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**A vegetation record based on charcoal analysis from Border Cave, KwaZulu-Natal,
South Africa, ~ 227 000 to ~ 44 000 years ago**

Sandra Lennox^{a, *}, Lucinda Backwell^{a, b, c}, Francesco d'Errico^{d, e}, Lyn Wadley^a

^a *Evolutionary Studies Institute, University of the Witwatersrand, 1 Jan Smuts Avenue,
Johannesburg, South Africa*

^b *Centre of Exploration for the Deep Human Journey, University of the Witwatersrand, 1 Jan
Smuts Avenue, Johannesburg, South Africa*

^c *Instituto Superior de Estudios Sociales (ISES-CONICET), Córdoba 191, San Miguel de
Tucumán, CP4000, Tucumán, Argentina*

^d *UMR 5199 CNRS de la Préhistoire à l'Actuel: Culture, Environnement, et Anthropologie
(PACEA), Université de Bordeaux, Allée Geoffroy Saint Hilaire, CS 50023, F - 33615,
Pessac CEDEX, Talence, France*

^e *Centre for Early Sapiens Behaviour, Øysteinsgate 3, Postboks 7805, 5020, University of
Bergen, Norway*

* Corresponding author: sandralennoxj@gmail.com

Abstract

Border Cave is a key Middle Stone Age (MSA) site in southern Africa, with a 4 m-deep sedimentary sequence that dates from more than 227,000 (227 ka) to 44 ka ago. Lithic assemblages vary considerably during this period and artefacts made from organic materials become common at the end of the MSA sequence. Here we describe charcoal from the 10 members that comprise the stratigraphic sequence. Anatomical features of charcoal were studied by means of reflected light microscopy, the use of the International Association of Wood Anatomists code and modern wood charcoal reference collections. Most woody plants represented by charcoal at the site are evergreen trees. Indicator plants from bushveld and open woodland taxa were most common in Member 6 BS (>227 ka) and Member 5 WA (~227 ka). Moist forest was most common in Members 5 BS (~161–144 ka) and 4 WA (~168–113 ka), while Member 1 RGBS (~74 ka) had a combination of bushveld and moist forest. At about 64 ka, dry bushveld predominated, while in Members 3 BS (72–56 ka) and 2 WA (~60 ka) moist forest was the predominant vegetation type. Member 2 BS.UP (49–44 ka) mostly included bushveld and moist forest patches, while Member 1 WA (~43 ka) was predominantly dry bushveld. The Border Cave occupations seem to have taken place in drier conditions than those at present. The driest members were 5 BS, 4 WA, 1 RGBS and 3 WA, followed by Members 2 BS and 1 WA. Member 3 BS was only slightly drier than present, while Member 2 WA was moderately drier than present. The past vegetation is similar to the modern vegetation profile and there appears to have been remarkable stability through time, suggesting that cultural changes in the sequence may not be linked to environmental change.

Keywords Anthracology, Environment, Late Pleistocene, Quaternary, Vegetation communities, human exploitation of plants

1. Introduction

The last two decades have witnessed a flourishing of hypotheses, often contradictory, trying to link climate change with the emergence of our species in Africa, its dispersal within and out of this continent, and its biological and cultural evolution. It has been proposed for example that a population bottleneck would have been produced c. 71 ka ago by the climatic deterioration triggered by the Toba eruption (Ambrose, 1998, but see Torosin et al., 2020). Ziegler and colleagues (2013) have argued that cultural innovations during the MSA in southern Africa were triggered by periods of humidity that produced higher levels of biomass and consequent increases in human population density. Other authors have proposed that Heinrich events, entailing strong reduction in the North Atlantic sea temperature following the break off from North America and European glaciers, may have rendered large regions of North, East, and West Africa unsuitable for hominin occupation, thus compelling *Homo sapiens* to migrate out of Africa (Carto et al., 2009). Low-latitude insolation has been posited as a prominent driver governing the evolution of vegetation and mammal communities in eastern and western Africa by increasing stable ecotonal settings, which would have in turn played a role in early modern human adaptation (Kabothe-Bahr et al., 2021). Humid intervals in the Levant have been proposed as a potential trigger of modern human dispersal out of Africa (Langgut et al., 2018). Rapid climatic variability has been modelled as a possible cause for the loss of complex cultural innovations (Kolodny et al., 2015). A varied climate towards the end of the penultimate glacial, followed by an abrupt change to relatively stable moist climate during the last interglacial would have favoured selection for behavioural versatility, population growth, and range expansion, supporting scenarios of early, multiple dispersals of modern humans from Africa (Lamb et al., 2018). By applying ecological niche modelling techniques d'Errico and colleagues (2018) have identified a niche shift characterized by a significant expansion in the breadth of the Howiesons Poort ecocultural niche compared with the preceding Still Bay. This expansion is coincident with aridification

occurring across Marine Isotope Stage 4 (c. 72–60 ka) and especially pronounced at 60 ka. Climate change would have acted during the last 300 ka as a factor favouring in some instances, and preventing in others, biological and cultural contact across African regions, thus supporting a multiregional and long term scenario for the emergence of our species in Africa (Scerri et al., 2018; Bergström et al., 2021). In a recent study, more weight is given instead to the impact of astronomically forced changes in temperature, rainfall and terrestrial net primary production on the distribution and evolution of *Homo* populations, as well as the emergence of the first members of our species (Timmermann et al., 2022). Global climate change producing contrasting vegetation changes in the two hemispheres may have caused regional niche contractions or expansions affecting movements of hominin populations and therefore human evolution (Sánchez Goñi, 2020). The precocious appearance 92–80 ka ago, following the disappearance, of cultural innovations at a site located in southern Africa's arid Succulent Karoo Biome, has recently been explained by suggesting that climate change modified cultural connectivity between regions during the southern African MSA (Mackay et al., 2022).

Most of the above propositions, however, lack the means, apart from contemporaneity and recurrence, by which to verify hypotheses that climate may have influenced cultural shifts, to identify the suite of environmental parameters within which each archaeological culture operated, or to evaluate how these relationships varied through space and time (d'Errico and Banks, 2013). The emergence of key cultural innovations in our lineage may reflect changes in the nature of such relationships. The more robust connections between cultural and biological evolution on the one hand, and climate on the other, arguably come from approaches that create means for quantification and verification of their findings. Eriksson and colleagues (2012) have for example combined patterns of genetic variation in modern human populations and climatic reconstructions to create a model accounting for

human demography and expansion over the past 120 ka. They show that the model is fully consistent with known trends in modern human expansion, which support a clear effect of climate on past population densities and dispersal (Eriksson et al., 2012). In most regions, however, the evidence needed to test these hypotheses rigorously is scant, and simply lacking in others. Existing regional palaeoenvironmental records remain spatially and chronologically disconnected from the archaeological record. Very few continuous terrestrial climate archives exist that would permit an integration of climate and behavioural variability, and even when they exist, chronological uncertainties do not allow clear correlations between the two records. High-resolution regional palaeoclimate simulations can only partially overcome the problem and they only provide a rough representation of past climate and vegetation. They need data-model comparisons to be accepted as real. Despite its recognized importance for the biological and cultural evolution of Middle and Later Stone Age populations, southern Africa records only a few continuous climatic sequences covering the large span of the last climatic cycles (Dupont, 2011; Daniau et al., 2013; Urrego et al., 2015; Ziegler et al., 2013; Dupont et al., 2019, 2022; Chevalier et al., 2021; Strobel et al., 2022). Most of these records are not high resolution, and rarer are those allowing reconstruction of the evolution of the climate and vegetation of the eastern side of this vast region.

Pollen, in combination with sediment chemistry and carbon isotope analysis from Core MD96-2048, retrieved in the middle of the Delagoa Bight and covering the last 2 Ma, provide at present the best record to identify long term trends in the evolution of vegetation in the area during the Quaternary (Dupont et al., 2022). Pollen source areas cover the region north of the Delagoa Bight in southern Mozambique and the region west of the Lebombo Mountains and the Drakensberg escarpment. The pollen record allows for a detailed reconstruction of the biome developments over the last 790 ka (Dupont et al., 2022). This recently extended record and the presence in the region of an archaeological site, Border

Cave, preserving a well-dated stratigraphic sequence covering the last seven climatic cycles, and presenting exceptional preservation of organic matter, provides the opportunity to contrast the evolution of vegetation at a regional scale and the choices made by human groups visiting the site when selecting the plant taxa in their immediate environment to burn for heating and pyrotechnology. The identification of archaeological charcoal from abandoned fireplaces and living areas enables the reconstruction of vegetation communities around the site. Anthracology in northern (Thery-Parisot et al., 2010) and southern latitudes (Scheel-Ybert, 2020) has demonstrated that different firewood gathering scenarios result in most local vegetation types being represented in archaeological charcoal assemblages. On the one hand, firewood collection for daily domestic use generally has low species selectivity, with dead wood randomly gathered. On the other hand, multiple fire functions tend to result in the selection of multiple types of wood. In both cases, the charcoal remains of an occupation that lasted for a sufficiently long time would include most of the species in the different vegetation types around the settlement (Thery-Parisot et al., 2010; Scheel-Ybert, 2020). While human selection may account for under- or over-representation of specific taxa in an archaeological charcoal assemblage, it may not be the only explanation. Other factors should also be considered, such as the reliability of the analysed samples in terms of the number of charcoal pieces identified, the duration of site occupation, the context in which the charcoal was found, whether concentrated in combustion features or scattered in sediments, and whether the taxa concerned occur in low or high frequency in the surrounding environment. Here we present results of the study of archaeological charcoal from Border Cave, South Africa, where stratigraphic members have been dated between ~227 ka and ~24 ka (Table 1).

