The last glacial maximum climate at Boomplaas Cave, South Africa

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ABSTRACT

With a rich sequence of floral and faunal remains spanning the past >65,000 years, Boomplaas Cave is among the more important paleoenvironmental archives from South Africa's southern Cape. However, over the last several decades, its paleoenvironmental records have been the subject of conflicting interpretations, fueling uncertainty over fundamental aspects of Quaternary climate change in the region. Most significantly, researchers have variably interpreted the fossil plant and animal assemblages dating to the Last Glacial Maximum (LGM) as indicating harsh and arid or humid and productive conditions. This review critically examines the paleoenvironmental evidence from Boomplaas Cave, focusing on its LGM deposits and how they relate to the contentious problem of moisture availability through time. We show that interpretations of aridity during the LGM either (i) lack robust ecological links between the evidence and the paleoenvironmental interpretation, or (ii) are based on spurious patterns arising from sampling effects. In contrast, interpretations of relatively humid conditions during the LGM are grounded in present-day ecological observations and are consistent with both local and regional paleoenvironmental datasets. Overall, the evidence strongly supports the characterization of the LGM as a time of relatively humid conditions, with the transition to the Holocene characterized by increasing aridity. Several lines of evidence from Boomplaas Cave further suggest that this phase of increased humidity was associated with a dominance of winter rainfall, in contrast to the aseasonal rainfall regime that characterizes the southern Cape today.

Keywords: charcoal, mammals, paleoclimate, paleoecology, pollen, South Africa

1. INTRODUCTION

South Africa's southern Cape has long been a focus of research on Quaternary climate change and its influence on terrestrial ecosystems (e.g., Cockcroft et al., 1987; Deacon and Lancaster, 1988; van Zinderen Bakker, 1976). Encompassing the southern coastal plains and the east-west trending ranges of the Cape Fold Belt, the southern Cape is situated at the transition between regions of temperate and tropical climate dominance (**Figure 1**). To the west, the winter rainfall zone (WRZ; sensu Chase and Meadows, 2007) receives most of its rainfall during the austral winter, as frontal systems associated with the southern hemisphere westerlies shift northwards. In contrast, most of southern Africa falls within the summer rainfall zone (SRZ), which receives rainfall during the austral summer when tropical easterly flow strengthens and transports moisture from the Indian Ocean (Tyson, 1986). The southern Cape falls within the aseasonal rainfall zone (ARZ). It receives rainfall throughout the year from both sources, such that changes in the dominance of temperate and tropical climate systems, and the interactions between them, are reflected in the region's Quaternary paleoenvironmental archives (Chase et al., 2017; Chase and Meadows, 2007).

Among the more important Quaternary paleoenvironmental archives in the region is Boomplaas Cave. Located on the southern flanks of the Swartberg range (**Figure 1**), archaeological excavations at Boomplaas Cave in the 1970s uncovered a rich sequence of floral and faunal remains spanning the last >65,000 years (Deacon, 1979). A substantial body of research over the last four decades has drawn from this evidence to reconstruct ancient plant and animal communities (e.g., Avery, 1982; Klein, 1978; Scholtz, 1986), inform on climate dynamics (e.g., Faith et al., 2019; Sealy et al., 2016; Thackeray, 1987), and evaluate how human populations responded to environmental changes through time (e.g., Chase et al., 2018; Deacon and Thackeray, 1984; Deacon, 1984; Pargeter and Faith, 2020). This literature has grown considerably since the first syntheses of the paleoenvironmental records from Boomplaas Cave (Deacon, 1983a; Deacon et al., 1984; Deacon and Lancaster, 1988), but so too has the divergence of opinions concerning their interpretation (e.g., Chase and Meadows, 2007; Faith et al., 2019; Marean et al., 2014; Thackeray, 2020).

Disagreements over climatic conditions during the Last Glacial Maximum (LGM; 26-19 ka) are especially consequential for paleoenvironmental research in southern Africa. Early research on the paleoenvironmental records from Boomplaas Cave reconstructed the LGM as exceptionally arid and ‘harsh’ (e.g., Avery, 1982; Deacon et al., 1984; Deacon and Lancaster, 1988; Scholtz, 1986). Archaeologist Hilary Deacon, who directed the initial research at the site, was so confident in this assessment that he described the evidence for a dry LGM as “incontrovertible” (Deacon, 1983a:326). The interpretation of LGM aridity was echoed in subsequent syntheses and regional overviews (Chase and Meadows, 2007; Deacon et al., 1984; Deacon and Lancaster, 1988), though Chase and Meadows (2007) questioned the incontrovertible nature of the evidence, suggesting that some presumed indicators of aridity (e.g., expansion of grassy vegetation; Deacon et al., 1984) from Boomplaas Cave and elsewhere in the southern Cape could be tracking climatic variables unrelated to precipitation. This initial seed of doubt has given way to a rejection of the early characterizations of the LGM, with recent work interpreting the evidence from Boomplaas Cave as indicative of humid and highly productive conditions (Chase et al., 2018; Faith, 2013a, b; Faith et al., 2019). These incompatible interpretations have stimulated debate (Faith et al., 2019, 2020; Thackeray, 2020) and fueled uncertainty about the climate history of southernmost Africa (see review in Marean et al., 2014).

The conflicting assessments of the LGM at Boomplaas Cave mean that fundamental aspects of Quaternary climate dynamics in the southern Cape—e.g., were glacial periods wetter or drier than interglacial periods?—currently elude consensus (Chase and Meadows, 2007; Marean et al., 2014; Thackeray, 2020). This uncertainty demands resolution, especially in light of ongoing work at Boomplaas Cave (Pargeter and Faith, 2020; Pargeter et al., 2018), the continued development of regional paleoenvironmental records (e.g., Braun et al., 2020; Chase et al., 2017, 2020, 2021), and the creation of downscaled LGM climate models for southern Africa (Engelbrecht et al., 2019), which are now providing a basis for inferring other aspects of LGM ecosystems (Cowling et al., 2020; Grobler et al., 2023; Kraiij et al., 2020). As Boomplaas Cave is a key LGM archive for the southern Cape, progress in understanding Quaternary climate dynamics in southern Africa, from both empirical and modelling perspectives, will require greater certainty over the paleoclimatic implications of its proxy records. With this in mind, we

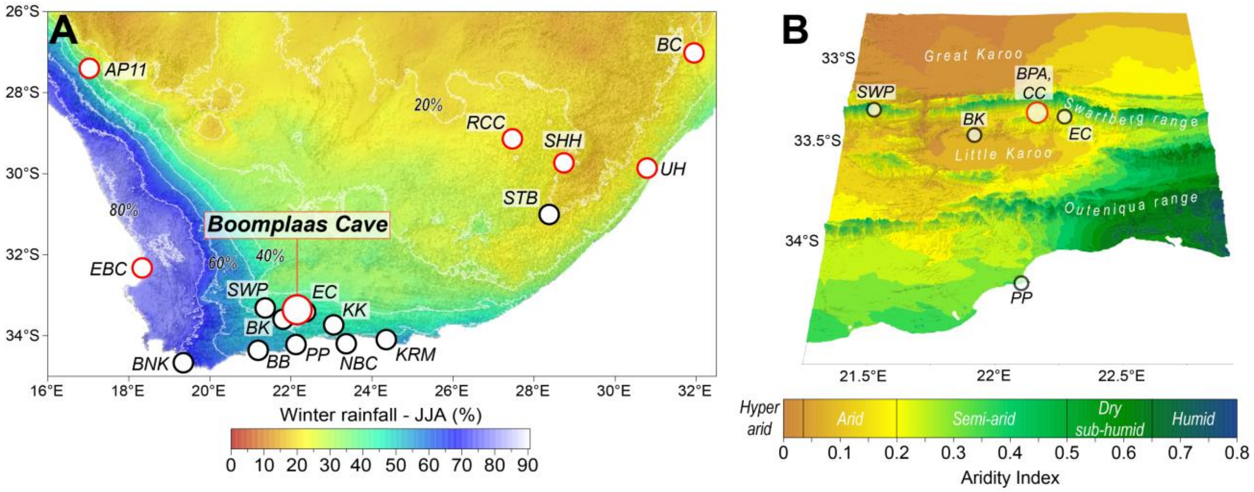

Figure 1. (A) Map of southern Africa showing the location of Boomplaas Cave [BPA] relative to other sites in the region: Buffelskloof [BK], Blombos Cave [BB], Border Cave [BC]), Byneskranskop [BNK], Cango Cave [CC], Efflux Cave [EC], Kangkara [KK], Klasies River Mouth [KRM], Nelson Bay Cave [NBC], Pinnacle Point [PP], Rose Cottage Cave [RCC], Seweweekspoort [SWP], Strathalan B [STB], Sehonghong [SHH], Umhlatuzana Rockshelter [UH]. The color gradient reflects the percentage of annual precipitation that falls during the austral winter months (JJA) (precipitation data from Hijmans et al. 2005). (B) Map of the region surrounding Boomplaas Cave (red circle) highlighting spatial variation in aridity. Aridity index = MAP/MAE; MAP = mean annual precipitation; MAE = mean annual evapotranspiration (data from Trabucco and Zomer 2009; classifications follow UNEP 1997).

aim to critically review the paleoenvironmental data from Boomplaas Cave, focusing on its LGM deposits. We examine this evidence as it relates to the contentious problem of moisture availability (i.e., precipitation relative to evapotranspiration), incorporating additional insights into rainfall seasonality where available.

2. BOOMPLAAS CAVE

Boomplaas Cave overlooks the Cango Valley from the southern flanks of the Swartberg range, which separates the arid to semi-arid Great Karoo to the north from the Little Karoo to the south (**Figure 1**). The site falls within a transitional shrubland whose component species vary as moisture increases from the valley floor up the slopes of the Swartberg (Vlok and Schutte-Vlok, 2010). Succulent Karoo and Subtropical Thicket vegetation historically dominated the lowlands ~10-15 km south of the cave, giving way to renosterveld at the base of the Swartberg, with fynbos occurring at higher elevations north of the cave. Thicket and closed woodland occur along watercourses draining the Swartberg and flowing through the Cango Valley (Moffett and Deacon, 1977), including the Grobbelaars River, located ~300 m south of the cave. The annual rainfall of ~400 mm is evenly distributed throughout the year, contributing to a mix of C_3 and C_4 grasses in the local environment (Vogel et al., 1978; Grobler et al., 2023). Large mammal communities in the region were historically dominated by small-bodied browsers and mixed feeders, including klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), and grey rhebok (*Pelea capreolus*), with the less abundant large-bodied grazers including hartebeest (*Alcelaphus buselaphus*) and mountain zebra (*Equus zebra*) (Boshoff and Kerley, 2001; Skead, 2011; Vlok and Schutte-Vlok, 2010).

