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The last glacial maximum climate at Boomplaas Cave, South Africa

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1 **ABSTRACT**

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

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

21 1. INTRODUCTION

22 South Africa's southern Cape has long been a focus of research on Quaternary climate change
23 and its influence on terrestrial ecosystems (e.g., Cockcroft et al., 1987; Deacon and Lancaster,
24 1988; van Zinderen Bakker, 1976). Encompassing the southern coastal plains and the east-west
25 trending ranges of the Cape Fold Belt, the southern Cape is situated at the transition between
26 regions of temperate and tropical climate dominance (**Figure 1**). To the west, the winter rainfall
27 zone (WRZ; sensu Chase and Meadows, 2007) receives most of its rainfall during the austral
28 winter, as frontal systems associated with the southern hemisphere westerlies shift northwards. In
29 contrast, most of southern Africa falls within the summer rainfall zone (SRZ), which receives
30 rainfall during the austral summer when tropical easterly flow strengthens and transports
31 moisture from the Indian Ocean (Tyson, 1986). The southern Cape falls within the aseasonal
32 rainfall zone (ARZ). It receives rainfall throughout the year from both sources, such that changes
33 in the dominance of temperate and tropical climate systems, and the interactions between them,
34 are reflected in the region's Quaternary paleoenvironmental archives (Chase et al., 2017; Chase
35 and Meadows, 2007).

36 Among the more important Quaternary paleoenvironmental archives in the region is
37 Boomplaas Cave. Located on the southern flanks of the Swartberg range (**Figure 1**),
38 archaeological excavations at Boomplaas Cave in the 1970s uncovered a rich sequence of floral
39 and faunal remains spanning the last >65,000 years (Deacon, 1979). A substantial body of
40 research over the last four decades has drawn from this evidence to reconstruct ancient plant and
41 animal communities (e.g., Avery, 1982; Klein, 1978; Scholtz, 1986), inform on climate
42 dynamics (e.g., Faith et al., 2019; Sealy et al., 2016; Thackeray, 1987), and evaluate how human
43 populations responded to environmental changes through time (e.g., Chase et al., 2018; Deacon

44 and Thackeray, 1984; Deacon, 1984; Pargeter and Faith, 2020). This literature has grown
45 considerably since the first syntheses of the paleoenvironmental records from Boomplaas Cave
46 (Deacon, 1983a; Deacon et al., 1984; Deacon and Lancaster, 1988), but so too has the divergence
47 of opinions concerning their interpretation (e.g., Chase and Meadows, 2007; Faith et al., 2019;
48 Marean et al., 2014; Thackeray, 2020).

49 Disagreements over climatic conditions during the Last Glacial Maximum (LGM; 26-19
50 ka) are especially consequential for paleoenvironmental research in southern Africa. Early
51 research on the paleoenvironmental records from Boomplaas Cave reconstructed the LGM as
52 exceptionally arid and ‘harsh’ (e.g., Avery, 1982; Deacon et al., 1984; Deacon and Lancaster,
53 1988; Scholtz, 1986). Archaeologist Hilary Deacon, who directed the initial research at the site,
54 was so confident in this assessment that he described the evidence for a dry LGM as
55 “incontrovertible” (Deacon, 1983a:326). The interpretation of LGM aridity was echoed in
56 subsequent syntheses and regional overviews (Chase and Meadows, 2007; Deacon et al., 1984;
57 Deacon and Lancaster, 1988), though Chase and Meadows (2007) questioned the
58 incontrovertible nature of the evidence, suggesting that some presumed indicators of aridity (e.g.,
59 expansion of grassy vegetation; Deacon et al., 1984) from Boomplaas Cave and elsewhere in the
60 southern Cape could be tracking climatic variables unrelated to precipitation. This initial seed of
61 doubt has given way to a rejection of the early characterizations of the LGM, with recent work
62 interpreting the evidence from Boomplaas Cave as indicative of humid and highly productive
63 conditions (Chase et al., 2018; Faith, 2013a, b; Faith et al., 2019). These incompatible
64 interpretations have stimulated debate (Faith et al., 2019, 2020; Thackeray, 2020) and fueled
65 uncertainty about the climate history of southernmost Africa (see review in Marean et al., 2014).

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

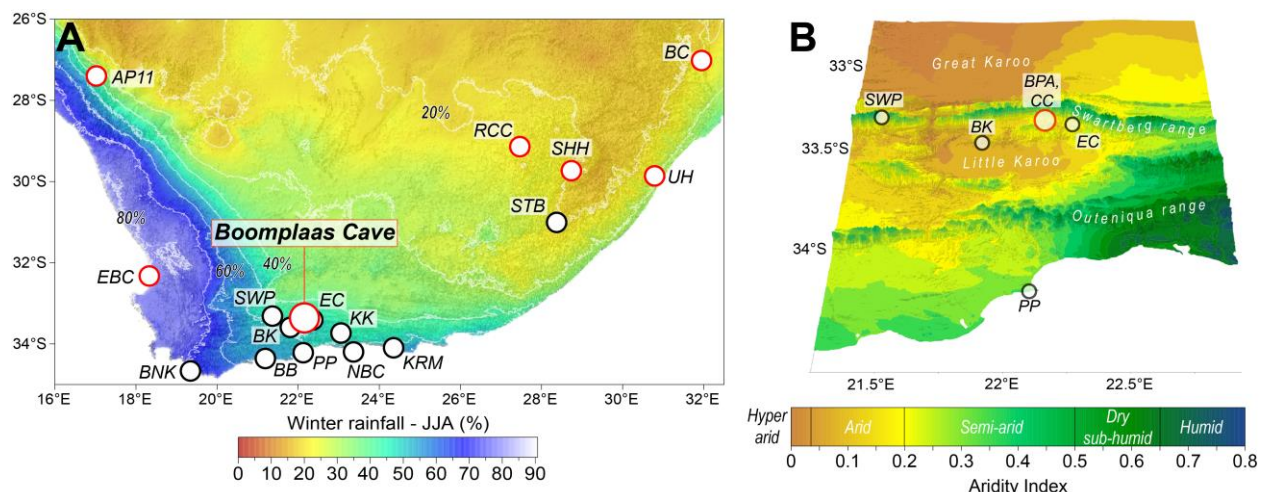


Figure 1. (A) Map of southern Africa showing the location of Boomplaas Cave [BPA] relative to other sites in the region: Buffelskloof [BK], Blombos Cave [BB], Border Cave [BC]), Byneskranskop [BNK], Cango Cave [CC], Efflux Cave [EC], Kangkara [KK], Klasies River Mouth [KRM], Nelson Bay Cave [NBC], Pinnacle 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).

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

82

83 **2. BOOMPLAAS CAVE**

84 Boomplaas Cave overlooks the Cango Valley from the southern flanks of the Swartberg range,
85 which separates the arid to semi-arid Great Karoo to the north from the Little Karoo to the south
86 (**Figure 1**). The site falls within a transitional shrubland whose component species vary as
87 moisture increases from the valley floor up the slopes of the Swartberg (Vlok and Schutte-Vlok,
88 2010). Succulent Karoo and Subtropical Thicket vegetation historically dominated the lowlands
89 ~10-15 km south of the cave, giving way to renosterveld at the base of the Swartberg, with
90 fynbos occurring at higher elevations north of the cave. Thicket and closed woodland occur
91 along watercourses draining the Swartberg and flowing through the Cango Valley (Moffett and
92 Deacon, 1977), including the Grobbelaars River, located ~300 m south of the cave. The annual
93 rainfall of ~400 mm is evenly distributed throughout the year, contributing to a mix of C₃ and C₄
94 grasses in the local environment (Vogel et al., 1978; Grobler et al., 2023). Large mammal
95 communities in the region were historically dominated by small-bodied browsers and mixed
96 feeders, including klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), and
97 grey rhebok (*Pelea capreolus*), with the less abundant large-bodied grazers including hartebeest
98 (*Alcelaphus buselaphus*) and mountain zebra (*Equus zebra*) (Boshoff and Kerley, 2001; Skead,
99 2011; Vlok and Schutte-Vlok, 2010).