1.1. *Site location and modern vegetation*

Border Cave is a large, West-facing shelter located about 82 km West of the Indian Ocean, in the Lebombo Mountains on the border between KwaZulu-Natal in South Africa, and eSwatini, formerly known as Swaziland (Fig. 1). The cave is just below the rim of an escarpment at approximately 600 m above mean sea level (a.m.s.l.) (Backwell et al., 2018). It overlooks eSwatini, and is 2 km North of the Ngwavuma River where the altitude is about 100 m a.m.s.l. and riverine vegetation occurs. The modern Lebombo vegetation around Border Cave provides the vegetation baseline for the anthracology. A mosaic of vegetation communities exists within a 5 km radius of the cave and the variability of vegetation in this part of the Lebombo is linked to the elevation, moisture availability and soil type. We make use of several commonly-used names to describe the local vegetation communities, for example, bushveld, sourveld, woodland, and forest. Bushveld is defined as sub-tropical woodland (Mucina and Rutherford, 2006); sourveld is grassland which occurs in cool, moist areas (Ellery, 1992; Cowling et al., 2004); woodland consists of trees and shrubs with an open canopy (Coates-Palgrave, 2002; Scholes, 2004), while forest consists of closed stands of trees where the crowns of the trees are continuous and some trees are taller than 10 m (Scholes and Walker, 1993; Midgley et al., 2004: 278; Mucina and Rutherford, 2006). All of these plant communities, as well as the riverine vegetation near the Ngwavuma River, could have been exploited by inhabitants of Border Cave. Mucina and Rutherford (2006) have classified the Lebombo vegetation zones more precisely as Lebombo Summit Sourveld (SVI 17) and Northern (SVI 15) and Southern (SVI 16) Lebombo Bushveld (Mucina and Rutherford, 2006: 500-502). All these vegetation zones occur near Border Cave (Fig. 1). Southern Lebombo Bushveld includes *Androstachys johnsonii* (Lebombo ironwood) thickets, *Acacia* spp. (including herein *Vachellia* and *Senegalia* spp.), and *Combretum* spp., *Olea europaea*, *Atalaya alata*, *Bridelia cathartica*, *Commiphora harveyii*, *Croton gratissimus*, *Diospyros dichrophylla*, *Encephalartos lebomboensis*, *Erythroxylum emarginatum*,

Euphorbia tirucalli, *Manilkara concolor*, *Peltophorum africanum*, *Pterocarpus rotundifolius*, *Strychnos gerrardii*, *Teclea gerrardii*, *Turraea floribunda*, *Vepris reflexa*, and *Vitex obovata* subsp. *obovata* (Mucina and Rutherford, 2006: 502). Lebombo Summit Sourveld (sour grassland) includes some woody plants that also occur in other vegetation zones: *Diospyros dichrophylla*, *Grewia monticola* and *Acacia caffra* (*Senegalia caffra*) (Mucina and Rutherford, 2006: 502). This grassland vegetation type is not further described in our study, which relies on woody plants.

A recent vegetation survey near the cave (see Backwell et al., 2018) confirms several plant species and adds new ones to those recorded by Anderson (1978), whose list of common taxa include *Acacia* spp., *Combretum kraussii*, *Dichrostachys cinerea*, *Diospyros dichrophylla*, *Ehretia rigida*, *Euclea divinorum*, *Euphorbia tirucalli*, *Maytenus* spp., *Spirostachys africana*, *Strychnos henningsii* and *Vitex wilmsii*.

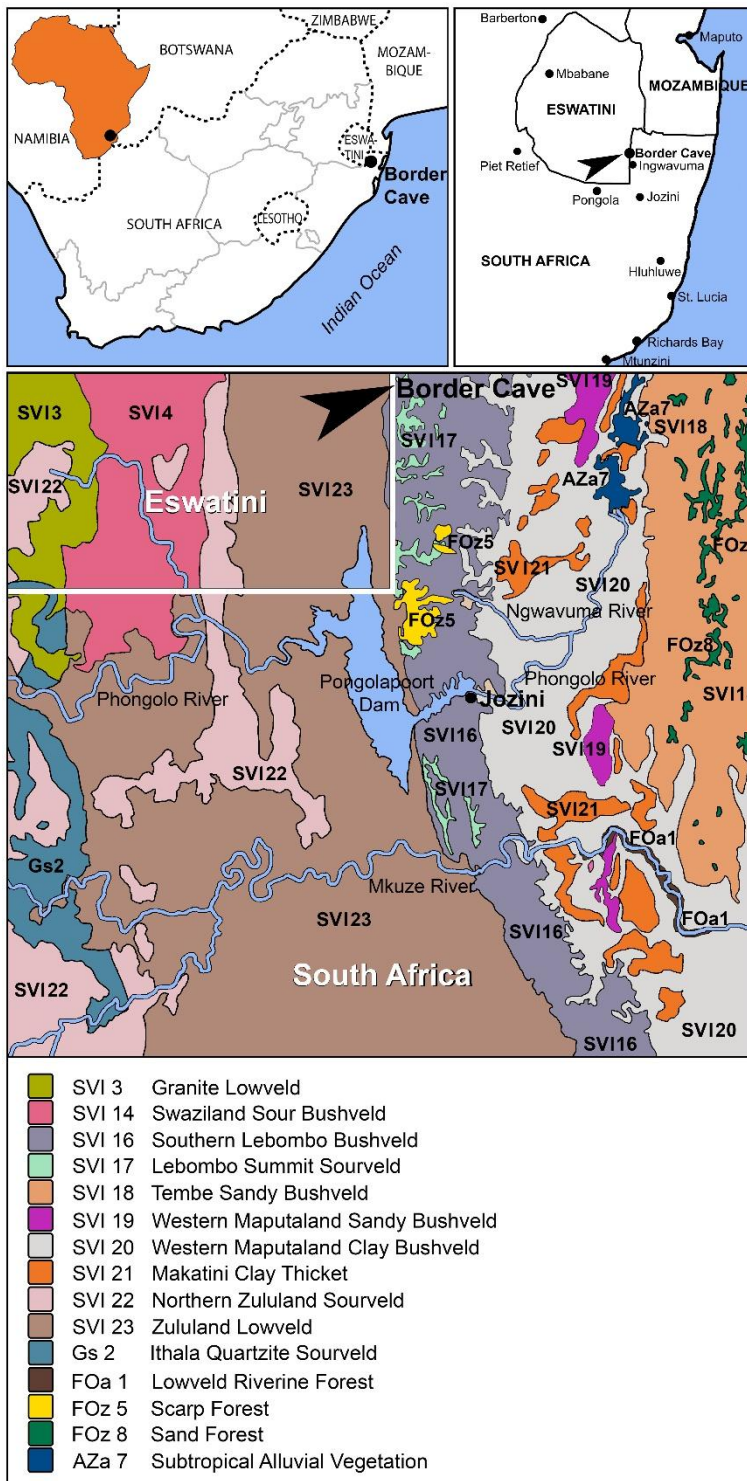


Fig. 1. Location of Border Cave and the surrounding vegetation types. **a.** Map of South Africa with the locality of Border Cave; **b.** location of Border Cave near the Ngwavuma River; **c.** vegetation of the area (modified after Mucina and Rutherford, 2006).

In the broader context, Border Cave is within an area of high biodiversity. The Maputaland centre of endemism is not far from the cave, and nor is the Gwalaweni Forest, which may once have encompassed a greater area of the Lebombo, though at present only about 500 hectares survive. Gwalaweni is a scarp forest (with several endemics) that borders the Lebombo Summit Sourveld (Mucina and Rutherford, 2006). Plants found in Gwalaweni Forest and nowhere else include: a combination of three types of *Celtis* (*C. africana*, *C. gomphophylla* and *C. mildbraedii*), important canopy trees *Brachylaena uniflora*, *Combretum kraussii* and *Homalium dentatum*, and a combination of *Heywoodia lucens*, *Drypetes gerrardii* and *Chrysophyllum viridifolium* (Moll, 1977; Midgley et al., 2004). *Buxus natalensis* is a common shrub in the understorey. Forest trees of about 30 m tall occur in deep, moist valleys, and on South-facing slopes. Lower canopy and dense shrub grade into bushveld. This type of grading also occurs elsewhere in the Lebombo Mountains where forest (Scarp Forest FOz5) in valleys transforms to bushveld (Lebombo Summit Sourveld SVI 17) on the plateau (Mucina and Rutherford, 2006: 790). This type of variability may have once occurred in the Border Cave area.

The complexity of the modern environment has made it necessary for us to simplify the vegetation types used for our analysis at Border Cave, so we have concentrated on four types based on plant habitat. Habitat is defined by shrub or tree height and plant community (Hammer et al., 2001; Hammer, 2019). We have chosen forest and closed woodland as two types that will be used in our interpretations, and of course there is some overlap between the genera found in each. Bushveld and open woodland are the other two vegetation types, and once again, there is overlap between the genera found in each of these vegetation types.

1.2. Excavations at Border Cave

At Border Cave, five archaeological excavations have taken place, as well as one non-archaeological excavation, namely ‘Horton’s Pit’ that was purportedly for the collection of bat guano for agricultural purposes. R.A. Dart was the first professional excavator; B.D. Malan, L.H. Wells and H.B.S. Cooke undertook the second expedition, and P.B. Beaumont was responsible for the next two excavations (Beaumont, 1978; Beaumont et al., 1992). These early excavations demonstrated that the site contains a wealth of organic material, but archaeological charcoal was not studied prior to the Backwell-led excavations between 2015 and 2019. The new campaign aims primarily to produce a high-resolution multi-proxy record of climate change and contemporaneous human behaviour that extends from MIS 7 to MIS 2; contribute to an understanding of the impact of climate change on subsistence strategies in this region through time; gain insight into site formation processes; identify cultural trends within a secure chronological framework; document the emergence of cultural innovations, and collect and study all organic remains, including grass bedding, seeds, leaves, wood, rhizomes and charcoal (Backwell et al., 2018; this volume).

