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Small mammals from Marine Isotope Stage 5 at Klasies River, South Africa—Reconstructing the local palaeoenvironment

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ABSTRACT

Klasies River, a significant Middle Stone Age (MSA) site, preserves remains of anatomically modern humans and a 21 m sequence of human habitation that shows use of sophisticated lithic technology and systematic exploitation of marine and terrestrial resources. In this paper micromammals recovered from the lower MSA sequence (MSA I and MSA II) at Klasies River Main site have been analysed to provide proxy data for palaeoenvironmental reconstruction. Small mammals recovered from 183 separate layers ensure a detailed record of local climate and vegetation during Marine Isotope Stage (MIS) 5. Taphonomic analyses indicate that avian predators accumulated the micromammals. Analysis of post-depositional processes has provided information on intra-site variability and utilisation. The palaeoenvironmental reconstruction shows changes in rainfall seasonality within MIS 5. There was transient movement towards more aseasonal rainfall and significant alterations in the vegetation composition from MIS 5e to MIS 5a. Our study adds new insights to palaeoenvironmental conditions on the Cape coast during MIS 5.

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1. Introduction

During the Middle Stone Age (MSA) of southern Africa, climatic fluctuations may have had an important impact on the environment in which modern humans evolved. Obtaining palaeoenvironmental information to gain holistic contexts for interpreting MSA people's subsistence strategies, technological innovations and site choices is increasingly prominent (e.g. Clark, 2011; Compton, 2011; Blome et al., 2012; Ziegler et al., 2013; Backwell et al., 2014; Mackay et al., 2014; Wurz, 2016).

Past local environments can be reconstructed by analyses of micromammal species that become incorporated into archaeological sites. Micromammals are suitable as palaeoenvironmental indicators due to their limited territorial ranges, precise ecological requirements and their role as primary consumers in the food chain. Analyses of modern micromammal samples have demonstrated close correlation between relative abundance of species and composition of vegetation substrate in the vicinity of sample sites (Andrews, 1990; Reed, 2003, 2005; Avery et al., 2005). Local alterations in vegetation substrate and climatic conditions may thus be reflected in presence/absence and/or variations in proportions of micromammal species in an archaeological assemblage. Our palaeoenvironmental reconstruction of the lower MSA sequences, c. 120 ka to c. 85 ka, at Klasies River Main site aims at gaining further knowledge of local environmental conditions that prevailed during Marine Isotope Stage (MIS) 5 (Fig. 1).

The MSA I (MIS 5e/d), MSA II Lower (MIS 5c) and MSA II Upper (MIS 5b/a) phases at Klasies River were relatively intense human occupation periods. This sequence contains remains of anatomically modern Homo sapiens, the oldest dated to c. 115 ka (Singer and Wymer, 1982; Rightmire and Deacon, 1991, 2001; Grine et al., 2017). The lithic traditions are characterised by a recurrent strategy to produce elongated products in MSA I (Klasies River technocomplex), followed by manufacturing of products using unipolar convergent Levallois strategies in MSA II (Mossel Bay technocomplex) (Wurz, 2012). Bone tools and ochre are recovered from the MIS 5 levels (Wurz, 2000, 2016; d'Errico and Henshilwood, 2007; d'Errico et al., 2012) and there was systematic exploitation

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Fig. 1. Location of Klasies River and other sites mentioned in the text. Blue and red lines mark approximate positions of the winter rainfall (WRZ) and summer rainfall zones (SRZ) respectively. The area between the contour lines is the intermediate gradient rainfall zone (YRZ), characterised by all year rainfall at transient intervals moving from west to east. Satellite maps: NASA Earth Observatory (public domain): http://earthobservatory.nasa.gov/, insert from Maplibrary.org (public domain): http://www.maplibrary.org/index. php. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of terrestrial and marine resources (Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Deacon, 2001; Wurz, 2000, 2012; 2016). The results of the micromammal analysis add context to lithic technologies and resource procurement strategies employed by human occupants of the site.

1.1. Site background

The Klasies River Main site (34°06′S, 24°24′E) is situated on the Tsitsikamma coast in the Eastern Cape Province, South Africa, approximately 43 km northwest of Cape St. Francis (Singer and Wymer, 1982; Deacon and Geleijnse, 1988) (Fig. 2). Main site consists of a number of openings cut into quartz arenite of the Silurian Cape Supergroup. A 21 m shell midden has accumulated in and against two caves (1 and 2) and two overhangs (1A and 1B) (Deacon and Geleijnse, 1988; Deacon, 2001; Wurz, 2012, 2016) (Fig. 2).

1.1.1. Stratigraphy, dating and previous analysis of micromammals

There have been several excavations at Klasies River Main site, first by Singer and Wymer (1982), later by Deacon (2001) and currently by Wurz. The MSA deposits comprise multiple human occupation units containing shell, fish, bone and cultural artefacts, hearths and carbonisation of organic matter. Naturally accumulated culturally sterile sands containing terrestrial microfauna and ichthyofauna separate these units. The sediments built up and eventually covered the entrance of cave 1 and at a later stage filled up cave 2 (Singer and Wymer, 1982; Deacon, 2001) (Figs. 2 and 3).

