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Stable isotope ecology of Cape dune mole-rats (*Bathyergus suillus*) from Elandsfontein, South Africa: Implications for C_4 vegetation and hominin paleobiology in the Cape Floral Region

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The archaeological and paleontological records from the west coast of South Africa have potential to provide insights into ecosystem dynamics in the region during the mid-Pleistocene. Although the fossil record suggests an ecosystem quite different than that of the region today, we understand little about the ecological factors that contributed to this disparity. The site of Elandsfontein (EFT) dates to between 1.0 and 0.6 million years ago (Ma), preserves *in situ* lithic and faunal materials found in direct association with each other, and provides the rare opportunity to examine the relationship between hominin behavioral variability and landscape heterogeneity in a winter rainfall ecosystem. In this study, we examine the stable carbon isotopic composition of a large sample ($n = 81$) of Cape dune mole-rats (*Bathyergus suillus*) and contemporaneous large mammals (>6 kg; $n = 194$) from EFT. We find that $\delta^{13}C$ values of *B. suillus* are significantly different to those of contemporaneous large mammals from EFT indicating a significant presence of plants utilizing the C_4 photosynthetic pathway during the mid-Pleistocene, in contrast to present C_3 dominated ecosystems along the west coast of South Africa. Additionally, we find that artifact density at EFT localities is positively correlated with $\delta^{13}C$ values in *B. suillus* enamel suggesting that evidence of more intense hominin occupation may be associated with the presence of more C_4 vegetation. Lastly, we hypothesize that this unique distribution of vegetation 1) provided abundant resources for both hominin and non-hominin taxa and 2) may have concentrated hominin and animal behavior in certain places on the ancient landscape.

1. Introduction

1.1. Southern African paleoecosystems

Differing combinations of climatological factors influence ecosystem dynamics in eastern and southern Africa. As a result, placing the rich Quaternary fossil records of these two regions within a resolute ecological framework requires the integration of marine and terrestrial proxies reflective of a variety of spatial and temporal scales (deMenocal, 2004; Bobe and Behrensmeyer, 2004; Behrensmeyer, 2006; Behrensmeyer and Reed, 2013). The last 1 million years of the African fossil record is particularly interesting because it witnesses many important shifts in mammal clades (Vrba, 1995; Faith, 2011; Patterson et al., 2014), as well as the blossoming of what many consider the behavioral repertoire of modern humans (McBrearty and Brooks, 2000; Marean et al., 2007). Although the integration of high-resolution paleoecological data has proved successful at many eastern African localities (Potts, 1998; Tryon et al., 2014, 2015; Faith et al., 2015), much less is understood about ecosystems and faunal communities in southern Africa during a critical time period in mammalian evolution. As a result, extrapolating the paleoenvironmental conditions of eastern Africa to concurrent time periods in southern Africa has been especially challenging (Patterson et al., 2014).

In southern Africa, differences in the seasonal distribution of precipitation are largely responsible for the geographic distribution of vegetation (Chase and Meadows, 2007). In the summer rainfall zone (SRZ), the majority of precipitation falls between October and March. In contrast,

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the winter rainfall zone (WRZ), a narrow band incorporating the western and part of the southern coasts, receives the majority of its rainfall between April and September (Fig. 1). Between these two regions is the year-round rainfall zone (YRZ) that receives rainfall throughout the year. Although the extent of these zones is clearly discernable in contemporary southern Africa, their distribution over the past million years is far from understood. It is, however, becoming increasingly clear that oscillations in atmospheric and oceanic circulation as well as glacial and interglacial cycles affected the location, duration and intensity of rainfall in these regions during the Quaternary (Chase and Meadows, 2007).

The relationship between precipitation and vegetation in southern Africa is most evident in the distribution of plants utilizing the C_3 and C_4 photosynthetic pathways. Globally, C_4 plants are adapted to low- to mid-elevation tropical systems with high temperatures and warm season precipitation, while C_3 plants are dominant in regions of higher elevation with lower temperatures and cool season precipitation (Tieszen et al., 1979; Ehleringer et al., 1997). In the SRZ, C_4 plants dominate plant communities (Vogel et al., 1978; Rebelo et al., 2006; Radloff, 2008). In the WRZ, however, with the exception of a few common plant communities (e.g., strandveld, renosterveld) that contain species that utilize the C_4 pathway, C_3 vegetation dominates in the form of the low-height, shrubby, fire-adapted fynbos (Cowling, 1992). This unique vegetation system primarily within the WRZ, classified as the Cape Floral Region (CFR), is host to nearly 9000 plant species, a majority (69%) of which are endemic (Cowling, 1992; Cowling and Lombard, 2002; Goldblatt and Manning, 2002; see Marean, 2010 for summary). Within the CFR, differences in the proportion of C_3 and C_4 vegetation are primarily related to the relative abundance of C_3 and C_4 grasses (Bar-Matthews et al., 2010). C_3 grasses are the most common grasses in the WRZ, while the YRZ contains a mixture of C_3 and C_4 grasses. In the SRZ, C_4 grasses are more abundant. The vegetative diversity within the CFR is not mirrored in mammalian diversity (Klein, 1983). Due to the dominance of nutrient-poor fynbos vegetation, the contemporary CFR does not support a sizable community of large-bodied grazing and browsing ungulates, but rather is dominated by small-bodied, browsing taxa (Skead, 1980; Klein, 1983).