1.3. Border Cave chronostratigraphic sequence

The 4 m-deep sedimentary sequence comprises six alternating brown sand (BS) and white ash (WA) members. Beaumont (1973, 1978) and Butzer et al. (1978) named the Border Cave members based on whether the layers were predominantly white from accumulated ash (WA members) or whether they were brown sandy layers (BS members). The new excavations directed by Backwell retain the Beaumont nomenclature. At the base of the sequence, Members 6 BS and 5 WA are older than 227 ka. A portion of the older part of the sequence (Members 6 BS–4 BS) is illustrated in Figure 2. Above the long MSA sequence are Members 1 WA and 1 BS Lower dated to between 43 ka and 24 ka and they are said to belong to the Early Later Stone Age (ELSA) (Beaumont et al., 1992 ; d’Errico et al, 2012; Villa et al, 2012;

d'Errico and Backwell, 2016). Directly above the ELSA deposits is Member 1 BS Upper (Iron Age). In order to avoid the possibility of Iron Age intrusions in our sample, we chose not to analyse charcoal from Member 1 BS Lower in this study. In the new excavations, small layers separated at the centimetre scale have been recognized within each member, and anthropogenic features such as hearths and bedding layers (Fig. 3) have been carefully mapped (Backwell et al., 2018; Wadley et al., 2020).

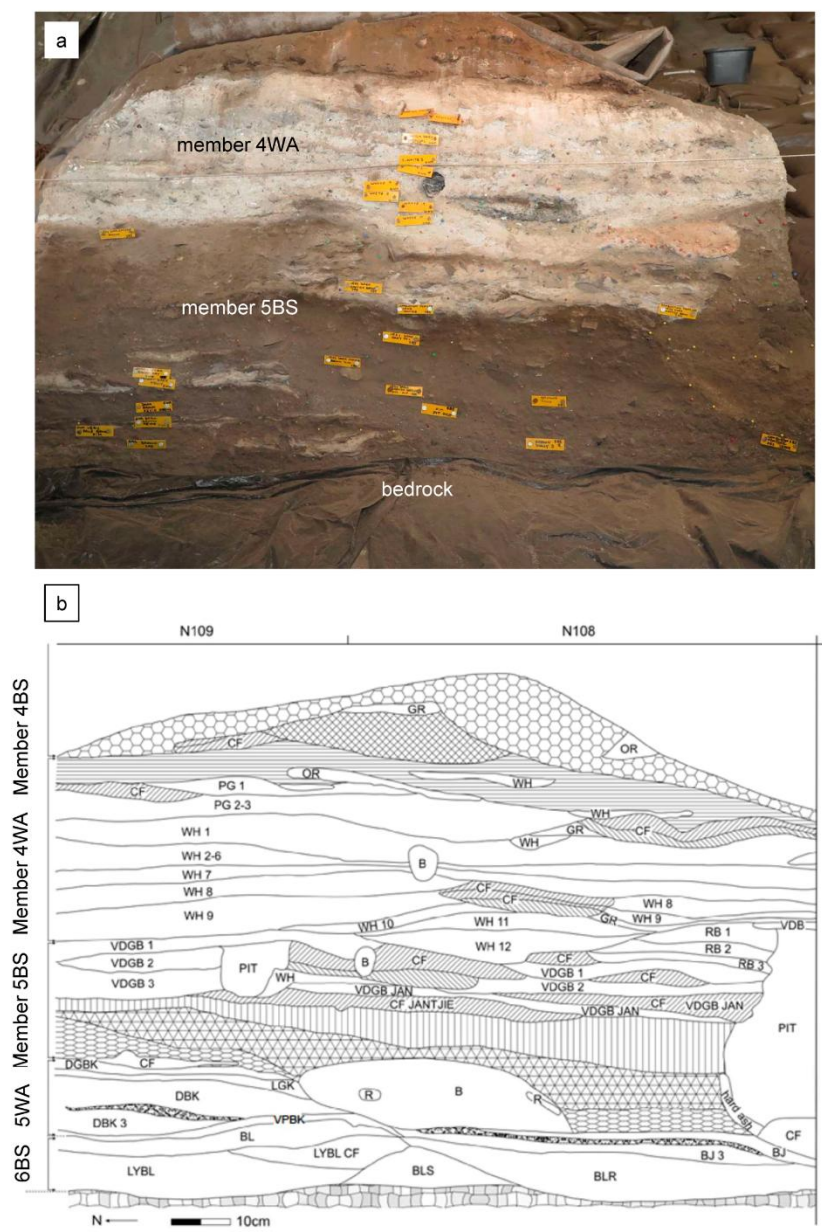


Fig. 2. Lower part of the Border Cave sequence showing the East profile in squares N108 E113 and N109 E113. **a.** Photograph showing the alternating white ash and brown sand members above bedrock: Members 6 BS, 5 WA, 5 BS, 4 WA and 4 BS; **b.** stratigraphic drawing illustrating the same sequence. The abbreviations denote the layers within each member. Modified after Backwell et al. (2018) and Wadley et al. (2020).



Fig. 3. Border Cave Member 2 WA combustion features. Stacked combustion features show black charcoal-rich bases with white or yellow/pink ash above. **A** and **C** are lens-shaped combustion features that might be burned grass bedding, while **B** and **D** are basin-shaped and are probably hearths.

The Border Cave sequence has been dated by electron spin resonance (ESR) (Grün and Beaumont, 2001; Grün et al., 2003; Millard, 2006), amino acid racemisation (Miller and Beaumont, 1989; Miller et al., 1999), and radiocarbon methods (Vogel and Beaumont, 1972; Beaumont et al., 1978; Beaumont, 1980; Vogel et al., 1986; Beaumont et al., 1992; Bird et al., 2003; d’Errico et al., 2012; Villa et al., 2012; Backwell et al., 2018), see Table 1. Lithic assemblages at the site were divided by Beaumont (1978) into MSA 1, MSA 2/Howiesons Poort (HP), MSA 3/post-HP and ELSA. The MSA 1 lithic assemblages (Members 5 WA, 5

BS, 4 WA, 4 BS) span 238 ka to 71 ka when minimum and maximum standard deviations are included. Beaumont's MSA 2/HP assemblages (Members 1 RGBS, 3 WA, 3 BS) range between 82 ka and 54 ka, and the MSA 3/post-HP assemblages (Members 2 WA; 2 BS.LR C, B and A; 2 BS.UP) fall between 63 ka and 42 ka. The ELSA assemblages (Members 1 WA, 1 BS.LR) date to between 44 ka and 24 ka. The new dating results (Tribolo et al., this volume) generally support the earlier chronologies.

1.4. *Research hypothesis*

Here, the hypothesis is that global climate changes caused similar vegetation change at Border Cave to that demonstrated at the mouth of the Limpopo River by Dupont and colleagues (2019). The hypothesis for change through time was also informed by a micromammalian study suggesting that miombo woodland occurred before ~150 ka at Border Cave and that miombo was later replaced by vegetation similar to mopane woodland (Avery, 1992). *Colophospermum mopane* charcoal was indeed found in layer Faan (Member 1 RGBS) (Zwane and Bamford, 2021b), but has not previously been located in the cave's sequence, and the tree does not grow near the cave nowadays. Miombo woodland also does not occur near Border Cave today, but a small relic miombo woodland survives in northern South Africa, in the Soutpansberg mountains (Pienaar, 2015). The southern range of miombo is in Zimbabwe, though it extends through Mozambique and into Zambia (Smith and Allen, 2004). Miombo taxa are described by Smith and Allen (2004) and den Outer and van Veenendaal (1996). What is clear from vegetation community descriptions is that *Brachystegia* spp. and *Julbernardia* spp. (Fabaceae Caesalpinioideae) are characteristic miombo woodland genera, and they would be expected in the Border Cave charcoal assemblage if miombo woodland was represented there in the past.

We aim to depict shifts in the Lebombo woodland vegetation through time by carrying out anthracological analysis on the well-preserved assemblage retrieved from the Border Cave sequence. Identified woody taxa in the various archaeological members will be used to reconstruct vegetation communities through time. Border Cave charcoal is better preserved than that from Sibudu, a site about 300 km South of Border Cave, where the charcoal was fragmented into tiny pieces (Allott, 2006; Lennox et al., 2015; Lennox, 2016; Lennox et al., 2017; Lennox and Wadley, 2019; Bamford, 2021; Zwane and Bamford, 2021a). We recognise, however, that anthropogenic choice is an important factor to consider when interpreting the presence of taxa collected for firewood.

2. Materials and methods

During recent excavations between 2015 and 2018, all charcoal, whether recovered from combustion features (hearths and burned bedding layers) or scattered in sediments, was collected from all members. All pieces 20 mm or larger were point-plotted by means of a total station, and were curated individually. Smaller pieces were collected after dry sieving the sediment through 2 mm and 1 mm mesh, and they were curated according to standard procedures for archaeobotany (Popper and Hastorf, 1988; Pearsall, 2000). Flotation was not used because the site preserves some delicate unburnt plant material that would be destroyed by water.