100 Deacon conducted excavations at Boomplaas Cave from 1974 to 1979 as part of a
 101 broader effort to understand the effects of Quaternary paleoenvironmental change on human

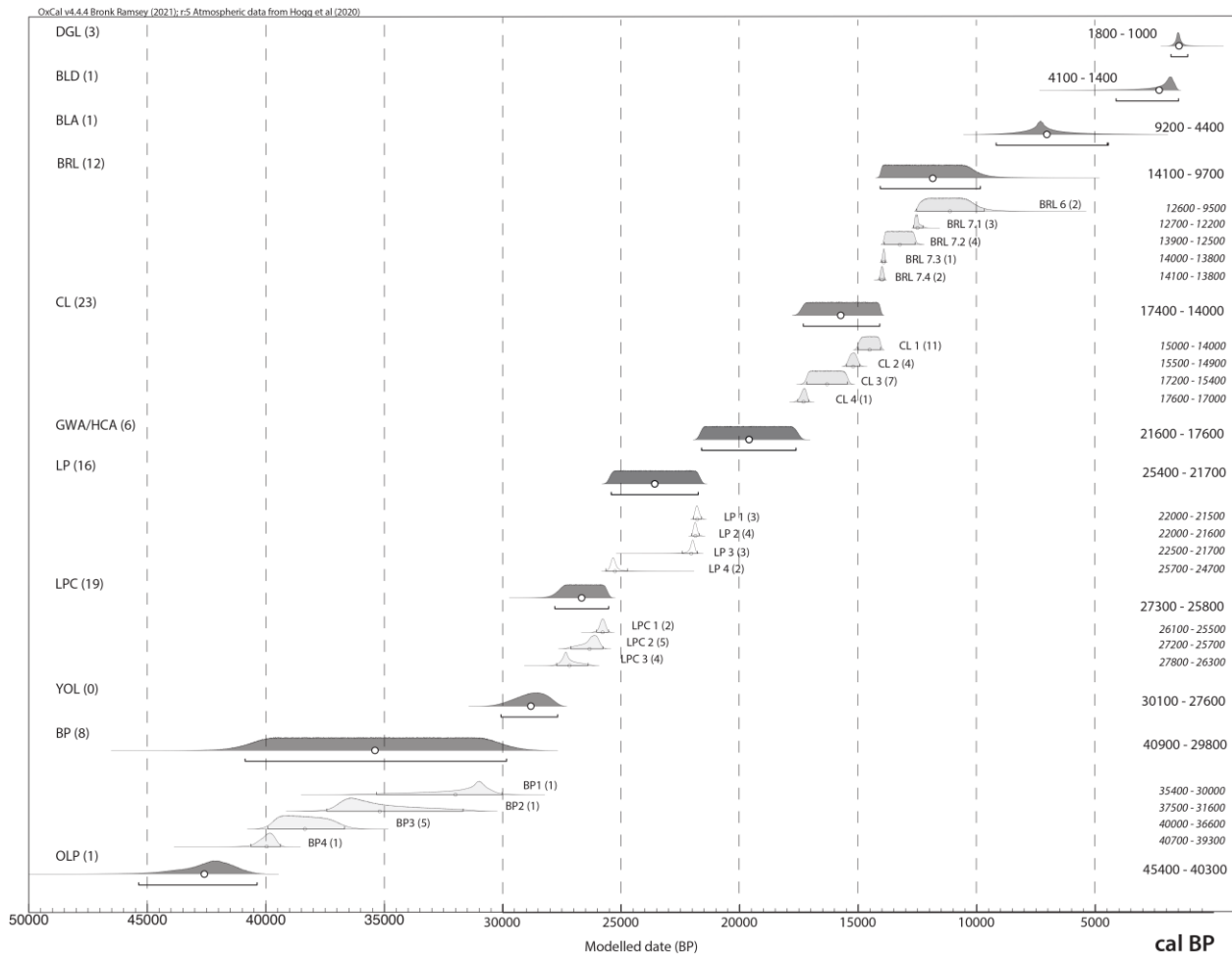


Figure 2. The radiocarbon chronology of the Boomplaas Cave sequence. Ages for each member and for select units are modelled ^{14}C ages with 2σ ranges. The chronology is updated from Pargeter et al. 2018 in OxCal 4.4 (Bronk Ramsy (2009) using ShCal20 (Hogg et al. 2020). Values in parentheses indicate 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).

102 behavioral evolution in the southern Cape (Deacon, 1979; Deacon, 1995). His excavations
 103 uncovered a well-stratified sedimentary sequence extending from >65 ka to the protohistoric
 104 period, with the main stratigraphic aggregates divided into a hierarchical scheme of members,
 105 units, and subunits (**Figure 2**). The deposits overlapping in age with at least parts of the LGM
 106 include members LPC (27.3-25.8 cal ka BP), LP (25.4-21.7 cal ka BP), and GWA/HCA (21.6-
 107 17.6 cal ka BP), with the overlying subunits of members CL (17.4-14.0 cal ka BP) and BRL

108 (14.1-9.7 cal ka BP) providing a finely resolved record of the last glacial-interglacial transition
109 (LGIT) (Pargeter et al., 2018). Pargeter directs the current excavations focused on members
110 GWA/HCA to BP.

111 The primary sources of paleoenvironmental evidence derived from Deacon’s excavations,
112 and which have been the subject of varied interpretations, include the large mammal (Faith,
113 2013a; Klein, 1978, 1983; Sealy et al., 2016), micromammal (Avery, 1982, 1983b), charcoal
114 (Deacon et al., 1983; Deacon and Lancaster, 1988; Scholtz, 1986), and pollen assemblages
115 (Deacon et al., 1984; Deacon and Lancaster, 1988). Below, we examine these datasets, outlining
116 the nature of the evidence and how it has been used to infer LGM moisture availability. Because
117 these climate proxies are more directly influenced by the amount of water in the environment
118 rather than total precipitation, we focus our discussion on moisture availability, which is
119 primarily influenced by the combination of precipitation and temperature via its effect on
120 evapotranspiration (e.g., Chevalier and Chase, 2016). This is important here because lower LGM
121 temperatures (e.g., Heaton et al., 1986; Talma and Vogel, 1992; Chevalier and Chase, 2015), and
122 the associated decline in evapotranspiration, could drive an increase in moisture availability in
123 the absence of precipitation change. Following the UNEP (1997) climate classification scheme,
124 we discuss moisture availability in terms of a gradient from relatively arid (i.e., less precipitation
125 relative to evapotranspiration) to relatively humid (i.e., more precipitation relative to
126 evapotranspiration). Throughout our evaluation of Boomplaas Cave, we limit our discussion to
127 ordinal-scale trends (e.g., more or less arid/humid), as the kinds of proxy records examined here
128 are poorly suited for more precise numerical estimates of paleoclimate variables (e.g., Faith and
129 Lyman, 2019).

130

131 **3. LARGE MAMMALS**

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

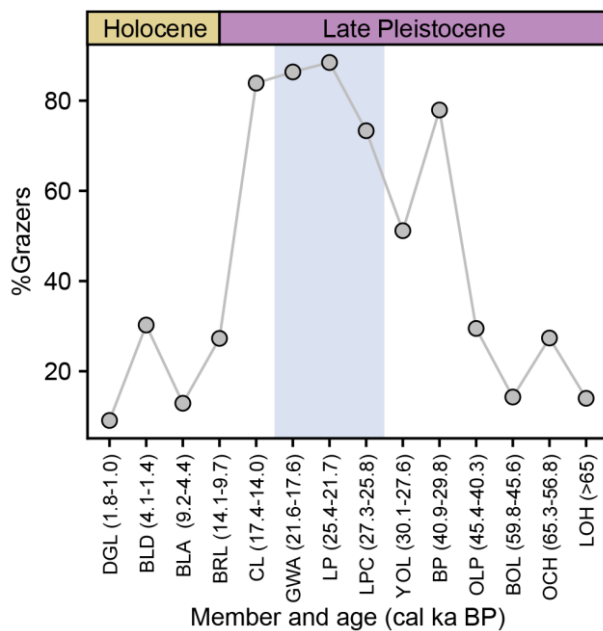


Figure 3. Changes in the abundance (% of specimens) of ungulate grazers through the Boomplaas Cave sequence (data from Klein, 1983 for DGL; Faith 2013a for BLD through LOH). Vertical bar denotes the LGM members.

change, suggesting that environmental forcing is a primary driver of faunal turnover through the sequence (Faith, 2013a).

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

149 Holocene levels at Boomplaas, the faunas from member BP (40.9-29.8 cal ka BP) through CL
 150 (17.4-14.0 cal ka BP) are dominated by grazers, including various alcelaphin antelopes
 151 (*Alcelaphus buselaphus*, *Connochaetes taurinus*, *C. gnou*, and *Damaliscus pygargus*), equids
 152 (*Equus capensis* and likely both *E. quagga* and *E. zebra*), and an extinct caprin (see Brink, 1999
 153 for details on the caprin; see Faith, 2013a for the latest faunal list). Klein (1978, 1983)

154 interpreted these changes in terms of vegetation structure, suggesting that grasses were more
155 widespread when grazers were dominant, particularly during the LGM. This interpretation
156 remains uncontroversial, mirroring faunal changes observed elsewhere in the region (e.g., Klein,
157 1972; Schweitzer and Wilson, 1982).

