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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

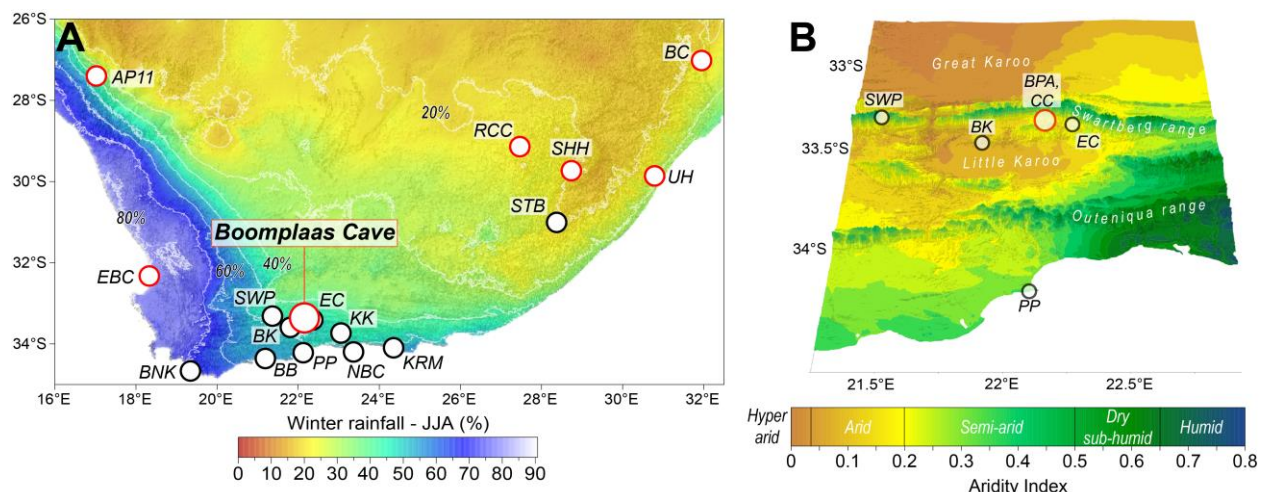
22 South Africa's southern Cape has long been a focus of research on Quaternary climate change  
23 and its influence on terrestrial ecosystems (e.g., Cockcroft et al., 1987; Deacon and Lancaster,  
24 1988; van Zinderen Bakker, 1976). Encompassing the southern coastal plains and the east-west  
25 trending 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).

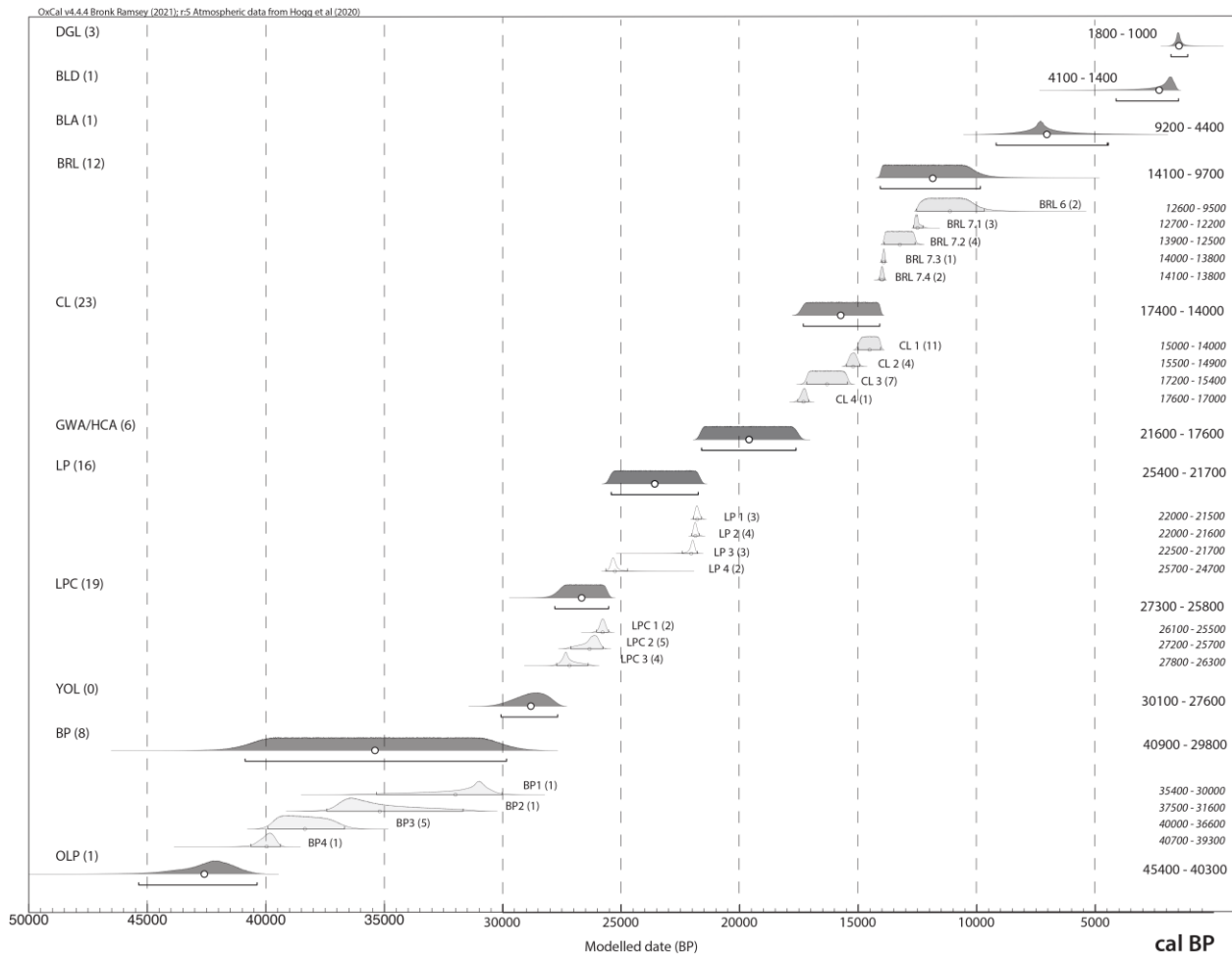
78 aim to critically review the paleoenvironmental data from Boomplaas Cave, focusing on its LGM  
79 deposits. We examine this evidence as it relates to the contentious problem of moisture  
80 availability (i.e., precipitation relative to evapotranspiration), incorporating additional insights  
81 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 C<sub>3</sub> and C<sub>4</sub>  
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  $^{14}\text{C}$  ages with  $2\sigma$  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