Deacon conducted excavations at Boomplaas Cave from 1974 to 1979 as part of a broader effort to understand the effects of Quaternary paleoenvironmental change on human behavioral evolution in the southern Cape (Deacon, 1979; Deacon, 1995). His excavations uncovered a well-stratified sedimentary sequence extending from >65 ka to the protohistoric period, with the main stratigraphic aggregates divided into a hierarchical scheme of members, units, and subunits (**Figure 2**). The deposits overlapping in age with at least parts of the LGM include members LPC (27.3-25.8 cal ka BP), LP (25.4-21.7 cal ka BP), and GWA/HCA (21.6-17.6 cal ka BP), with the overlying subunits of members CL (17.4-14.0 cal ka BP) and BRL

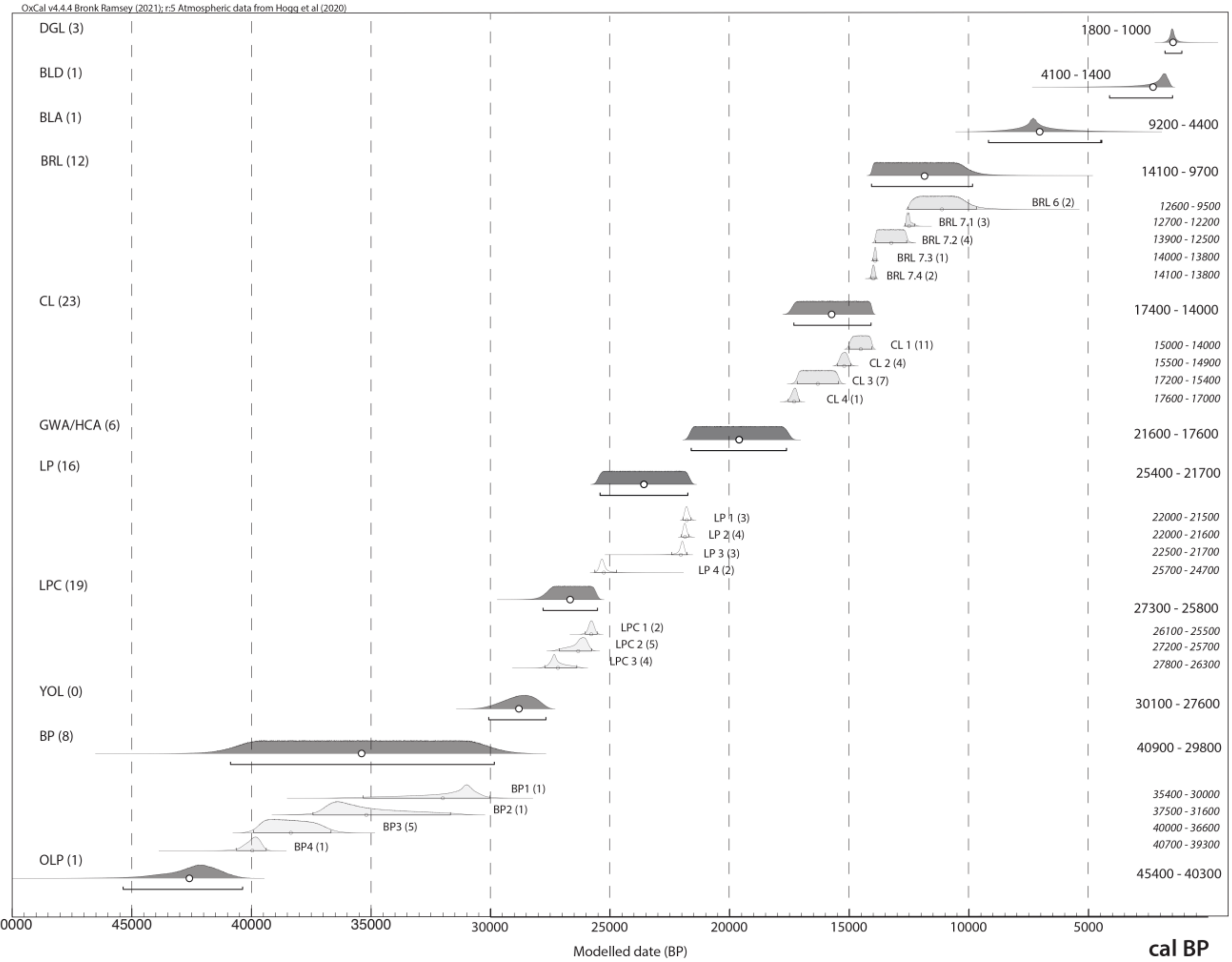

Figure 2. The radiocarbon chronology of the Boomplaas Cave sequence. Ages for each member and for select units are modelled ^{14}C ages with 2σ ranges. The chronology is updated from Pargeter et al. 2018 in OxCal 4.4 (Bronk Ramsy (2009) using ShCal20 (Hogg et al. 2020). Values in parentheses indicate the number of dates. The ages of the underlying members (BOL, OCH, and LOH) are poorly constrained, though OCH is associated with U-series and amino acid racemization age estimates of ~60-65 ka (Miller et al., 1999; Vogel, 2001).

(14.1-9.7 cal ka BP) providing a finely resolved record of the last glacial-interglacial transition (LGIT) (Pargeter et al., 2018). Pargeter directs the current excavations focused on members GWA/HCA to BP.

The primary sources of paleoenvironmental evidence derived from Deacon's excavations, and which have been the subject of varied interpretations, include the large mammal (Faith, 2013a; Klein, 1978, 1983; Sealy et al., 2016), micromammal (Avery, 1982, 1983b), charcoal (Deacon et al., 1983; Deacon and Lancaster, 1988; Scholtz, 1986), and pollen assemblages (Deacon et al., 1984; Deacon and Lancaster, 1988). Below, we examine these datasets, outlining the nature of the evidence and how it has been used to infer LGM moisture availability. Because these climate proxies are more directly influenced by the amount of water in the environment rather than total precipitation, we focus our discussion on moisture availability, which is primarily influenced by the combination of precipitation and temperature via its effect on evapotranspiration (e.g., Chevalier and Chase, 2016). This is important here because lower LGM temperatures (e.g., Heaton et al., 1986; Talma and Vogel, 1992; Chevalier and Chase, 2015), and the associated decline in evapotranspiration, could drive an increase in moisture availability in the absence of precipitation change. Following the UNEP (1997) climate classification scheme, we discuss moisture availability in terms of a gradient from relatively arid (i.e., less precipitation relative to evapotranspiration) to relatively humid (i.e., more precipitation relative to evapotranspiration). Throughout our evaluation of Boomplaas Cave, we limit our discussion to ordinal-scale trends (e.g., more or less arid/humid), as the kinds of proxy records examined here are poorly suited for more precise numerical estimates of paleoclimate variables (e.g., Faith and Lyman, 2019).

3. LARGE MAMMALS

The large mammals (>500 g) from Boomplaas Cave were first studied by Klein (1978, 1983), with subsequent studies undertaken by Brink (1999) and Faith (2013a). Humans were the primary accumulators of the large mammals from member CL (17.4-14.0 cal ka BP) through the Holocene, with the faunal remains derived from the LGM and underlying deposits accumulated by a combination of humans, carnivores, and raptors (Faith, 2013a). Despite this complex taphonomic history, major changes in taxonomic composition are unassociated with taphonomic change, suggesting that environmental forcing is a primary driver of faunal turnover through the sequence (Faith, 2013a).

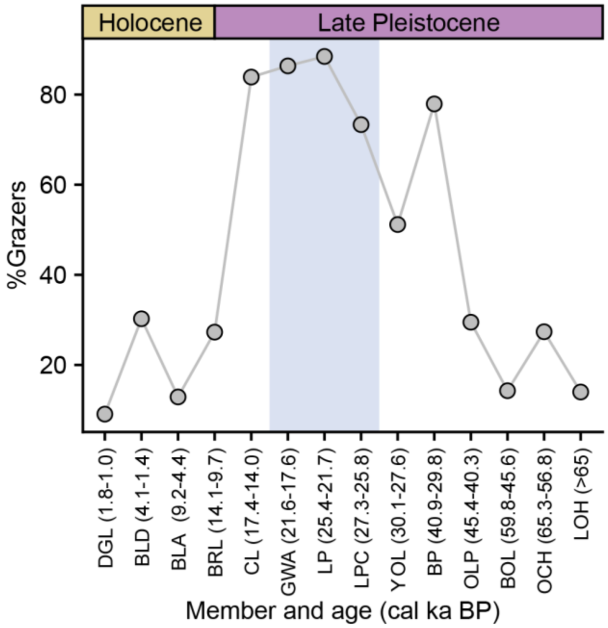

Figure 3. Changes in the abundance (% of specimens) of ungulate grazers through the Boomplaas Cave sequence (data from Klein, 1983 for DGL; Faith 2013a for BLD through LOH). Vertical bar denotes the LGM members.