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

177 Grobbelaars River and the Swartberg range (Moffett and Deacon, 1977; Vlok and Schutte-Vlok,
 178 2010). In light of these observations, and acknowledging that a detailed understanding of LGM

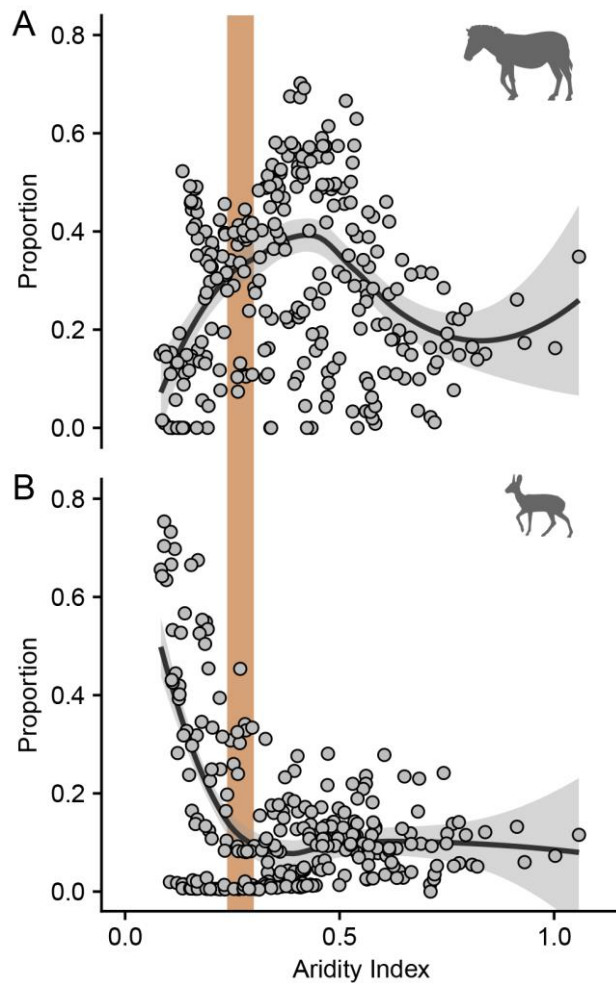


Figure 4. A: The proportion of equids and alcelaphins across southern Africa as a function of aridity (Aridity index = MAP/MAE; MAP = mean annual precipitation; MAE = mean annual evapotranspiration; larger values indicate greater moisture). B: The relative abundance of *Raphicerus* spp., *Oreotragus 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.

vegetation will also require consideration of fire regimes (Kraaij and van Wilgen, 2014), lower temperature (Duker et al., 2014), reduced atmospheric pCO₂ (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).

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**

200 illustrates the relative abundance of equids and alcelaphin antelopes, the dominant ungulates
201 during the LGM (60-64% of specimens; counts from Faith, 2013a), as a function of aridity
202 across southern Africa. These taxa tend to be rare in relatively arid environments, reaching peak
203 abundance at intermediate levels of moisture availability, where grass availability and quality are
204 highest (Hempson et al., 2015). Conversely, the small-bodied ungulates that dominate the
205 Holocene levels at Boomplaas Cave, including steenbok, Cape grysbok, klipspringer, grey
206 rhebok, and mountain reedbuck (*Redunca fulvorufula*) (collectively 87% of specimens in late
207 Holocene member BLD; counts from Faith, 2013a), tend to be most abundant in relatively arid
208 environments, in part because limited primary productivity precludes an abundance of larger-
209 bodied ungulates (**Figure 4**). Using these observations to guide our interpretations, the temporal
210 shifts in ungulate community composition at Boomplaas Cave (**Figure 3**) are most consistent
211 with a relatively humid LGM and a relatively arid Holocene.

212 Temporal shifts in ungulate diversity further support this inference (Faith, 2013a, b).
213 Within Africa (Faith, 2013b; Patterson et al., 2022), and more broadly (Olf et al., 2002),
214 ungulate diversity peaks at intermediate levels of moisture availability (typically ~600-800 mm
215 annual rainfall). This pattern represents the ‘Goldilocks zone’ that favors the co-occurrence of
216 smaller-bodied species limited by forage quality alongside larger-bodied species limited by
217 forage quantity (Olf et al., 2002). When moisture availability declines below this zone, the
218 associated decline in productivity results in lower diversity, particularly among larger-bodied
219 species that require large amounts of forage. When moisture availability exceeds this zone, the
220 associated decline in forage quality excludes the smaller-bodied species. These quantity-quality
221 interactions result in a unimodal relationship between moisture availability and ungulate
222 diversity (**Figure 5**). Based on this relationship, the expectation is that aridification of the arid-

223 to-semi-arid Little Karoo (relative to today) would be associated with a decline in species
 224 richness. In contrast, increased moisture availability would be associated with increased richness,
 225 though richness would eventually decline in
 226 particularly wet environments. At Boomplaas
 227 Cave, as well as other sites in the southern
 228 Cape (e.g., Nelson Bay Cave, Byneskranskop
 229 1), temporal trends in diversity are consistent
 230 with aridification since the LGM—ungulate
 231 richness is highest during the LGM and
 232 Lateglacial, declining in the Holocene (Faith,
 233 2013a, b) (Figure 5). This observation
 234 reinforces the evidence species-environment
 235 relationships (Figure 4) that suggest the
 236 LGM was a time of relatively humid
 237 conditions.

238 Subsequent isotopic analysis indicates
 239 a dominance of C₃ vegetation on the
 240 landscape (Sealy et al., 2016), with LGM
 241 alcelaphins consuming on average ~71% C₃
 242 plants and equids consuming ~76% C₃ plants
 243 (percentages from Robinson, 2023). Provided
 244 that these taxa were consuming primarily
 245 grasses, as is the case among their present-

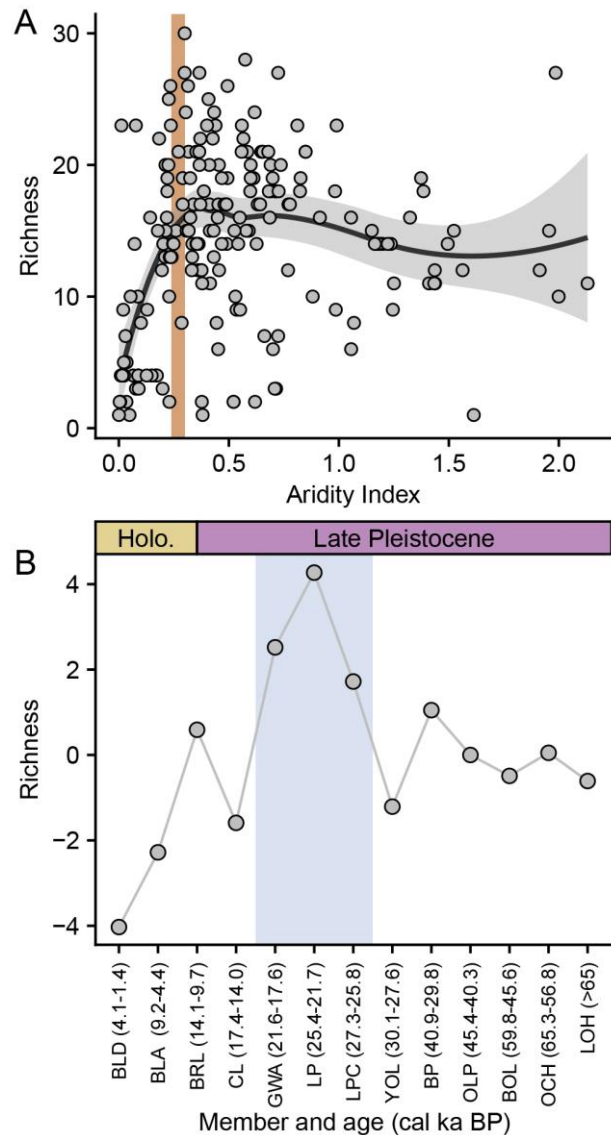


Figure 5. A: Ungulate richness as a function of aridity across Africa (Aridity Index = MAP/MAE; larger values indicate greater moisture). Solid lines are LOESS curves (span = 0.75) with 95% confidence interval in gray. Vertical bar denotes range of aridity index values in the vicinity of Boomplaas Cave 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.