Although C_3 plants are present in high frequencies in the modern vegetative communities in the CFR (Cowling, 1992), this may not always have been the case. The timing and underlying climatological drivers of plant distributions in the CFR remain enigmatic. Marine records from the region beginning in the Miocene indicate an overall increase in aridity with multiple phases of vegetation change alongside relative stability in moisture availability (Maslin et al., 2012; Hoetzel et al., 2013, 2015). More recent stable carbon isotopic analyses of mammalian enamel suggest the presence of C_4 vegetation in the CFR during certain periods of the Quaternary (Luyt et al., 2000; Hare and Sealy, 2013). Much like elsewhere on the African continent, however, the integration of C_4 vegetation into the CFR plant biome would have likely been highly heterogeneous within a C_3 dominated system (Feakins et al., 2013). This scenario is supported by the lack of evidence for C_4 grasses at Langebaanweg approximately 5 Ma (Ma = million years ago; Franz-Odendall et al., 2002; Rossouw et al., 2009), and evidence of their presence at younger sites of Elandsfontein (Luyt et al., 2000) and Hoedjiespunt (Hare and Sealy, 2013) dating to approximately 1.0–0.6 Ma and 0.35–0.25 Ma respectively. Thus, although these data

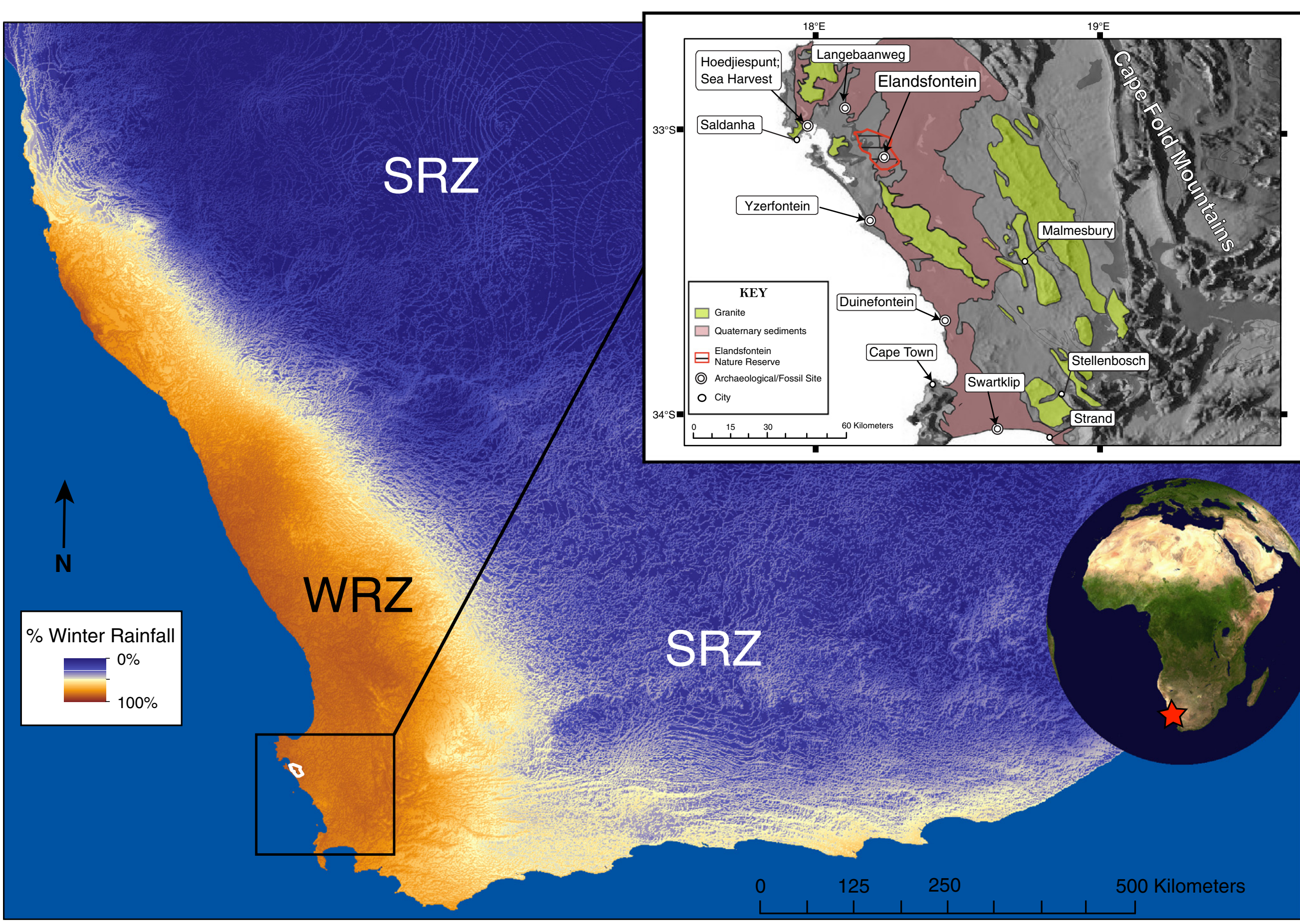

Fig. 1. Modern rainfall seasonality in southern Africa. Inset: location of Elandsfontein (EFT) and other important archaeological locations along the west coast of southern Africa (rainfall data: www.worldclim.org; Inset: modified from Braun et al., 2013a).

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