Paleoenvironmental interpretations derived from the large mammals have focused on the ungulates (Artiodactyla and Perissodactyla). In his initial reports, Klein (1978, 1983) emphasized dramatic changes in the relative abundance of ungulate grazers through time (**Figure 3**). In contrast to the historic faunas, as well as those from the Holocene levels at Boomplaas, the faunas from member BP (40.9-29.8 cal ka BP) through CL (17.4-14.0 cal ka BP) are dominated by grazers, including various alcelaphin antelopes (*Alcelaphus buselaphus*, *Connochaetes taurinus*, *C. gnou*, and *Damaliscus pygargus*), equids (*Equus capensis* and likely both *E. quagga* and *E. zebra*), and an extinct caprin (see Brink, 1999 for details on the caprin; see Faith, 2013a for the latest faunal list). Klein (1978, 1983) interpreted these changes in terms of vegetation structure, suggesting that grasses were more widespread when grazers were dominant, particularly during the LGM. This interpretation remains uncontroversial, mirroring faunal changes observed elsewhere in the region (e.g., Klein, 1972; Schweitzer and Wilson, 1982).

In the first synthesis of the paleoenvironmental evidence from Boomplaas Cave, Deacon et al. (1984) also emphasized the grassy conditions implied by the LGM faunas, and they further suggested that this was consistent with dry conditions. Others subsequently associated grasses with aridity (Deacon and Lancaster, 1988), but the empirical basis for this interpretation is lacking (e.g., Chase, 2010). Plant communities in the southern Cape are mediated by complex relationships between climate, soil characteristics, and fire (e.g., Bergh et al. 2014; Cowling and Holmes, 1992), with geological and topographic variability the Cape Fold Belt contributing to abrupt spatial changes in vegetation structure (e.g., Moffett and Deacon, 1977; Campbell, 1986; Cowling and Campbell, 1983; Vlok and Schutte-Vlok, 2010). On nutrient-rich soils that are particularly attractive to large herbivores, including those occurring on the shale bedrock of the Cango Valley (le Roux, 1977; Moffett and Deacon, 1977), increased rainfall is generally associated with a succession from succulent karoo, renosterveld, grassland or thicket, and finally to afrotemperate forest (e.g., Cowling, 1983). Grasses generally become more prevalent across this gradient, only declining when moisture is sufficiently high to promote dense tree cover. The contemporary vegetation near Boomplaas Cave echoes this succession. Succulent shrubs with limited grassy cover dominate the more arid parts of the Little Karoo basin ~15 km south of Boomplaas (Vlok and Schutte-Vlok, 2010). Grasses become more prevalent as moisture availability increases closer to the Swartberg range, especially in the renosterveld occurring on shale-derived soils of the Cango Valley and in the thicket on the limestone hills between the

Grobbelaars River and the Swartberg range (Moffett and Deacon, 1977; Vlok and Schutte-Vlok, 2010). In light of these observations, and acknowledging that a detailed understanding of LGM vegetation will also require consideration of fire regimes (Kraaij and van Wilgen, 2014), lower temperature (Duker et al., 2014), reduced atmospheric pCO_2 (Gerhart and Ward, 2010), and herbivory (Staver et al. 2020), the expansion of grasses signaled by the LGM faunas at Boomplaas Cave is most parsimoniously interpreted as a response to wetter conditions (*contra* Deacon et al., 1984; Deacon and Lancaster, 1988).

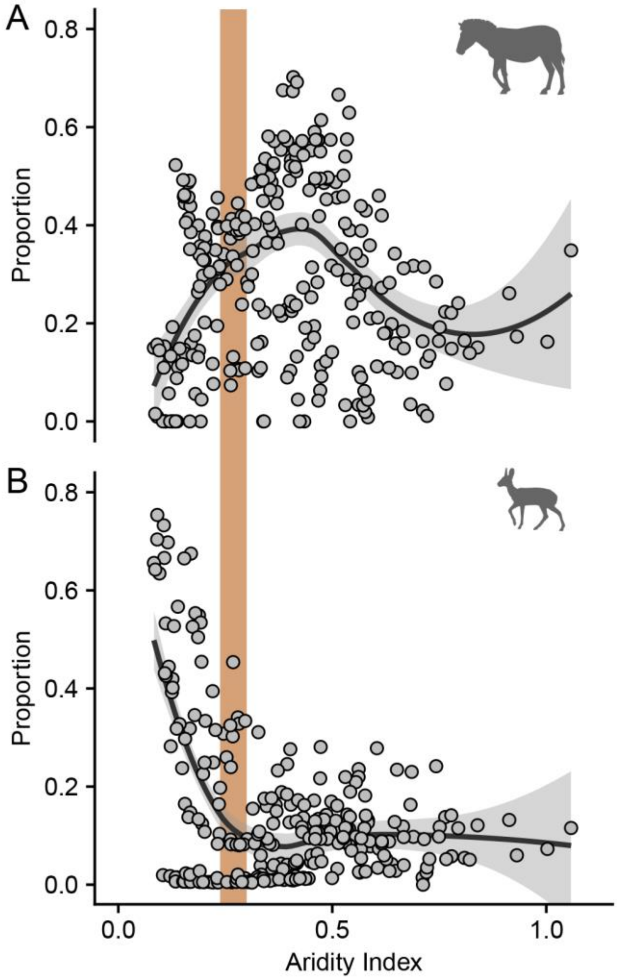

Figure 4. A: The proportion of equids and alcelaphins across southern Africa as a function of aridity (Aridity index = MAP/MAE; MAP = mean annual precipitation; MAE = mean annual evapotranspiration; larger values indicate greater moisture). B: The relative abundance of *Raphicerus* spp., *Oreotragus oreotragus*, *Pelea capreolus*, and *Redunca fulvorufula* as a function of aridity. Solid lines are LOESS curves (span = 0.75) with 95% confidence interval in gray. Vertical bar denotes range of aridity index values within a 2.5 km radius of Boomplaas Cave today (from Trabucco and Zomer 2009). Herbivore data are from Hempson et al. (2015) for the following ecoregions: Albany thickets, Drakensberg Escarpment savanna and thicket, Drakensberg grassland, fynbos shrubland, highveld grassland, Limpopo lowveld, Nama Karoo shrubland, Renosterveld shrubland, Succulent karoo xeric shrubland.

Contemporary herbivore-environment relationships further support a link between grazer-dominated faunas and humid environments. Hempson et al. (2015) developed models relating herbivore densities from wildlife censuses to various environmental variables (e.g., rainfall, soil nutrient status, vegetation types), allowing them to estimate the potential densities of large herbivore species across Africa. Drawing from their models, **Figure 4** illustrates the relative abundance of equids and alcelaphin antelopes, the dominant ungulates during the LGM (60-64% of specimens; counts from Faith, 2013a), as a function of aridity across southern Africa. These taxa tend to be rare in relatively arid environments, reaching peak abundance at intermediate levels of moisture availability, where grass availability and quality are highest (Hempson et al., 2015). Conversely, the small-bodied ungulates that dominate the Holocene levels at Boomplaas Cave, including steenbok, Cape grysbok, klipspringer, grey rhebok, and mountain reedbuck (*Redunca fulvorufula*) (collectively 87% of specimens in late Holocene member BLD; counts from Faith, 2013a), tend to be most abundant in relatively arid environments, in part because limited primary productivity precludes an abundance of larger-bodied ungulates (**Figure 4)**. Using these observations to guide our interpretations, the temporal shifts in ungulate community composition at Boomplaas Cave (**Figure 3**) are most consistent with a relatively humid LGM and a relatively arid Holocene.

Temporal shifts in ungulate diversity further support this inference (Faith, 2013a, b). Within Africa (Faith, 2013b; Patterson et al., 2022), and more broadly (Olff et al., 2002), ungulate diversity peaks at intermediate levels of moisture availability (typically ~600-800 mm annual rainfall). This pattern represents the 'Goldilocks zone' that favors the co-occurrence of smaller-bodied species limited by forage quality alongside larger-bodied species limited by forage quantity (Olff et al., 2002). When moisture availability declines below this zone, the associated decline in productivity results in lower diversity, particularly among larger-bodied species that require large amounts of forage. When moisture availability exceeds this zone, the associated decline in forage quality excludes the smaller-bodied species. These quantity-quality interactions result in a unimodal relationship between moisture availability and ungulate diversity (**Figure 5**). Based on this relationship, the expectation is that aridification of the arid-to-semi-arid Little Karoo (relative to today) would be associated with a decline in species richness. In contrast, increased moisture availability would be associated with increased richness, though richness would eventually decline in particularly wet environments. At Boomplaas Cave, as well as other sites in the southern Cape (e.g., Nelson Bay Cave, Byneskranskop 1), temporal trends in diversity are consistent with aridification since the LGM—ungulate richness is highest during the LGM and Lateglacial, declining in the Holocene (Faith, 2013a, b) (**Figure 5**). This observation reinforces the evidence species-environment relationships (**Figure 4**) that suggest the LGM was a time of relatively humid conditions.

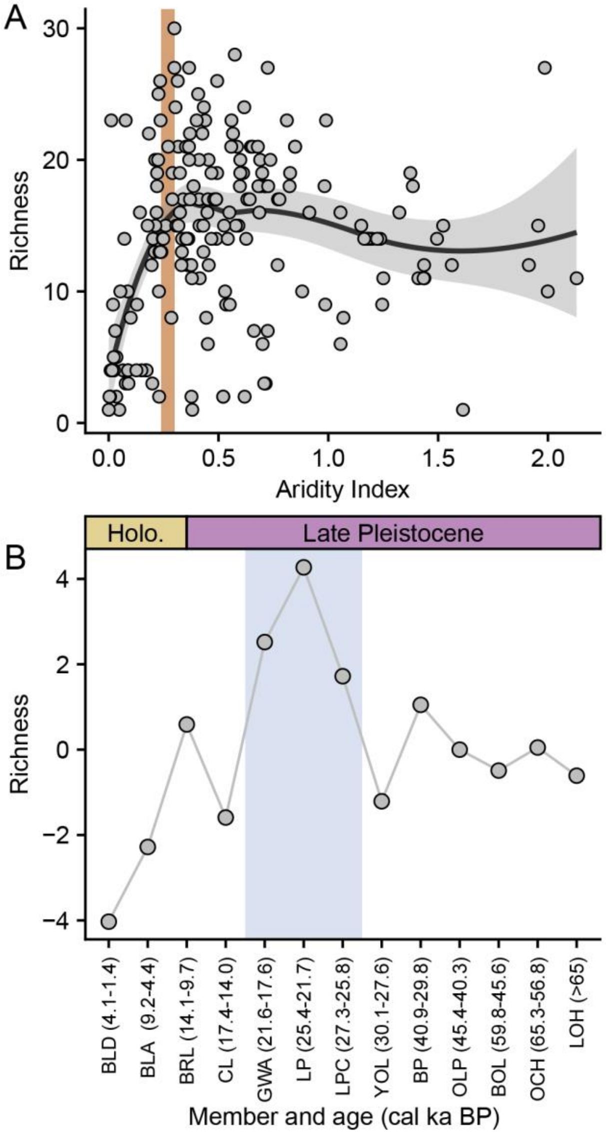

Figure 5. A: Ungulate richness as a function of aridity across Africa (Aridity Index = MAP/MAE; larger values indicate greater moisture). Solid lines are LOESS curves (span = 0.75) with 95% confidence interval in gray. Vertical bar denotes range of aridity index values in the vicinity of Boomplaas Cave today (as in Figure 4). Faunal data from Faith et al. (2019). B: Temporal trends in ungulate richness across the Boomplaas Cave sequence (from Faith 2013a). Values represent residuals calculated from a linear regression of richness as a function of assemblage sample size. Vertical bar denotes the LGM members.