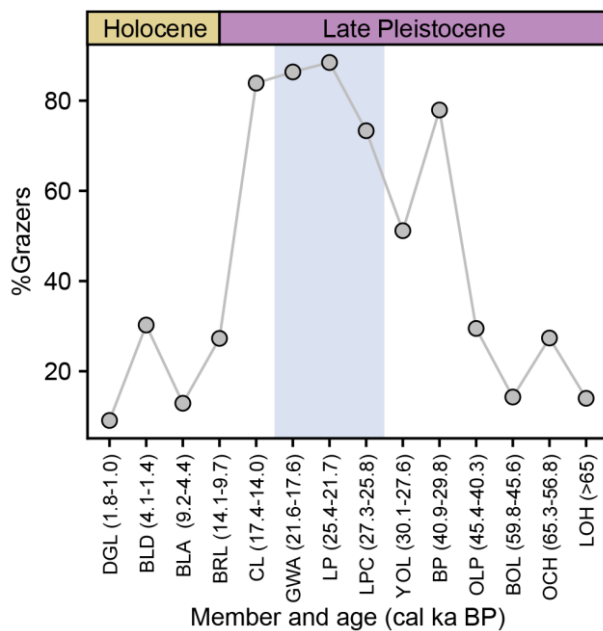
108 (14.1-9.7 cal ka BP) providing a finely resolved record of the last glacial-interglacial transition  
109 (LGIT) (Pargeter et al., 2018). Pargeter directs the current excavations focused on members  
110 GWA/HCA to BP.

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).

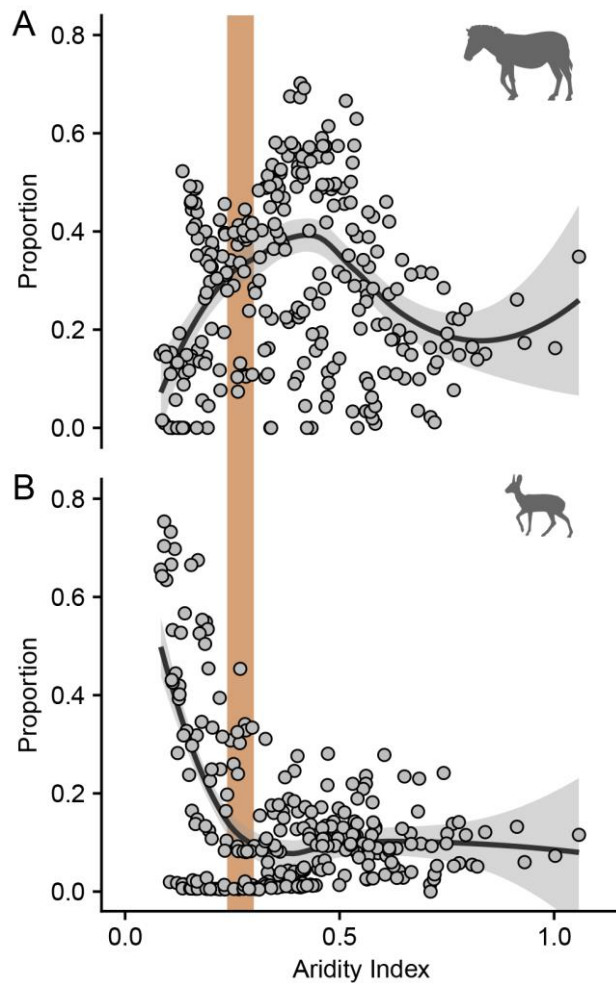
Paleoenvironmental interpretations derived from the large mammals have focused on the ungulates (Artiodactyla and Perissodactyla). In his initial reports, Klein (1978, 1983) emphasized dramatic changes in the relative abundance of ungulate grazers through time (**Figure 3**). In contrast to the historic 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 pCO<sub>2</sub> (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.

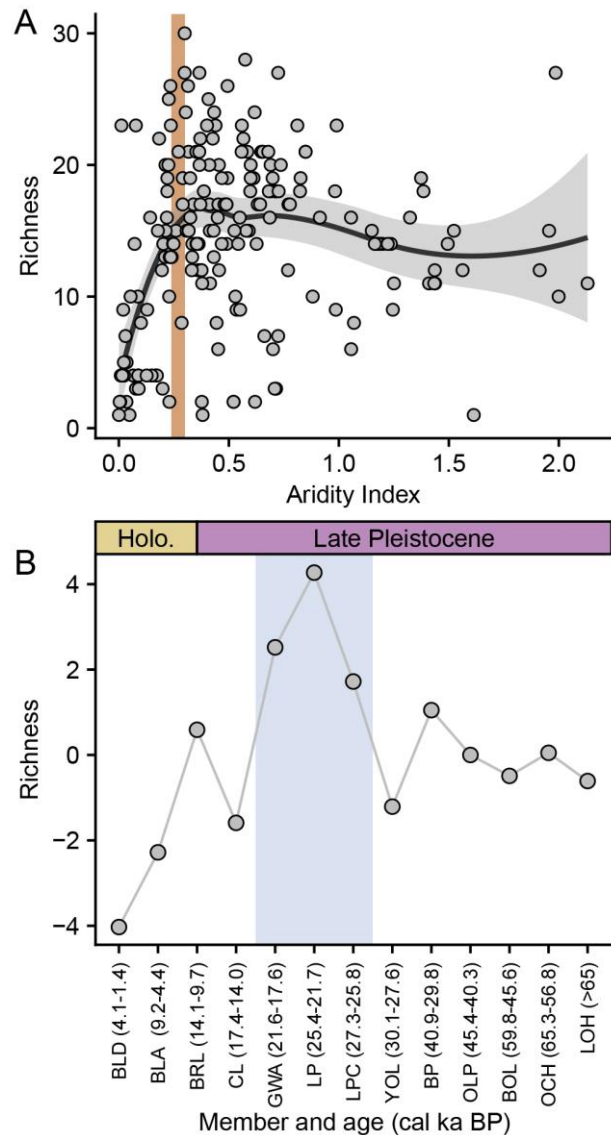
Drawing from their models, **Figure 4**

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 C<sub>3</sub> vegetation on the  
 240 landscape (Sealy et al., 2016), with LGM  
 241 alcelaphins consuming on average ~71% C<sub>3</sub>  
 242 plants and equids consuming ~76% C<sub>3</sub> 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.

