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Ungulate diversity and precipitation history since the Last Glacial Maximum in the Western Cape, South Africa

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ABSTRACT

This study reviews the precipitation history of the winter and year-round rainfall zones in the Western Cape (South Africa) in light of its fossil ungulate communities. Fossil sequences spanning the Last Glacial Maximum (LGM) and Lateglacial through the Holocene document a decline in ungulate richness through time. Based on the observed relationship between ungulate community richness and annual precipitation in Southern and East Africa, this implies increased effective precipitation during the LGM-Lateglacial at sites located in both the winter and year-round rainfall zones. These results are consistent with other lines of paleoenvironmental evidence from the winter rainfall zone, although they contradict records from the year-round rainfall zone that have been interpreted as reflecting aridity. A critical review of these records suggests that the patterns interpreted in terms of aridity can be explained by other mechanisms, including vegetation change. Current evidence is consistent with paleoclimatic models indicating that altered rainfall patterns during the LGM-Lateglacial were primarily related to the position of westerly frontal systems, which were displaced northward due to the expansion of Antarctic sea ice. Seasonal migration of these systems resulted in an expanded winter rainfall zone across much of southwestern Africa, but perhaps with some summer rains reaching the southern coast.

1. Introduction

The nature of late Quaternary climate change in the Western Cape of South Africa is a major focus of research and debate (van Zinderen Bakker, 1976; Deacon et al., 1983; Deacon and Lancaster, 1988; Partridge et al., 1990; Meadows and Baxter, 1999; Chase and Meadows, 2007), with important implications for understanding southern hemisphere climate dynamics (Tyson et al., 2001; Scott and Woodborne, 2007; Chase et al., 2011), the distribution of its endemic flora (Cowling and Lombard, 2002; Linder, 2003; Linder and Hardy, 2004), and modern human origins (Bar-Matthews et al., 2010; Chase, 2010; Marean, 2010). Today the Western Cape lies at the intersection of winter and summer rainfall systems (Chase and Meadows, 2007) and includes a winter and year-round rainfall zone (Fig. 1). The west coast receives the majority of its rainfall during the winter months, resulting from the annual migration of westerly storm tracks and associated frontal systems. The south coast receives rainfall more evenly throughout the year, including winter rains from the west and summer rains from easterly flows associated with the migration of the Intertropical Convergence Zone (ITCZ). To the north and east of the Western Cape (summer rainfall zone), summer rains are dominant.

Multiple lines of evidence from the winter rainfall zone suggest increased precipitation during the Last Glacial Maximum (LGM) and Lateglacial relative to the Holocene (Meadows and Baxter, 1999; Chase and Meadows, 2007). For example, at Elands Bay Cave (Fig. 1), where annual precipitation is 200–250 mm and the local vegetation is dominated by xeric shrubland, pollen and charcoal records from the LGM-Lateglacial indicate the presence of woodland and forest taxa, implying increased moisture availability (Cowling et al., 1999; Meadows and Baxter, 1999; Parkington et al., 2000). The presence of hedgehog (*Atelerix frontalis*) and the large body size of Cape dune molerats (*Bathyergus suillus*) from the same deposits further suggest greater precipitation (Klein and Cruz-Uribe, 1987; Klein, 1991). Increased precipitation at this time may result from the expansion of Antarctic sea ice and subsequent displacement of westerly frontal systems, bringing about more frequent and intense winter rains (van Zinderen Bakker, 1967, 1976; Stuut et al., 2004; Chase and Meadows, 2007).

Whereas several independent lines of evidence from the winter rainfall zone indicate increased precipitation during the LGM-Lateglacial, the signal from the year-round rainfall zone is unclear.

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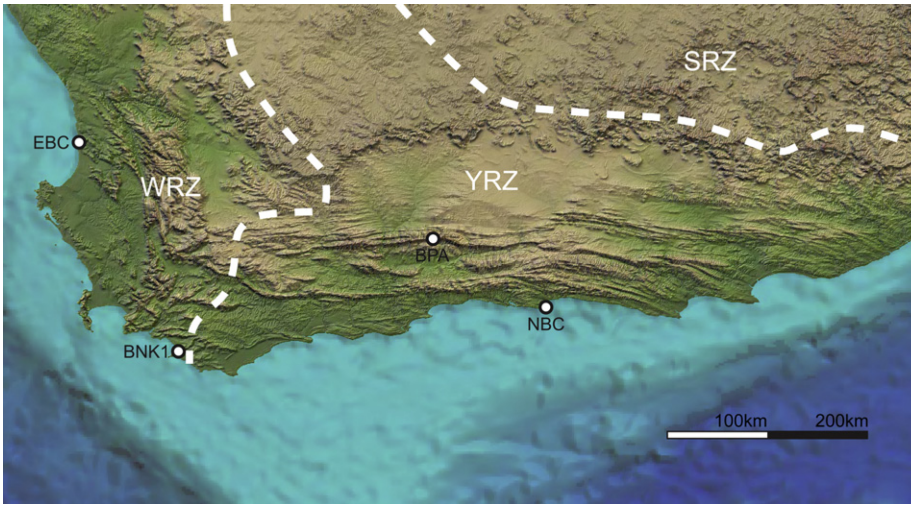

Fig. 1. Map of southern Africa indicating the locations of the sites examined in the text (BNK1 = Byneskranskop 1, BPA = Boomplaas Cave, EBC = Elands Bay Cave, NBC = Nelson Bay Cave). Dashed lines mark the boundaries of the modern winter rainfall zone (WRZ), year-round rainfall zone (YRZ), and summer rainfall zone (SRZ) following Chase and Meadows (2007).