Subsequent isotopic analysis indicates a dominance of C_3 vegetation on the landscape (Sealy et al., 2016), with LGM alcelaphins consuming on average ~71% C_3 plants and equids consuming ~76% C_3 plants (percentages from Robinson, 2023). Provided that these taxa were consuming primarily grasses, as is the case among their present-day counterparts (e.g., Skinner and Chimimba, 2005), the implication is that C_3 grasses were more abundant than in the present (Sealy et al., 2016). The distribution of C_3 and C_4 grasses depends largely on temperature during the growing season, with the proportion of C_3 grasses increasing with altitude and the relative dominance of winter rains (Vogel et al., 1978; Grobler et al., 2023). Changes in atmospheric pCO_2 have also been identified as an important determinant of C_3/C_4 grass distributions, with lower pCO_2—such as occurred during the LGM—favoring the expansion of C_4 grasses (Ehleringer et al., 1997; Collatz, et al., 1998). According to these studies, even with a 6°C LGM temperature depression (Talma and Vogel, 1992), low pCO_2 would promote C_4 grass expansion in the region, and a change in rainfall seasonality (i.e., a greater proportion of winter rain) would be required for the C_3 dominance observed by Sealy et al. (2016) in the LGM grazers from Boomplaas Cave. There is still an important C_4 signal in the isotope data (on average 29% among alcelaphins and 24% among equids), demonstrating that C_4 grasses were present, but they were less prevalent than in the terminal Pleistocene (member CL) and Holocene members of the sequence (Sealy et al., 2016).

4. MICROMAMMALS

The well-preserved micromammal assemblages, which include an assortment of rodents (Rodentia), shrews (Eulipotyphla), elephant shrews (Macroscelidea), golden moles (Afrosoricida), and bats (Chiroptera), represents a second key source of paleoenvironmental evidence from Boomplaas Cave. Avery (1982) conducted the initial taxonomic and paleoecological study of the microfauna (see also Avery, 1983a, b), with subsequent analyses conducted by Deacon et al. (1984), Thackeray (1987, 1990; Thackeray and Fitchett, 2016), and Faith et al. (2019). Based on the ecology of the likely predators and the represented micromammal species, barn owls (*Tyto alba*) are considered the main accumulator of the micromammal assemblages (Avery, 1982). However, detailed taphonomic analyses remain to be conducted.

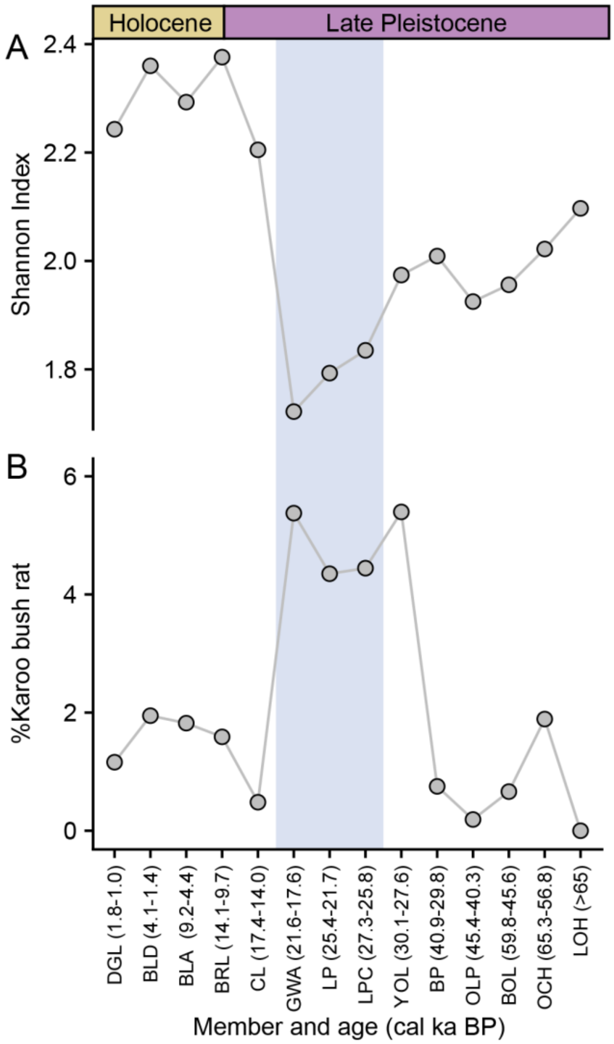

Figure 6. A: Taxonomic diversity (Shannon index) of micromammals (bats excluded) through the Boomplaas Cave sequence. B: Changes in the abundance of Karoo bush-rat through the Boomplaas Cave sequence. Data from Avery (1982). Vertical bar denotes the LGM members.

Avery (1982) drew primarily from two lines of evidence to build a case for an arid and harsh LGM at Boomplaas Cave. First, she observed that taxonomic diversity (richness, equitability, and heterogeneity) was lowest in the LGM assemblages (**Figure 6**), primarily due to the dominance of Saunders' vlei rat (*Otomys saundersiae*) and forest shrew (*Myosorex varius*). Referring to global latitudinal gradients, where diversity is greatest in the tropics and declines at higher latitudes, Avery (1982) interpreted the reduction in diversity during the LGM as indicative of harsh conditions (i.e., cold and dry). Though reference to large-scale diversity gradients often underpins paleoenvironmental inferences (Faith and Lyman, 2019), relationships between micromammal diversity and moisture availability are not substantiated in southern

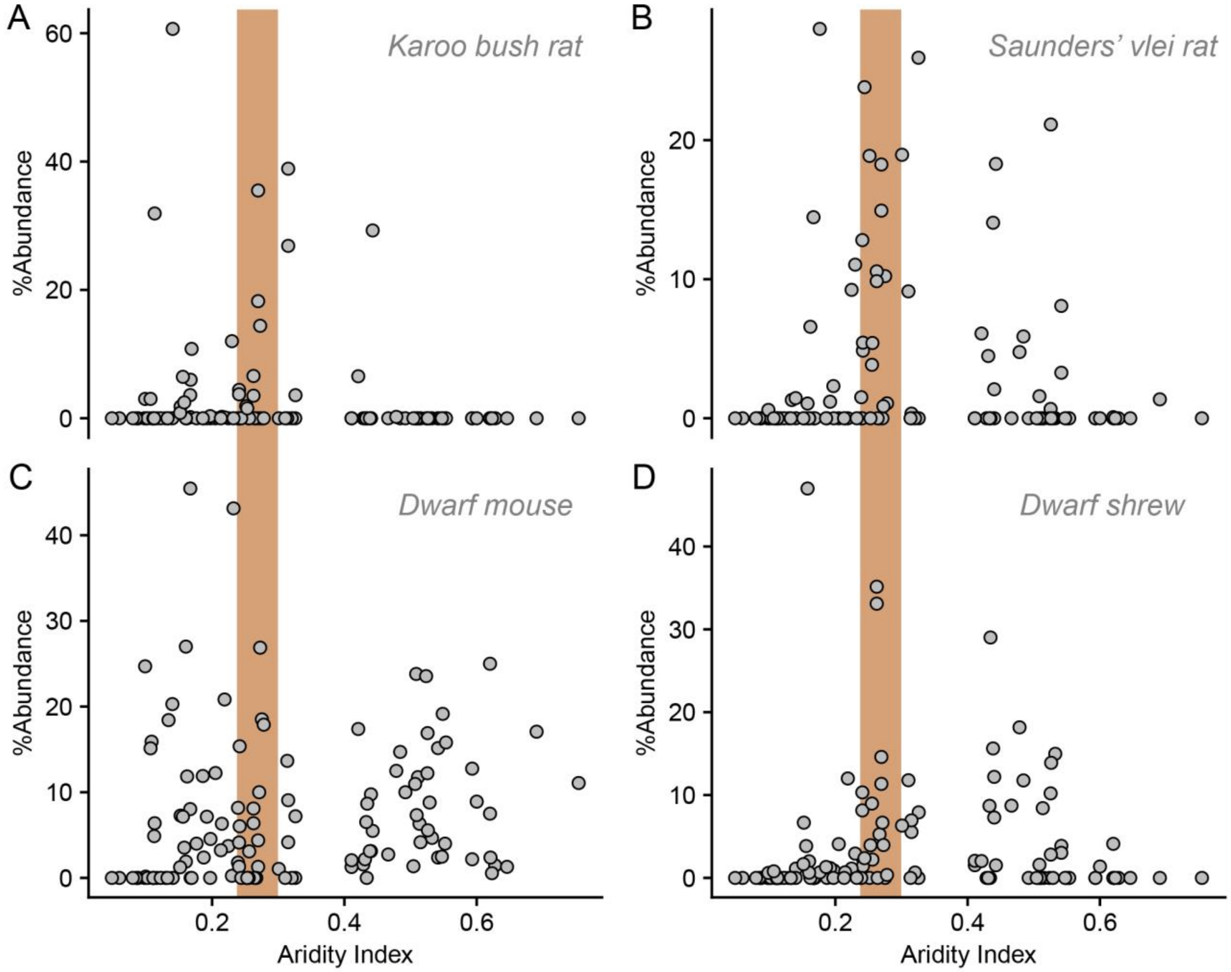

Figure 7. The percent abundance of (A) Karoo bush-rat, (B) Saunders' vlei rat, (C) dwarf mouse, and (D) dwarf shrew as a function of aridity (Aridity Index [AI] = MAP/MAE; larger values indicate greater moisture availability) in present-day southern Africa (data from Faith et al. 2019). Vertical bars denote range of aridity index values in the vicinity of Boomplaas Cave today (as in Figure 4).