The MSA sequence was divided into four main cultural phases, MSA I, MSA II, Howiesons Poort and MSA III by Singer and Wymer (1982). Deacon and Wurz further sub-divided the MSA II phase into MSA II Lower and MSA II Upper (Wurz, 2012). MSA I, also termed MSA 2a (Volman, 1981) and Klasies River techno-complex (Wurz, 2002), comprises the lowest cultural stratigraphic unit (Deacon
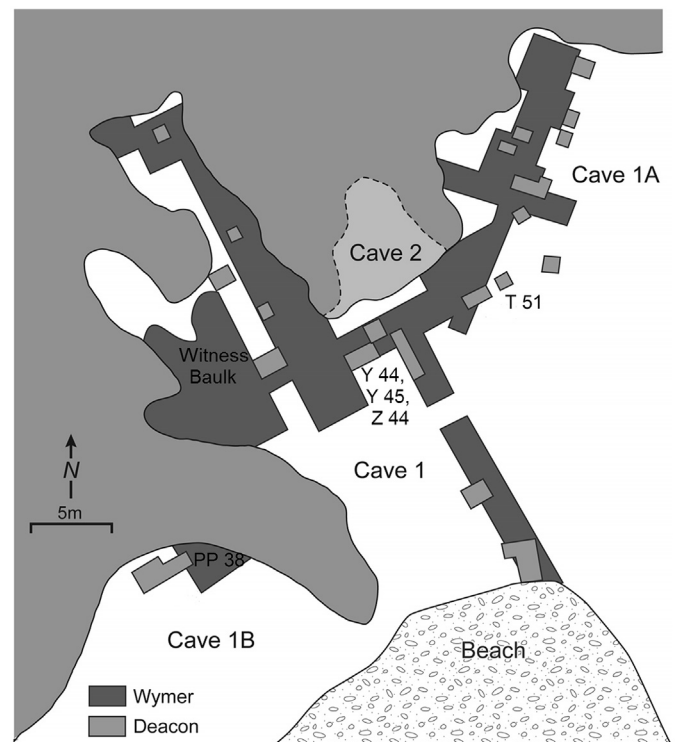

Fig. 2. Site layout of Klasies River main site. Our study assemblage is from the Deacon excavations; squares T 51, Y 44, Z 44 and Y 45 in cave 1A, Witness Baulk in cave 1 and square PP 38 in cave 1B. Site layout adapted with permission from Grine et al. (2017).
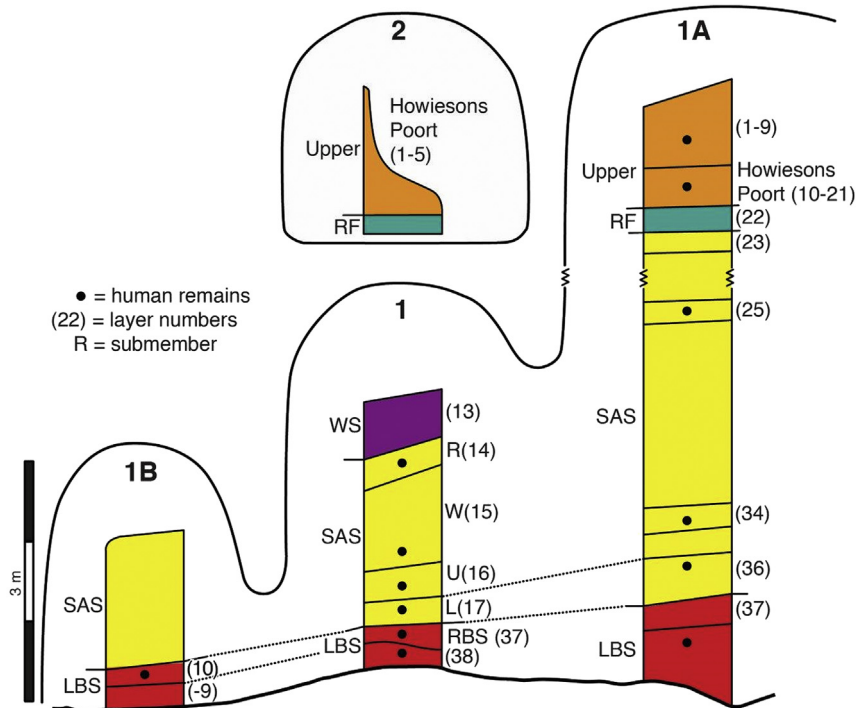
Fig. 3. Schematic of stratigraphic relationships at the main site repositories (**after** Grine et al. 2017, **adapted from** Deacon and Geleijnse 1988). Numbers in brackets are Layers as assigned by Singer and Wymer (1982). Letter designations to the left of the columns are Members and to the right are sub-Members as assigned by Deacon and Geleijnse (1988).