Approximately 80 specimens of charcoal (Stewart et al., 2016) were analysed from two layers from each member, except from Members 5 BS and 4 WA where more layers were examined (Table 1). Standard anthracological methods were applied to identify the charcoal (see for example Figueiral and Mosbrugger, 2000; Allott, 2006; Théry-Parisot, 2010; Cartwright, 2013; Backwell et al., 2014; Bamford, 2015a, b; Stewart et al., 2016; King et al., 2018; Bodin et al., 2020; Henry et al., 2020). Border Cave specimens were selected for

identification by means of random sampling within each sample using random number tables (Drennan, 2009). Consequently, specimen sizes vary between members. This is important because a study of the taphonomy in Escabasses Cave (southwestern France) showed that size class does not affect interpretations of floristic diversity (Henry et al., 2020). However, earlier studies by Chabal (1991,1992, 1997) demonstrated that the charcoal analyst's choice of larger or better conserved pieces introduced bias and interpretation errors in the analysis, by underestimating sample diversity. It was statistically demonstrated that larger fragment classes contained only the most frequent species, whereas most species, and all rare species, are represented only in the smallest fragments. Material excavated and records kept during the Backwell campaigns at Border Cave are stored at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg.

Table 1. Summary of the members and the layers within them that were used in the study of Border Cave charcoal. The bucket points are total station identification numbers from Backwell et al's. excavations. The dates were obtained during Beaumont's excavations. Abbreviations: ELSA (Early Later Stone Age) and HP (Howiesons Poort).

Member	Layers in Backwell excavation	Munsell colour	Sediment description	Bucket point (Backwell excavation)	Lithic industry (Beaumont's names)	Approx. age (ka) Beaumont excavation	Dating method (Beaumont excavation)
1 WA	Very Dark Brown Barry 1	10YR 2/2	fine silt	3126	ELSA	43	14C ^{1,2}
	Very Dark Greyish Brown Bill	10YR 6/2	-	3357			

2 BS.UP	Grass Mat Carly	-	organic, pebbly, sandy	3221	MSA 3/post- HP	49.0-44.2	14C ²
	Grass Mat Cassidy 1	10YR 4/3	silty, loose	4641			
2 WA	Grass Mat Dark Yellowish Brown Dossy 2	10YR 6/2	silty, loose, organic	4585	MSA 3/post- HP	60 ± 3	ESR ^{2,4}
	Dark Yellowish Brown Dossy	10YR 6/2	silty, loose, organic	5188			
3 BS	Grass Mat Eco 1	-	organic	4401	MSA 2b/HP, MSA 2a/HP	56 ± 2 64 ± 3	ESR ^{3,4}
	Dark Brown Elmo 1 Combustion Feature	7.5YR 4/3	silty, loose	5318		72 ± 4	
3 WA	Light Reddish Brown Faba, Plan 2	-	-	6173	MSA 2/HP	64 ± 2	ESR ^{3,4}
	Dark Reddish Brown Faddy, Plan 1	-	-	6231			
1 RGBS	Very Dark	-	-	6622	MSA 2/HP	74 ± 4	ESR ^{3,4}

	Brown Feba, Plan 1						
	Very Dark Brown Feba, Plan Base	-	-	6693			
4 WA	Reddish Brown Ian 3. Pinkish Grey 1, 2, 3	5YR 6/4 7,5YR 7/2	gritty/ashy loose cemented	Ian 3 is 3144. PG is 396, 433.	MSA 1	115 ± 8 113 ± 5 168 ± 5	ESR ^{3,4}
5 BS	Very Dark Greyish Brown Jan 1, 2, 4. Very Dark Grey Brown Jantjie. White Jet 1 CF 2. Very Dark Grey Jez 1, 2. Brown Jim. Brown John 1.	10YR 3/2 10YR 3/2 10YR 4/3 7.5YR 8/1 10YR 3/1 10YR 3/2 7.5YR 4/2	silty, loose silty, loose sandy ashy, cemented ashy, loose ashy, loose ashy, cemented	Jan 2 is 3312. Jan 4 is 3694. Jantjie is 3108. Jet 1 is 4199, 4224. Jez 1 is 4336, 4378, 4616, 4698, 4805. Jim is 5137, 5242, 5254, 5256, 5360, 5365, 5430. John 1 is 5425, 5469.	MSA 1	161 ± 10 144 ± 11	ESR ^{3,4}
5 WA	Dark	-	-	5645	MSA 1	183 ± 20	ESR ^{3,4}

	Greyish Brown Kay, Plan 1					227 ± 11	
	Brown Ken, Plan 1	-	-	6150			
6 BS	Brown Larry, Plan 1	-	-	6347	MSA 1	>227	ESR ^{3,4}
	Brown Larry, Plan 2	-	-	6881			

Dating methods are radiocarbon (¹⁴C) for the younger layers and electron spin resonance for the older ones. 1. d’Errico et al. (2012); 2. Bird et al. (2003); 3. Grün and Beaumont (2001); 4. Grün et al. (2003).

By way of reference, a list was compiled of several species occurring near Border Cave between 2016 and 2019, and the anatomical characteristics were recorded according to the IAWA (International Association of Wood Anatomists) code from the InsideWood database (Wheeler et al., 1989; Wheeler, 2011) and from published references (Kromhout, 1975; Ilic, 1991; Neumann et al., 2000; Jansen et al., 2002; Ruffinato and Crivellaro, 2019). In addition, charcoal reference collections are held at the Evolutionary Studies Institute, University of the Witwatersrand (Allott, 2005; Chikumbirike, 2014; Lennox, 2016; Scheel-Ybert, 2016).

Each charcoal specimen was pressure-fractured in order to obtain the three anatomical planes for observation: transverse, radial longitudinal and tangential longitudinal. The anatomical features were observed by means of light microscopy, utilising an Olympus SZX 16 stereomicroscope magnified up to 110 times, an Olympus USB camera and Soft Imaging Solutions software. Anatomical details were studied in greater detail by means of an

Olympus BX51 reflective, polarised light microscope magnified up to 600 times, and Olympus Stream Essentials image analysis software with Extended Focal Image (EFI) capability was used.

The anatomical characteristics were compared with those of reference charcoal (Allott, 2005; Höhn et al., 2008; Bamford, 2011; Hubau et al., 2012, 2013; Nelle et al., 2013; Asouti and Kabukcu, 2014; Chikumbirike, 2014; Dotte-Sarout et al., 2014; Hubau et al., 2014; Scheel-Ybert et al., 2014; Bamford, 2015a, b; Lennox and Bamford, 2015; Lennox, 2016, Lennox and Bamford, 2017; Lennox, 2019). The archaeological charcoal is identified by comparing the IAWA characters of reference material. Most anatomical characteristics are visible using reflective microscopy to 600x magnification. For example, pitting and perforation plates of *Curtisia dentata* (Fig. 4), and fibre thickness in *Brachylaena* and *Tarchonanthus* spp. (Lennox and Bamford, 2017) are observable, while crystals and silica bodies can be detected in Euphorbiaceae such as *Spirostachys africana* and *Sclerocroton* spp. (Lennox and Bamford, 2015), and radial canals can be seen in *Commiphora* spp., in addition to ray width in *Cryptocarya* spp. (Lennox, 2019). Nonetheless, IAWA characteristics are sometimes not visible because of post-depositional damage to charcoal, such as cracks caused by diagenesis, and fusion due to vitrification. Carbonisation fuses the structure of cell walls and middle lamellae, which may destroy the pits in vessels and fibres, thus it is not possible to use all IAWA features in anthracology (Kwon et al., 2009; Scheel-Ybert and Gonçalves, 2017).

While it is often not possible for anthracologists to distinguish the species within a woody genus, some African genera, such as *Curtisia dentata*, have only one species. In such cases we make use of the genus and species attribution. Where several species occur within a genus, we do not attempt to distinguish them, but list them as, for example, *Tarchonanthus* spp.

Since the micromammalian study mentioned earlier (Avery, 1992) implied that miombo woodland may once have occurred near Border Cave, particular attention was given to the anatomy of the Fabaceae found in the charcoal assemblage because their wood anatomy is highly variable, and often does not permit specific identifications. White (1983) lists 19 species of *Brachystegia*, two of *Julbernardia*, and *Isoberlinia angolensis*, which occur in miombo as dominant taxa. No miombo species presently grow near Border Cave, but may have been present in the past. Thus particular attention was given to the anatomy of *Brachystegia* and *Julbernardia* spp. (as listed in den Outer and van Veenendaal, 1996). The published anatomical features were compared with those of the Border Cave archaeological legumes, and with legumes that occur in the modern Lebombo environment. The anatomical features of the charred reference material were thus grouped according to the distinguishing characteristics, particularly ray width and parenchyma arrangement (abundant or sparse).

2.1. *Quantitative analysis methods*

Detrended correspondence analysis (DCA) was used to compare the woody taxa identifications from charcoal in the ten Border Cave members using Palaeontological Statistics, PAST 3.23 software (Hammer et al., 2001; Hammer, 2019). The PAST module uses the same algorithm as the Decorana software (Hill and Gauch, 1980). DCA is commonly used in paleoecology. In studies of plant ecology it can suggest the progression of plant communities over time. Correspondence analysis and principal coordinate analysis are particularly useful for dealing with large quantities of data, especially in cases of presence-absence data, for example plant species, or semi-quantitative data, such as rare, moderately present or abundant specimens. Such analyses allow for ordination of both fixed points like stratigraphic layers, and variables, for example plant taxa. The taxa are grouped into the four broad types of vegetation based on plant habitat that have previously been discussed, that is,

forest, closed woodland, bushveld and open woodland. The horse-shoe curve produced by correspondence analysis is straightened out by Decorana, enabling a comparison between values along a relatively horizontal line. Two of three axes are plotted, increasing from zero along the x and y axes. The scale is even and increases incrementally, not logarithmically or exponentially. The lines link similar values in the four groups. The position of each woody taxon (data row) is plotted once; Eigen values group woody taxa and the Border Cave stratigraphic members. The hulls represent correlations between plant habitat (determined by groups of woody taxa) and members (Hill and Gauch, 1980; Bloem et al., 1993; Hammer et al., 2001; Cruikshank, 2016; Hammer, 2019).

