



Hominin home ranges and habitat variability: Exploring modern African analogues using remote sensing



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ARTICLE INFO

Article history:

Received 17 December 2015

Received in revised form 9 June 2016

Accepted 26 June 2016

Available online xxxx

Keywords:

Human evolution

Landscape

Savannah

Africa

Landsat

Pedogenic carbonate

Fraction of woody cover

ABSTRACT

The palaeoanthropological literature contains numerous examples of putative home range sizes associated with various hominin species. However, the resolution of the palaeoenvironmental record seldom allows the quantitative analysis of the effects of different range sizes on access to different habitat types and resources. Here we develop a novel approach of using remote sensing data of modern African vegetation as an analogue for past hominin habitats, and examine the effects of different range sizes on the access to habitat types. We show that when the location of the ranges are chosen randomly then the number of habitat types within a range is surprisingly scale invariant – that is increasing range size makes only a very modest difference to the number of habitat types within an estimated hominin home range. However, when transects are placed perpendicular to a water body (such as a lake or river bank) it is apparent that the greatest number of habitats are seen near water bodies, and decline with distance. This suggests additional advantages to living by freshwater other than the obvious one associated with access to drinking water, and may indicate that the finding of hominins in fluvial and lacustrine deposits is not simply a taphonomic issue. Comparison of the distribution of modern canopy cover with the fraction of woody canopy cover (f_{wc}) calculated from fossil pedogenic carbonate stable isotopes also suggests that closed woodland may be under-represented at fossil sites.

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1. Introduction

In the nineteenth and early twentieth century relatively little emphasis was given to the environmental context in studies of human evolution – this started to change in the 1930's around the time of the 'evolutionary synthesis' (Bowler, 1986). While there is now some consensus in the literature that many early hominins in Africa lived in mosaic habitats (see Reynolds et al. (2015) for a review and history of this terminology), little work has been undertaken on how variable habitats might have been within hominin home ranges. While site-level analyses can produce highly detailed results (e.g. Kroll and Isaac, 1984; Magill et al., 2016), and analyses integrating climate and palaeoproxies have been undertaken at a continental scale (e.g. Blome et al., 2012), very little detailed landscape reconstruction has been attempted at the level of individual hominins or their social groups. Here we take a novel approach to hominin spatial ecology by using remote sensing to quantify patterns in the vegetation of modern Africa at hominin-relevant scales, to examine the distribution and habitat variability that may have been encountered in the past. Such an approach has the obvious disadvantage of characterising the modern vegetation,

rather than the vegetation at the time of interest for any given past hominin species. However, it does allow variation to be quantified at a far greater spatial and narrower temporal scale than is possible based on palaeoenvironmental proxies such as pollen, pedogenic carbonate analysis or phytoliths (although these can be incorporated, see below), or from traditional field-based approaches. We explore these advantages here, using data from seven separate regions of sub-Saharan Africa to quantify habitat variability at a variety of hominin-relevant scales.

We are particularly considering the range sizes and habitat variability associated with various species of *Australopithecus* and early *Homo*, although the methods are equally applicable to earlier and later hominin taxa. While it is obvious that hominins lived on and within the landscape, we have few tools at our disposal to examine exactly how different habitat types may have influenced their movements. Suggested key characteristics are the presence of water (Ashley et al., 2009; Finlayson, 2014; Quinn et al., 2013), trees for shade (Habermann et al., 2016), and river cobbles or rock outcrops for tool making (Harmand, 2009). It is rare, however, to have stone tools or cutmarked bones directly associated with palaeoenvironmental proxies that can be used to reconstruct that exact location (although FLK Zinj may be a notable exception, Magill et al., 2016). Rather than seeking to reconstruct a particular place at a specific point in time (which can usually only be

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achieved on a scale of tens to hundreds of metres, rather than the kilometres that hominins are likely to have ranged), we are examining vegetation at a larger scale to look for physical patterns – such as the number of different habitat types a hominin may have encountered in a daily round, or even within their lifetime. If the presence of a number of different habitat types such as trees, bushes, water, swamp or bare rock was important to hominins, then we can examine how likely it is that such variability would have been encountered on a regular basis or at specific locations (such as riversides) using vegetation classifications derived from modern remote sensing.

This new approach allows us to consider, for measures identified in the fossil record (e.g. % canopy cover, Cerling et al., 2011; Quinn et al., 2013) and vegetation patchiness (i.e. 'mosaic' habitats), how the land cover in modern Africa varies on a number of hominin-relevant scales. Questions such as 'how many vegetation types would typically be found within the putative range size of a given hominin species?' and 'how does this number vary as range size increases (or decreases)?'. In this paper we set out the basic ideas of this approach – which is intended to be complimentary to, rather than replacing, existing ways of addressing these questions. We use our data to address two specific points:

- 1) We look at randomly placed home ranges and calculate land cover within them. This allows us to quantify the effect of increasing range size on access to different vegetation types.
- 2) We focus on water, and examine how land cover and patchiness change as one moves away from water sources.

