



Small mammal insectivore stable carbon isotope compositions as habitat proxies in a South African savanna ecosystem



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ABSTRACT

Carbon isotope analysis of fossil micromammalian insectivores holds promise for resolving questions about past environments because these animals have restricted home ranges and are generalist feeders. Thus, their diets likely integrate ecological information about local habitats. In this study, we assessed the degree to which carbon isotope compositions of three sympatric shrew species record spatial changes in habitat in a mosaic southern African savanna environment. Sampling sites were located within 2 km of one another, and microhabitat conditions ranged from very open (<5% canopy cover) to wooded (~60% canopy cover). We compared shrew hair $\delta^{13}\text{C}$ values between microhabitat types, and across taxa, in order to test whether these data follow predictable patterns based on local vegetation.

Shrew carbon isotope compositions varied with habitat in a predictable manner within our study area. While taxonomy also influenced $\delta^{13}\text{C}$ values, this was largely due to differences in habitat preferences of individual taxa and the resultant variation in their relative abundance within each environment. Isotopic differences between habitat types were preserved within taxa where taxa occurred in multiple habitats. To complement this modern study, we performed isotopic analysis of the enamel of insect-eating fossil micromammals from the hominin sites Gladysvale and Sterkfontein in the Cradle of Humankind, South Africa. This subset of fossil micromammals consumed primarily C_4 -derived carbon.

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1. Introduction

Understanding the environmental context of hominin evolution is a primary focus of paleoanthropological research (e.g. Dart, 1925; Vrba, 1975, 1985, 1988; Reed, 1997; Potts, 1998, 2013; Bobe et al., 2002; Bonnefille et al., 2004; Kingston, 2007; Maslin et al., 2015). Though complicated and not unidirectional, there is strong evidence that during the Plio-Pleistocene, large-scale tectonic and climatic shifts influenced African ecosystems, driving the expansion of open environments at the expense of forested habitats (Vrba, 1975; deMenocal, 1995, 2004; Reed, 1997; Potts, 1998; Trauth et al., 2003, 2005, 2007, 2009; Kingston, 2007; Maslin and Christensen, 2007; Maslin and Trauth, 2009; Reed et al., 2014; Maslin et al., 2015). Against this larger backdrop of continental change, a wide diversity of mosaic habitats emerged that

many believe played an important role in hominin evolution (Domínguez-Rodrigo, 2014; Reynolds et al., 2015).

Carbon isotopic analysis of paleosol carbonates is a well-established tool in paleoenvironmental reconstruction (Cerling, 1992, 1999; Cerling and Hay, 1986; Cerling et al., 1989, 1991, 1997, 2011; Levin et al., 2008, 2011; Ségalen et al., 2007; Sikes, 1994, 1995; Wynn, 2000, 2004). Such analyses are based upon the different photosynthetic pathways used by most trees, shrubs and forbs (C_3 plants) and tropical grasses and sedges (C_4 plants). Plants using C_3 photosynthesis discriminate against ^{13}C resulting in a lower ratio of ^{13}C to ^{12}C in plant tissue relative to that of atmospheric CO_2 . C_4 plants discriminate less against ^{13}C , and therefore exhibit a relatively higher ratio of ^{13}C to ^{12}C . This differential discrimination results in distinct, non-overlapping carbon isotope distributions across the two types of plants (Smith and Epstein, 1971). Carbon isotopes are of particular utility in the savannas of Africa, where the landscape consists of a mix of C_3 and C_4 vegetation, distributed across the two major functional vegetation types in savanna environments

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(C₃ trees and shrubs; C₄ grasses). The carbon isotopic composition of paleosol carbonates reflects that of vegetation growing in soil during the time of soil formation (Cerling, 1984, 1999; Cerling et al., 1989, 1991; Quade et al., 1989; Cerling and Quade, 1993).

The carbon isotopic compositions of foods are incorporated into the tissues (e.g. bone, hair, enamel) of the animals that eat them (DeNiro and Epstein, 1978; Vogel, 1978; Cerling and Harris, 1999). Thus, the ratio of ¹³C/¹²C in body tissues reveals information about the relative contribution of C₃ and C₄ foods to the diet. For example, isotopic differences in tissue composition have been used to discriminate grazing (C₄ consuming), browsing (C₃ consuming), and mixed-feeding (mixed C₃/C₄ consuming) herbivores in both modern and fossil assemblages (Ambrose and DeNiro, 1986; Koch et al., 1994; Koch, 1998; Cerling and Harris, 1999; Zazzo et al., 2000; Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003; Cerling et al., 2003; Kingston and Harrison, 2007; Lee-Thorp et al., 2007; Levin et al., 2008; Bedaso et al., 2010, 2013). Diet, in turn, reveals information about habitat since an animal can only consume what is available in its environment. For example, if C₄ grasses heavily dominate a landscape, and C₃ resources are rare, it is likely that many animals foraging in that environment will consume C₄ foods given that they are the most abundant and readily available resource. Thus, by using carbon isotope analysis to reconstruct the diets of communities of herbivores, one can make inferences about the dominant vegetation on a given landscape.