and Geleijnse, 1988), and occurs in the LBS and RBS Members from caves 1, 1A and 1B (Fig. 3, Appendix, Table A1). It is dated by luminescence to between 115 and 108 ka (Vogel, 2001; Feathers, 2002), thus falling within MIS 5e/d (see Grine et al., 2017; for recent summary of the dating). MSA II, also labelled MSA 2b (Volman, 1981) and Mossel Bay techno-complex (Wurz, 2002), comprises the entire SAS Member, the thickest depositional unit at c. 10 m (Wurz, 2008, 2016). It has been dated using a variety of methods and MSA II Lower dates to between c. 101 and 90 ka corresponding to MIS 5c (Appendix, Table A1). MSA II Upper dates to c. 85 ka, associated with MIS 5b/a (Appendix, Table A1). Howiesons Poort, not discussed in this paper, is from the Upper Member and is associated with MIS 5a/4 and MSA III, also from the Upper Member, corresponds to MIS 3 (Grine et al., 2017).

There have been two previous analyses of micromammals from samples other than the study assemblages reported here. Avery (1979, 1982) analysed micromammal material from Singer and Wymer's excavation, but detailed quantitative analysis was not possible due to the excavators sampling method (Avery, 1979, 1982). Avery also analysed a sample from Deacon's excavations (1984-86 seasons) from MSA III, Howiesons Poort, MSA II and MSA I layers in cave 1A (Avery, 1986, 1987) (see 4.2 and 4.3). Thackeray (1987) used multivariate analyses to infer relative changes in temperature based on this sample.

1.2. Current climate and vegetation

Southern Africa is at the interface between tropical and temperate weather systems (Chase and Meadows, 2007). As a result of dynamics and seasonal variations of these systems, the southern African region can be divided into three distinct rainfall zones; winter, intermediate and summer (Chase and Meadows, 2007) (Fig. 1). The winter rainfall zone (WRZ) is influenced by seasonal migrations of the southern westerlies; high altitude winds from the west which define areas where cool dry air from the

Antarctic collides with warm, moist air from the tropics causing instability and convection, resulting in cloud formation and precipitation (Chase, 2010; Blome et al., 2012; Chase et al., 2015). More than 60% of precipitation occurs during the winter months in the WRZ. The intermediate gradient year round rainfall zone (YRZ) is a transient zone where the percentage of winter rainfall decreases in an easterly direction, while summer rainfall increases, which in essence creates an aseasonal rainfall pattern. Klasies River Main site is situated in the YRZ (Fig. 1) and rainfall is aseasonal with c. 39% precipitation in summer (October to March) (Avery, 1995; Climate Systems Analysis Group, 2016; Van Wijk et al., 2017). The summer rainfall zone (SRZ) where tropical easterly winds bring moisture from the Indian Ocean during summers lies to the east of the YRZ. Here winter months are arid with less than 30% rainfall (Chase, 2010; Chase et al., 2015). The extent of these rainfall zones are likely to have shifted in the past (Chase and Meadows, 2007; Chase et al., 2015).

Mean annual precipitation (MAP) varies in a 60 km radius. MAP is 875–1375 mm at the slopes of the Tsitsikamma Mountains (Hosking and Du Preez, 1999), while at Storms River, 25 km west it is 810 mm (Van Wijk et al., 2017) (Fig. 1). Further east at Cape St. Francis, MAP is 643 mm (average from 1880 to 2001) (Climate Systems Analysis Group, 2016) (Fig. 1). Average temperatures (1959–2001) at Cape St. Francis show a maximum/minimum of 18/11 °C in winter (July and August) and 23/18 °C in peak summer (January) (Climate Systems Analysis Group, 2016). At Storms River average temperatures in July are 18/10 °C and in February 24/17 °C (Climate Systems Analysis Group, 2016).

Klasies River is located in the Eastern fynbos and renosterveld bioregion of the fynbos biome (Mucina and Rutherford, 2006; Van Wijk et al., 2017). Here fynbos and renosterveld interdigitate and form mosaic structures with three other biomes; forest, subtropical thicket and grassland (Cowling and Potts, 2015; Van Wijk et al., 2017) (Table 1). Van Wijk et al. (2017) have documented a mosaic like pattern of thicket (33%), forest (20%), coastal species (22%) and

Table 1
Characteristics of vegetation components currently present in an approximately 5-km radius of Klasies River Main site. Data from Biodiversity Geographic Information Systems (BGIS) by South African National Biodiversity Institute (2012) at http://bgisviewer.sanbi.org/, Mucina and Rutherford (2006) with supplementary information from Van Wijk et al. (2017).