Africa (Avery, 1999). In an analysis of modern barn owl-accumulated micromammal assemblages from the region, Avery (1999) showed that taxonomic diversity is unrelated to rainfall and aridity, undercutting her previous argument that low diversity signals a harsh LGM. We suspect that the temporal trends in diversity are instead tracking vegetation change. The two species whose dominance drives the reduction in LGM diversity, Saunders' vlei rat and forest shrew, are associated with a range of environments in southern Africa, but both have affinities for grassy habitats in hilly and mountainous terrain (Happold, 2013; Happold and Happold, 2013). Together with the environmental implications of the large mammals (**Figure 3**), the dominance of Saunders' vlei rat and forest shrew during the LGM, and the associated decline in micromammal diversity, are consistent with an expansion of grassy vegetation.

As further support for aridity during the LGM, Avery (1982) cited the relatively high frequencies (~4 to 5% of individuals) of Karoo bush rat (*Myotomys unisulcatus*) from members YOL to GWA (**Figure 6**), which she interpreted as indicating the most arid interval of the sequence (Avery, 1982: 316). Avery based this inference on characterizations of the Karoo bush rat as a stenotopic species generally associated with arid scrub habitats within the Great Karoo. However, Avery's (1999) more recent data on contemporary southern African micromammal assemblages suggests that the Karoo bush rat is more eurytopic than implied by such characterizations. Though the Karoo bush rat tends to be excluded from dry sub-humid (aridity index [AI] = 0.5 to 0.65) and humid (AI > 0.65) environments, it can be quite abundant in environments that are both more humid and more arid than those that characterize the region surrounding Boomplaas Cave today (**Figure 7**). Thus, the peak abundance of Karoo bush rat immediately before and during the LGM is not a clear indicator of aridity at Boomplaas Cave.

Deacon et al. (1984) expanded on Avery's (1982) initial analysis, using factor analysis to identify environmental shifts reflected by the Boomplaas Cave micromammals (bats excluded). Their analysis identified two factors that collectively account for 84% of the total variance in assemblage composition. Based on the ecological associations of species with strongly positive or negative scores on these factors, they interpreted Factor 1 in terms of temperature and Factor 2 in terms of aridity. To quantify environmental changes through the Boomplaas Cave sequence, they subsequently multiplied the factor loadings for each taxon by its relative abundance in a given stratum and summed these values to provide 'summary statistics' for each stratigraphic interval (see Thackeray, 1987 for further details). The summary statistics for Factor 1 are low throughout the LGM, with the Factor 2 scores also reaching lows in two of the three LGM members (**Figure 8**). Deacon et al. (1984) interpreted these results as indicating very cold and dry conditions during the LGM, in contrast to a warmer and more humid Holocene.

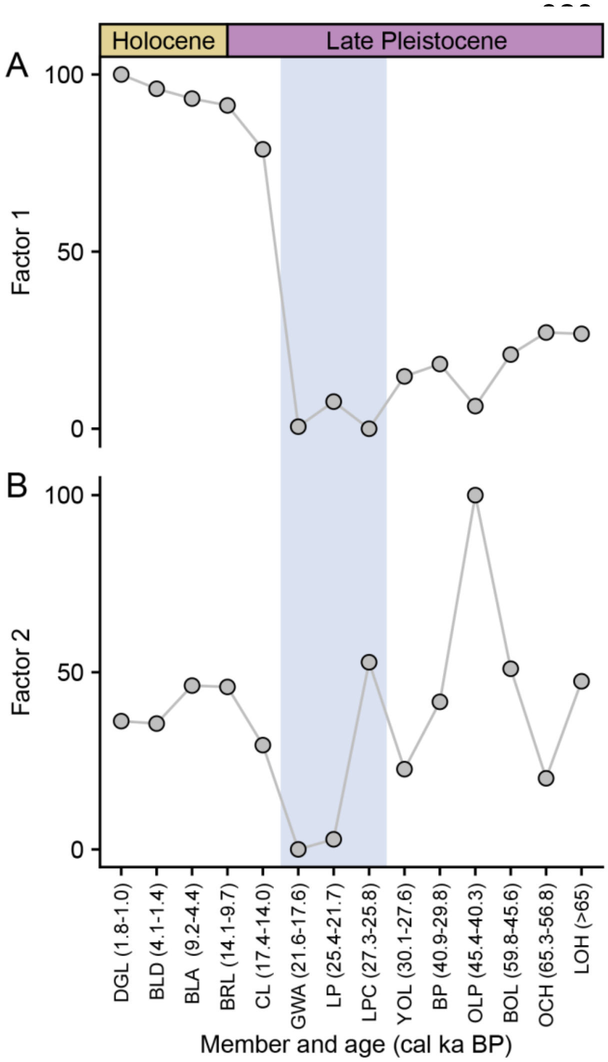

Figure 8. A: Factor 1 summary statistics derived from a factor analysis of micromammals across the Boomplaas Cave sequence (following Deacon et al., 1984). These values were interpreted as tracking temperature changes through the sequence, with larger values indicating warmer conditions (see Thackeray, 1987). B: Factor 2 summary statistics from the same analysis. These values were interpreted as tracking moisture availability across the sequence, with larger values indicating more humid conditions.

Deacon et al. (1984) based their interpretation of Factor 2 as indicative of a mesic-xeric gradient on an assessment of four taxa. They noted that the Factor 2 scores implied a dichotomy between dwarf mouse (*Mus minutoides*) and dwarf shrew (*Suncus varilla*) (greater Factor 2 scores) and Saunders' vlei rat and Karoo bush rat (smaller Factor 2 scores). Drawing from sparse zoological observations, they reasoned that the first two taxa are associated with relatively humid environments and that the latter two are tolerant of cold and dry extremes. Thus, the low

Factor 2 summary statistics during the LGM (except in member LPC; **Figure 8**), when Saunders' vlei rat and Karoo bush rat are particularly abundant, indicated aridity. **Figure 7** illustrates one of the problems with this interpretation, namely that data from present-day micromammal assemblages do not support the proposed mesic-xeric dichotomy for the species in question—they all can reach high abundances in relatively arid and humid environments. Perhaps more consequential are the results of a follow-up study by Thackeray (1987), who provided a more detailed analysis using a narrower set of micromammal taxa. He showed that the Factor 2 scores for each species were not tracking their environmental associations, but rather their body mass. The same is true of the Deacon et al. (1984) analysis, in which the Factor 2 scores for each species strongly correlate with their body mass ($r = -0.77$, $p < 0.001$) (factor scores from Deacon, 1983b; body masses from Smith et al., 2018). As Thackeray (1987) noted, the implication is that the Factor 2 summary statistics through the sequence are tracking the average body mass of the recovered species, likely due to taphonomic bias (e.g., differential preservation and recovery of the smallest species). This implies that the low Factor 2 summary statistics during parts of the LGM (**Figure 8**) are not indicating exceptional aridity, but instead a rarity of the very smallest species (e.g., the ~5 g dwarf shrew) and an abundance of the larger species (e.g., the ~100 g Saunders' vlei rat).

Though Thackeray's (1987) analysis undermined the interpretations made by Deacon et al. (1984), he went on to suggest an arid LGM at Boomplaas Cave by calling attention to the third factor (Factor 3) of his multivariate analysis. The Factor 3 scores for each taxon correlate moderately with the average precipitation across their geographic ranges, so Thackeray (1987)

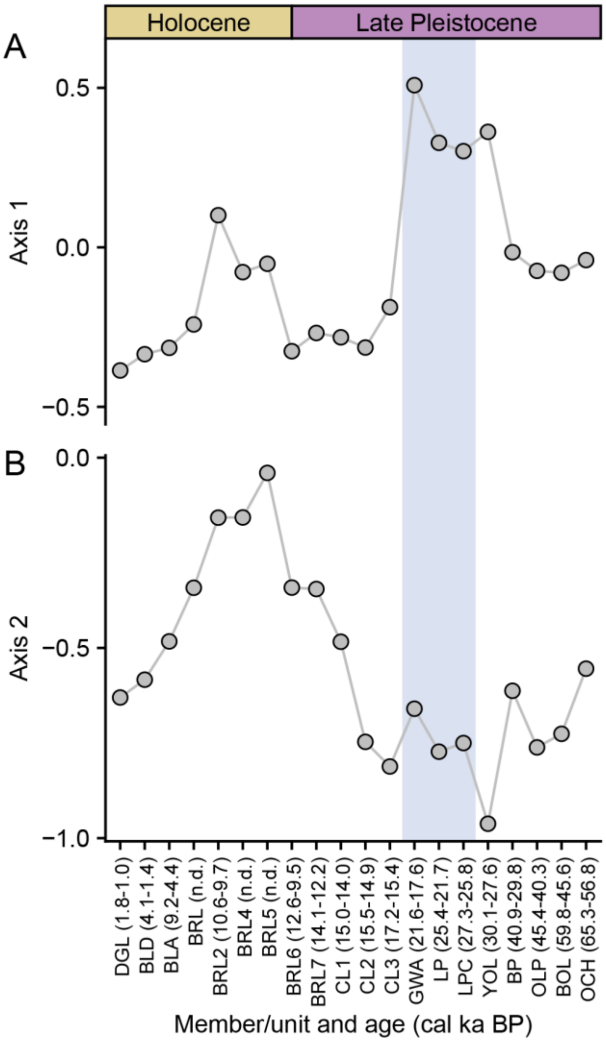

Figure 9. A: Axis 1 scores derived from a canonical correspondence analysis (CCA) of the micromammal assemblages across the Boomplaas Cave sequence (from Faith et al. 2019). These values strongly correlate with rainfall seasonality in modern assemblages (r = -0.88), with larger values indicating a greater proportion of winter rain. B: Axis 2 scores from the same analysis. These values strongly correlate with aridity in modern assemblages (r = -0.86), with larger values indicating greater aridity.

inferred that low Factor 3 summary statistics during the LGM indicated aridity. However, he also cautioned that the correlation underpinning this interpretation was not particularly robust—the weak coefficient of determination ($r^2 = 0.35$) implies that most of the variation (~65%) in Factor 3 reflects environmental or taphonomic parameters unrelated to precipitation. It follows that insofar as Factor 3 is informative of paleoenvironmental changes at Boomplaas Cave, it is not likely telling us much about moisture availability during the LGM.