Note that we are not attempting to reconstruct past environments, rather quantifying the landscape as it is today (with adjustment for anthropogenic change, see Methods) and using this as a surrogate for the unquantifiable spatial variation of the past. We also provide, as an illustrative example of the ways in which this approach could be developed, a brief case study which compares data from our analysis with data gained from pedogenic carbonates from East African hominin localities.

1.1. Home ranges

A home range may be defined as a circumscribed area in which an individual spends much of its life, and contains the requisite resources (food, water, shelter and conspecifics to mate with) (Barnard, 1999). This is somewhat different to a territory, which is the section of a home range that is actively defended (Manning and Dawkins, 2012). A territory may cover the entire home range or be restricted to around a particular resource, such as nesting site. Barnard (1999) points out that home range size is not always easy to quantify for extant animals, and it is even harder to infer for extinct taxa. However, there are some general rules that can be applied; for example, home range size (or feeding territory size) tends to be scaled with body mass (Clutton-Brock and Harvey, 1984). This is unsurprising as not only do larger animals require more physical space but they also require more food than smaller animals (McNab, 2012).

Following from these patterns established for extant species, for hominins an increase in range size has been inferred from increasing carnivory (Foley, 2001), a direct result of increasing body size and dietary quality (Leonard and Robertson, 2000, and see below). However, it has proved difficult to gain accurate estimates of home range size, even using modern isotopic techniques (e.g. Copeland et al., 2011), so we have used a variety of measures based on archaeological information and estimates based on data from extant human groups or other animals.

2. Methods

2.1. Calculating landcover

To quantify land cover heterogeneity in a variety of modern African landscapes, we analysed seven Landsat ETM+ satellite image pairs

ranging in latitude from Ethiopia to South Africa, and in habitat types from forest to semi-desert (Fig. 1). These were chosen from a larger study of sub-Saharan Africa land cover, in which sites were selected randomly and from these we chose seven sites that we considered representative of the main habitats and geographical locations most often discussed in studies of early human evolution in Africa.

Due to the highly seasonal nature of many African landscapes as a result of climate and rainfall patterns, both wet and dry season Landsat ETM+ satellite imagery was used in combination to generate a single land cover classification for each study area. This enabled land cover classes present, or only able to be discriminated, at certain times of the year (such as seasonal water) to be identified. A number of image pre-processing steps were performed on the images using ERDAS IMAGINE 2010 to ensure data quality was maintained. These included: error detection and recording; cloud and cloud shadow masking; image geometric accuracy checking; atmospheric correction; and finally compositing the wet and dry season images into a single dual-date composite image (Morton et al., 2011). For both the wet and dry season Landsat ETM+ images spectral bands 1 (0.45–0.52 μm wavelength), 2 (0.52–0.60 μm), 3 (0.63–0.69 μm), 4 (0.77–0.90 μm), 5 (1.55–1.75 μm) and 7 (2.09–2.35 μm) were used to enable characterisation of the varying wavelength-dependent spectral response of land surface features. Band 6 (thermal, 10.40–12.5 μm) was used only during the cloud masking stage, and was not included in the final composited image. The composite images were projected in the Universal Transverse Mercator (UTM) WGS84 coordinate system.

An unsupervised pixel-based classification technique with post-classification refinement was used to generate land cover maps of the study areas. Unsupervised classification algorithms aggregate all pixels within an image into groupings based on the spectral characteristics of those pixels, with the clustering process controlled by predetermined parameters for numbers of iterations and classes generated (Loveland and Belward, 1997). Unsupervised classification techniques are well established for land cover mapping applications, and have been used in the production of regional and global land cover maps (Loveland et al., 2000; McGwire et al., 1992; Fleischmann and Walsh, 1991). An unsupervised classification generating 75 spectral classes was produced for the composite image using the Iterative Self-Organising Data Analysis Technique (ISODATA) (Bezdek, 1973). This large number of classes was used to minimise the problem of split land cover class spectral clusters (Homer et al., 1997; Wayman et al., 2001).

High-resolution satellite imagery of the study areas available via public portals such as Google Earth were used as a reference to enable the unsupervised spectral classes to be assigned specific land cover class labels (Loveland et al., 2000; Juang et al., 2004; Cihlar, 2000) corresponding to the project classification nomenclature in Table 1. Additionally, field surveys conducted in the Kruger National Park, South Africa (shown as area F in Fig. 1), in July 2014 involved further identification of ground truthing locations of known land cover types for validation of the classification generated at this site. This field data was combined with the high resolution imagery-derived validation data and showed good congruence between methodologies (data not shown), however given the logistical challenges of collecting ground truthing data over such broad geographical areas, high resolution reference imagery provided the sole source of validation data for the other sites. The classification nomenclature used was designed to be applied broadly across sub-Saharan Africa and was based on a modified version of the Global Land Cover 2000 Land Cover Map of Africa classification system (Mayaux et al., 2003). Our classification also pays special attention to the forest – grassland gradient, and follows the approach of Torello-Raventos et al. (2013) which stratified this gradient into five forest to grassland categories at 25% intervals (100–75%, 75–50%, 50–25%, 25–5% and 5–0%). We have amalgamated the latter two categories to form a 25–0% canopy grouping. The generated classification maintained the 30 m spatial resolution of the input Landsat ETM+ imagery.

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