In the case of Border Cave where continuity and overlap in plant taxa are likely through time, the Decorana module in PAST offers potential to identify trends, for example recurrent ecological associations not detectable through a simple analysis of the data. Naturally, interpretations suggested by the Decorana need to be assessed using ecological insights and local knowledge about a particular environment.

3. Results

In the charcoal analysis, 1441 of the 1581 charcoal specimens were identified: 22 families and 28 genera were identified, 25 charcoal specimens remain unidentified and 115 were unidentifiable. Unidentified charcoal did not have enough IAWA features for identification. Unidentifiable charcoal was in some instances knotted (branched), or damaged beyond recognition by carbonisation, for example it was vitrified. A variety of woody taxa occur in each member (Table 2). The IAWA features of each are listed in Appendix Table 1. The wood anatomy of some of the taxa identified at Border Cave is illustrated in micrographs (Appendix Figs. 1–5) where diagnostic anatomical features are described in the captions.

Appendix Fig. A1 illustrates *Acacia* sp. (Fabaceae Mimosoideae) and *Azelia quanzenis* (Fabaceae Caesalpinioideae), both from Member 4 WA. Appendix Fig. A2 illustrates *Brachylaena* sp. (Asteraceae) and *Diospyros* sp. (Ebenaceae), both from Member 5 BS. Appendix Fig. A3 illustrates *Myroxylon aethiopicum* (Celastraceae) from Member 4 WA, and *Olea* sp. (Oleaceae) from Member 5 BS. Appendix Fig. A4 illustrates *Vitex* sp. (Lamiaceae) and *Ziziphus* sp. (Rhamnaceae), both from Member 5 BS. Appendix Fig. A5 illustrates *Combretum* sp. (Combretaceae) and *Commiphora* sp. (Burseraceae), both from Member 4 WA.

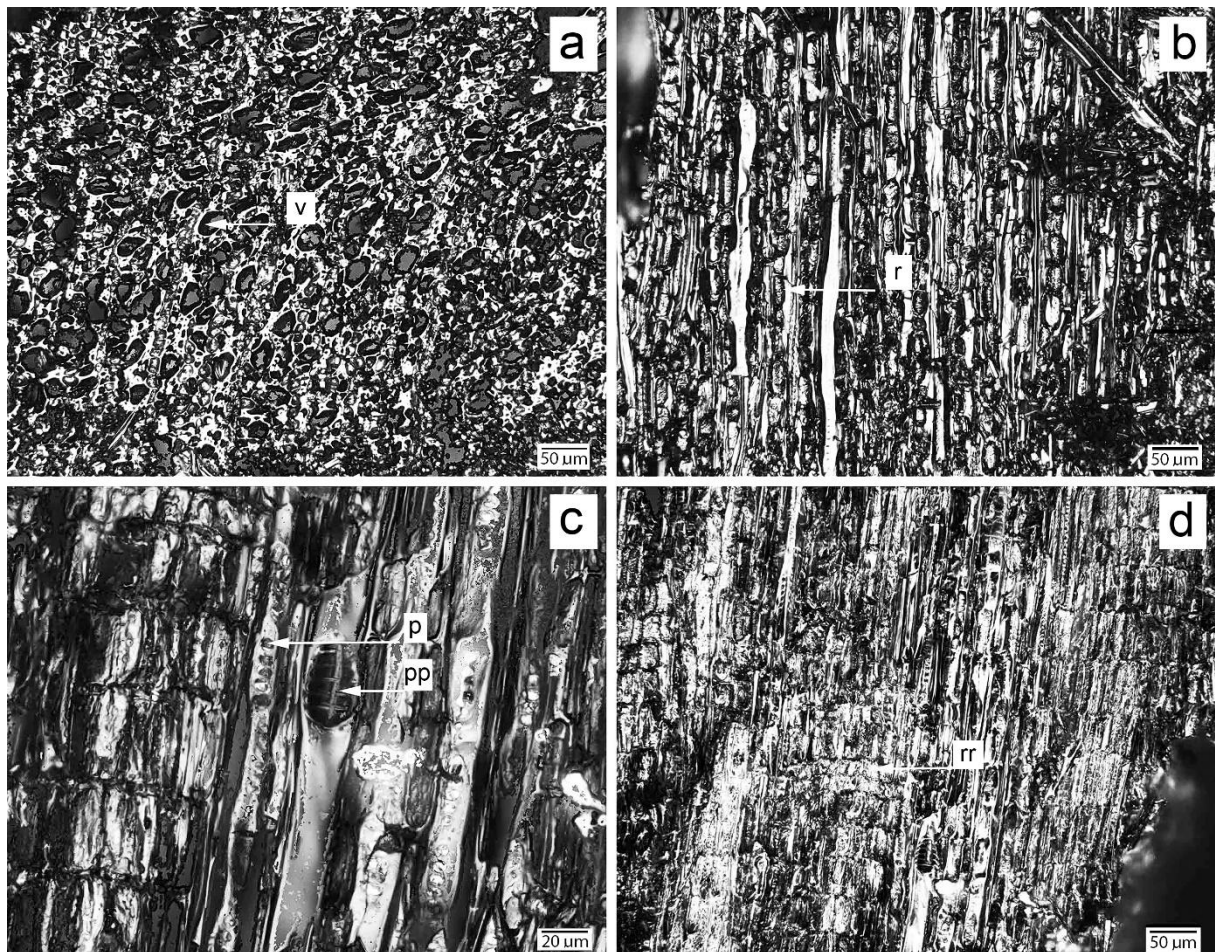


Fig. 4. Microphotographs of *Curtisia dentata*, Cornaceae (specimen #5430 from Member 5 BS, layer Brown Jim), identified from reference specimen LFA 47 (also, Kromhout, 1977; Noshiro and Baas, 1998; InsideWood, 2004 onwards; Allott, 2005). **a.** Transverse section,

diffuse porous wood with exclusively solitary vessels and diffuse parenchyma. The vessel diameters average ~50 μm , and frequencies range from 40-100 vessels/ mm^2 . Axial parenchyma is diffuse. **b.** Ray width is 1-3 cells and frequency is 12 rays/ mm . **c.** Perforation plates are scalariform. Vessel-ray pit arrangement is opposite and the mean diameter is ~7 μm . **d.** Rays are heterocellular and composed of procumbent and marginal upright body cells. Scale bars of 50 μm represent 200x (**a**, **b** and **d**) and 20 μm represents 500x (**c**) magnification. pp = perforation plate; p = vessel-ray pit; r = ray; v = vessel.

Several woody taxa from charcoal representing Fabaceae from subfamilies Caesalpinioideae and Mimosoideae were identified in the Border Cave charcoal assemblage (Appendix Table A1; Metcalfe and Chalk, 1950; den Outer and Van Veenendal, 1996; Neumann et al., 2000; InsideWood, 2004 onwards). Other archaeological charcoal identified as Fabaceae closely matches *Acacia* sp. and *Afzelia quanzenis*, Type 6 Caesalpinioideae, Type 7 Mimosoideae and Type 8 Papilionoideae (see Table 2 and IAWA features in Appendix Table 1). No Fabaceae charcoal in the Border Cave sample matches *Brachystegia* or *Julbernardia* spp. (as listed by White, 1983; Den Outer and Van Veenendaal, 1996; Höhn, 1999; InsideWood, 2004-onwards). The presence of *Brachystegia* and *Julbernardia* can therefore be ruled out amongst the archaeological charcoal identified at Border Cave.

The genera representing evergreen or deciduous plants (Fig. 5) or forest/closed woodland and bushveld/open woodland habitats (Fig. 6) are expressed as a percentage of the total number of genera identified in each member. Thus, the figure is not a measure of the percentage of fragment counts of identified material, but rather a measure of percentage ubiquity, present across samples (Kabukcu and Chabal, 2021).

Table 2. Summary of the woody taxa identified from 10 members (M) in Border Cave from ~227 ka (Member 6 BS) to ~43 ka (Member 1 WA). Totals (T) are the total number of charcoal pieces identified to the listed taxa. Preferred modern habitats for the listed taxa are presented as bushveld (B), forest (F), or woodland open (W. Op.) or closed (W. Cl). * = Taxa not recently observed in the Border Cave area.