More recent work aiming to tackle the problem of LGM moisture availability using microfaunal evidence has arrived at different conclusions. Drawing from Avery's (1999) data on recent micromammal assemblages across southern Africa, Faith et al. (2019) used canonical correspondence analysis to relate taxonomic composition to aridity and rainfall seasonality. In contrast to Thackeray's (1987) analysis, they observed strong relationships between assemblage composition and aridity ($r = -0.86$, $p < 0.001$), with the high coefficient of determination ($r^2 = 0.74$) providing greater confidence that there is a strong moisture availability signal. This relationship provides the basis for interpreting the ordination of the fossil assemblages in terms of aridity, with the Boomplaas Cave micromammals indicating relatively humid conditions before and during the LGM, followed by increased aridity across the last glacial-interglacial transition (LGIT) (**Figure 9**). The interval of peak aridity is not observed during the LGM, but rather during the early Holocene within member BRL.

Complementing interpretations derived from isotopic analysis of the Boomplaas Cave ungulates (Sealy et al., 2016), the micromammal assemblages further suggest that winter rainfall dominated during the LGM. The analysis provided by Faith et al. (2019) indicated that rainfall seasonality was a strong correlate of micromammal assemblage composition ($r^2 = 0.77$), with the LGM fossil assemblages providing the strongest winter rainfall signal for the sequence **(Figure 9**). Thackeray and Fitchett (2016) obtained equivalent observations in a previous study. They used climate data from across the geographic ranges of rodent species to develop transfer functions for estimating the seasonality of rainfall in the fossil record. Thus, the dominant signal from large mammals (Sealy et al., 2016) and micromammals (Faith et al., 2019; Thackeray and Fitchett, 2016) is a greater dominance of winter rainfall during the LGM.

5. CHARCOAL

The charcoal evidence from Boomplaas Cave has played a central role in characterizing the past vegetation and inferring climatic conditions through the sequence. Analyzed by two of Hilary Deacon's students (Anton Scholtz and David Daitz), the fossil charcoals were preliminarily described by Deacon (1979) and Deacon et al. (1983), with a detailed treatment provided in Scholtz's (1986) Master's thesis, which at the time was a pioneering study in anthracology. Scholtz (1986) presumed the charcoal assemblages were primarily derived from anthropogenic fires within the cave, though limited accumulation by other processes (e.g., colluvial processes) is possible (Deacon et al., 1983).

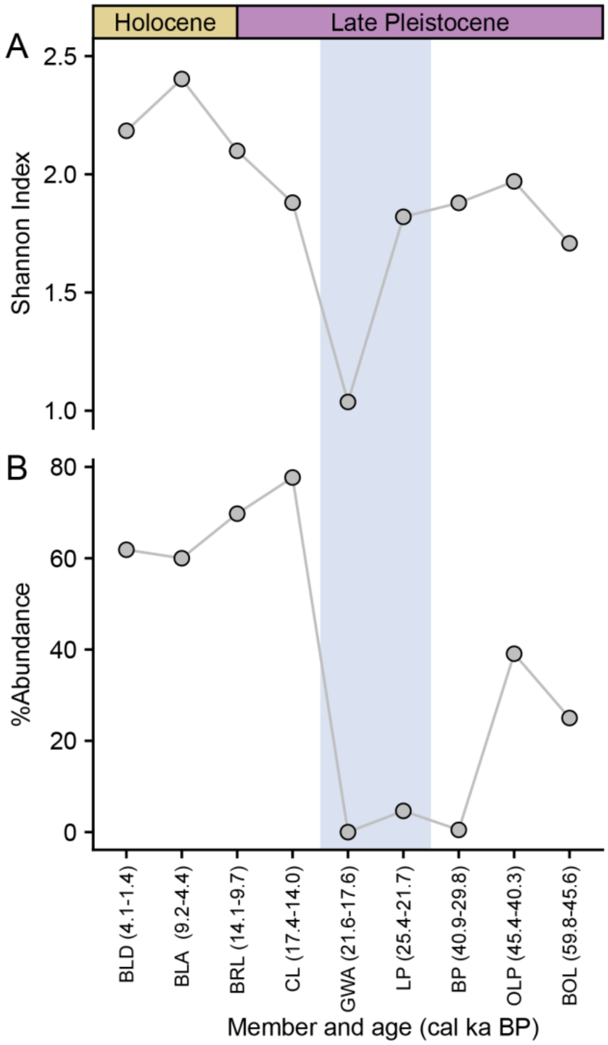

Figure 10. A: Taxonomic diversity (Shannon index) of the charcoal assemblages through the Boomplaas Cave sequence. B: The percent abundance of trees and tall shrubs recovered from Boomplaas Cave. Data from Scholtz (1986).

Like the faunas from Boomplaas Cave, the charcoal assemblages document marked temporal shifts in taxonomic composition, especially in the proportion of shrubs that are typical of the contemporary Fynbos Biome (e.g., Asteraceae) versus trees (e.g., *Acacia* and *Olea*) and other taxa that are today linked to Subtropical Thicket. Deacon et al. (1984; 1983) and Scholtz (1986) called attention to the taxonomically distinct assemblages from the LGM deposits, which are characterized by very low diversity (in member GWA/HCA), with few or no trees and a dominance of various Asteraceae, especially *Euryops* (**Figure 10**). This pattern contrasts starkly with the terminal Pleistocene (member CL) and Holocene assemblages (BLD to BRL), in which taxonomic diversity is high, trees and tall shrubs are abundant, and smaller shrubs (Asteraceae) are rare. They interpreted this as indicative of extremely cold and dry conditions during the LGM, such that only a few small shrubs could persist in the valley.

There are reasons to question both the evidence and its links to aridity. First, variation in the charcoal sampling strategy employed by Scholtz (1986) renders the temporal trends in diversity unreliable. Scholtz (1986) notes that in the upper levels of the sequence (BLD to CL), where the excavation was largest and charcoal fragments more numerous, he selected two specimens from each hearth or excavation square. For example, the large sample from the late Holocene member BLD (n = 215 specimens; Scholtz, 1986) derived from >100 different hearths and squares. This ensures a broad representation of charcoals from across the site, reducing the possibility of counting multiple fragments from the same fire or even the same piece of wood. Scholtz modified the sampling strategy to bolster sample sizes in the lower levels (from GWA/HCA and below) because the excavation extent was smaller and charcoal densities declined, increasing the sampling threshold to 10 or more specimens per hearth or square. In some cases, he analyzed all fragments from a hearth (Scholtz, 1986:74). Significantly, in the LGM sample from member GWA/HCA, where anomalously low diversity (**Figure 10A**) prompted inferences of extremely harsh conditions (Deacon et al., 1984; Deacon et al., 1983), only a single hearth was sampled (Scholtz, 1986: 95). This shift in sampling strategy increases the likelihood that identified

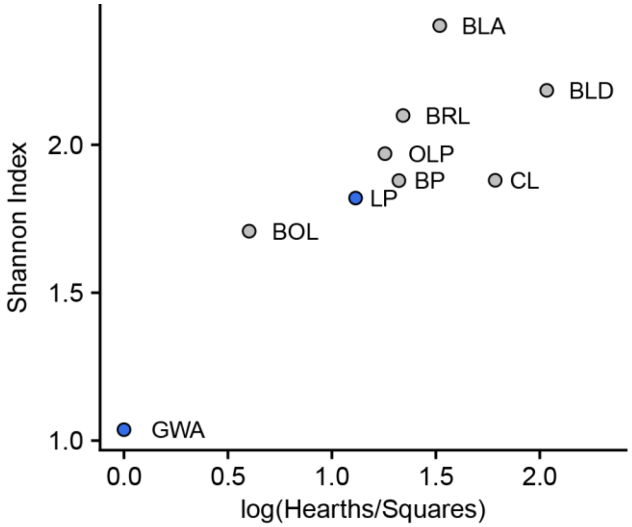

Figure 11. The relationship between sampling strategy (log-transformed number of hearths or squares) and taxonomic diversity (Shannon index) for the Boomplaas charcoal assemblages. Scholtz (1986) provided counts of the number of specimens analyzed from each member and following his description of the sampling strategy, we assume that two charcoal specimens were analyzed from each hearth or square from members BLD to CL and that 10 specimens were analyzed from each hearth or square in the underlying levels. Scholtz (1986) notes that only one hearth was sampled in member GWA/HCA. Data from Scholtz (1986).

charcoal fragments derived from the same piece of wood or burning event and complicates comparisons of taxonomic diversity across the sequence.

Scholtz (1986) quantified diversity using the Shannon index (**Figure 10A**), a heterogeneity index that increases with richness and evenness and that can be highly sensitive to sampling effects (Magurran, 1988, 2004). Though data on the exact number of hearths or excavation squares that Scholtz (1986) analyzed are unavailable, we can use his counts of identified specimens from each member to estimate the number of hearths or squares that were sampled (assuming two specimens from each hearth/square from BLD to CL and 10 specimens from each hearth/square in the underlying levels). Consistent with our understanding of how sampling affects diversity (Magurran, 1988, 2004), this value (log-transformed) is a strong predictor of the observed Shannon index values ($r = 0.845$, $p = 0.004$), with diversity increasing with the number of sampled hearths/squares (**Figure 11**). It follows that taxonomic diversity cannot be meaningfully compared across the sequence and that the anomalously low diversity in member GWA/HCA arises from the decision to sample only a single hearth.