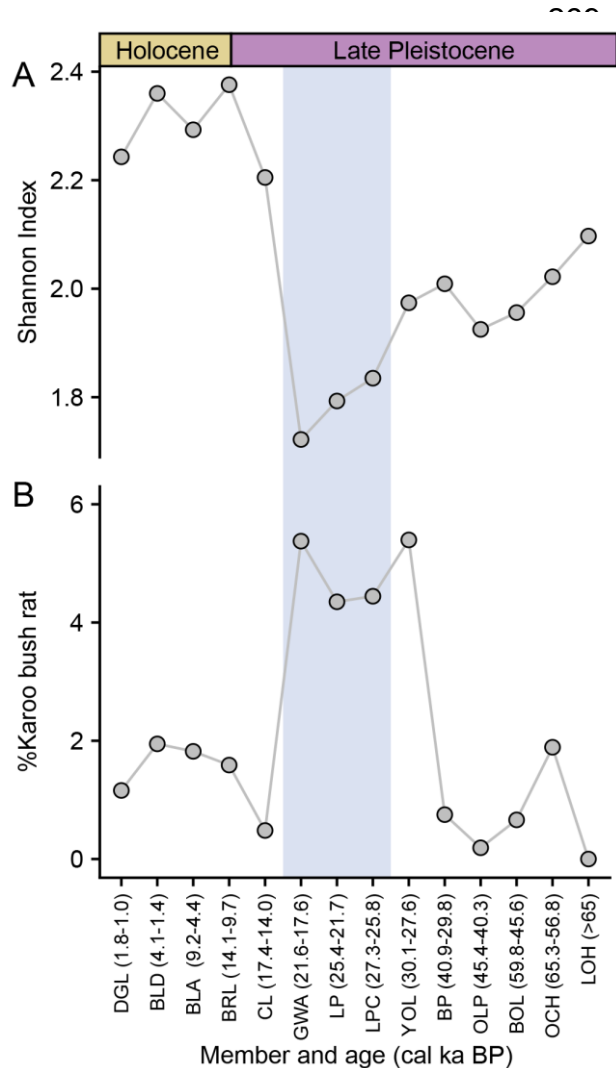
246 day counterparts (e.g., Skinner and Chimimba, 2005), the implication is that C<sub>3</sub> grasses were  
247 more abundant than in the present (Sealy et al., 2016). The distribution of C<sub>3</sub> and C<sub>4</sub> grasses  
248 depends largely on temperature during the growing season, with the proportion of C<sub>3</sub> grasses  
249 increasing with altitude and the relative dominance of winter rains (Vogel et al., 1978; Grobler et  
250 al., 2023). Changes in atmospheric pCO<sub>2</sub> have also been identified as an important determinant  
251 of C<sub>3</sub>/C<sub>4</sub> grass distributions, with lower pCO<sub>2</sub>—such as occurred during the LGM—favoring the  
252 expansion of C<sub>4</sub> 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 pCO<sub>2</sub>  
254 would promote C<sub>4</sub> 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 C<sub>3</sub> dominance observed by Sealy et  
256 al. (2016) in the LGM grazers from Boomplaas Cave. There is still an important C<sub>4</sub> signal in the  
257 isotope data (on average 29% among alcelaphins and 24% among equids), demonstrating that C<sub>4</sub>  
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.

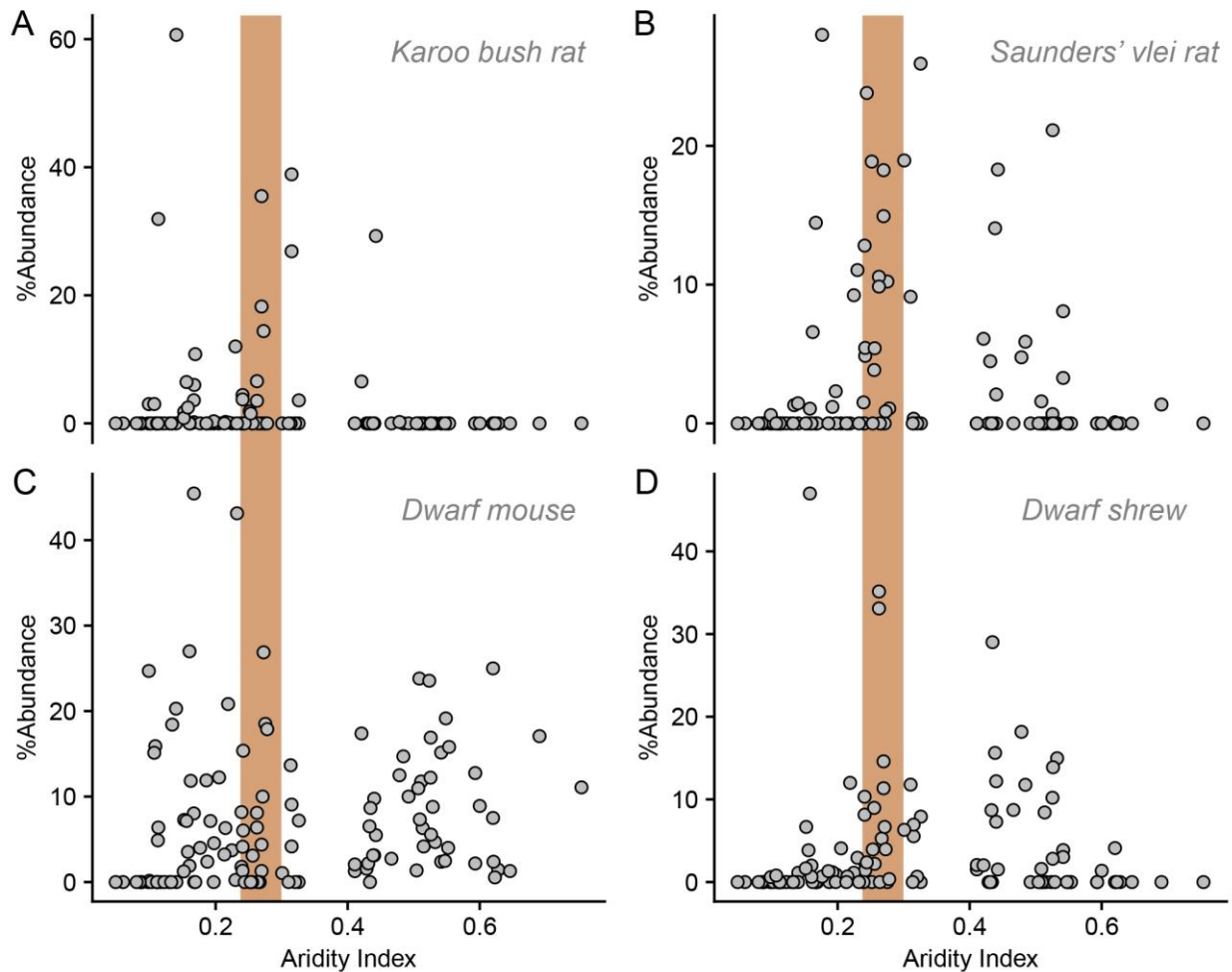
Avery (1982) drew primarily from two lines of evidence to build a case for an arid and harsh LGM at Boomplaas Cave. First, she observed that taxonomic diversity (richness, equitability, and heterogeneity) was lowest in the LGM assemblages (Figure 6), primarily due to the dominance of Saunders' vlei rat

(*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).