Bioregion	Vegetation	Description	Occurs on
Azonal vegetation	Albany alluvial vegetation	Riverine thicket (narrow coastal floodplains) and thornveldt (inland floodplains)	Floodplains close to coast
	Algoa dune strandveldt	Tall (up to 5 m) dense thickets dominated by stunted trees, thorn and spine shrubs, sparse herbaceous and grassy cover	Dunes beyond influence of salt spray from sea
	Cape lowland freshwater wetlands	Tall reeds, restoids, sedge and rush-beds, macrophytic vegetation embedded in permanent waters	Flats and landscape depressions, fine sandy, silty, clayey soils, floods
	Cape seashore vegetation	Open, grassy herbaceous and dwarf-shrubby vegetation, often dominated by single pioneering species	Beaches, coastal dunes, dune slacks and coastal cliffs
Eastern fynbos and renosterveldt	Eastern coastal shale band vegetation	Shrubland consisting of thicket, renosterveld and fynbos (usually grassy)	Shale bands; smooth and flat landscape features
	Garden route shale fynbos	Tall, dense proteoid and ericaceous fynbos (wetter areas), and graminoid fynbos or shrubby grassland (drier areas)	Undulating hills and plains on coastal foreland, acidic, moist clay-loam
	Humansdorp shale renosterveldt	Low, grassy and cupressoid-leaved shrubland, dominated by renosterbos, both grassland and shrubland forms can be present	Moderately undulating plains and hills
	Southern Cape dune fynbos	Fynbos heath dominated by sclerophyllous shrub with rich restio undergrowth	Coastal dune cordons, steep slopes, outside influence of sea salt spray
	Tsitsikamma sandstone fynbos	Medium dense, tall proteoid shrubland over dense ericoid-leaved shrubland — mainly proteoid, restioid and ericoid fynbos, with fynbos thicket in wetter areas	Tsitsikamma coastal mountain range
Forest	Southern coastal/afrotemperate forest	Tall, multi-layered afro-temperate forest with a well-developed shrub and herb layer especially in mesic and wet habitats	Sheltered seaward slopes, plateaux and coastal scarps

fynbos (15%) in a 5 km radius of Klasies River. Due to this mosaic structure, small climate changes may have had great implications for vegetation diversity and distribution at Klasies River in the past (Avery, 1987).

2. Material and methods

2.1. Material

Micromammal remains from MSA II Upper, MSA II Lower and MSA I recovered during Deacon's excavations (1984—1995) were analysed in this study. Deacon and his team carried out detailed stratigraphic excavations and wet sieved excavated material (standard mesh size 3 mm, control squares 2 mm and 1 mm).

We have analysed 183 separate layers from cave 1, cave 1A and cave 1B (Fig. 2). Organisation of layers into units suitable for statistical interpretations, while maintaining geographic provenance within the site and thereby detailed palaeoenvironmental information, was based on Wurz (2000) (Appendix, Table A2). Taphonomic analyses are presented by units, while taxonomic and palaeoenvironmental results are presented by phase.

2.2. Methods

2.2.1. Taphonomy

Taphonomic analyses determine potential bias and serve to identify predator(s) or agent(s) responsible for accumulation of the micromammals (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992; Avery, 2002; Matthews et al., 2009, 2011; Fernandez-Jalvo and Avery, 2015; Fernandez-Jalvo et al., 2016). Analyses include assessing representation of skeletal elements, digestion (grade and frequency), breakage and post-depositional damage to bones, of which the first three categories were emphasized when identifying predator species (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992).

A predator preying on micromammals will most likely consume much, or all, of the body of the prey. Modern samples indicate that predators have characteristic patterns for the proportional abundances of prey elements (Andrews, 1990). Skeletal element abundance was calculated as $Ri = Ni/(MNI \times Ei)$ where Ri is the relative abundance of the element i, Ni is the number of elements i in the assemblage, MNI is the minimum number of individuals and Ei is the number of elements i in the prey skeleton (Andrews, 1990). The problematic feature of breakage and skeletal element abundance as predator indicators have been questioned due to post-depositional site-specific processes also affecting these categories (e.g. Matthews et al., 2011; Nel, 2013; Fernandez-Jalvo and Avery, 2015; Belmaker et al., 2016; Nel and Henshilwood, 2016). The implications of these observations are discussed in 4.1.1.

Protocols of previous research on micromammals in South Africa (Avery, 2002; Matthews, 2004; Matthews et al., 2009, 2011) led to minor changes of digestion classification. In our study Rodentia incisors, both in situ and isolated, humeri and femora, were microscopically analysed for predator-related digestion. Incisor digestion classes were based on Andrews (1990). The suitability of Rodentia incisors for digestive analysis is further described in Nel and Henshilwood (2016).