Scientific name	Family	Habitat	6 BS	5 WA	5 BS	4 WA	1 RG BS	3 WA	3 BS	2 WA	2 BS	1 WA	T	M
<i>Acacia</i> sp.	Fabaceae Mimosoideae	B	2	1	5	13	1	9	20	8	6	10	75	10
<i>Afrocarpus/ Podocarpus</i> sp.	Podocarpaceae	F					1	1	1				3	3
<i>Azelia quanzenis</i>	Fabaceae Caesalpinioideae	B	1			1			1				3	3
<i>Brachylaena</i> sp.	Asteraceae	W. Op.	30	4	106	22	2	1	26	45	19	30	285	15
<i>Celtis</i> sp.	Celtidaceae	W. Op.				1				1	1	1	4	4
<i>Combretum</i> sp.	Combretaceae	W. Cl.	2			3		16		2			23	4
<i>Commiphora</i> sp. *	Burseraceae	W. Op., B	2	3		4	1	12	4	1	4	4	35	14
<i>Cryptocarya</i> spp.	Lauraceae	W. Cl.	4	1	9	16			3	1	13		47	7
<i>Curtisia dentata</i>	Cornaceae	F			6	1			5	8			20	4
<i>Diospyros</i> sp.	Ebenaceae	B., W. Op.	5	1	12	4		16	9	6	7	5	65	9
<i>Diospyros</i> sp. 2	Ebenaceae	W. Op.		2	29	1			6	5		2	45	6
<i>Erica</i> * sp.	Ericaceae	W. Op.			5				2				7	2
<i>Harpephyllum caffrum</i>	Anacardiaceae	F							4				4	1
<i>Leucosidea sericea</i> *	Rosaceae	W. Op.								6		3	9	2

<i>Mystroxydon aethiopicum</i>	Celastraceae	F., B	10	2	10	19		6	7	10	2	1	6	9
<i>Olea</i> sp.	Oleaceae	F., W. Op.	2		5	4			4	7	7	1	3	8
<i>Pappea capensis</i>	Sapindaceae	B	18	11			4	2			17	3	5	6
<i>Phoenix</i> sp.	Arecaceae Monocot.	W. Op.					1	1		1		1	4	4
<i>Protea</i> . sp.*	Proteaceae	W. Op.			3		1						4	2
<i>Ptaeroxylon obliquum</i>	Ptaeroxylaceae	F				1							1	1
<i>Rapanea melanophloeos</i>	Myrsinaceae	W. Cl.			2				1				3	2
<i>Sclerocarya birrea</i>	Anacardiaceae	W. Op., B			2		1		3				6	3
<i>Sclerocroton integerrimum</i>	Euphorbiaceae	W. Cl.					2						2	1
<i>Searsia</i> . sp.	Anacardiaceae	W. Op.	2	8	4			13	1	6	2	18	5	1
<i>Tarchonanthus</i> spp.	Asteraceae	F., B	4	9			3			1	7	1	2	6
<i>Spirostachys africana</i>	Euphorbiaceae	B		1		1							2	2
<i>Vitex</i> sp.	Lamiaceae	W. Op.			3				5	2		1	1	4
<i>Ziziphus</i> sp.	Rhamnaceae	W. Op.	1		6	8	1		1	4	1		2	7
Type 1	Anacardiaceae					12	7				4		2	3
Type 2	Araliaceae										3		3	1
Type 3	Boraginaceae								1				1	1
Type 4	Cunoniaceae							20			17		3	2
Type 5	Euphorbiaceae					1			1	1			3	3
Type 6	Fabaceae Caesalpinioideae						1	17		1			1	3
Type 7	Fabaceae Mimosoideae								1				1	1
Type 8	Fabaceae Papilionoideae									4			4	1
Type 9	Flacourtiaceae								2		4		6	2
Type 10	Heteropyxidaceae								9	2	3		1	3
Type 11	Kirkiaceae				6							1	7	2
Type 12	Lamiaceae				10	3		1	4	4			2	5
													2	

Type 13	Meliaceae					4	1						5	2
Type 14	Melanthaceae											1	1	1
Type 15	Ochnaceae		3			21				1		2	2	4
Type 16	Olacaceae								1	2			3	2
Type 17	Rhizophoraceae											1	1	1
Type 18	Rubiaceae		26	36	27	26	13	25	26	21	11	44	2	1
Type 19	Rutaceae				1	2	3				2	6	1	5
Type 20	Sterculiaceae								2		1		3	2
sp.	Ebenaceae								1		3	1	5	3
sp.	Erythroxylaceae				1								1	1
sp.	Fabaceae		1		40	14			6	4			6	5
sp.	Fabaceae Caesalpinioideae		1	1				1	3			1	7	5
sp.	Fabaceae Papilionoideae									2	1	2	5	3
sp.	Rosaceae				20								2	1
IDENTIFIED	IDENTIFIED		11	80	28	186	46	14	16	15	135	14	1	
			4		4			0	0	6		0	4	
													4	
													1	
UNIDENTIFIED	UNIDENTIFIED		0	0	12	5	4	0	0	4	0	0	2	
													5	
UNIDENTIFIABLE	UNIDENTIFIABLE		42	19	18	9	0	6	4	5	2	10	1	
													1	
													1	
STUDIED	STUDIED		15	99	31	200	50	14	16	16	137	15	1	
			6		4			6	4	5		0	5	
													8	
													1	

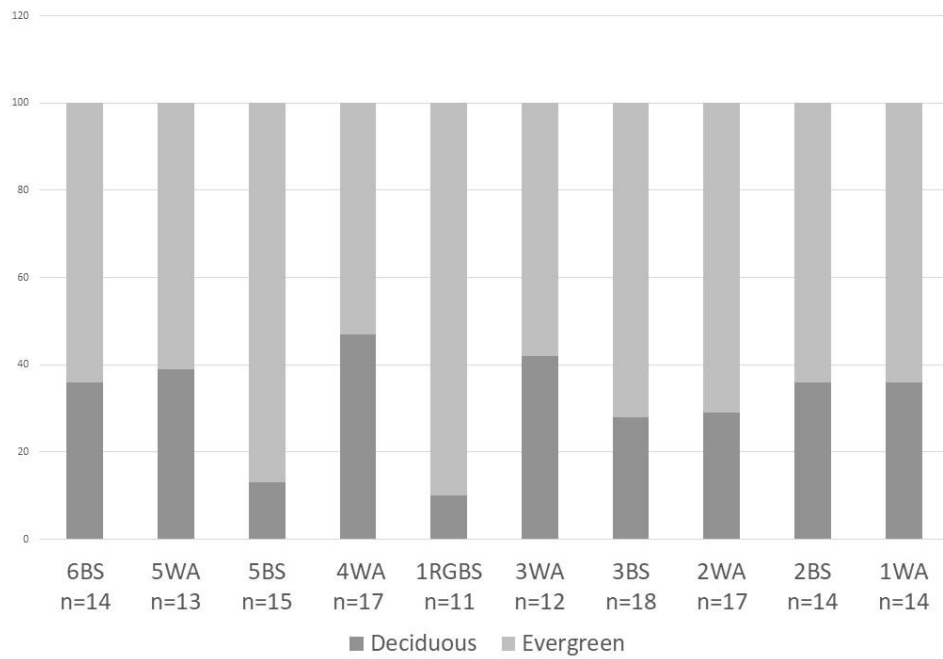


Fig. 5. Percentage of evergreen and deciduous woody genera in Members 6 BS to 1 WA at Border Cave.

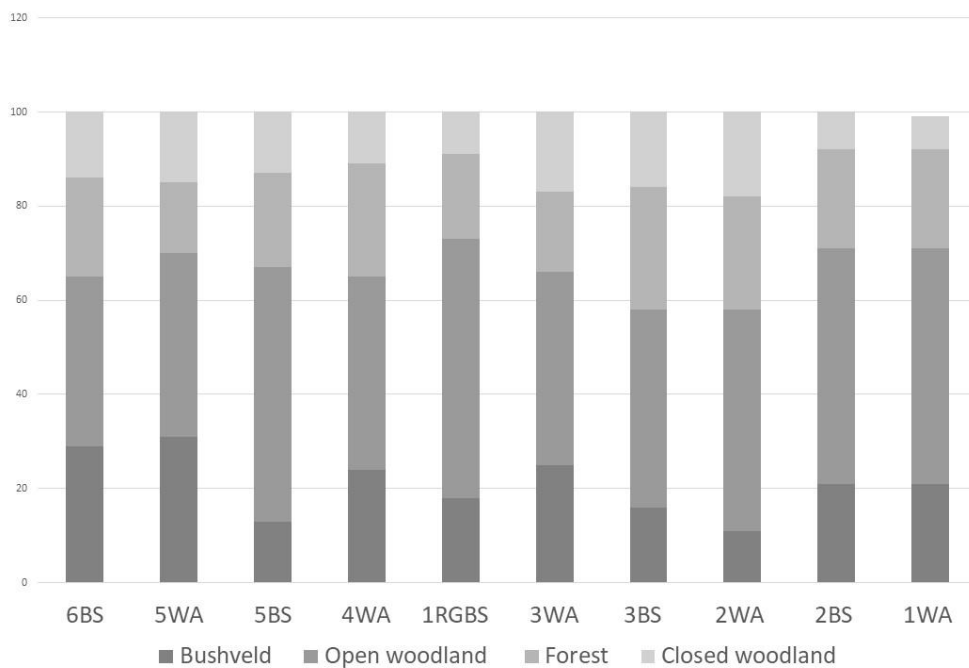


Fig. 6 Border Cave percentage of woody genera from forest/closed woodland and bushveld/open woodland from Members 6 BS to 1 WA.

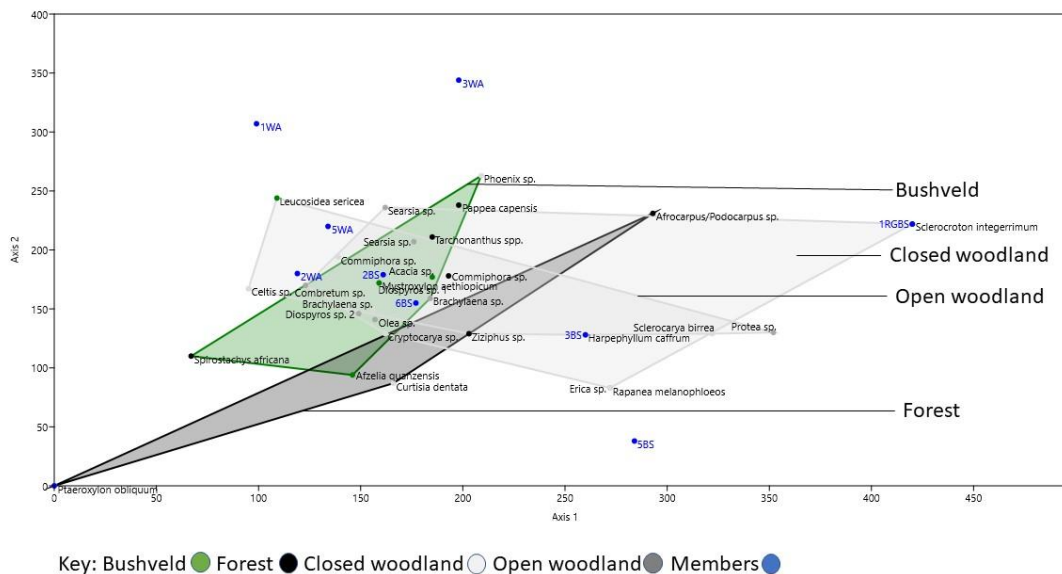


Fig. 7. Detrended correspondence analysis convex hulls of woody taxa habitats represented at Border Cave. The hulls overlap from bushveld to woodland and forest in the various members.