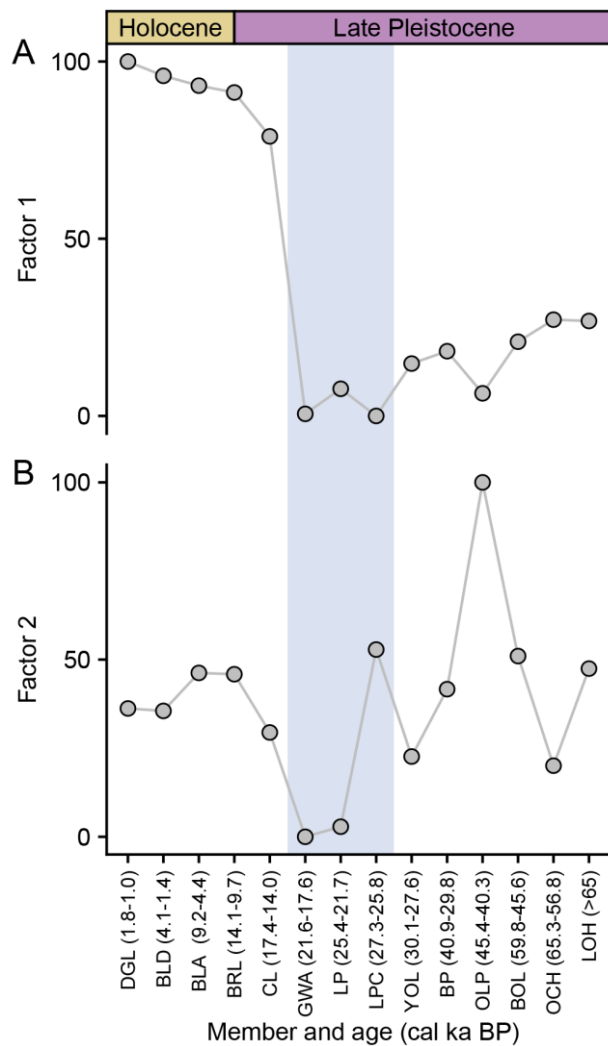
290 Africa (Avery, 1999). In an analysis of modern barn owl-accumulated micromammal  
291 assemblages from the region, Avery (1999) showed that taxonomic diversity is unrelated to  
292 rainfall and aridity, undercutting her previous argument that low diversity signals a harsh LGM.  
293 We suspect that 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.

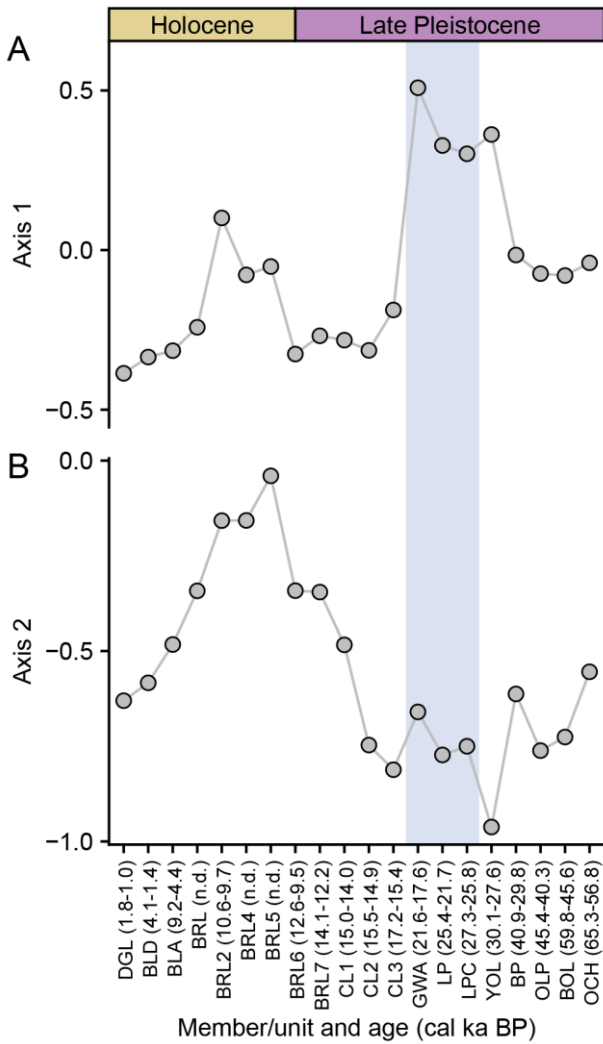
interval (see Thackeray, 1987 for further details). The summary statistics for Factor 1 are low throughout the LGM, with the Factor 2 scores also reaching lows in two of the three LGM members (**Figure 8**). Deacon et al. (1984) interpreted these results as indicating very cold and dry conditions during 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.

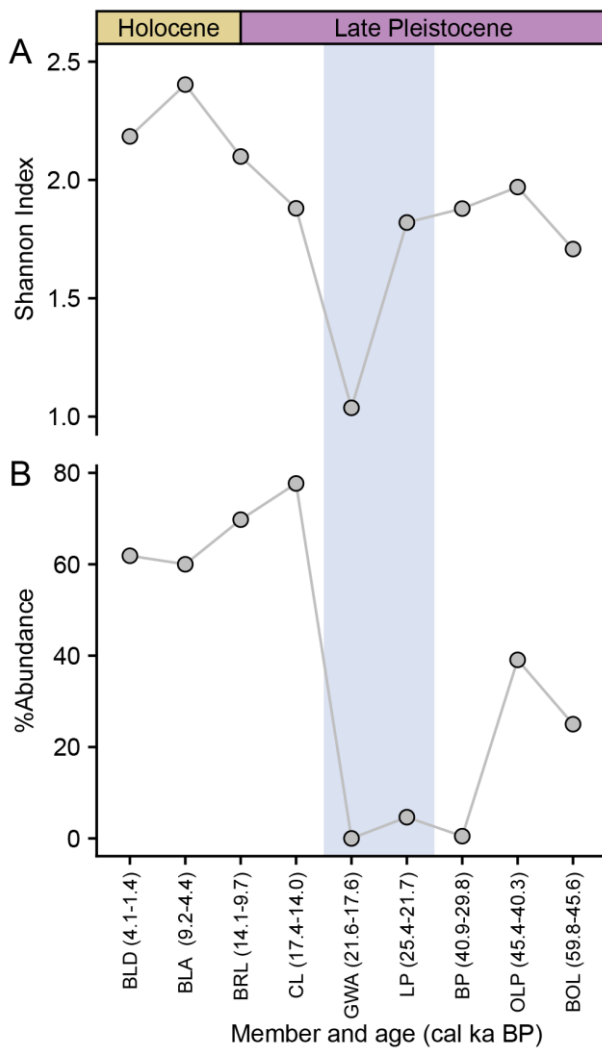
390         Complementing interpretations derived from isotopic analysis of the Boomplaas Cave  
391 ungulates (Sealy et al., 2016), the micromammal assemblages further suggest that winter rainfall  
392 dominated during the LGM. The analysis provided by Faith et al. (2019) indicated that rainfall  
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).

