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A 12,000 year record of changes in herbivore niche separation and palaeoclimate (Wonderwerk Cave, South Africa)

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ABSTRACT

The large mammalian fauna of southern Africa is characterised by strong niche separation into grazer and browser species, with few falling into the intermediate mixed-feeder niche. Moreover, the modern fauna is reduced in species diversity compared to the Pleistocene, following the extinction of several specialized grazers in the late Pleistocene and early Holocene. How did this state develop, and how might it be connected to climatic change during the Holocene? To better understand this development, we obtained extensive carbon and oxygen stable light isotope data from herbivore tooth enamel samples from Wonderwerk Cave, South Africa, spanning about 12,000–500 cal. BP. This is a unique dataset since it is the only site in the southern Kalahari with a robust chronometric record and well-preserved faunal remains for the last 12,000 years without significant gaps. Combining the stable isotopes with pollen and micromammal data from Wonderwerk Cave, we have explored shifts in the proportions of C_3 and C_4 plants and moisture availability. Although climate remained generally semi-arid for much of this period, the results show significant hydrological and vegetation shifts in the sequence, particularly with the strengthening of summer rainfall in the mid-Holocene. The results for the sixteen herbivore species reveal a reinforcement of the grazer-browser niche partitioning through the Holocene and shows how niche specialization follows changes in local vegetation composition. In the light of this reconstruction of the local ecology we discuss grazer extinctions, human adaptations, and the drivers behind climatic changes in the summer rainfall zone of southern Africa.

1. Introduction

Ecological changes prevailed in faunal communities worldwide at the end of the Pleistocene. Although more muted, on the African continent the prevalent trend was an environmentally driven decline in species of grazers that began in the late Pleistocene (c. 13,000 BP) and continued into the early Holocene (c. 6000 BP), apparently without direct influence of humans (Faith, 2011, 2013, 2014). In southern Africa, the change was marked with the replacement of the Florisian Land Mammal Age, which is defined by specialist grazers and wetland species, and a faunal community reduced in species diversity and encompassing a higher percentage of generalists (e.g. Brink, 2005; Faith, 2013; Faith and Behrensmeyer, 2013). Species that went extinct were mainly the highly specialized grazers, including *Equus capensis*, *Equus lylei*, *Syncerus antiquus*, *Megalotragus priscus*, *Damaliscus niro* and *Antidorcas bondi* (Brink, 2005, 2016; Faith, 2013, 2014). The mechanisms proposed as causes of this faunal turnover in southern Africa vary: increased aridification and reduced productivity of grasslands (Brink and Lee-Thorp, 1992; Brink, 2016), increased competition between grazer species (Thackeray, 1984, 2015), increasing niche specialization (Codron et al., 2008), changes in the structure of grassland habitats (Faith, 2014), or increased seasonality (Faith, 2011), but are not mutually exclusive. Although it is clear that climate and environmental change impacted the faunal

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communities, the primary drivers behind this turnover remain unclear. To a large degree, this is due to a lack of clarity on the timing and nature of climate and environmental change through the Holocene.

The current climate in southern Africa is dry with strongly seasonal precipitation, which influences its biome structure (Fig. 1). Rainfall reaches the south-western Cape from the Atlantic Ocean mainly in the winter (June to August), whereas rain arrives from the Indian Ocean in northern and eastern southern Africa in summer (December to February). A small intermediate zone on the southern coast receives year-round rainfall, while the northern intermediate zone lies in a rain shadow. Holocene climate conditions in southern Africa are largely reconstructed from pollen records. Recent statistical models of pollen data show contrasting records in the summer rainfall zone. For example, in one set of records a modest increase in moisture availability is observed over the course of the Holocene (e.g. at Wonderkrater, Tswaing Crater), and another set shows dry periods 5–7 cal. BP (e.g. at Blydefontein, Braamhoek, Equus Cave, Lake Eteza) (Chevalier and Chase, 2015; Scott, 2016). A review of pollen records using principal component analysis demonstrates decreased moisture at 7-8ka at several sites and slightly cooler temperatures after 6ka in the Holocene (Scott et al., 2012; Scott, 2016). Around 2ka many records show drying and reduced summer rainfall (Nicholson, 2011; Scott et al., 2012). The drawback of pollen records lies in that they cannot distinguish between temperature and aridity signals using principal components analysis. Another issue is the difficulty in establishing a robust chronology for pollen accumulation sites. Thus, in addition to pollen records, independent, chronologically sound environmental data is needed to mediate information on regional climate. However, palaeoclimatic records are extremely sparse for the arid interior of southern Africa. Finally, most pollen, and other proxy records such as speleothems, dune records as well as lake sediment cores represent short sequences, from disparate areas located at a significant distance from each other, that inevitably show a large degree of variability (e.g. Burrough and Thomas, 2013) (Fig. 1).

