. Each scenario offers suitable habitat opportunities, but the first two landscape models have very little variable surface topography and are profoundly influenced by the level of the water table, and this in turn is affected by large-scale climate changes (deMenocal, 1995,