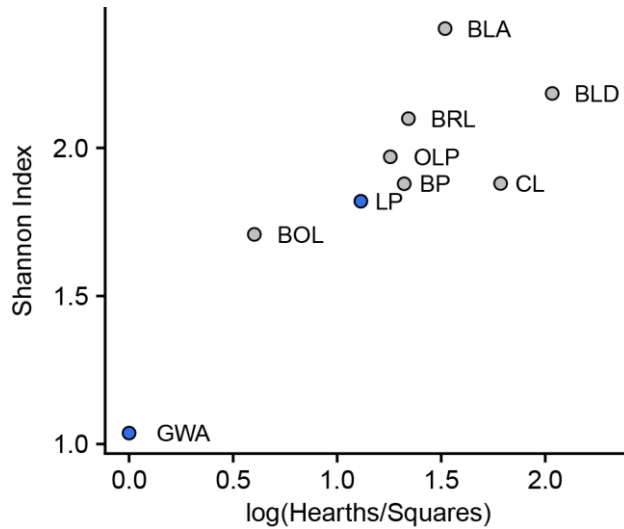


**Figure 10.** A: Taxonomic diversity (Shannon index) of the charcoal assemblages through the Boomplaas Cave sequence. B: The percent abundance of trees and tall shrubs recovered from Boomplaas Cave. Data from Scholtz (1986).

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



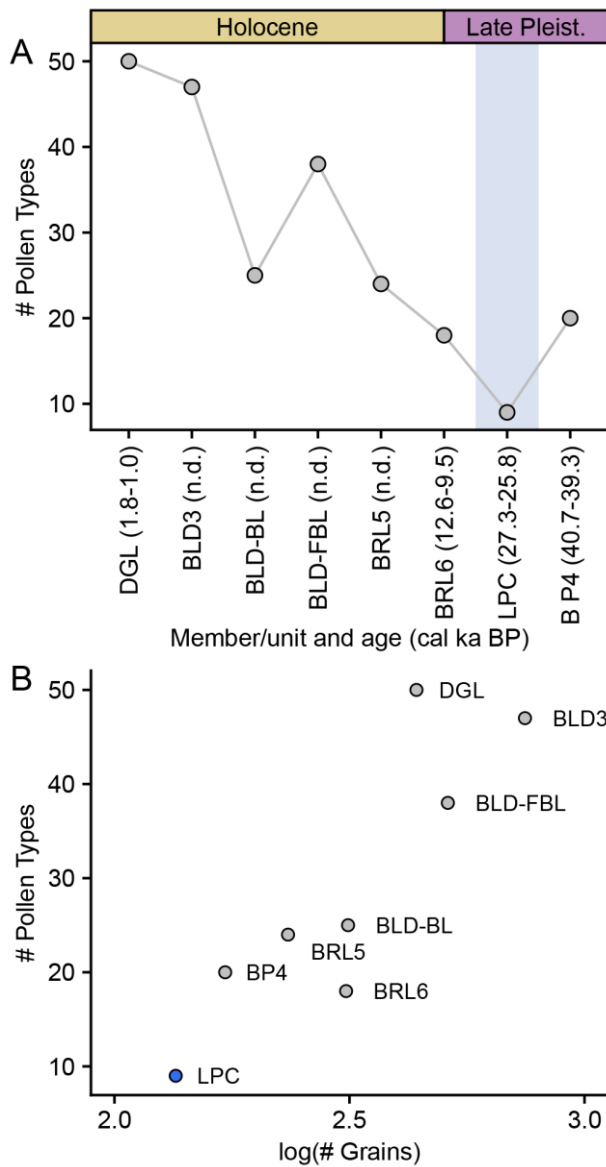
452 charcoal fragments derived from the same piece of wood or burning event and complicates  
453 comparisons of taxonomic diversity across the sequence.

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  $\text{pCO}_2$  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 C<sub>3</sub> 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 C<sub>3</sub>  
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 C<sub>4</sub> grass component during the LGM  
623 (Braun et al., 2020). Taken together, the speleothem records indicate spatial heterogeneity in the  
624 distribution of C<sub>3</sub> and C<sub>4</sub> grasses within the Little Karoo during the LGM. Because C<sub>3</sub> grasses  
625 tend to be more prevalent on south-facing slopes and C<sub>4</sub> 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 C<sub>3</sub> signal from Cango Caves need not imply a dominance of winter rains  
630 whereas the C<sub>4</sub> 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 C<sub>3</sub> signal observed in LGM grazers implies that C<sub>3</sub> grasses were dominant relative to C<sub>4</sub> 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 pCO<sub>2</sub>  
647 concentrations that would otherwise favor C<sub>4</sub> grasses (Ehleringer et al., 1997; Collatz, et al.,  
648 1998). The herbivore isotope data do not agree well with modelled outputs predicting mostly C<sub>4</sub>  
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 C<sub>3</sub> and C<sub>4</sub> 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 C<sub>4</sub> 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 C<sub>4</sub> grass component implied by herbivore isotope data  
661 (Sealy et al., 2016) would underestimate the importance of C<sub>4</sub> relative to C<sub>3</sub> 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 C<sub>3</sub> and C<sub>4</sub> 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 C<sub>4</sub> 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

### 719 **REFERENCES**

- 720 Avery, D.M., 1982. Micromammals as palaeoenvironmental indicators and an interpretation of  
721 the late Quaternary in the southern Cape Province, South Africa. *Annals of the South*  
722 *African Museum* 85, 183-374.
- 723 Avery, D.M., 1983a. Micromammalian population dynamics and environmental change: the last  
724 18,000 years in the southern Cape, in: Vogel, J.C. (Ed.), *Late Cainozoic Palaeoclimates*  
725 *of the Southern Hemisphere*. Balkema, Rotterdam, pp. 361-369.