246 day counterparts (e.g., Skinner and Chimimba, 2005), the implication is that C₃ grasses were
247 more abundant than in the present (Sealy et al., 2016). The distribution of C₃ and C₄ grasses
248 depends largely on temperature during the growing season, with the proportion of C₃ grasses
249 increasing with altitude and the relative dominance of winter rains (Vogel et al., 1978; Grobler et
250 al., 2023). Changes in atmospheric pCO₂ have also been identified as an important determinant
251 of C₃/C₄ grass distributions, with lower pCO₂—such as occurred during the LGM—favoring the
252 expansion of C₄ grasses (Ehleringer et al., 1997; Collatz, et al., 1998). According to these
253 studies, even with a 6°C LGM temperature depression (Talma and Vogel, 1992), low pCO₂
254 would promote C₄ grass expansion in the region, and a change in rainfall seasonality (i.e., a
255 greater proportion of winter rain) would be required for the C₃ dominance observed by Sealy et
256 al. (2016) in the LGM grazers from Boomplaas Cave. There is still an important C₄ signal in the
257 isotope data (on average 29% among alcelaphins and 24% among equids), demonstrating that C₄
258 grasses were present, but they were less prevalent than in the terminal Pleistocene (member CL)
259 and Holocene members of the sequence (Sealy et al., 2016).

260

261 **4. MICROMAMMALS**

262 The well-preserved micromammal assemblages, which include an assortment of rodents
263 (Rodentia), shrews (Eulipotyphla), elephant shrews (Macroscelidea), golden moles
264 (Afrosoricida), and bats (Chiroptera), represents a second key source of paleoenvironmental
265 evidence from Boomplaas Cave. Avery (1982) conducted the initial taxonomic and

266 paleoecological study of the microfauna (see also Avery, 1983a, b), with subsequent analyses
 267 conducted by Deacon et al. (1984), Thackeray (1987, 1990; Thackeray and Fitchett, 2016), and
 268 Faith et al. (2019). Based on the ecology of the likely predators and the represented

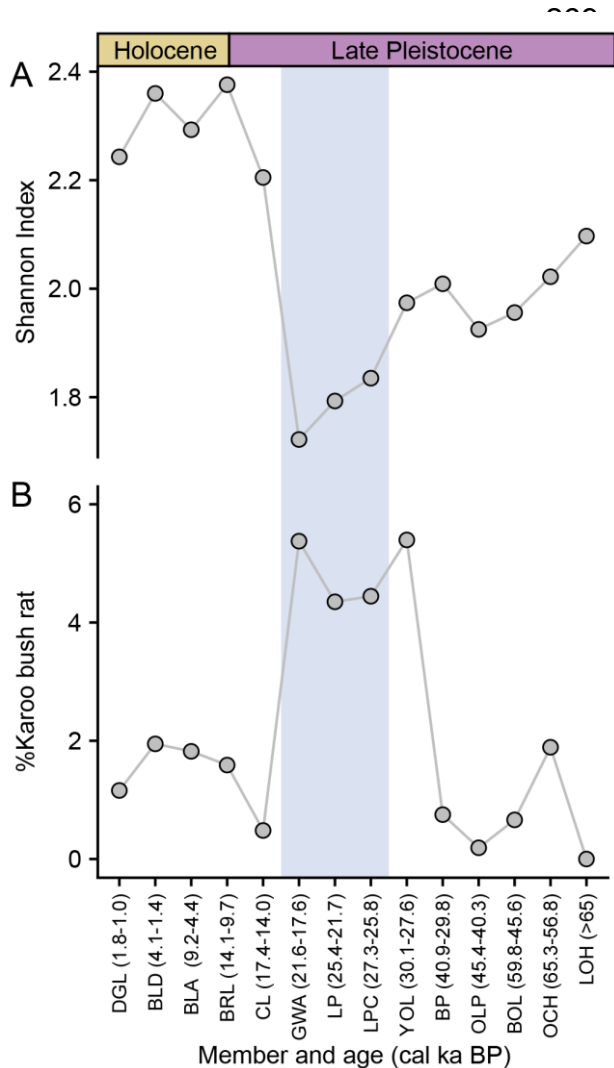


Figure 6. A: Taxonomic diversity (Shannon index) of micromammals (bats excluded) through the Boomplaas Cave sequence. B: Changes in the abundance of Karoo bush-rat through the Boomplaas Cave sequence. Data from Avery (1982). Vertical bar denotes the LGM members.

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.

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

287 indicative of harsh conditions (i.e., cold and dry). Though reference to large-scale diversity

288 gradients often underpins paleoenvironmental inferences (Faith and Lyman, 2019), relationships
289 between micromammal diversity and moisture availability are not substantiated in southern

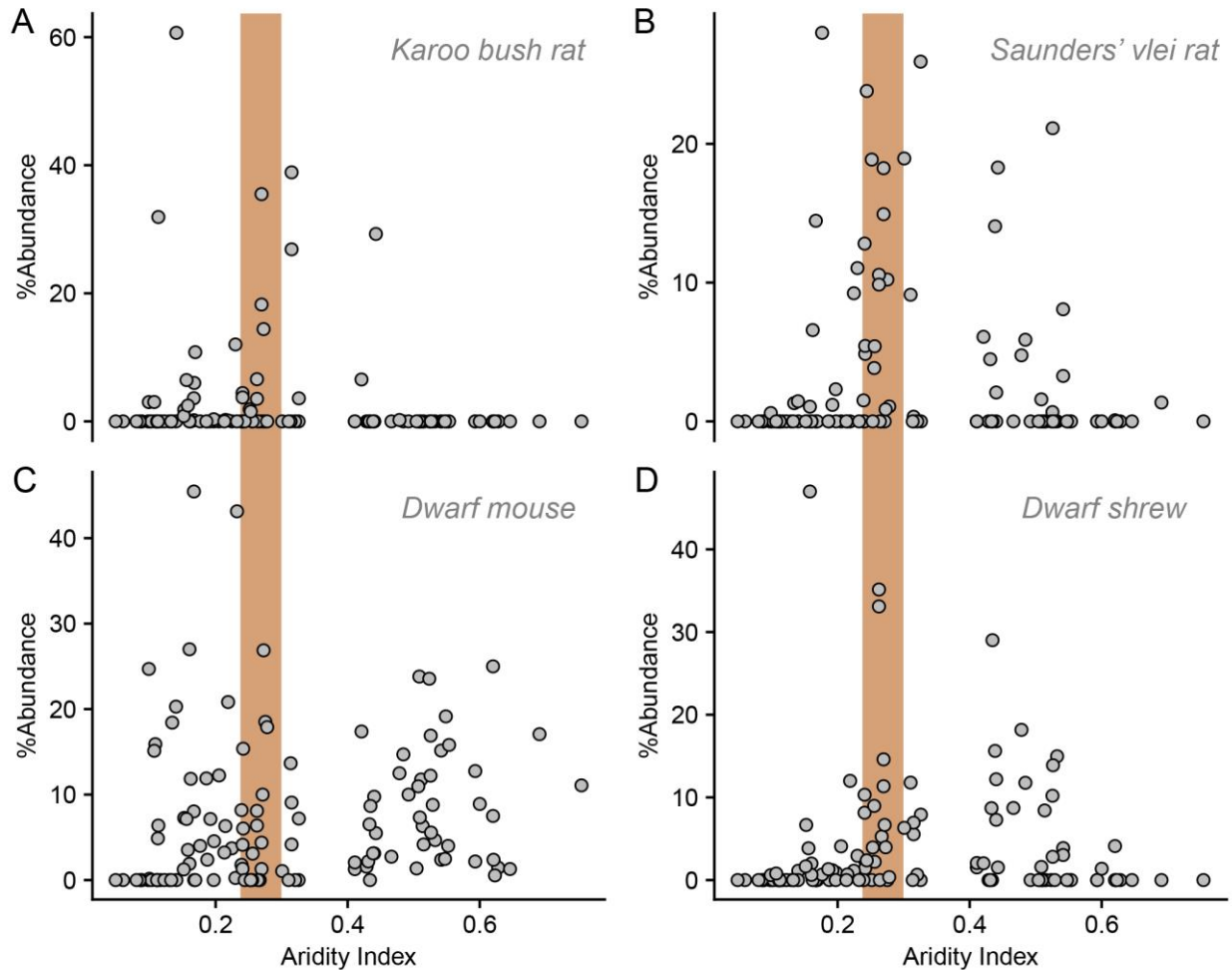


Figure 7. The percent abundance of (A) Karoo bush-rat, (B) Saunders' vlei rat, (C) dwarf mouse, and (D) dwarf shrew as a function of aridity (Aridity Index [AI] = MAP/MAE; larger values indicate greater moisture availability) in present-day southern Africa (data from Faith et al. 2019). Vertical bars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

290 Africa (Avery, 1999). In an analysis of modern barn owl-accumulated micromammal
291 assemblages from the region, Avery (1999) showed that taxonomic diversity is unrelated to
292 rainfall and aridity, undercutting her previous argument that low diversity signals a harsh LGM.
293 We suspect that the temporal trends in diversity are instead tracking vegetation change. The two
294 species whose dominance drives the reduction in LGM diversity, Saunders' vlei rat and forest
295 shrew, are associated with a range of environments in southern Africa, but both have affinities

296 for grassy habitats in hilly and mountainous terrain (Happold, 2013; Happold and Happold,
297 2013). Together with the environmental implications of the large mammals (**Figure 3**), the
298 dominance of Saunders' vlei rat and forest shrew during the LGM, and the associated decline in
299 micromammal diversity, are consistent with an expansion of grassy vegetation.