Carbon isotope analyses of tooth enamel have been widely employed by paleoanthropologists to understand past habitats (Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003; Kingston and Harrison, 2007; Lee-Thorp et al., 2007; Levin et al., 2008; Bedaso et al., 2010, 2013). Such studies use a variety of analytical approaches based on both intra-specific comparisons (e.g., within Bovidae) (Sponheimer, 1999; Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003) and comparisons across multiple taxonomic groups, specific dietary guilds, and whole ecological communities (Zazzo et al., 2000; Kingston and Harrison, 2007; Levin et al., 2008; Sponheimer and Lee-Thorp, 2009; Bedaso et al., 2010, 2013). These studies use $\delta^{13}\text{C}$ values to determine percentages of dietary categories (e.g., C₃ consumers, C₄ consumers) within assemblages (Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003; Lee-Thorp et al., 2007), or use $\delta^{13}\text{C}$ distribution or summary data for a site to compare with other modern or fossil datasets (Kingston and Harrison, 2007; Levin et al., 2008; Sponheimer and Lee-Thorp, 2009), while some incorporate relative abundance data or biomass calculations (Luyt and Lee-Thorp, 2003; Sponheimer and Lee-Thorp, 2003, 2009; Lee-Thorp et al., 2007; Bedaso et al., 2010, 2013).

In practice, it is usually not difficult to distinguish C₃ forests from environments where C₄ grasses are present (Ambrose and DeNiro, 1986; Cerling et al., 2003; MacFadden and Higgins, 2004). Such environments range from woodland with some grass to treeless grassland, but using carbon isotopes to reconstruct specific habitats within this broad range of environments is complex (Sponheimer and Lee-Thorp, 2009). Such reconstructions are limited by a poor understanding of how carbon isotopes are distributed in modern foodwebs, both at the level of the individual species and at the community level (Gannes et al., 1997; Codron et al., 2007b). For instance, how do we quantify the difference between “wooded grassland” and “grassland” (sensu Reed et al., 2013)? What differences should be manifest isotopically in environments with 10%, 25%, or 50% tree cover? These distinctions are important because all African ecosystems associated with fossil hominins contain a mix of C₃ and C₄ vegetation, and are often generalized as mosaics, although the relative abundance of C₃ and C₄ plants, as well as the nature and distribution of plant types at many sites, are heavily debated (Reynolds et al., 2015). The consensus in the field is that mosaic habitats require better characterization and more detailed study in modern contexts to evaluate their role in hominin evolution (Reynolds et al., 2015).

So how do we improve our understanding of carbon isotope distributions across modern African habitats? Since it is often impractical to

sample an entire ecological community, much less incorporate data on the relative abundance of each taxon (especially given taphonomic considerations in fossil assemblages), an ideal approach would be to identify a reliable isotopic ecological “integrator” – an organism whose isotopic signature accurately and consistently reflects the actual proportion of C₃ and C₄ vegetation in its habitat. This could be achieved by looking for taxa that are highly opportunistic, eclectic feeders that shift their diets in response to their ecological setting. Isotopically, most individual species are relatively poor indicators of environmental characteristics. Most African bovids are C₃ or C₄ specialists and maintain their specialized diets in heterogeneous environments (Sponheimer et al., 2003a; Cerling et al., 2003). Even flexible, generalist herbivores do not seem to reliably record environmental characteristics isotopically, instead tending to browse or graze preferentially. For instance, both nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*) are classified as “mixed-feeders”, yet the former prefers browse and the latter grass (Codron et al., 2007b). Similarly, the diets of mixed-feeding African elephants (*Loxodonta africana*) do not always accurately reflect regional differences in grass biomass, tree density, or canopy cover (Koch et al., 1995; Codron et al., 2006, 2011). Even most rodents, which are widely considered generalist feeders, were not found to change their diets across different habitats within a savanna environment (Codron et al., 2015).

Traditionally, organisms at lower trophic levels, such as herbivores, have been used to make inferences about habitat under the assumption that their direct interaction with vegetation reflects the distribution of C₃ and C₄ resources on a landscape. However, it has been suggested that organisms at higher trophic levels might actually better reflect overall environmental characteristics by acting as ecological integrators, concentrating signals from multiple variable sources and averaging inputs from lower trophic levels through space and time (de Ruiter et al., 2005). Many carnivores are opportunistic dietary generalists, and select their prey primarily on the basis of body size, abundance, and availability (Vézina, 1985; Murray et al., 1994; Radloff and du Toit, 2004; Hayward and Kerley, 2008), all variables that are intrinsically linked to habitat. Isotopic sampling of predators increases effective “sample size” because predators integrate the tissues of multiple herbivore species which themselves consume many different primary producers (Bump et al., 2007).

The argument that predators can serve as isotopic integrators has been tentatively supported by data from fossil carnivores (Lee-Thorp et al., 2000, 2007; Bump et al., 2007; Hopley and Maslin, 2010). The idea has not been well tested in the context of modern isotopic ecology, but some support for its validity does exist. Bump et al. (2007) determined that environmental isotope patterns were better represented by higher trophic levels in both experimental and observational contexts. For example, using carbon isotope data they determined that wolves record historical trends in atmospheric CO₂ more accurately than tree rings. Similarly, data from Codron et al. (2007a) suggests that South African savanna-dwelling carnivores differ in $\delta^{13}\text{C}$ based on feeding behavior and associated habitat preferences of different prey types. In particular, lions foraging in open grasslands were found to have higher $\delta^{13}\text{C}$ values than lions associated with more wooded habitats.

However, large to medium bodied carnivores are capable of ranging significant distances in search of prey and likely sample from a variety of habitat types (Gittleman and Harvey, 1982). While demonstrably useful in recording large-scale spatial and temporal patterns of carbon isotopes in the palaeontological record (e.g. changes in atmospheric CO₂ levels) (Kohn et al., 2005; Bump et al., 2007; Hopley and Maslin, 2010), they may offer poorer resolution at smaller spatial scales. In a paleoecological context, there is the added complication that predators are somewhat rare in the fossil record relative to other organisms (Brain, 1981; Werdelin and Lewis, 2005; Patterson et al., 2014).

Smaller bodied, insectivorous mammals such as Soricidae (shrews) are ideal potential candidates for carbon isotopic studies. Unlike larger

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