- 726 Avery, D.M., 1983b. Palaeoenvironmental implications of the small Quaternary mammals of the  
727 fynbos region, in: Deacon, H.J., Hendey, Q.B., Lambrechts, J.J.N. (Eds.), Fynbos  
728 Palaeoecology: A Preliminary Synthesis, South African National Scientific Programmes  
729 Report No 75. Mills Litho, Cape Town, pp. 139-155.
- 730 Avery, D.M., 1999. A preliminary assessment of the relationship between trophic variability in  
731 southern African Barn owls *Tyto alba* and climate. *Ostrich* 70, 179-186.
- 732 Bergh, N.G., Verboom, G.A., Rouget, M., Cowling, R.M., 2014. Vegetation types of the Greater  
733 Cape Floristic Region, in: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), Fynbos:  
734 Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University  
735 Press, Oxford, pp. 26-46.
- 736 Boshoff, A.F., Kerley, G.I.H., 2001. Potential distributions of the medium- to large-sized  
737 mammals in the Cape Floristic Region, based on historical accounts and habitat  
738 requirements. *African Zoology* 36, 245-273.
- 739 Braun, K., Bar-Matthews, M., Matthews, A., Ayalon, A., Zilberman, T., Cowling, R.M., Fisher,  
740 E.C., Herries, A.I.R., Brink, J.S., Marean, C.W., 2020. Comparison of climate and  
741 environment on the edge of the Palaeo-Agulhas Plain to the Little Karoo (South Africa)  
742 in Marine Isotope Stages 5-3 as indicated by speleothems. *Quaternary Science Reviews*  
743 235, 105803.
- 744 Brink, J.S., 1999. Preliminary report on a caprine from the Cape mountains, South Africa.  
745 *Archaeozoologia* 10, 11-26.
- 746 Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337-360.
- 747 Campbell, B.M., 1985. A classification of the mountain vegetation of the fynbos biome. No. 50.  
748 Botanical Research Institute, Department of Agriculture and Water Supply, South Africa.

749 Chase, B.M., 2010. South African palaeoenvironments during marine oxygen isotope stage 4: a  
750 context for the Howiesons Poort and Still Bay industries. *Journal of Archaeological*  
751 *Science* 37, 1359-1366.

752 Chase, B.M., Boom, A., Carr, A.S., Quick, L.J., Reimer, P.J., 2020. High-resolution record of  
753 Holocene climate change dynamics from southern Africa's temperate-tropical boundary,  
754 Baviaanskloof, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 539,  
755 109518.

756 Chase, B.M., Chevalier, M., Boom, A., Carr, A.S., 2017. The dynamic relationship between  
757 temperate and tropical circulation systems across South Africa since the last glacial  
758 maximum. *Quaternary Science Reviews* 174, 54-62.

759 Chase, B.M., Faith, J.T., Mackay, A., Chevalier, M., Carr, A.S., Boom, A., Lim, S., Reimer, P.J.,  
760 2018. Climatic controls on Later Stone Age human adaptation in Africa's southern Cape.  
761 *Journal of Human Evolution* 114, 35-44.

762 Chase, B.M., Harris, C., de Wit, M.J., Kramers, J., Doel, S., Stankiewicz, J., 2021. South African  
763 speleothems reveal influence of high- and low-latitude forcing over the past 113.5 k.y.  
764 *Geology* 49, 1353-1357.

765 Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter  
766 rainfall zone. *Earth-Science Reviews* 84, 103-138.

767 Chevalier, M., Chase, B.M., 2015. Southeast African records reveal a coherent shift from high-  
768 to low-latitude forcing mechanisms along the east African margin across last glacial-  
769 interglacial transition. *Quaternary Science Reviews* 125, 117-130.

770 Chevalier, M., Chase, B.M., 2016. Determining the drivers of long-term aridity variability: a  
771 southern African case study. *Journal of Quaternary Science* 31, 143-151.

772 Chevalier, M., Chase, B.M., Quick, L., Scott, L. (2021). An atlas of southern African pollen  
773 types and their climatic affinities. *Palaeoecology of Africa*, in: Runge, J., Gosling, W.D.,  
774 Lézine, A.-M., Scott, L. (Eds.), *Quaternary Vegetation Dynamics – The African Pollen*  
775 *Database*. CRC Press, London, pp. 239-257.

776 Cockcroft, M.J., Wilkinson, M.J., Tyson, P.D., 1987. The application of a present-day climate  
777 model to the Late Quaternary in southern Africa. *Climatic Change* 10, 161-181.

778 Collatz, G.J., Berry, J.A., Clark, J.S., 1998. Effects of climate and atmospheric CO<sub>2</sub> partial  
779 pressure on the global distribution of C<sub>4</sub> grasses: present, past, and future. *Oecologia* 114,  
780 441-454.

781 Cowling, R.M., 1983. Phytochorology and vegetation history in the south-eastern Cape, South  
782 Africa. *Journal of Biogeography* 10, 393-419.

783 Cowling, R.M., Campbell, B.M., 1983. A Comparison of Fynbos and Non-Fynbos Coenoclines  
784 in the Lower Gamtoos River Valley, Southeastern Cape, South Africa. *Vegetatio* 53, 161-  
785 178.

786 Cowling, R.M., Holmes, P.M., 1992. *Flora and Vegetation*, in: Cowling, R.M. (Ed.), *The*  
787 *Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town,  
788 pp. 23-61.

789 Cowling, R.M., Potts, A.J., Franklin, J., Midgley, G.F., Engelbrecht, F., Marean, C.W., 2020.  
790 Describing a drowned Pleistocene ecosystem: Last Glacial Maximum vegetation  
791 reconstruction of the Palaeo-Agulhas Plain. *Quaternary Science Reviews* 235, 105866.

792 Cowling, R.M., Procheş, Ş., Vlok, J.H.J., van Staden, J., 2005. On the origin of southern African  
793 subtropical thicket vegetation. *South African Journal of Botany* 71, 1-23.

- 794 Croft, D.A., Su, D.F., Simpson, S.W., 2018. *Methods in Paleoecology: Reconstructing Cenozoic*  
795 *Terrestrial Environments and Ecological Communities*. Springer, Cham, Switzerland.
- 796 Deacon, H.J., 1979. Excavations at Boomplaas cave – a sequence through the Upper Pleistocene  
797 and Holocene in South Africa. *World Archaeology* 10, 241-257.
- 798 Deacon, H.J., 1983a. Another look at the Pleistocene climates of South Africa. *South African*  
799 *Journal of Science* 79, 325-328.
- 800 Deacon, H.J., 1983b. Late Quaternary environment and culture relationships in the southern  
801 Cape. Human Sciences Research Council. Ad Hoc Larger Grant Final Report.
- 802 Deacon, H.J., 1995. Two late Pleistocene-Holocene archaeological depositories from the  
803 Southern Cape, South Africa. *South African Archaeological Bulletin* 50, 121-131.
- 804 Deacon, H.J., Deacon, J., Scholtz, A., Thackeray, J.F., Brink, J.S., Vogel, J., 1984. Correlation of  
805 palaeoenvironmental data from the Late Pleistocene and Holocene deposits at Boomplaas  
806 Cave, southern Cape, in: Vogel, J.C. (Ed.), *Late Cainozoic Palaeoclimates of the*  
807 *Southern Hemisphere*. Balkema, Rotterdam, pp. 339-351.
- 808 Deacon, H.J., Scholtz, A., Daitz, L.D., 1983. Fossil charcoals as a source of palaeoecological  
809 information in the fynbos region, in: Deacon, H.J., Hendey, Q.B., Lambrechts, J.J.N.  
810 (Eds.), *Fynbos Palaeoecology: A Preliminary Synthesis*, South African National  
811 Scientific Programmes Report No 75. Mills Litho, Cape Town.
- 812 Deacon, H.J., Thackeray, J.F., 1984. Late Pleistocene environmental changes and implications  
813 for the archaeological record in southern Africa, in: Vogel, J.C. (Ed.), *Late Cainozoic*  
814 *Palaeoclimates of the Southern Hemisphere*. Balkema, Rotterdam, pp. 375-390.
- 815 Deacon, J., 1984. *The Later Stone Age of southernmost Africa*. *British Archaeological Reports*,  
816 *International Series* 213, Oxford.