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

312 Deacon et al. (1984) expanded on Avery's (1982) initial analysis, using factor analysis to
313 identify environmental shifts reflected by the Boomplaas Cave micromammals (bats excluded).
314 Their analysis identified two factors that collectively account for 84% of the total variance in
315 assemblage composition. Based on the ecological associations of species with strongly positive
316 or negative scores on these factors, they interpreted Factor 1 in terms of temperature and Factor 2
317 in terms of aridity. To quantify environmental changes through the Boomplaas Cave sequence,

318 they subsequently multiplied the factor loadings for each taxon by its relative abundance in a
 319 given stratum and summed these values to provide ‘summary statistics’ for each stratigraphic

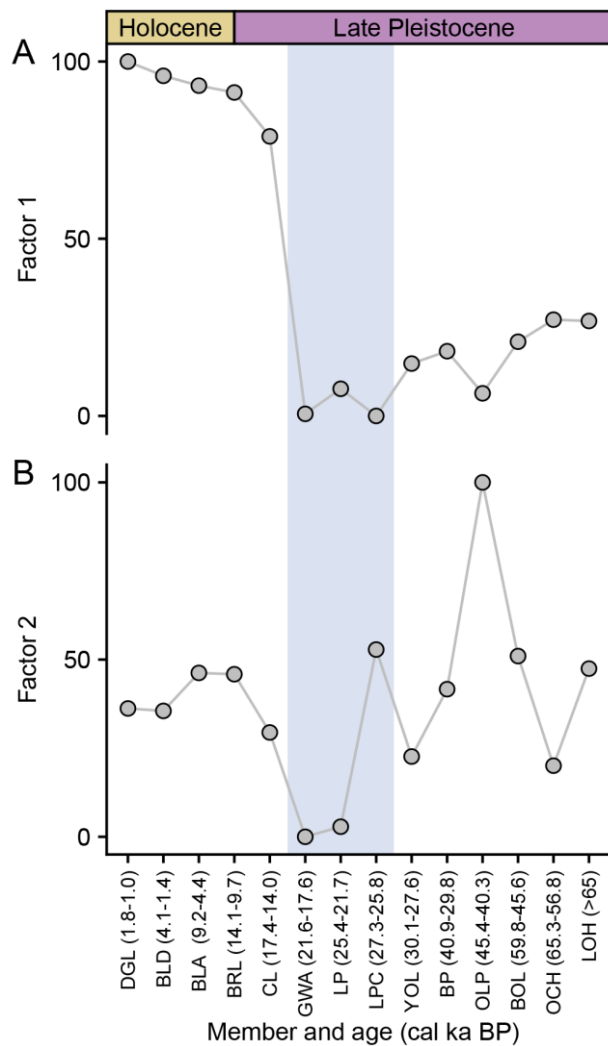


Figure 8. A: Factor 1 summary statistics derived from a factor analysis of micromammals across the Boomplaas Cave sequence (following Deacon et al., 1984). These values were interpreted as tracking temperature changes through the sequence, with larger values indicating warmer conditions (see Thackeray,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

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.

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

340 humid environments and that the latter two are tolerant of cold and dry extremes. Thus, the low

341 Factor 2 summary statistics during the LGM (except in member LPC; **Figure 8**), when Saunders'
342 vlei rat and Karoo bush rat are particularly abundant, indicated aridity. **Figure 7** illustrates one of
343 the problems with this interpretation, namely that data from present-day micromammal
344 assemblages do not support the proposed mesic-xeric dichotomy for the species in question—
345 they all can reach high abundances in relatively arid and humid environments. Perhaps more
346 consequential are the results of a follow-up study by Thackeray (1987), who provided a more
347 detailed analysis using a narrower set of micromammal taxa. He showed that the Factor 2 scores
348 for each species were not tracking their environmental associations, but rather their body mass.
349 The same is true of the Deacon et al. (1984) analysis, in which the Factor 2 scores for each
350 species strongly correlate with their body mass ($r = -0.77$, $p < 0.001$) (factor scores from Deacon,
351 1983b; body masses from Smith et al., 2018). As Thackeray (1987) noted, the implication is that
352 the Factor 2 summary statistics through the sequence are tracking the average body mass of the
353 recovered species, likely due to taphonomic bias (e.g., differential preservation and recovery of
354 the smallest species). This implies that the low Factor 2 summary statistics during parts of the
355 LGM (**Figure 8**) are not indicating exceptional aridity, but instead a rarity of the very smallest
356 species (e.g., the ~5 g dwarf shrew) and an abundance of the larger species (e.g., the ~100 g
357 Saunders' vlei rat).

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

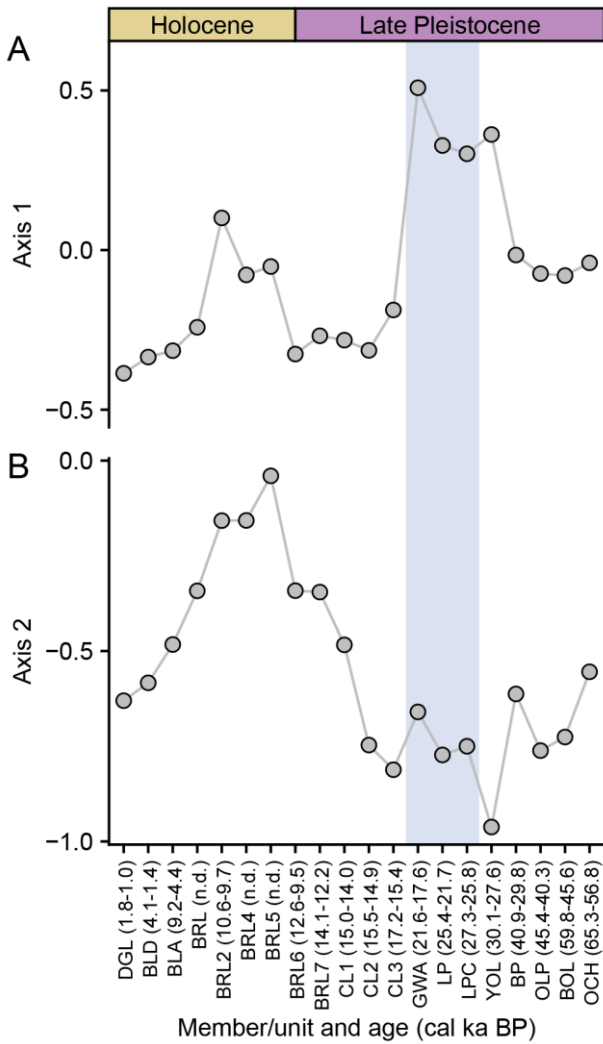


Figure 9. A: Axis 1 scores derived from a canonical correspondence analysis (CCA) of the micromammal assemblages across the Boomplaas Cave sequence (from Faith et al. 2019). These values strongly correlate with rainfall seasonality in modern assemblages ($r = -0.88$), with larger values indicating a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

381 used canonical correspondence analysis to relate taxonomic composition to aridity and rainfall
 382 seasonality. In contrast to Thackeray's (1987) analysis, they observed strong relationships
 383 between assemblage composition and aridity ($r = -0.86$, $p < 0.001$), with the high coefficient of
 384 determination ($r^2 = 0.74$) providing greater confidence that there is a strong moisture availability

385 signal. This relationship provides the basis for interpreting the ordination of the fossil
386 assemblages in terms of aridity, with the Boomplaas Cave micromammals indicating relatively
387 humid conditions before and during the LGM, followed by increased aridity across the last
388 glacial-interglacial transition (LGIT) (**Figure 9**). The interval of peak aridity is not observed
389 during the LGM, but rather during the early Holocene within member BRL.