Several processes may affect osseous assemblages after deposition (e.g. Andrews, 1990; Matthews et al., 2005; Fernandez-Jalvo and Avery, 2015). The bone surfaces were consequently investigated for post-depositional alterations caused by weathering, sediment-related corrosion, transport, breakage due to trampling and etching from roots. It could be problematic to discern post-depositional damages from digestion by predators (e.g. Fernandez-Jalvo et al., 2016). Rounding of breaks could occur prior to deposition due to predator digestion (Andrews, 1990). Mammalian carnivores are particularly associated with this type of rounding as bones pass through their entire digestive system, thus subjecting them to greater digestive damage than diurnal birds or raptors (Andrews, 1990; Fernandez-Jalvo et al., 2016). Post-deposition rounding of broken bones may occur when flowing water and sediment interacts, and it produces a surface polishing effect (Fernandez-Jalvo et al., 2016). Etching may also be a result of various processes such as predator digestion, roots of plants or micro-morphological features of soil affecting bones after deposition (Nel, 2013).

2.2.2. Identification of micromammal taxa

Taxonomic identification was based on mandibles, maxillae and dental morphology following standard methods (Avery, 1982;

Matthews et al., 2005; Nel, 2013). Specimens not identified to species were assigned to either family or sub-family. Comparative specimens from Iziko South African Museum aided identification. Previously identified specimens (by D. M. Avery) from Klasies River and Boomplaas Cave and identification keys (Avery, 1979; De Graaff, 1981) were used as reference. Post-cranial elements were identified by general assignation. The systematic classification followed Wilson and Reeder (2005).

2.2.3. Species richness and diversity

Biodiversity was assessed by species richness, general diversity and dominance. The palaeoenvironmental information these indices provide are linked to measures of vegetation structure and abundance of plant species. Complex vegetation structures, which contain a range of plant species and comprise a variety of habitats, are associated with both general abundance and diversity of micromammal species (López Antoñanzas et al., 2002; Cuenca-Bescós et al., 2009). Thus, numbers of taxa (richness) and individuals per species (diversity) serve as measure of vegetation structure in the immediate vicinity of Klasies River. Small mammal species richness is expected to be greater where seasonal variability in the thermal, energy production (i.e. vegetation) and precipitation regimes are limited (Andrews & O'Brien, 2000; Belmaker and Hovers, 2011). In southern Africa, small mammal species richness also correlates with seasonal distribution of rainfall and maximum monthly precipitation (MMP) (Andrews & O'Brien, 2000).

Species richness was calculated as the number of species present in each phase (Hammer and Harper, 2006). It is influenced by sample size, and to investigate whether variation in taxonomic abundance is a result of sample size rarefaction curves were calculated (Hammer and Harper, 2006). The curves were based on minimum number of individuals (MNI) per phase.

General diversity of micromammal populations was assessed by the Shannon Wiener index, H, where; $H = - \Sigma P_i (\ln P_i)$ where P_i is the proportion (P) of taxon i in the assemblage. The Simpson index indicates the probability that two randomly picked individuals are of the same species (Hammer and Harper, 2006). The Simpsons index of dominance, D, is given as $D = \Sigma (p^2_i)$ where $p_i = n_i/n$ (the proportion of species i). The value will be close to 1 if there is a single dominant taxon in the sample. The results of the general diversity and dominance indices were subject to a t-test. All statistical calculations were done using the free software program for data analysis; Paleontological Statistics (PAST) (Hammer et al., 2001).

2.2.4. Taxonomic composition − palaeoenvironmental implications

Taxonomic composition reveals information on vegetation, temperature and rainfall seasonality and on the potential alterations of these environmental factors through time. The distribution of taxa was analysed by presence-absence, relative abundance and a taxonomic habitat index (THI). The preferred habitats and habits of micromammal taxa are based on Skinner and Chimimba (2005), with supplementary information from Avery (1979, 1982; 1987; 1992; 2001; 2002; 2007), Avery et al. (2005); Bigalke (1979), Bond et al. (1980), De Graaff (1981) Du Toit et al. (2012); Engelbrecht et al. (2011), Fleming and Nicolson (2002), Hopley et al. (2006), Matthews (2004), Matthews et al. (2005, 2009; 2011), Meester et al. (1979), Perrin (1980, 1986), Rautenbach (1971), Schraden and Pillay (2005), Stuart and Stuart (2001), Willows-Munro and Matthee (2011) and Wilson and Reeder (2005).

Taxonomic composition was compared by applying two similarity indices. The Jaccard index based on binary data evaluates the assemblage on a high level (presence absence). The Bray-Curtis index based on distance measures converted by subtracting from one to obtain similarity indices assesses the taxonomic assemblage

on a low level (proportional abundance) (Hammer and Harper, 2006). Relative abundance of each species was expressed as percentage representation per phase. Grouped taxa were excluded as these could potentially create an artificial variation in the species assemblage.