4. Discussion

Wood could not have entered the deep cave without being brought there; certainly no plants can grow in the dry sediments and darkness in Border Cave. Humans brought wood to the cave and used it predominantly as fuel in their fireplaces. The practice occurred prior to 227 ka and continued throughout the occupation of the site. Some of the taxa identified are known to be good fuelwoods in the sense that they produce charcoal that retains heat, for example *Protea* spp., *Acacia* spp. and *Leucosidea sericea* (Allott, 2006). Possibly some taxa were also collected for their medicinal properties. Of particular interest in this regard, are *Tarchonanthus* spp. (from Members 6 BS, 5 WA, 1 RGS, 2 WA, 2 BS and 1 WA), *Spirostachys africana* (from Members 5 WA and 4 WA) and *Cryptocarya* spp. (from Members 6 BS to 4 WA, and 3 BS to 2 BS) that may have served an insecticidal or medicinal

purpose, as seems to have been the case at Sibudu (Wadley et al., 2011; Lennox and Bamford, 2015, 2017). Fresh leaves and wood of *Tarchonanthus* spp. and *Cryptocarya* spp. are aromatic, and *Spirostachys africana* wood creates noxious smoke when burned (Lennox and Bamford, 2015). People select their firewood and tinder deliberately from the best available woody plants, and for this purpose modern gatherers are prepared to collect from about 2 km from their homesteads (Archer 1990, 1994; Cunningham, 2001). It is likely that people in the past also had good knowledge of the properties of various woods; thus the list of woody taxa may reflect human choice, and need not fully represent the vegetation profile in the vicinity of the archaeological site. The absence of taxa does not imply that they were not growing in the area. Furthermore, an abundance of charcoal from some species may imply human preference rather than high frequency in the environment (Cunningham, 2001; Wadley, 2013, 2015). Nonetheless, the suites of archaeological charcoal do provide useful clues for the reconstruction of ancient environments.

Through the long sequence of human occupation that began before 227 ka, woody plants representing at least 22 families and 28 genera were brought to the cave. The greatest diversity is recorded in Member 3 BS (n = 18) dated from about 72–56 ka. The least diversity is in 1 RGBS (n = 11) where diagenesis may have played a role in selectively preserving charcoal dated to 74 ± 4 ka. This period is approximately the time of both the Toba eruption and the start of the last glacial episode in the northern hemisphere (Svensson et al., 2008). While both events potentially affected southern African vegetation, this remains to be clearly demonstrated. Certainly, we find no evidence at Border Cave to support Ambrose's 1998 suggestion that the Toba eruption caused depopulation. Although not present in our charcoal collection, nor present near the cave nowadays, a small amount of *Colophospermum mopane* charcoal was recently identified in Member 1 RGBS (Zwane and Bamford, 2021b). This tree thrives in hot, dry conditions. Mopane produces excellent firewood that would have been

selected when available in the area. Reduced woody plant diversity as a result of anthropogenic impact on the stability of woodland vegetation due to long-term hunter-gatherer presence in the vicinity of a site (Asouti and Kabukcu, 2014) is an improbable scenario at Border Cave. Occupation in Member 1 RGBS was sporadic, likely by small groups of people for short periods of time, as evidenced by the low number of archaeological finds per sediment volume (de la Pena et al., this volume). In addition, the site is located in Southern Lebombo Bushveld, a vast sub-tropical woodland (see Fig. 1) that would have been impervious to the wood gathering activities of MSA people, no matter how large the size of the group or the length of their stay.

Details of the habitats and modern environmental requirements of the woody taxa identified at Border Cave are presented in Appendix Table 2. These help to explain conditions that may have existed in the past, when the taxa concerned grew in the Border Cave area. The shrubs and trees identified here from the wood anatomy of Border Cave charcoal include evergreen and deciduous taxa (Fig. 5) from the broadly-defined habitats of forest/closed woodland, and bushveld/open woodland (Fig. 6). In other words, all the vegetation communities that have already been described for the area in modern times seem to have created a mosaic of communities in the past, perhaps within close proximity to each other. Of the taxa listed as important to the modern Southern Lebombo Bushveld by Mucina and Rutherford (2006: 502), several were found in the Border Cave charcoal record, suggesting continuity between past and present. These persistent taxa include *Acacia* and *Combretum* sp., *Olea* sp., *Commiphora* sp., *Diospyros* sp. and *Vitex* sp. Yet, each Border Cave member has some woody taxa no longer found nearby. This may sometimes be because the modern environment is anthropogenically altered by subsistence farmers. Frequent burning of the area by farmers may have eliminated some taxa, like *Protea* sp. (Poultney, 2014), and overexploitation may have played a role in other cases. Among the taxa absent

today, but present in the past at Border Cave are: *Curtisia dentata* that prefers moist forests, and the pioneer *Leucosidea sericea* that favours scrub thicket near water. Other taxa absent from the modern Lebombo environment, like *Commiphora* sp., are bushveld taxa. Since there are still many bushveld taxa in the Border Cave region, the absence of those listed above may imply minor recent loss of diversity rather than a change in the vegetation type. The ancient forests, suggested by various taxa at Border Cave, may have been relatively small, and they probably occupied the deep, cool, moist valleys near the site. The forest taxa represented in the charcoal assemblage do not imply that the Gwalaweni Forest was near Border Cave in the past.

Several environmental implications arise from this study of Border Cave's woody plants. The vegetation communities implied by the identified woody plants comprise some shrubs, together with large numbers of small- or medium-sized trees and some large trees. Many of the taxa are evergreen, particularly in the older members 5 BS and 1 RGS. While evergreen taxa are often associated with forest, this is not necessarily the case because some evergreens, like *Olea* spp. and *Tarchonanthus* spp., can occur in bushveld, while some deciduous taxa, like *Celtis* sp. and *Commiphora* sp., also grow in forests. Evergreen and deciduous taxa are almost evenly distributed in the Border Cave members. The woody taxa at Border Cave do, indeed, appear to come from a mosaic of vegetation communities that must have co-existed contemporaneously relatively near to the cave, but the size of the various communities may have altered through time. To some extent this could be described as niche contraction or expansion, to use the Sánchez Goñi (2020) terminology mentioned in the introduction, but in the case of the Border Cave vegetation communities, the changes seem not to have been dramatic. If *Curtisia dentata*, *Cryptocarya* sp., *Harpephyllum caffrum*, and *Podocarpus* spp. are used as forest/closed woodland indicators and *Pappea capensis*, is taken as a bushveld/open woodland marker (Table 3), it is possible to suggest some broad

environmental changes through time, even though we acknowledge that this is an oversimplification of the data, not least because of the anthropogenic influence on archaeologically-retrieved charcoal. Moister conditions than present seem to have existed at least for part of the occupations in Members 5 BS, 4 WA, 3 BS, and 2 WA, based on the presence of *Curtisia dentata*. In Members 4 WA (168 ± 5 – 113 ± 5 ka) and 2 BS (60–44 ka) the percentage frequencies of forest and bushveld taxa are similar, and in both cases evergreen taxa are more common than deciduous ones. More (than 50%) bushveld/open woodland than forest/closed woodland trees were represented in all members.

Table 3. Selected bushveld/open woodland and forest/closed woodland indicators present in Border Cave through time. The conclusions in the fifth column are highly simplified, but the vegetation types suggested may represent the important communities in the mosaic of habitats.