In addition to problems with the diversity metrics, it is also unclear that aridity accounts for the taxonomic composition of the LGM charcoal assemblages. For instance, temperature alone is likely a key driver of taxonomic change from the LGM to the Holocene (e.g., Potts et al., 2013). It was ~6°C colder in the Boomplaas region during the LGM (Talma and Vogel, 1992), and many of the thicket taxa found in the Holocene assemblages are intolerant of frost (Cowling et al., 2005; Duker et al., 2015). Community distribution modelling predicts that cooler LGM temperatures drove a major contraction of Subtropical Thicket in southern Africa, eliminating this vegetation type from the Boomplaas Cave (Potts et al., 2013) and contributing to a relative dominance of Asteraceae. Furthermore, lower atmospheric pCO_2 could facilitate a contraction of tree cover (e.g., Kgope et al., 2010), perhaps also contributing to the lack of trees in parts of the Pleistocene sequence (**Figure 10B**). However, the study of charcoal fragments from recent (Pargeter et al., 2018) and ongoing radiocarbon dating efforts provides reason to question the extent to which the LGM was a treeless landscape. There are many LGM hearths that were never sampled in the initial studies (Deacon et al., 1983, 1984; Scholtz, 1986), and which attest to the presence of a diversity of trees that are closely linked to moist habitats (e.g., *Cunonia*, *Salix, Maytenus*; A. House pers. comm.). It is unclear why these hearth features were never studied, especially considering that Scholtz (1986) sampled only one LGM hearth from member GWA/HCA, but the identification of these trees, which are often found in afrotemperate forest today, indicates the nearby presence of well-watered environments. This observation further suggests that the *Euryops*-dominated assemblage reported by Scholtz (1986) is unlikely to be a robust reflection of the woody plants growing on the ancient landscape during the LGM.

Considering our analyses, it is clear that initial interpretations of the Boomplaas Cave charcoal assemblages are problematic. Temporal trends in taxonomic diversity, especially the anomalously low values in member GWA/HCA (**Figure 10A**), are driven by sampling artifacts that are well-known to affect diversity metrics. Likewise, more recent work demonstrates that the absence of thicket elements and relative dominance of Asteraceae during the LGM was in part a consequence of cooler temperature (Potts et al. 2013), whereas ongoing observations attest to the presence of several tree taxa that are incompatible with interpretations of a harsh, arid, and treeless landscape. Pending a study of the charcoal assemblages that implements a more consistent sampling strategy and includes greater representation of the unstudied LGM hearth features, the paleoenvironmental implications of the Boomplaas Cave charcoals are equivocal.

6. POLLEN

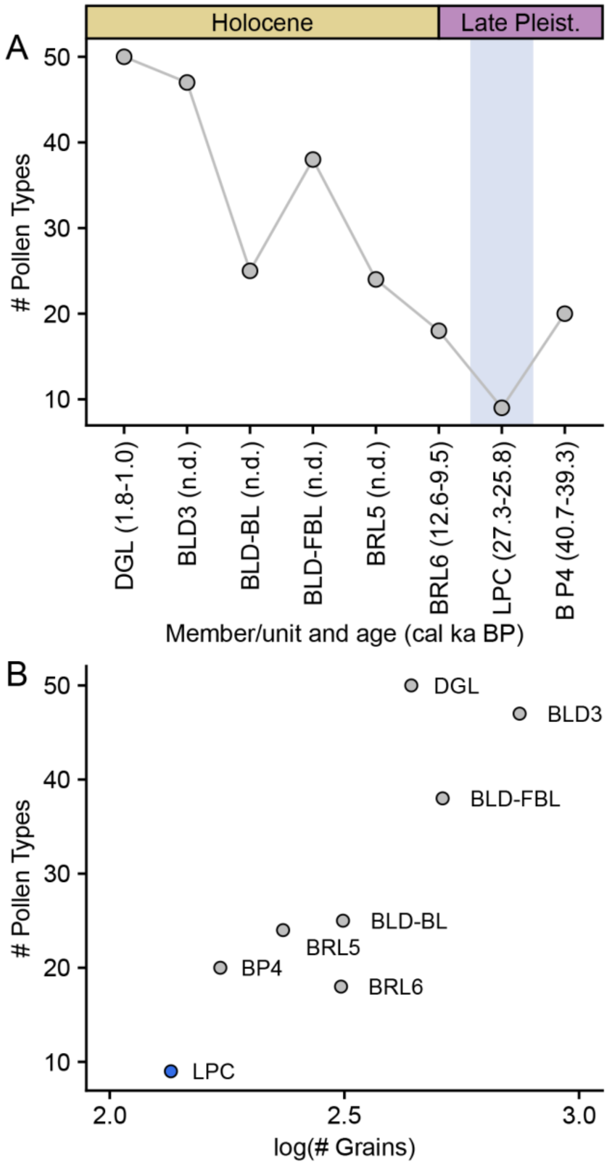

Figure 12. A: The number of pollen types across the Boomplaas Cave sequence. B: the relationship between sample size (# of grains counted) and the number of pollen types. The LGM member (LPC) is indicated in blue. Data from Deacon (1983b).

A pilot study of the pollen preserved through the Boomplaas Cave sequence remains incompletely reported, but it also has been used to support interpretations of aridity during the LGM. Both Deacon et al. (1984) and Deacon and Lancaster (1988) provide brief descriptions of the pollen assemblage in their syntheses of the paleoenvironmental data from the site, with the most detailed account provided in an unpublished report (Deacon, 1983b). These examinations emphasize the contrast between the LGM sample from member LPC (27.3-25.8 cal ka BP) relative to the Holocene samples. Most notably, diversity is very low in the LGM sample, which preserved only nine different pollen types, many of which are Asteraceae (cold-tolerant *Elytropappus*-type being most abundant). The Holocene samples are similarly dominated by Asteraceae, but there is also much greater diversity, with dozens of different types identified from each member (**Figure 12**). Paralleling the initial inferences made for the micromammal and the charcoal assemblages, Deacon et al. (1983b) interpreted this temporal shift in diversity as evidence for an arid LGM followed by a more mesic Holocene.

As we demonstrated with the charcoal evidence, sampling artifacts also drive the diversity trends observed in the pollen record. Though it is well-documented that taxonomic richness increases as a function of sample size (Gotelli and Colwell, 2001; Grayson, 1984; Lyman, 2008; Magurran, 2004), Deacon et al. (1983b) did not consider variable sampling effort in the initial pollen diversity examinations. Deacon's (1983b) report provides the number of pollen grains counted and the number of pollen types identified through the sequence. Consistent with the understanding of how sampling influences richness, the correlation between the number of grains (log-transformed) and the number of pollen types is strong ($r = 0.88$, $p = 0.004$; **Figure 12**), implying that the anomalously low diversity observed during the LGM reflects the lack of grains counted (135 in member LPC vs. ~545-826 for each of the Holocene members) rather than any meaningful aspect of the paleoenvironment.

Furthermore, the dominance of Asteraceae, especially *Elytropappus*-type (also known as Stoebe-type), in the LGM pollen sample need not imply aridity. This pollen type has associations with both arid and humid environments in southern Africa (Chevalier et al., 2021), such that any direct interpretation in terms of LGM moisture availability should be treated with caution. However, insofar as present-day vegetation gradients in the vicinity of Boomplaas Cave can be extrapolated to the past, the dominance of *Elytropappus*-type pollen is most parsimoniously interpreted as indicative of a more humid climate. In the transitional shrublands near Boomplaas Cave, renosterveld (the vegetation type dominated by *Elytropappus*) is associated with relatively humid environments closer to the Swartberg range (Vlok and Schutte-Vlok, 2010). As aridity increases further south of the Swartberg (**Figure 1**), renosterveld is replaced by asbosveld, which is dominated by *Pteronia incana*, and then by Subtropical Thicket (Vlok and Schutte-Vlok, 2010). Keeping in mind that cooler temperatures during the LGM would have eliminated many taxa presently associated with Subtropical Thicket (Potts et al., 2013), present-day vegetation gradients imply that increased aridity might have favored expansion of *Pteronia* as the dominant cold-tolerant Asteraceae, whereas increased humidity would have favored expansion of *Elytropappus* in the Cango Valley. It follows that the abundance of *Elytropappus* in the LGM pollen assemblage is reasonably interpreted as a consequence of both cold temperatures (eliminating thicket elements) and increased humidity. Importantly, renosterveld supports a dense understory of palatable grasses (e.g., Vlok and Schutte-Vlok, 2010), such that an expansion of grassy renosterveld-like habitats during the LGM is also consistent with the faunal evidence from Boomplaas Cave.

7. DISCUSSION

7.1. Moisture availability during the LGM

The many ways that researchers can use fossil remains to reconstruct paleoenvironments are unified by the same fundamental approach (Croft et al., 2018; Faith and Lyman, 2019). Different techniques typically begin with observing present-day relationships between organisms (e.g., their taxonomic identity, functional traits, community structure) and an environmental variable, such as temperature, moisture availability, or vegetation cover. These relationships provide the uniformitarian basis for inferring paleoenvironmental conditions from fossil assemblages (Faith and Lyman, 2019).

With respect to the large mammal and micromammal assemblages from Boomplaas Cave, interpretations of harsh and arid conditions during the LGM (Avery, 1982; Deacon et al., 1984; Deacon and Lancaster, 1988; Thackeray, 1987) lack this fundamental inferential link. Grazer-dominated ungulate communities and the grassy environments they imply do not signal an arid environment (**Figure 4**); low micromammal diversity is not associated with low precipitation in southern Africa (Avery, 1999); and the abundance of certain micromammal taxa during the LGM (e.g., Saunders' vlei rat and Karoo bush rat) need not imply drier conditions relative to today (**Figure 7**). In contrast, present-day observations substantiate interpretations of relatively humid conditions during the LGM. The taxonomic composition of the large mammal and micromammal assemblages, as well as ungulate community diversity, can all be linked to moisture availability, and they are indicative of relatively humid conditions during the LGM (**Figure 4-5**; Faith, 2013b; Faith et al., 2019). The inferences derived from ungulate community diversity are particularly robust, as the ecological mechanisms underpinning the link between diversity and moisture availability are well understood (Olff et al., 2002).