390 Complementing interpretations derived from isotopic analysis of the Boomplaas Cave
391 ungulates (Sealy et al., 2016), the micromammal assemblages further suggest that winter rainfall
392 dominated during the LGM. The analysis provided by Faith et al. (2019) indicated that rainfall
393 seasonality was a strong correlate of micromammal assemblage composition ($r^2 = 0.77$), with the
394 LGM fossil assemblages providing the strongest winter rainfall signal for the sequence (**Figure**
395 **9**). Thackeray and Fitchett (2016) obtained equivalent observations in a previous study. They
396 used climate data from across the geographic ranges of rodent species to develop transfer
397 functions for estimating the seasonality of rainfall in the fossil record. Thus, the dominant signal
398 from large mammals (Sealy et al., 2016) and micromammals (Faith et al., 2019; Thackeray and
399 Fitchett, 2016) is a greater dominance of winter rainfall during the LGM.

400

401 **5. CHARCOAL**

402 The charcoal evidence from Boomplaas Cave has played a central role in characterizing the past
403 vegetation and inferring climatic conditions through the sequence. Analyzed by two of Hilary
404 Deacon's students (Anton Scholtz and David Daitz), the fossil charcoals were preliminarily
405 described by Deacon (1979) and Deacon et al. (1983), with a detailed treatment provided in
406 Scholtz's (1986) Master's thesis, which at the time was a pioneering study in anthracology.
407 Scholtz (1986) presumed the charcoal assemblages were primarily derived from anthropogenic

408 fires within the cave, though limited accumulation by other processes (e.g., colluvial processes)
 409 is possible (Deacon et al., 1983).

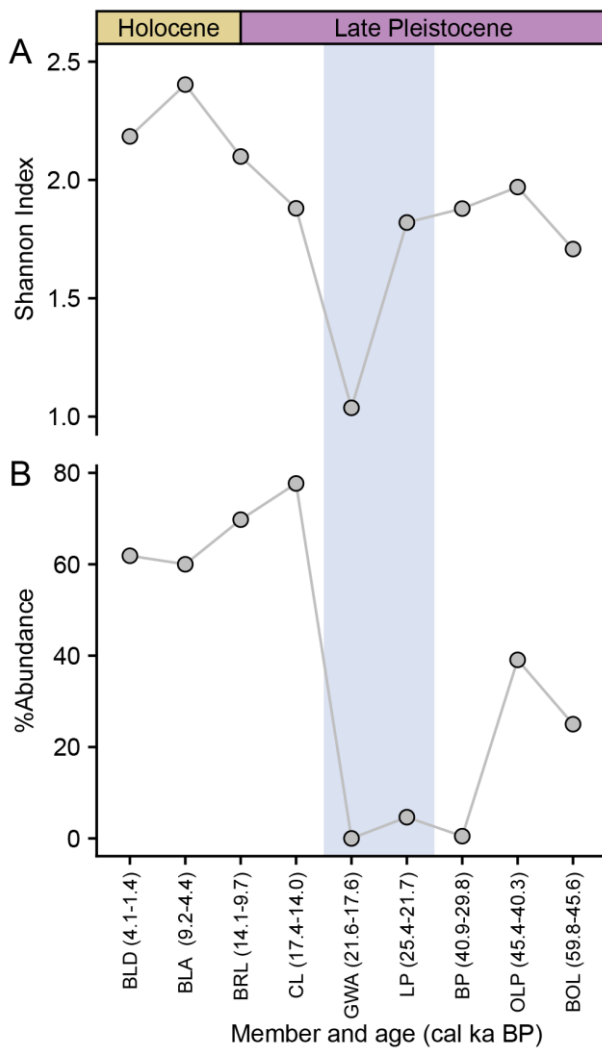


Figure 10. A: Taxonomic diversity (Shannon index) of the charcoal assemblages through the Boomplaas Cave sequence. B: The percent abundance of trees and tall shrubs recovered from Boomplaas Cave. Data from Scholtz (1986).

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

427 (BLD to BRL), in which taxonomic diversity is high, trees and tall shrubs are abundant, and
 428 smaller shrubs (Asteraceae) are rare. They interpreted this as indicative of extremely cold and
 429 dry conditions during the LGM, such that only a few small shrubs could persist in the valley.

430 There are reasons to question both the evidence and its links to aridity. First, variation in
 431 the charcoal sampling strategy employed by Scholtz (1986) renders the temporal trends in
 432 diversity unreliable. Scholtz (1986) notes that in the upper levels of the sequence (BLD to CL),

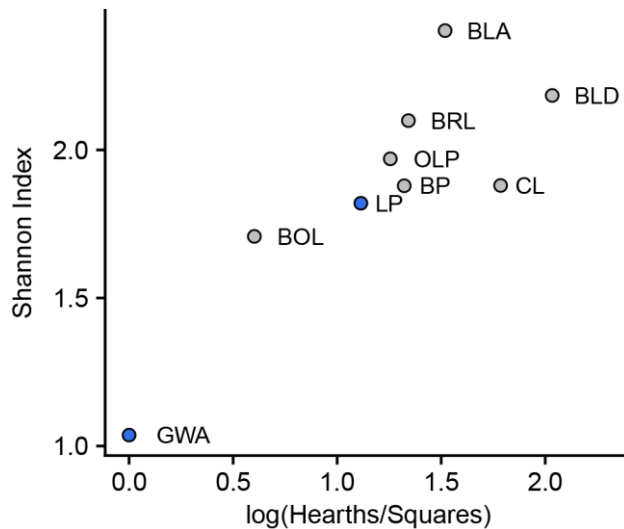


Figure 11. The relationship between sampling strategy (log-transformed number of hearths or squares) and taxonomic diversity (Shannon index) for the Boomplaas charcoal assemblages. Scholtz (1986) provided counts of the number of specimens analyzed from each member and following his description of the 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).

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)

446 because the excavation extent was smaller and charcoal densities declined, increasing the
 447 sampling threshold to 10 or more specimens per hearth or square. In some cases, he analyzed all
 448 fragments from a hearth (Scholtz, 1986:74). Significantly, in the LGM sample from member
 449 GWA/HCA, where anomalously low diversity (**Figure 10A**) prompted inferences of extremely
 450 harsh conditions (Deacon et al., 1984; Deacon et al., 1983), only a single hearth was sampled
 451 (Scholtz, 1986: 95). This shift in sampling strategy increases the likelihood that identified

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

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

466 In addition to problems with the diversity metrics, it is also unclear that aridity accounts
467 for the taxonomic composition of the LGM charcoal assemblages. For instance, temperature
468 alone is likely a key driver of taxonomic change from the LGM to the Holocene (e.g., Potts et al.,
469 2013). It was $\sim 6^{\circ}\text{C}$ colder in the Boomplaas region during the LGM (Talma and Vogel, 1992),
470 and many of the thicket taxa found in the Holocene assemblages are intolerant of frost (Cowling
471 et al., 2005; Duker et al., 2015). Community distribution modelling predicts that cooler LGM
472 temperatures drove a major contraction of Subtropical Thicket in southern Africa, eliminating
473 this vegetation type from the Boomplaas Cave (Potts et al., 2013) and contributing to a relative
474 dominance of Asteraceae. Furthermore, lower atmospheric pCO_2 could facilitate a contraction of

475 tree cover (e.g., Kgope et al., 2010), perhaps also contributing to the lack of trees in parts of the
476 Pleistocene sequence (**Figure 10B**). However, the study of charcoal fragments from recent
477 (Pargeter et al., 2018) and ongoing radiocarbon dating efforts provides reason to question the
478 extent to which the LGM was a treeless landscape. There are many LGM hearths that were never
479 sampled in the initial studies (Deacon et al., 1983, 1984; Scholtz, 1986), and which attest to the
480 presence of a diversity of trees that are closely linked to moist habitats (e.g., *Cunonia*, *Salix*,
481 *Maytenus*; A. House pers. comm.). It is unclear why these hearth features were never studied,
482 especially considering that Scholtz (1986) sampled only one LGM hearth from member
483 GWA/HCA, but the identification of these trees, which are often found in afrotemperate forest
484 today, indicates the nearby presence of well-watered environments. This observation further
485 suggests that the *Euryops*-dominated assemblage reported by Scholtz (1986) is unlikely to be a
486 robust reflection of the woody plants growing on the ancient landscape during the LGM.