Microfaunal evidence from Boomplaas Cave (Fig. 1) provides contradictory signals, with taxonomic composition and diversity interpreted as indicating drier conditions (Avery, 1982; Thackeray, 1987) but the large size of common molerat (*Cryptomys hottentotus*) consistent with increased precipitation (Avery, 2004). Large mammals from Boomplaas Cave and Nelson Bay Cave indicate an expansion of grasslands during the LGM-Lateglacial (Klein, 1983; Faith, 2012), which has been interpreted by some as evidence for reduced precipitation (reviewed in Chase and Meadows, 2007). The charcoal assemblage from Boomplaas Cave shows diminished diversity and an absence of woodland taxa, also interpreted as indicating aridity (Deacon et al., 1984). However, low diversity may instead be related to reduced atmospheric CO_2 concentrations or changes in rainfall seasonality (Chase and Meadows, 2007).

In their survey of late Quaternary climate changes in southern Africa, Chase and Meadows (2007) conclude that the year-round rainfall zone of the Western Cape witnessed a reduction in precipitation during the LGM-Lateglacial. A lack of confidence in this assessment, however, is suggested by numerous cautionary statements suggesting that the evidence for aridity could be driven by factors other than annual precipitation. Because the record from the year-round rainfall zone plays a central role in understanding the dominance of winter versus summer rainfall systems in southern Africa, it is clear that new evidence bearing on late Quaternary precipitation change is needed. This study provides such evidence through an examination of ungulate diversity at four Western Cape fossil sites spanning the LGM through the Holocene.

2. Methods

2.1. Ungulate diversity and precipitation

Paleoecologists and biogeographers have long explored the relationship between species diversity and precipitation (e.g., Thackeray, 1980; Avery, 1982; Rosenzweig and Abramsky, 1993; Rosenzweig, 1995; Grayson, 1998; Faith, 2011b). Evidence from African ecosystems indicates that precipitation mediates ungulate diversity through its effects on forage availability and quality (Coe et al., 1976; Thackeray, 1980; Bell, 1982; East, 1984; Olff et al., 2002). The interaction between these variables is complex, with enhanced precipitation contributing to an increase in forage availability (Rosenzweig, 1968; Coe et al., 1976; Thackeray, 1980; Olff et al., 2002) but a decrease in forage quality (Olff et al., 2002). These opposing effects translate to an increase in ungulate diversity from low to intermediate levels of rainfall and a decrease at higher levels of rainfall (Olff et al., 2002). The threshold beyond which diversity declines remains to be established for African ecosystems, although previous studies have documented a decline in herbivore biomass, a variable related to species diversity, between 700 and 800 mm/yr (Bell, 1982; East, 1984).

Table 1 reports annual precipitation and ungulate richness (the number of species) for 25 modern wildlife areas in Southern and East Africa (references reported in SI Table 1). These sites are characterized by a wide range of rainfall regimes (140–1050 mm/yr) and habitat types, including shrublands, grasslands, woodlands, and forests (habitat designations follow Reed, 1998). Consistent with the predicted effect of rainfall on diversity, ungulate richness increases with precipitation up to ~750 mm/yr and declines thereafter (Fig. 2A). This can be modeled by a least-squares quadratic regression ($r = 0.575$, $p = 0.012$), which shows an inflection point at 755 mm/yr. For those sites with annual precipitation values ≤755 mm/yr ($n = 17$), there is a significant linear relationship between precipitation and richness ($r = 0.692$, $p = 0.002$), with nearly half the variance in richness explained by precipitation alone (coefficient of determination: $r^2 = 0.478$). Because the wildlife areas examined here differ in geographic area by several orders of magnitude (Table 1), some of the unexplained variance is likely to be driven by the influence of geographic area on richness (i.e., the species–area curve, Rosenzweig, 1995). To provide an estimate of richness that is independent of area, the residuals of the reduced major axis (RMA) regression between log-transformed area and richness are reported in Table 1. Controlling for geographic area leads to an improved quadratic relationship between annual precipitation and richness (residuals) across all sites ($r = 0.641$, $p = 0.003$; inflection point = 781 mm/yr) and a stronger linear relationship across sites with precipitation ≤755 mm/yr (Fig. 2B, $r = 0.800$, $r^2 = 0.640$, $p < 0.001$).

These observations indicate that ungulate richness is linked to annual precipitation across a broad range of Southern and East African ecosystems, consistent with Thackeray's (1980) observations based on a smaller sample of Namibian data. For those wildlife areas receiving up to ~755 mm annual precipitation, ungulate richness is tightly correlated with rainfall, irrespective of habitat type or complexity and regional differences in faunal composition