817 Deacon, J., Lancaster, N., 1988. Late Quaternary Palaeoenvironments of Southern Africa.  
818 Oxford University Press, New York.

819 Duker, R., Cowling, R.M., du Preez, D.R., van der Vyver, M.L., Weatherall-Thomas, C.R.,  
820 Potts, A.J., 2015. Community-level assessment of freezing tolerance: frost dictates the  
821 biome boundary between Albany subtropical thicket and Nama-Karoo in South Africa.  
822 *Journal of Biogeography* 42, 167-178.

823 Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C<sub>4</sub> photosynthesis, atmospheric CO<sub>2</sub>, and  
824 climate. *Oecologia* 112, 285-299.

825 Faith, J.T., 2013a. Taphonomic and paleoecological change in the large mammal sequence from  
826 Boomplaas Cave, Western Cape, South Africa. *Journal of Human Evolution* 65, 715-730.

827 Faith, J.T., 2013b. Ungulate diversity and precipitation history since the Last Glacial Maximum  
828 in the Western Cape, South Africa. *Quaternary Science Reviews* 68, 191-199.

829 Faith, J.T., Chase, B.M., Avery, D.M., 2019. Late Quaternary micromammals and the  
830 precipitation history of the southern Cape, South Africa. *Quaternary Research* 91, 848-  
831 860.

832 Faith, J.T., Chase, B.M., Avery, D.M., 2020. Late Quaternary micromammals and the  
833 precipitation history of the southern Cape, South Africa: response to comments by F.  
834 Thackeray, *Quaternary Research* 95, 154–156. *Quaternary Research* 95, 157-159.

835 Faith, J.T., Lyman, R.L., 2019. *Paleozoology and Palaeoenvironments: Fundamentals,*  
836 *Assumptions, Techniques.* Cambridge University Press, Cambridge.

837 Gerhart, L.M., Ward, J.K., 2010. Plant responses to low [CO<sub>2</sub>] of the past. *New Phytologist* 188,  
838 674-695.

839 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the  
840 measurements and comparison of species richness. *Ecology Letters* 4, 379-391.

841 Grayson, D.K., 1984. *Quantitative Zooarchaeology*. Academic Press, Orlando, Florida.

842 Grobler, B.A., Franklin, J., Marean, C.W., Gravel-Miguel, C., Cowling, R.M., 2023. The  
843 importance of C<sub>3</sub> and C<sub>4</sub> grasses and CAM shrubs in the Greater ape Floristic Region  
844 under contemporary and Last Glacial Maximum climates. *Quaternary Science Reviews*  
845 318, 108294.

846 Happold, D., 2013. *Mammals of Africa. Volume III: Rodent, Hares and Rabbits*. Bloomsbury  
847 Publishing, London.

848 Happold, M., Happold, D., 2013. *Mammals of Africa. Volume IV: Hedgehogs, Shrews and Bats*.  
849 Bloomsbury Publishing, London.

850 Heaton, T.H.E., Talma, A.S., Vogel, J.C., 1986. Dissolved gas paleotemperatures and <sup>18</sup>O  
851 variations derived from groundwater near Uitenhage, South Africa. *Quaternary Research*  
852 25, 79-88.

853 Hempson, G.P., Archibald, S., Bond, W.J., 2015. A continent-wide assessment of the form and  
854 intensity of large mammal herbivory in Africa. *Science* 350, 1056-1061.

855 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution  
856 interpolated climate surfaces for global land areas. *International Journal of Climatology*  
857 25, 1965-1978.

858 Hogg, A., Heaton, T., Hua, Q., Palmer, J., Turney, C., Southon, J., Bayliss, A., Blackwell, P.,  
859 Boswijk, G., Ramsey, C., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L.,  
860 2020. SHCal20 southern hemisphere calibration, 0-55,000 years cal BP. *Radiocarbon* 62,  
861 759-778.

862 Kgope, B.S., Bond, W.J., Midgley, G.F., 2010. Growth responses of African savanna trees  
863 implication atmospheric [CO<sub>2</sub>] as a driver of past and current changes in savanna tree  
864 cover. *Austral Ecology* 35, 451-463.

865 Klein, R.G., 1972. The late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province,  
866 South Africa): its implications for megafaunal extinctions and environmental and cultural  
867 change. *Quaternary Research* 2, 135-142.

868 Klein, R.G., 1978. A preliminary report on the larger mammals from the Boomplaas stone age  
869 cave site, Cango Valley, Oudtshoorn District, South Africa. *South African*  
870 *Archaeological Bulletin* 33, 66-75.

871 Klein, R.G., 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos  
872 region, in: Deacon, H.J., Hendey, Q.B., Lambrechts, J.J.N. (Eds.), *Fynbos Palaeoecology:*  
873 *A Preliminary Synthesis*, South African National Scientific Programmes Report No 75.  
874 Mills Litho, Cape Town, pp. 116-138.

875 Kraaij, T., Engelbrecht, F., Frankling, J., Cowling, R.M., 2020. A fiery past: a comparison of  
876 glacial and contemporary fire regimes on the Palaeo-Agulhas Plain, Cape Floristic  
877 Region. *Quaternary Science Reviews* 235, 106059.

878 Kraaij, T., van Wilgen, B.W., 2014. Drivers, ecology, and management of fire in fynbos, in:  
879 Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Fynbos: Ecology, Evolution, and*  
880 *Conservation of a Megadiverse Region*. Oxford University Press, Oxford, pp. 47-73.

881 Lyman, R.L., 2008. *Quantitative Paleozoology*. Cambridge University Press, Cambridge.

882 le Roux, J.P., 1977. The stratigraphy, sedimentology and structure of the Cango Group north of  
883 Oudtshoorn, MA Thesis, University of Stellenbosch, South Africa.

884 Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Princeton University Press,  
885 Princeton.

886 Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, MA.

887 Marean, C.W., Cawthra, H.C., Cowling, R.M., Esler, K.J., Fisher, E., Milewski, A., Potts, A.J.,  
888 Singels, E., De Vynck, J., 2014. Stone Age people in a changing South African Greater  
889 Cape Floristic Region, in: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), Fynbos:  
890 Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University  
891 Press, Oxford, pp. 164-199.