487 Considering our analyses, it is clear that initial interpretations of the Boomplaas Cave
488 charcoal assemblages are problematic. Temporal trends in taxonomic diversity, especially the
489 anomalously low values in member GWA/HCA (**Figure 10A**), are driven by sampling artifacts
490 that are well-known to affect diversity metrics. Likewise, more recent work demonstrates that the
491 absence of thicket elements and relative dominance of Asteraceae during the LGM was in part a
492 consequence of cooler temperature (Potts et al. 2013), whereas ongoing observations attest to the
493 presence of several tree taxa that are incompatible with interpretations of a harsh, arid, and
494 treeless landscape. Pending a study of the charcoal assemblages that implements a more
495 consistent sampling strategy and includes greater representation of the unstudied LGM hearth
496 features, the paleoenvironmental implications of the Boomplaas Cave charcoals are equivocal.
497

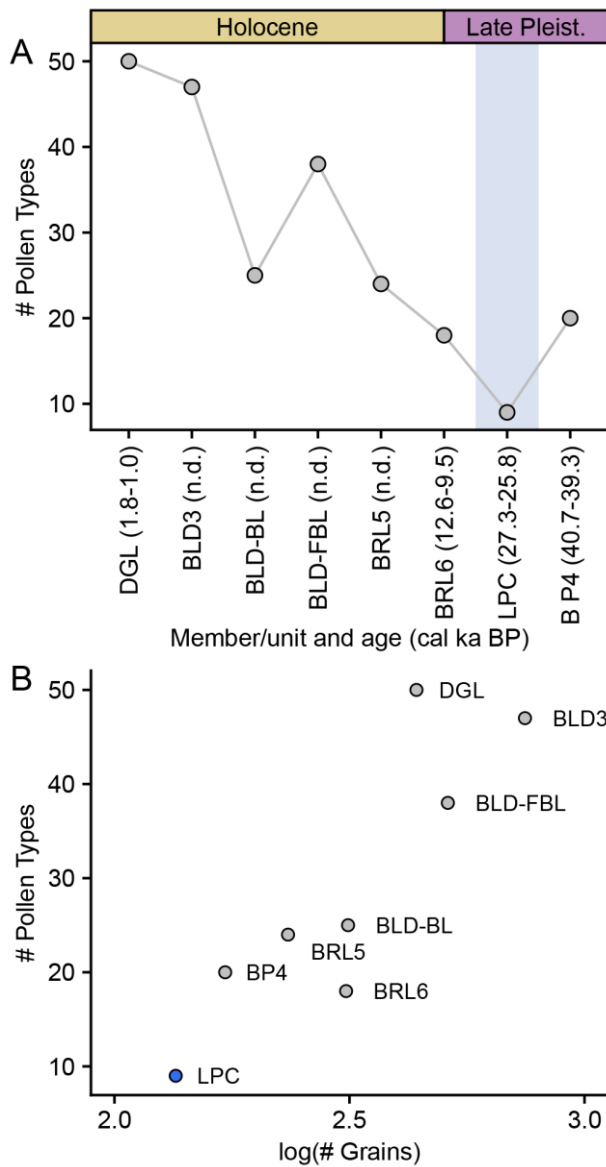


Figure 12. A: The number of pollen types across the Boomplaas Cave sequence. B: the relationship between sample size (# of grains counted) and the number of pollen types. The LGM member (LPC) is indicated in blue. Data from Deacon (1983b).

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

518 Asteraceae, but there is also much greater diversity, with dozens of different types identified
 519 from each member (**Figure 12**). Paralleling the initial inferences made for the micromammal and

520 the charcoal assemblages, Deacon et al. (1983b) interpreted this temporal shift in diversity as
521 evidence for an arid LGM followed by a more mesic Holocene.

522 As we demonstrated with the charcoal evidence, sampling artifacts also drive the
523 diversity trends observed in the pollen record. Though it is well-documented that taxonomic
524 richness increases as a function of sample size (Gotelli and Colwell, 2001; Grayson, 1984;
525 Lyman, 2008; Magurran, 2004), Deacon et al. (1983b) did not consider variable sampling effort
526 in the initial pollen diversity examinations. Deacon's (1983b) report provides the number of
527 pollen grains counted and the number of pollen types identified through the sequence. Consistent
528 with the understanding of how sampling influences richness, the correlation between the number
529 of grains (log-transformed) and the number of pollen types is strong ($r = 0.88$, $p = 0.004$; **Figure**
530 **12**), implying that the anomalously low diversity observed during the LGM reflects the lack of
531 grains counted (135 in member LPC vs. ~545-826 for each of the Holocene members) rather
532 than any meaningful aspect of the paleoenvironment.

533 Furthermore, the dominance of Asteraceae, especially *Elytropappus*-type (also known as
534 Stoebe-type), in the LGM pollen sample need not imply aridity. This pollen type has associations
535 with both arid and humid environments in southern Africa (Chevalier et al., 2021), such that any
536 direct interpretation in terms of LGM moisture availability should be treated with caution.
537 However, insofar as present-day vegetation gradients in the vicinity of Boomplaas Cave can be
538 extrapolated to the past, the dominance of *Elytropappus*-type pollen is most parsimoniously
539 interpreted as indicative of a more humid climate. In the transitional shrublands near Boomplaas
540 Cave, renosterveld (the vegetation type dominated by *Elytropappus*) is associated with relatively
541 humid environments closer to the Swartberg range (Vlok and Schutte-Vlok, 2010). As aridity
542 increases further south of the Swartberg (**Figure 1**), renosterveld is replaced by asbosveld, which

543 is dominated by *Pteronia incana*, and then by Subtropical Thicket (Vlok and Schutte-Vlok,
544 2010). Keeping in mind that cooler temperatures during the LGM would have eliminated many
545 taxa presently associated with Subtropical Thicket (Potts et al., 2013), present-day vegetation
546 gradients imply that increased aridity might have favored expansion of *Pteronia* as the dominant
547 cold-tolerant Asteraceae, whereas increased humidity would have favored expansion of
548 *Elytropappus* in the Congo Valley. It follows that the abundance of *Elytropappus* in the LGM
549 pollen assemblage is reasonably interpreted as a consequence of both cold temperatures
550 (eliminating thicket elements) and increased humidity. Importantly, renosterveld supports a
551 dense understory of palatable grasses (e.g., Vlok and Schutte-Vlok, 2010), such that an
552 expansion of grassy renosterveld-like habitats during the LGM is also consistent with the faunal
553 evidence from Boomplaas Cave.

554

555 **7. DISCUSSION**

556 *7.1. Moisture availability during the LGM*

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

564 With respect to the large mammal and micromammal assemblages from Boomplaas
565 Cave, interpretations of harsh and arid conditions during the LGM (Avery, 1982; Deacon et al.,

566 1984; Deacon and Lancaster, 1988; Thackeray, 1987) lack this fundamental inferential link.
567 Grazer-dominated ungulate communities and the grassy environments they imply do not signal
568 an arid environment (**Figure 4**); low micromammal diversity is not associated with low
569 precipitation in southern Africa (Avery, 1999); and the abundance of certain micromammal taxa
570 during the LGM (e.g., Saunders' vlei rat and Karoo bush rat) need not imply drier conditions
571 relative to today (**Figure 7**). In contrast, present-day observations substantiate interpretations of
572 relatively humid conditions during the LGM. The taxonomic composition of the large mammal
573 and micromammal assemblages, as well as ungulate community diversity, can all be linked to
574 moisture availability, and they are indicative of relatively humid conditions during the LGM
575 (**Figure 4-5**; Faith, 2013b; Faith et al., 2019). The inferences derived from ungulate community
576 diversity are particularly robust, as the ecological mechanisms underpinning the link between
577 diversity and moisture availability are well understood (Olf et al., 2002).

578 Interpretations of arid conditions derived from the charcoal and pollen assemblages are
579 problematic for these and other reasons. The lack of thicket elements in the LGM charcoal
580 assemblage, which contributes to a relative dominance of Asteraceae (**Figure 10B**), is likely a
581 consequence of cooler temperature (Potts et al., 2013; Duker et al. 2014) rather than aridity
582 (Deacon et al., 1984; Deacon et al., 1983; Scholtz, 1986). Additionally, ongoing work documents
583 the presence of trees that are closely linked to moist habitats (e.g., *Cunonia*, *Salix*, *Maytenus*),
584 contradicting interpretations of the LGM as a dry and treeless landscape. With respect to the
585 pollen, present-day vegetation gradients in the region indicate that the dominance of cold-
586 tolerant *Elytropappus* in the LGM pollen record is best explained as a consequence of wetter
587 (and cooler) rather than drier conditions. Critically, though Deacon et al. (1984) placed
588 considerable emphasis on the evidence for low diversity in both the LGM charcoal and pollen

589 records, our analyses show that variation in taxonomic diversity is driven by sampling artifacts
590 (**Figure 11-12**). Low plant diversity in the LGM assemblages is a consequence of relatively
591 limited sampling and not a reflection of low plant diversity on the landscape.