Interpretations of arid conditions derived from the charcoal and pollen assemblages are problematic for these and other reasons. The lack of thicket elements in the LGM charcoal assemblage, which contributes to a relative dominance of Asteraceae (**Figure 10B**), is likely a consequence of cooler temperature (Potts et al., 2013; Duker et al. 2014) rather than aridity (Deacon et al., 1984; Deacon et al., 1983; Scholtz, 1986). Additionally, ongoing work documents the presence of trees that are closely linked to moist habitats (e.g., *Cunonia*, *Salix, Maytenus*), contradicting interpretations of the LGM as a dry and treeless landscape. With respect to the pollen, present-day vegetation gradients in the region indicate that the dominance of cold-tolerant *Elytropappus* in the LGM pollen record is best explained as a consequence of wetter (and cooler) rather than drier conditions. Critically, though Deacon et al. (1984) placed considerable emphasis on the evidence for low diversity in both the LGM charcoal and pollen records, our analyses show that variation in taxonomic diversity is driven by sampling artifacts (**Figure 11-12**). Low plant diversity in the LGM assemblages is a consequence of relatively limited sampling and not a reflection of low plant diversity on the landscape.

Beyond relying on present-day ecological observations, we can strengthen confidence in paleoenvironmental reconstruction when independent records support them (Faith and Lyman, 2019). This is also where the early interpretations of a harsh and arid LGM fall short. One of the primary independent records available to Deacon et al. (1984) is the stalagmite from the nearby (~3 km east of Boomplaas) Cango Caves (Talma and Vogel, 1992; Vogel, 1983). The Cango stalagmite formed over much of the past ~50 kyr, except for a hiatus during the late glacial and early Holocene that may imply a lack of water in the system. Because speleothem formation requires water, Deacon et al. (1984) struggled to reconcile this hiatus with LGM aridity, suggesting that lack of formation at a time they believed to be relatively humid resulted from unspecified interactions between vegetation and groundwater. No special pleading is required if we accept that the LGM was an interval of relatively humid conditions, though a much larger sample of speleothems would be required to confidently link growth patterns to climate change (e.g., Vaks et al., 2007).

More recent independent evidence reinforces our interpretation of a wetter LGM at Boomplaas Cave. Isotopic analysis of the Seweweekspoort hyrax middens, located ~70 km west of Boomplaas Cave in the Swartberg range (**Figure 1**), indicates a relatively humid LGM followed by a more arid Holocene (Chase et al., 2017, 2018). In addition, downscaled climate models for southern Africa imply greater precipitation during the LGM relative to the present (Engelbrecht et al., 2019), though not all features of the Boomplaas Cave evidence align with these models (see below). Thus, the sum of the existing evidence, including proxy records and climate models, is consistent with relatively humid conditions during the LGM within the southern Cape.

7.2. Rainfall seasonality during the LGM

The Boomplaas Cave proxy records suggest that increased moisture availability during the LGM was associated with a greater dominance of C_3 grasses and enhanced winter precipitation, implying a more seasonal rainfall regime than at present (Sealy et al., 2016; Thackeray and Fitchett, 2016; Faith et al., 2019). This interpretation is consistent with the dominance of C_3 vegetation indicated by the Cango Caves speleothem (Talma and Vogel, 1992), though more recent work complicates the picture. Isotopic analysis of speleothems from Efflux Cave (~15 km east of Boomplaas Cave; **Figure 1**) suggests an important C_4 grass component during the LGM (Braun et al., 2020). Taken together, the speleothem records indicate spatial heterogeneity in the distribution of C_3 and C_4 grasses within the Little Karoo during the LGM. Because C_3 grasses tend to be more prevalent on south-facing slopes and C_4 grasses favor north-facing slopes (Cowling and Campbell, 1983), differences between the Cango Caves and Efflux Cave speleothem records may reflect localized topographic factors (Braun et al., 2020). If so, then the baseline isotope values of the two nearby records should not be interpreted in terms of regional climate—i.e., the C_3 signal from Cango Caves need not imply a dominance of winter rains whereas the C_4 signal from Efflux Cave need not imply stronger summer rains. However, temporal trends within those records should be reliable (see Chase et al., 2021), as topography is unlikely to have changed in any meaningful way since the LGM. Efflux Cave lacks a post-LGM record (Braun et al., 2020), but the isotope record from the Cango Caves speleothem (Talma and Vogel, 1992), suggest a greater proportion of summer rain during the Holocene. The same pattern is also seen in the Seweweekspoort hyrax middens (Chase et al., 2017, 2018), Thus, the overall signal from Boomplaas Cave, Cango Caves, and Seweweekspoort is that the LGM was characterized by a greater dominance of winter rains compared to today.

Relative to carbon isotope records derived from speleothems or hyrax middens, the large mammal isotope record from Boomplaas Cave should document vegetation at larger spatial scales, reflecting the geographic ranges over which herbivores foraged and the distances over which humans and carnivores transported their remains to the site. With this in mind, the strong C_3 signal observed in LGM grazers implies that C_3 grasses were dominant relative to C_4 grasses (Sealy et al., 2016). As argued by Sealy et al. (2016), and in agreement with the micromammal evidence (Thackeray and Fitchett, 2016; Faith et al., 2019), a reasonable explanation is a greater proportion of winter rainfall, as the regional LGM temperature depression of 6°C (Talma and Vogel, 1992) would not in itself be sufficient to offset the impact of reduced atmospheric pCO_2 concentrations that would otherwise favor C_4 grasses (Ehleringer et al., 1997; Collatz, et al., 1998). The herbivore isotope data do not agree well with modelled outputs predicting mostly C_4 grasses near Boomplaas Cave during the LGM (Grobler et al., 2023). One possible explanation for this discrepancy is that the modelled distribution of C_3 and C_4 grasses (Grobler et al., 2023) is based on climate models that predict an increase in summer precipitation within the southern Cape and across much of southern Africa during the LGM (Engelbrecht et al., 2019). While this should favor an expansion of C_4 grasses, some proxy records suggest a reduction in summer rainfall during the LGM (e.g., Chevalier and Chase, 2015; Sealy et al., 2020), paralleling previous analyses suggesting that significant features of the general circulation model simulations of LGM climate employed in the Engelbrecht et al. (2019) study do not perform well in southern Africa (Chevalier et al. 2017). Alternatively, it is also plausible that the LGM taxa assumed to be grazers at Boomplaas Cave were consuming more dicots than their contemporary counterparts, as has been demonstrated for early Pleistocene faunas in southern Africa (e.g., Stynder, 2009). If so, then the small C_4 grass component implied by herbivore isotope data (Sealy et al., 2016) would underestimate the importance of C_4 relative to C_3 grass in the diet. Whatever the explanation, this data-model discrepancy highlights the need for future work. This includes generating additional empirical records that speak to rainfall seasonality and the distribution of C_3 and C_4 grasses across southern Africa, as well as continued development, evaluation, and refinement of climate and paleodistribution models.

7.3. Synthesis of the Boomplaas Cave evidence

The sum of the evidence from Boomplaas Cave supports early conceptual models of Quaternary climate dynamics in southern Africa, whereby the expansion of Antarctic sea ice during glacial phases translated to an equatorward shift of the southern hemisphere westerlies, resulting in more intense and more frequent winter storms across southernmost Africa (Chase and Meadows, 2007; Cockcroft et al., 1987; van Zinderen Bakker, 1976). Together with a proposed weakening of the tropical systems that bring summer rain to the region, an observation supported by multiple paleoenvironmental records (see reviews in Chase et al., 2017; Chase and Meadows, 2007), the outcome is an expansion of the winter rainfall zone (but see Engelbrecht et al., 2020). In agreement with this scenario, research aiming to infer rainfall seasonality from the Boomplaas Cave records has consistently indicated a dominance of winter rain during the LGM (Faith et al., 2019; Sealy et al., 2016; Thackeray and Fitchett, 2016). Cooler conditions during the LGM must have played a role in increasing moisture availability, with the ~6°C drop in average temperatures near Boomplaas Cave (Talma and Vogel, 1992) resulting in a considerable decline in evapotranspiration. Whether annual precipitation increased is less clear from the Boomplaas Cave record, as the environmental proxies derived from the site are more directly influenced by moisture availability (i.e., precipitation relative to evapotranspiration) than by the overall rainfall amount (Chevalier and Chase, 2016; Faith et al., 2020). The downscaled climate models produced by Engelbrecht et al. (2019) suggests that increased precipitation may account for a wetter LGM, though other aspects of these models, namely an increase in summer rains that should facilitate expansion of C_4 grasses (Grobler et al., 2023) do not agree well with the proxy records from Boomplaas Cave. This discrepancy aside, when it comes to understanding the terrestrial ecosystems in which plants, animals, and human populations were embedded, Boomplaas Cave's records strongly indicate a relatively humid LGM.

8. CONCLUSION

Boomplaas Cave is a critical archive of Quaternary environments in the southern Cape, yet ongoing uncertainty over the interpretation of its paleoenvironmental records compromises its value. Disagreement surrounding climatic conditions during the LGM has been especially consequential, promoting uncertainty about Quaternary climate dynamics throughout the region. We believe it is time to move beyond this uncertainty. Though the early literature proposing exceptional aridity during the LGM at Boomplaas Cave occupies an important place in the intellectual history of paleoenvironmental research in southern Africa, the interpretations lack strong ecological links between the evidence and the interpretation, and some critical observations derive from spurious patterns driven by sampling artifacts. In the absence of robust evidence to the contrary, we see little reason to view the sum of the evidence from Boomplaas Cave as ambiguous or indicative of an arid LGM. In contrast, present-day ecological observations support interpretations of a relatively humid LGM, consistent with independent paleoenvironmental records. Though future research will surely refine the general pattern of climate dynamics through time, the evidence from Boomplaas Cave now allows us to make definitive statements: the LGM was a time of relatively humid conditions, with the transition to the Holocene characterized by increased aridity.

Acknowledgments

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