The taxonomic habitat index (THI) is a cumulative index, obtained by combining niche models of all species in an assemblage (Andrews, 1990). The habitat of each taxon is partitioned into several vegetation types as percentages of its occurrence frequency across these types (Matthews et al., 2005; Geraads et al., 2013; Nel and Henshilwood, 2016). Niche models are based on extant species and their preferred habitat and cumulative score of each taxon's niche model is 1. We used available literature regarding species current distribution and ecological requirements to allocate scores with the greatest possible accuracy. Combined values for all species indicate dominant habitats and variations in vegetation composition (Andrews, 1990; Reed, 2003; Cuenca-Bescós et al., 2009). By adding the relative abundance of the various micromammal species, it is possible to gain a nuanced picture of proportion of vegetation types in the area at the time.

Our niche models focus specifically on vegetation microhabitat typical of the southern coast of South Africa. They were developed for the Blombos Cave micromammal assemblage (Nel and Henshilwood, 2016) and have been modified to accommodate variations in taxonomic composition and vegetation microhabitat at Klasies River.

3. Results

3.1. Taphonomy

3.1.1. Skeletal element abundance (SEA)

The cave 1 sample, with the exception of TSM, OHO and HHH, has a lower percentage representation of smaller and delicate post-cranial elements (scapulae, ulnae, radii and vertebrae) and a greater representation of mandibles than other units (Fig. 4). Despite this, SEA displays a generally similar pattern for all units, comparable to mammalian carnivores such as serval, black-backed jackal (Matthews, 2008), mongoose species or small-spotted genet (Andrews, 1990) (Fig. 4). However, post depositional processes are likely to have influenced this result (see 3.1.4 and 4.1.2).

3.1.2. Digestion

There are traces of digestion on *in situ* and isolated incisors, femurs and humeri from all units (Tables 2–4); though the intensity and percentage of digested elements vary. In general, digestion of post-crania is more frequent, but digestive traces on these elements are harder to discern from other post-depositional alterations, and thus digestion on incisors are better indicators of predators responsible for accumulation (see 4.1.1).

The majority of digested incisors in MSA II Upper fall within the light category (Table 2). A small number of incisors had a greater degree of digestion, with exception of T51 BS1 where 23.4% had moderate to extreme digestive traces and in T51 SL5, 15.2% were moderate to heavily digested.

In MSA II Lower, digestion was least frequent in the upper units in cave 1 (Table 3). Otherwise all units throughout the phase had mostly light digestive traces and the frequency of digestion ranged from 28.9% (OHO) to 52.7% (DC Gr. 2) (Table 3). Digestion on humeri and femurs was consistent throughout MSA II Lower.

The MSA I sample displayed a similar pattern to the MSA II phases, although some differences occur. In cave 1A unit Z44 SBS had more incisors with moderate digestion and a higher frequency of digestion than Z44 SCB & SAS (Table 4). Overall, RS units in cave 1B had light digestion where the frequency ranged between 18.7%
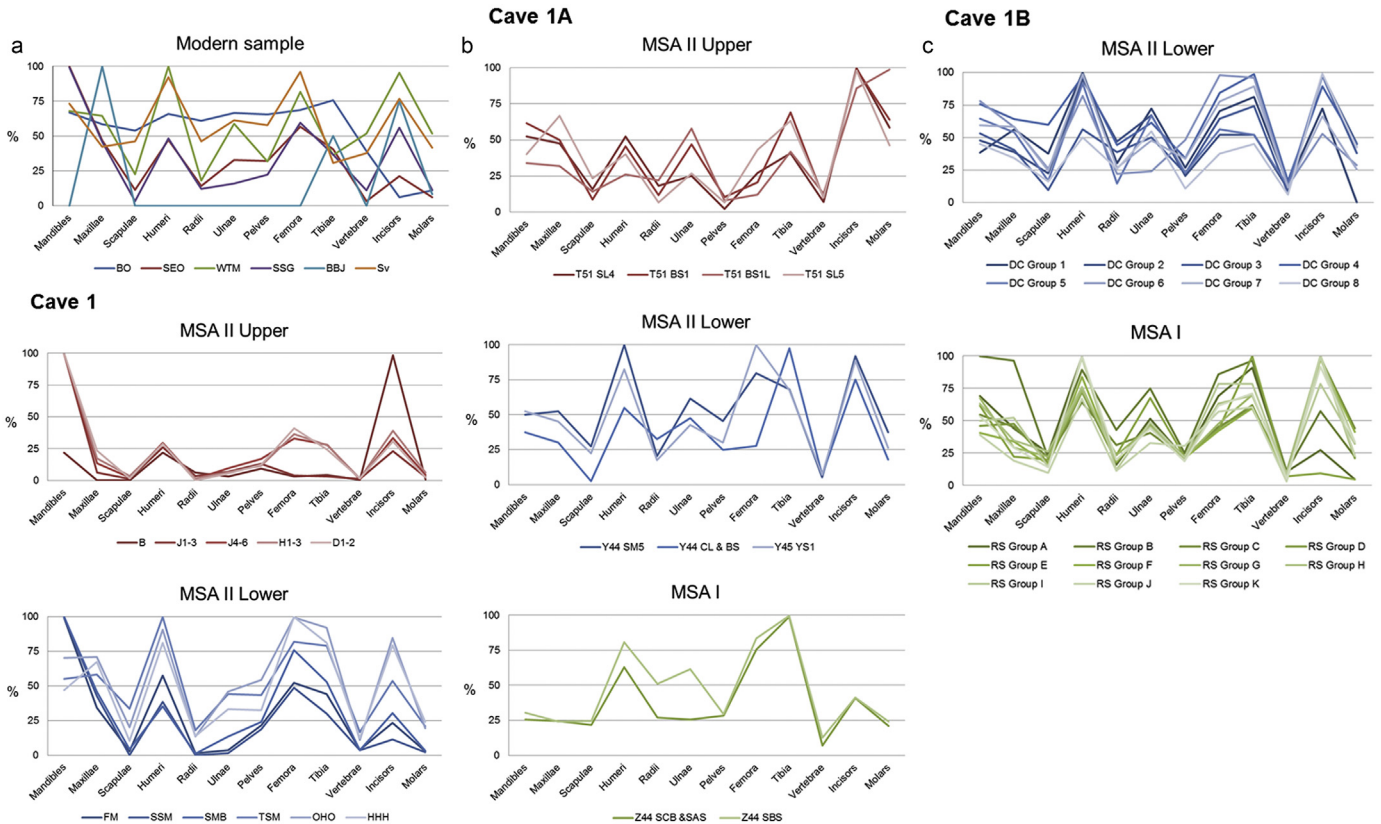
Fig. 4. Skeletal element abundance for the units in MSA II Upper (green), MSA II Lower (blue) and MSA I (red) presented by cave provenance; (A) Modern sample and cave 1, (B) cave 1A, (C) cave 1B. Examples of modern skeletal element abundances (multi-coloured) from Matthews (2008): Black-backed jackal (BBJ), Serval (SV), Andrews (1990): Barn owl (BO), Spotted eagle owl (SEO), White-tailed mongoose (WTM), Small-spotted genet (SSG). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Percentage of digested incisors (*in situ* and isolated), humeri and femurs in the MSA II Upper units.