592 Beyond relying on present-day ecological observations, we can strengthen confidence in
593 paleoenvironmental reconstruction when independent records support them (Faith and Lyman,
594 2019). This is also where the early interpretations of a harsh and arid LGM fall short. One of the
595 primary independent records available to Deacon et al. (1984) is the stalagmite from the nearby
596 (~3 km east of Boomplaas) Cango Caves (Talma and Vogel, 1992; Vogel, 1983). The Cango
597 stalagmite formed over much of the past ~50 kyr, except for a hiatus during the late glacial and
598 early Holocene that may imply a lack of water in the system. Because speleothem formation
599 requires water, Deacon et al. (1984) struggled to reconcile this hiatus with LGM aridity,
600 suggesting that lack of formation at a time they believed to be relatively humid resulted from
601 unspecified interactions between vegetation and groundwater. No special pleading is required if
602 we accept that the LGM was an interval of relatively humid conditions, though a much larger
603 sample of speleothems would be required to confidently link growth patterns to climate change
604 (e.g., Vaks et al., 2007).

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

612 climate models, is consistent with relatively humid conditions during the LGM within the
613 southern Cape.

614

615 *7.2. Rainfall seasonality during the LGM*

616 The Boomplaas Cave proxy records suggest that increased moisture availability during the LGM
617 was associated with a greater dominance of C₃ grasses and enhanced winter precipitation,
618 implying a more seasonal rainfall regime than at present (Sealy et al., 2016; Thackeray and
619 Fitchett, 2016; Faith et al., 2019). This interpretation is consistent with the dominance of C₃
620 vegetation indicated by the Cango Caves speleothem (Talma and Vogel, 1992), though more
621 recent work complicates the picture. Isotopic analysis of speleothems from Efflux Cave (~15 km
622 east of Boomplaas Cave; **Figure 1**) suggests an important C₄ grass component during the LGM
623 (Braun et al., 2020). Taken together, the speleothem records indicate spatial heterogeneity in the
624 distribution of C₃ and C₄ grasses within the Little Karoo during the LGM. Because C₃ grasses
625 tend to be more prevalent on south-facing slopes and C₄ grasses favor north-facing slopes
626 (Cowling and Campbell, 1983), differences between the Cango Caves and Efflux Cave
627 speleothem records may reflect localized topographic factors (Braun et al., 2020). If so, then the
628 baseline isotope values of the two nearby records should not be interpreted in terms of regional
629 climate—i.e., the C₃ signal from Cango Caves need not imply a dominance of winter rains
630 whereas the C₄ signal from Efflux Cave need not imply stronger summer rains. However,
631 temporal trends within those records should be reliable (see Chase et al., 2021), as topography is
632 unlikely to have changed in any meaningful way since the LGM. Efflux Cave lacks a post-LGM
633 record (Braun et al., 2020), but the isotope record from the Cango Caves speleothem (Talma and
634 Vogel, 1992), suggest a greater proportion of summer rain during the Holocene. The same

635 pattern is also seen in the Seweweekspoort hyrax middens (Chase et al., 2017, 2018), Thus, the
636 overall signal from Boomplaas Cave, Cango Caves, and Seweweekspoort is that the LGM was
637 characterized by a greater dominance of winter rains compared to today.

638 Relative to carbon isotope records derived from speleothems or hyrax middens, the large
639 mammal isotope record from Boomplaas Cave should document vegetation at larger spatial
640 scales, reflecting the geographic ranges over which herbivores foraged and the distances over
641 which humans and carnivores transported their remains to the site. With this in mind, the strong
642 C₃ signal observed in LGM grazers implies that C₃ grasses were dominant relative to C₄ grasses
643 (Sealy et al., 2016). As argued by Sealy et al. (2016), and in agreement with the micromammal
644 evidence (Thackeray and Fitchett, 2016; Faith et al., 2019), a reasonable explanation is a greater
645 proportion of winter rainfall, as the regional LGM temperature depression of 6°C (Talma and
646 Vogel, 1992) would not in itself be sufficient to offset the impact of reduced atmospheric pCO₂
647 concentrations that would otherwise favor C₄ grasses (Ehleringer et al., 1997; Collatz, et al.,
648 1998). The herbivore isotope data do not agree well with modelled outputs predicting mostly C₄
649 grasses near Boomplaas Cave during the LGM (Grobler et al., 2023). One possible explanation
650 for this discrepancy is that the modelled distribution of C₃ and C₄ grasses (Grobler et al., 2023) is
651 based on climate models that predict an increase in summer precipitation within the southern
652 Cape and across much of southern Africa during the LGM (Engelbrecht et al., 2019). While this
653 should favor an expansion of C₄ grasses, some proxy records suggest a reduction in summer
654 rainfall during the LGM (e.g., Chevalier and Chase, 2015; Sealy et al., 2020), paralleling
655 previous analyses suggesting that significant features of the general circulation model
656 simulations of LGM climate employed in the Engelbrecht et al. (2019) study do not perform well
657 in southern Africa (Chevalier et al. 2017). Alternatively, it is also plausible that the LGM taxa

658 assumed to be grazers at Boomplaas Cave were consuming more dicots than their contemporary
659 counterparts, as has been demonstrated for early Pleistocene faunas in southern Africa (e.g.,
660 Stynder, 2009). If so, then the small C₄ grass component implied by herbivore isotope data
661 (Sealy et al., 2016) would underestimate the importance of C₄ relative to C₃ grass in the diet.
662 Whatever the explanation, this data-model discrepancy highlights the need for future work. This
663 includes generating additional empirical records that speak to rainfall seasonality and the
664 distribution of C₃ and C₄ grasses across southern Africa, as well as continued development,
665 evaluation, and refinement of climate and paleodistribution models.

666

667 *7.3. Synthesis of the Boomplaas Cave evidence*

668 The sum of the evidence from Boomplaas Cave supports early conceptual models of Quaternary
669 climate dynamics in southern Africa, whereby the expansion of Antarctic sea ice during glacial
670 phases translated to an equatorward shift of the southern hemisphere westerlies, resulting in more
671 intense and more frequent winter storms across southernmost Africa (Chase and Meadows, 2007;
672 Cockcroft et al., 1987; van Zinderen Bakker, 1976). Together with a proposed weakening of the
673 tropical systems that bring summer rain to the region, an observation supported by multiple
674 paleoenvironmental records (see reviews in Chase et al., 2017; Chase and Meadows, 2007), the
675 outcome is an expansion of the winter rainfall zone (but see Engelbrecht et al., 2020). In
676 agreement with this scenario, research aiming to infer rainfall seasonality from the Boomplaas
677 Cave records has consistently indicated a dominance of winter rain during the LGM (Faith et al.,
678 2019; Sealy et al., 2016; Thackeray and Fitchett, 2016). Cooler conditions during the LGM must
679 have played a role in increasing moisture availability, with the ~6°C drop in average
680 temperatures near Boomplaas Cave (Talma and Vogel, 1992) resulting in a considerable decline

681 in evapotranspiration. Whether annual precipitation increased is less clear from the Boomplaas
682 Cave record, as the environmental proxies derived from the site are more directly influenced by
683 moisture availability (i.e., precipitation relative to evapotranspiration) than by the overall rainfall
684 amount (Chevalier and Chase, 2016; Faith et al., 2020). The downscaled climate models
685 produced by Engelbrecht et al. (2019) suggests that increased precipitation may account for a
686 wetter LGM, though other aspects of these models, namely an increase in summer rains that
687 should facilitate expansion of C₄ grasses (Grobler et al., 2023) do not agree well with the proxy
688 records from Boomplaas Cave. This discrepancy aside, when it comes to understanding the
689 terrestrial ecosystems in which plants, animals, and human populations were embedded,
690 Boomplaas Cave's records strongly indicate a relatively humid LGM.

691

692 **8. CONCLUSION**

693 Boomplaas Cave is a critical archive of Quaternary environments in the southern Cape, yet
694 ongoing uncertainty over the interpretation of its paleoenvironmental records compromises its
695 value. Disagreement surrounding climatic conditions during the LGM has been especially
696 consequential, promoting uncertainty about Quaternary climate dynamics throughout the region.
697 We believe it is time to move beyond this uncertainty. Though the early literature proposing
698 exceptional aridity during the LGM at Boomplaas Cave occupies an important place in the
699 intellectual history of paleoenvironmental research in southern Africa, the interpretations lack
700 strong ecological links between the evidence and the interpretation, and some critical
701 observations derive from spurious patterns driven by sampling artifacts. In the absence of robust
702 evidence to the contrary, we see little reason to view the sum of the evidence from Boomplaas
703 Cave as ambiguous or indicative of an arid LGM. In contrast, present-day ecological

704 observations support interpretations of a relatively humid LGM, consistent with independent
705 paleoenvironmental records. Though future research will surely refine the general pattern of
706 climate dynamics through time, the evidence from Boomplaas Cave now allows us to make
707 definitive statements: the LGM was a time of relatively humid conditions, with the transition to
708 the Holocene characterized by increased aridity.

709

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718

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