Member	Age (ka)	Bushveld/ Open Woodland indicator	Forest/ Closed Woodland indicator	Possible vegetation type
6 BS	>227	<i>Pappea capensis</i>		bushveld/ open woodland
5 WA	227 ± 11 183 ± 20	<i>Pappea capensis</i>		bushveld/ open woodland
5 BS	161 ± 10 144 ± 11		<i>Curtisia dentata</i> <i>Cryptocarya</i> spp.	forest/ closed woodland
4 WA	168 ± 5 115 ± 8 113 ± 5		<i>Curtisia dentata</i> <i>Cryptocarya</i> spp.	forest/ closed woodland
1 RGBS	74 ± 4	<i>Pappea capensis</i>	<i>Curtisia dentata</i> . <i>Podocarpus</i> sp. <i>Cryptocarya</i> spp.	bushveld/ open woodland and forest
3 WA	64 ± 2	<i>Pappea capensis</i>	<i>Podocarpus</i> sp.	bushveld/ open woodland and forest
3 BS	72 ± 4 64 ± 3 56 ± 2		<i>Curtisia dentata</i> <i>Podocarpus</i> sp. <i>Harpephyllum caffrum</i>	forest
2 WA	60 ± 3		<i>Curtisia dentata</i> <i>Cryptocarya</i> spp.	forest
2 BS.UP	49–44	<i>Pappea capensis</i>	<i>Cryptocarya</i> spp.	bushveld and closed woodland
1 WA	43	<i>Pappea capensis</i>		bushveld/ open woodland

The woody taxa represented in Border Cave suggest not only that a mosaic of habitats occurred in the area for hundreds of thousands of years, but also that conditions enabled gradual transitions between the habitats. What is clear from this study is that miombo woodland was not represented during the occupations of Border Cave. This inference is significant because it contradicts part of the micromammalian study by Avery (1992) that concluded that micromammals in the early part of the Border Cave sequence were proxies for miombo woodland. Nonetheless, there is some overlap between climatic conclusions reached by Avery and ones presented here. The identification of mopane wood in Member 1 RGBS by Zwane and Bamford (2021b) supports the Avery interpretation of this woodland type. Avery (1992) suggested that Members 4 WA and 2 BS (lower) represent the warmest phases of the sequence with sub-humid conditions. Our results imply conditions favouring evergreen forest (*Curtisia dentata*) in Member 4 WA and evergreen bushveld (*Pappea capensis*) and closed woodland (*Cryptocaya* sp.) in Member 2 BS. There are higher proportions of forest and closed woodland taxa than elsewhere in Members 3 BS and 2 WA (including forest taxa requiring moist conditions). We concur with Avery that Member 1 WA has low forest and closed woodland representation (as low as 2 BS) and is probably one of the most arid of the members in the Border Cave sequence. In the introduction we mentioned that Ziegler and colleagues (2013) predicted that cultural innovations during the MSA would have been triggered by periods of humidity. Our findings do not support this hypothesis since dry Member 1 WA is replete with innovative artefacts (d’Errico et al., 2012; Villa et al., 2012).

Table 4. Border Cave forest/closed woodland and bushveld/open woodland taxa in Members 6 BS to 1 WA.

Plant habitat	Examples of taxa
Forest/Closed Woodland	Forest: <i>Afrocarpus/Podocarpus</i> , <i>Curtisia dentata</i>

	Closed Woodland: <i>Cryptocarya</i> spp., <i>Rapanea melanophloeos</i> , <i>Tarchonanthus</i> spp.
Bushveld/Open Woodland	Bushveld: <i>Azelia quanzensis</i> , <i>Pappea capensis</i> , <i>Spirostachys africana</i> Open Woodland: <i>Celtis</i> sp., <i>Leucosidea sericea</i> , <i>Protea</i> sp.

In the Decorana, *Afrocarpus/Podocarpus* spp. are forest indicators, *Cryptocarya* spp. is a closed woodland indicator; *Celtis* sp. is an open woodland indicator and *Pappea capensis* and *Spirostachys africana* are bushveld indicators (for further examples, see Table 4; Fig. 7). The oldest member, 6 BS, shows a positive correlation (overlap) with woody taxa from three habitats (bushveld, closed and open woodland) that may have occurred as mosaics near the site. Members 5 WA and 2 WA have a strong positive correlation with open woodland and both have charcoal representing *Commiphora* sp. (Fig. 7). Member 3 BS correlates positively with closed and open woodland (Fig. 5). Member 2 BS includes *Tarchonanthus* sp., a taxon that fits well with other closed woodland taxa. There is a close correlation between *Cryptocarya* spp., a closed woodland indicator, and Members 6 BS, 5 WA and 2 BS. There is a strong positive correlation between bushveld-indicator, *Acacia* sp., and Members 6 BS and 2 BS. Member 6 BS has a strong positive correlation with *Olea* sp. from open woodland, as well as with bushveld indicators and closed woodland taxa like *Cryptocarya* spp. These data support our earlier suggestion that a mosaic of habitats probably occurred near Border Cave during the occupation of Member 6 BS as well as during other periods. Thus, the results of the detrended correspondence analysis support the intuitive observation that mosaic vegetation communities had a long-standing existence in the area.

Overall the vegetation record at Border Cave appears to have been stable through time. Notwithstanding this, forest and closed woodland patches may occasionally have

occurred as part of a mosaic alongside bushveld and open vegetation. A varied vegetation mosaic was also suggested from archaeobotanical research at Sibudu (Wadley, 2004; Allott, 2006; Sievers, 2006; Bamford, 2021; Zwane and Bamford, 2021a). The Border Cave record might also be compared to an East African paleoenvironmental simulation using temperature and precipitation coupled with a biome model for the MSA (Timbrell et al., 2022). Here, in MIS 5 and MIS 3, people may have inhabited ecotones to take advantage of resources in both open and forested areas.

The relative stability found through time in the vegetation record at Border Cave compares favourably with the climate-modeled vegetation stability through time during both glacial and interglacial cycles in East Africa (Sánchez Goñi, 2020). Nonetheless, a combination of stable isotopes, geochemical proxies and a pollen record from a marine core taken near the mouth of the Limpopo River (Dupont et al., 2019) demonstrates that vegetation did undergo some changes between glacial and interglacial periods in south east Africa. The pollen study yielded four time-related assemblages implying heathland, mountain forest, shrubland and woodland biomes (Dupont et al., 2019). The results from this research suggest that forests grew in moderate glacial conditions and that open ericaceous vegetation only occurred during extremely cold conditions (Dupont et al., 2019). However, Chevalier et al. (2020) used these data to show, further, that the south-eastern part of southern Africa followed global climatic trends at the time, with differences of only $\sim 4^{\circ}\text{C}$ between glacial minima and interglacial maxima. The results from Dupont and colleagues (2019) are only partly applicable to the inland Border Cave scenario. The pollen in the marine core is purely an environmental signal, whereas the cave charcoal represents firewood that people deliberately selected from a range of potential taxa. Nonetheless, the suggestion that ericaceous vegetation only occurred during very cold conditions might explain why *Erica* sp., a popular kindling in mountainous regions even presently, is uncommon in the cave. Indeed, heathland seems not represented in its

sequence. The suggestion by Chevalier et al. (2020) that only about 4°C separated glacial and interglacial maxima in south east Africa is also helpful to explain the relative stability observable in the Border Cave vegetation record through time. The other noteworthy observation is that we see no correlation between the timing of vegetation changes at Border Cave and the technological changes that were identified by Beaumont (summarised in Table 1). Our charcoal results do not, on their own, support the idea that climate change caused cultural change. We acknowledge, however, that our anthracology results must be taken as distant proxies in archaeological debates, and that time lag is an important consideration.

5. Conclusion

The 10 archaeological members at Border Cave studied here are dated between ~227 and 43 ka, and all have evidence of human occupation and combustion features in the form of fireplaces and burned grass bedding. Charcoal analysed from the 10 members resulted in the identification of woody plants representing 22 families. These comprised a few shrubs, mostly small- or medium-sized trees, and some large trees. The plants represent taxa from forests, forest margins, closed and open woodland and bushveld habitats. The vegetation succession suggests a past environment that supported gradual transitions. Overall, the archaeological charcoal from all members implies that the area contained trees that were mostly evergreen in habit, and that more bushveld and open woodland trees than forest and closed woodland trees were represented.

Notwithstanding the likely presence of mosaic vegetation communities through much of the time that Border Cave was occupied, it is possible to suggest some predominant habitats. In terms of indicator species, for example, in Member 6 BS (>227 ka) bushveld and open woodland taxa were most common, as was also the case in Member 5 WA (~227 ka). Moist forest was most common in Members 5 BS (~161–144 ka) and 4 WA (~168–113 ka),

while Member 1 RGBS (~74 ka) had a combination of bushveld and moist forest present. In Member 3 WA (~64 ka) dry bushveld predominated, while in Members 3 BS (72–56 ka) and 2 WA (~60 ka) moist forest was the predominant vegetation habitat. Member 2 BS.UP (49–44 ka) mostly included bushveld and moist forest patches, while Member 1 WA (~43 ka) was predominantly dry bushveld. In comparison with modern vegetation, the Border Cave occupations from approximately 227 ka seem to have taken place in a dry environment, beginning with Members 6 BS and 5 WA. The dryness ameliorated in Members 5 BS, 4 WA and 1 RGBS, but recurred in Member 3 WA, then became less dry in 3 BS, moderately dry in 2 WA, and finally it was considerably drier in Members 2 BS and 1 WA. Overall, however, the past vegetation seems similar to the modern vegetation profile and there appears to have been remarkable stability through time.

Plants once represented in the area, but are no longer near the site, include *Commiphora* sp. (an open woodland and bushveld taxon), *Protea* sp. (an open woodland taxon) and *Curtisia dentata* (an evergreen forest taxon). All these taxa have a wide southern African distribution and their absence today need not imply anything other than a gradual reduction of species in the modern environment. The modern environment appears to be somewhat impoverished compared with that in the past. We suggest this because of the suite of taxa occurring near Border Cave in the past, but absent from the area today. One reason for the difference could be the considerable firewood exploitation by the large, modern rural population.

The stable plant habitats present at Border Cave between ~227 ka and ~44 ka ago suggest that the area would have been a suitable refugium for plants during periods of instability elsewhere in the region. This may well explain its repeated occupation during the MSA. There are, of course, observable shifts in the proportions of, for example, bushveld and forest species. While this might imply changing sizes in vegetation communities when

effective precipitation increased or decreased, we also acknowledge human agency in the presence of wood in Border Cave. Firewood preferences may have changed through time for reasons that we cannot now decipher, though we can speculate that issues like negotiating a precipitous cliff to collect wood from forest trees when their patch size decreased may have deterred foragers.

Importantly, the emergence of cultural innovations in Border Cave cannot be chronologically linked to the changes that we see in the vegetation record. If such relationships do exist, they will need to be demonstrated using other climate proxies from the site.

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