Digestion % Incisors	Cave 1					Cave 1A			
	B	J1-3	J4-6	H1-3	D1-2	T51 SL4	T51 BS1	T51 BS1L	T51 SL5
No digestion	77.4	39.4	51.7	63.3	72.9	76.2	55.0	81.6	75.9
Light	16.1	53.5	43.3	34.6	26.5	15.2	21.7	13.2	8.9
Moderate	6.6	2.8	4.2	1.4	0.0	1.9	10.6	1.3	7.6
Heavy	0.0	4.2	0.4	0.3	0.6	6.7	11.7	3.9	7.6
Extreme	0.0	0.0	0.4	0.3	0.0	0.0	1.1	0.0	0.0
Total digested	22.6	60.6	48.3	36.7	27.1	23.8	43.9	18.4	24.1
Number analysed	*62*	*71*	*240*	*286*	*166*	*105*	*180*	*152*	*79*
Humeri									
No digestion	100	37.5	39.3	30.0	51.4	27.3	46.2	18.2	77.8
Digested	0.0	62.5	60.7	70.0	48.6	72.7	53.8	81.8	22.2
Number analysed	*7*	*16*	*56*	*40*	*35*	*11*	*26*	*11*	*9*
Femurs									
No digestion	60.0	18.2	28.6	16.4	24.1	10.0	11.1	0.0	30.0
Digested	40.0	81.8	71.4	83.6	75.9	90.0	88.9	100	70.0
Number analysed	*10*	*22*	*63*	*73*	*58*	*10*	*9*	*6*	*10*

(RS Gr. A) to 44.6% (RS Gr. J) (Table 4).

3.1.3. Breakage of skeletal elements

Breakage of skeletal elements is expressed by fragmentation of humeri and average relative abundance of skeletal elements (ARA) (Appendix, Table A3). All units had considerable fragmentation of humeri and loss of skeletal elements. Unit B in MSA II Upper has lowest ARA at 4.2, while DC Group 4 in MSA II Lower is highest at 48.3. ARA is generally lower in cave 1 comparably to the two other caves. The cave 1 units, with exception of the bottom three units

(TSM, OHO and HHH) in MSA II Lower, have a higher percentage of complete humeri compared to the rest of the assemblage.

3.1.4. Post-depositional modification

Etching on elements and rounding of breaks were the most frequent modifications (Appendix, Tables A4, A5 and A6). The frequency varied according to provenance and was greatest in cave 1A, particularly in MSA II Upper. Here etching affected between 58.3% (T51 SL4) and 68.2% (T51 BS1) of limb bones and rounding of breaks occurred on 45.8% and 37.9% respectively (Appendix, Table A4). The

Table 3
Percentage of digested incisors (*in situ* and isolated), humeri and femurs in the MSA II Lower units.