892 Miller, G.H., Beaumont, P.B., Deacon, H.J., Brooks, A.S., Hare, P.E., Jull, A.J.T., 1999. Earliest  
893 modern humans in southern Africa dated by isoleucine epimerization in ostrich eggshell.  
894 Quaternary Science Reviews 18, 1537-1548.

895 Moffett, R.O., Deacon, H.J., 1977. The flora and vegetation in the surrounds of Boomplaas  
896 Cave: Cango Valley. South African Archaeological Bulletin 32, 127-145.

897 Olf, H., Ritchie, M.E., Prins, H.H.T., 2002. Global environmental controls of diversity in large  
898 herbivores. Nature 415, 901-905.

899 Pargeter, J., Faith, J.T., 2020. Lithic miniaturization as adaptive strategy: a case study from  
900 Boomplaas Cave, South Africa. Archaeological and Anthropological Sciences 12, 225.

901 Pargeter, J., Loftus, E., Mackay, A., Mitchell, P., Stewart, B., 2018. New ages from Boomplaas  
902 Cave, South Africa, provide increased resolution on late/terminal Pleistocene human  
903 behavioral variability. Azania: Archaeological Research in Africa 53, 156-184.

904 Patterson, D.B., Du, A., Faith, J.T., Rowan, J., Uno, K., Behrensmeier, A.K., Braun, D.R.,  
905 Wood, B.A., 2022. Did vegetation change drive the extinction of *Paranthropus boisei*?  
906 Journal of Human Evolution 173, 103154.

- 907 Potts, A.J., Hedderson, T.A., Franklin, J., Cowling, R.M., 2013. The Last Glacial Maximum  
908 distribution of South African subtropical thicket inferred from community distribution  
909 modelling. *Journal of Biogeography* 40, 310-322.
- 910 Robinson, J.R., 2023. A context for connectivity: insights to environmental heterogeneity in the  
911 Late Pleistocene and Holocene of southern Africa through measuring isotope space and  
912 overlap. *Journal of Paleolithic Archaeology* 6, 34.
- 913 Scholtz, A., 1986. Palynological and Palaeobotanical Studies in the Southern Cape, MA Thesis,  
914 University of Stellenbosch, South Africa.
- 915 Schweitzer, F.R., Wilson, M.L., 1982. Byneskranskop 1, a late Quaternary living site in the  
916 southern Cape Province, South Africa. *Annals of the South African Museum* 88, 1-203.
- 917 Sealy, J., Lee-Thorp, J., Loftus, E., Faith, J.T., Marean, C.W., 2016. Late Quaternary  
918 environmental change in the Southern Cape, South Africa, from stable carbon and  
919 oxygen isotopes in faunal tooth enamel from Boomplaas Cave. *Journal of Quaternary*  
920 *Science* 31, 919-927.
- 921 Sealy, J., Naidoo, N., Hare, V.J., Brunton, S., Faith, J.T., 2020. Climate and ecology of the  
922 palaeo-Agulhas Plain from stable carbon and oxygen isotopes in bovid tooth enamel from  
923 Nelson Bay Cave, South Africa. *Quaternary Science Reviews* 235, 105974.
- 924 Skead, C.J., 2011. Historical incidence of the larger land mammals in the broader Western and  
925 Northern Cape. Centre for African Conservation Ecology, Nelson Mandela Metropolitan  
926 University, Port Elizabeth.
- 927 Skinner, J.D., Chimimba, C.T., 2005. *The Mammals of the Southern African Subregion*.  
928 Cambridge University Press, Cambridge.

929 Smith, F.A., Elliot Smith, R.E., Lyons, S.K., Payne, J.L., 2018. Body size downgrading of  
930 mammals over the late Quaternary. *Science* 360, 310-313.

931 Staver, A.C., Abraham, J.O., Hempson, G.P., Karp, A.T., Faith, J.T., 2021. The past, present,  
932 and future of herbivore impacts on savanna vegetation. *Journal of Ecology* 109, 2804-  
933 2822.

934 Stynder, D.D., 2009. The diets of ungulates from the hominid fossil-bearing site of  
935 Elandsfontein. *Quaternary Research* 71, 62-70.

936 Talma, A.S., Vogel, J.C., 1992. Late Quaternary palaeotemperatures derived from a speleothem  
937 from Cango Caves, Cape Province, South Africa. *Quaternary Research* 37, 203-213.

938 Thackeray, J.F., 1987. Late Quaternary environmental changes inferred from small mammalian  
939 fauna, southern Africa. *Climatic Change* 10, 285-305.

940 Thackeray, J.F., 1990. Temperature indices from late Quaternary sequences in South Africa:  
941 comparisons with the Vostok core. *South African Geographic Journal* 72, 47-49.

942 Thackeray, J.F., 2020. Late Quaternary micromammals and the precipitation history of the  
943 southern Cape, South Africa — comment on the published paper by Faith et al.,  
944 *Quaternary Research* (2019), Vol. 91, 848–860. *Quaternary Research* 95, 145-146.

945 Thackeray, J.F., Fitchett, J.M., 2016. Rainfall seasonality captured in micromammalian fauna in  
946 Late Quaternary contexts, South Africa. *Palaeontologia Africana* 51, 1-9.

947 Trabucco, A., Zomer, R.J., 2009. Global Aridity Index (Global-Aridity) and Global Potential  
948 Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium for Spatial  
949 Information, <http://www.cgiar-csi.org/>.

950 Tyson, P.D., 1986. *Climatic change and variability in southern Africa*. Oxford University Press,  
951 Cape Town.

- 952 UNEP, 1997. World Atlas of Desertification. UNEP, London.
- 953 Vaks, A., Bar-Matthews, M., Ayalon, A., Matthews, A., Halicz, L., Frumkin, A., 2007. Desert  
954 speleothems reveal climatic window for African exodus of early modern humans.  
955 Geology 35, 831-834.
- 956 van Zinderen Bakker, E.M., 1976. The evolution of late Quaternary paleoclimates of southern  
957 Africa. Palaeoecology of Africa 9, 160-202.
- 958 Vlok, J., Schutte-Vlok, A.L., 2010. Plants of the Klein Karoo. Umdaus Press, Hatfield, South  
959 Africa.
- 960 Vogel, J.C., 1983. Isotopic evidence for the past climates and vegetation of southern Africa.  
961 Bothalia 14, 391-394.
- 962 Vogel, J.C., 2001. Radiometric dates for the Middle Stone Age in South Africa, in: Tobias, P.V.,  
963 Raath, M.A., Maggi-Cecchi, J., Doyle, G.A. (Eds.), Humanity from African Naissance to  
964 Coming Millenia: Colloquia in Human Biology and Paleoanthropology. Florence  
965 University Press, Florence, pp. 261-268.
- 966 Vogel, J.C., Fuls, A., Ellis, R.P., 1978. The geographical distribution of Kranz grasses in South  
967 Africa. South African Journal of Science 74, 209-215.