In this paper we present carbon and oxygen stable isotope values for enamel from sixteen herbivore species from Wonderwerk Cave, located in the arid interior of South Africa. Our research represents the first detailed study of a single site in southern Africa that spans the entire Holocene from the late Pleistocene to historic periods (from ~12ka cal. BP to 500 cal. BP, Ecker et al., 2017). Moreover, the Wonderwerk Cave record offers a range of other environmental and climate proxies (microfauna, macrofauna, pollen, speleothems) with which to compare and contrast the isotopic results. Together, these records allow us to investigate regional trends through most of the Holocene and to discuss the drivers behind climatic changes in the summer rainfall zone.

1.1. Background to the site

Wonderwerk Cave is located on the eastern flank of the Kuruman Hills in the Northern Cape Province of South Africa. It lies at the base of a 121 m high conical hill overlooking the Ghaap plateau (Fig. 1). The current climate is characterised by summer rainfall of c.400 mm MAP (mean annual precipitation) with dry winters where frost is possible (Beaumont, 1990). Today the area falls within the Savannah biome and the local vegetation is defined as *Kuruman mountain bushveld* (Mucina and Rutherford, 2006), with C_4 grasses and C_3 trees, shrubs and herbs. Historic records of European travellers in the 19th century describe a wide range of typical savannah herbivores and carnivores inhabiting the Kuruman Hills and surrounding region (Skead, 1980; Thackeray, 1981), but today's biomass is significantly reduced due to modern development and farming (Brink et al., 2016).

The cave is a ca. 140 m long dolomitic cavity, which was initially explored and excavated in the 1930s and 1940s (for a review see Horwitz and Chazan, 2015). The late Peter Beaumont undertook extensive excavations near the cave's entrance (known as Excavation 1) in 1978, to be joined in 1979 by Anne and J. Francis Thackeray, who were specifically interested in documenting the Holocene cultural, faunal and sedimentary record (Thackeray, 1981,

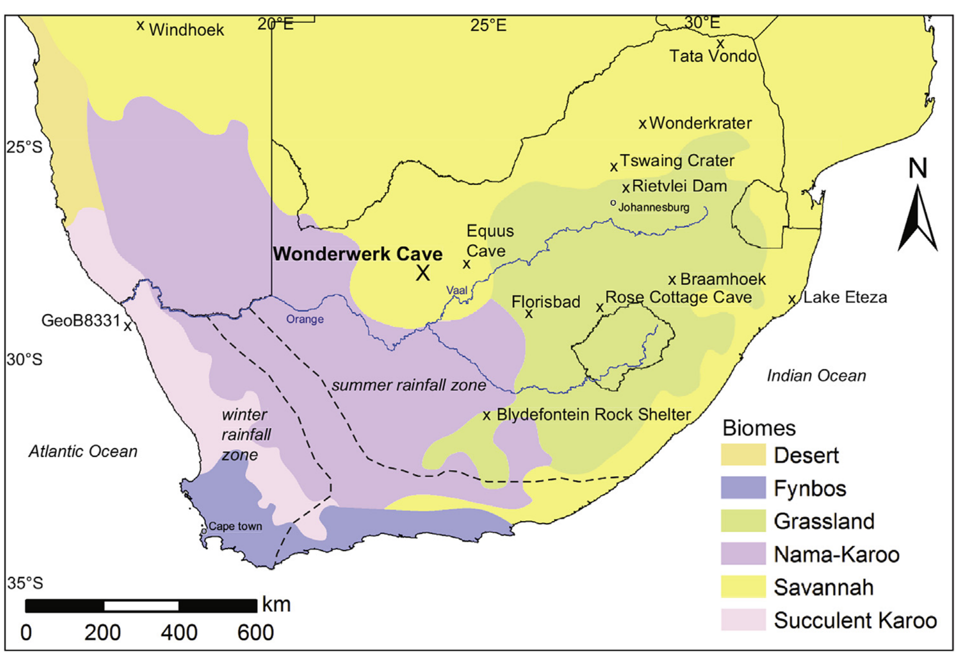

Fig. 1. Location of Wonderwerk Cave, as well as environmental records mentioned in the text. Rose Cottage Cave has a stable isotope record on enamel, all other records represent pollen data. The marine core GeoB8331 additionally has a microcharcoal record. The dashed lines mark the approximate boundary of the winter rainfall zone, and the approximate boundary of the year-round rainfall zone to the summer rainfall zone, respectively (Chase and Meadows, 2007). Biome distribution after Rutherford (1997) and Mucina and Rutherford (2006).