Digestion % Incisors	Cave 1						Cave 1A			Cave 1B							
	FM	SSM	SMB	TSM	OHO	HHH	Y44 SM5	Y44 CL&BS	Y45 YS1	DC Gr.1	DC Gr.2	DC Gr.3	DC Gr.4	DC Gr. 5	DC Gr.6	DC Gr.7	DC Gr.8
No digestion	83.3	80.0	80.7	67.6	71.1	67.1	62.0	48.4	51.7	59.3	47.3	64.9	60.5	69.8	59.4	64.4	52.1
Light	15.3	18.5	17.6	26.7	26.8	28.3	26.0	38.7	43.7	35.5	40.4	31.8	33.3	24.8	34.8	31.3	40.2
Moderate	0.7	1.5	0.8	4.9	1.2	1.2	12.0	9.7	3.4	4.0	8.6	3.2	3.7	3.1	2.9	2.5	5.2
Heavy	0.7	0.0	0.8	0.4	0.4	2.3	0.0	3.2	0.0	0.4	2.4	0.0	1.2	2.3	2.9	1.8	5.2
Extreme	0.0	0.0	0.0	0.4	0.4	1.2	0.0	0.0	1.1	0.8	1.2	0.0	1.2	0.0	0.0	0.0	1.0
Total digested	16.7	20.0	19.3	32.4	28.9	32.9	38.0	51.6	47.1	40.7	52.7	35.1	39.5	30.2	40.6	35.6	47.9
Number analysed	*150*	*65*	*119*	*247*	*246*	*173*	*100*	*62*	*87*	*248*	*245*	*154*	*162*	*129*	*69*	*163*	*194*
Humeri																	
No digestion	52.2	70.4	50.0	33.9	43.3	44.7	59.5	53.9	34.8	61.8	35.0	39.4	41.8	42.4	37.5	45.2	47.3
Digested	47.8	29.6	50.0	66.1	56.6	55.3	40.5	46.2	65.2	38.2	65.0	60.6	58.2	57.6	62.5	54.8	52.7
Number analysed	*69*	*27*	*32*	*115*	*122*	*132*	*37*	*13*	*23*	*89*	*80*	*33*	*55*	*33*	*32*	*62*	*55*
Femurs																	
No digestion	35.5	39.4	33.8	33.3	25.4	28.8	41.9	42.9	23.3	23.3	34.0	19.4	20.0	21.7	13.6	22.6	10.0
Digested	64.5	60.6	66.2	66.7	74.6	71.2	58.1	57.1	76.7	76.7	66.0	80.6	80.0	78.3	86.4	77.4	90.0
Number analysed	*62*	*33*	*71*	*120*	*134*	*163*	*31*	*7*	*30*	*73*	*50*	*36*	*50*	*23*	*44*	*62*	*50*

Table 4
Percentage of digested incisors (*in situ* and isolated), humeri and femurs in the MSA I units.

Digestion % Incisors	Cave 1A		Cave 1B										
	Z44 SCB& SAS	Z44 SBS	RS Gr. A	RS Gr. B	RS Gr. C	RS Gr. D	RS Gr. E	RS Gr. F	RS Gr. G	RS Gr. H	RS Gr. I	RS Gr. J	RS Gr. K
Light	18.2	24.0	20.8	13.2	14.8	16.8	29.3	26.6	21.2	18.5	20.4	37.4	31.9
Moderate	0.0	14.0	0.0	3.8	1.0	1.9	0.0	1.8	0.8	0.9	4.5	7.2	4.9
Heavy	2.3	8.0	0.0	1.9	3.0	0.0	0.0	0.9	0.8	0.9	1.3	0.0	0.7
Extreme	0.0	2.0	0.0	0.0	1.0	0.0	0.0	0.9	0.0	0.0	0.6	0.0	0.7
Total digested	*20.5*	*48.0*	*20.8*	*18.9*	*19.8*	*18.7*	*29.3*	*30.3*	*22.9*	*20.4*	*26.8*	*44.6*	*38.2*
Number analysed	*44*	*100*	*53*	*53*	*101*	*155*	*41*	*109*	*118*	*108*	*157*	*139*	*144*
Humeri													
No digestion	29.0	41.8	37.6	41.2	40.9	54.1	51.1	18.2	42.5	51.7	47.8	30.8	43.7
Digested	71.0	58.2	62.4	58.8	59.1	45.9	48.9	81.8	57.5	48.3	52.2	69.2	56.3
Number analysed	*38*	*91*	*109*	*17*	*22*	*159*	*45*	*33*	*47*	*29*	*67*	*65*	*71*
Femurs													
No digestion	25.0	25.0	7.6	25.0	0.0	20.6	25.8	22.7	20.7	8.0	20.7	1.7	23.9
Digested	75.0	75.0	92.4	75.0	100	79.4	74.2	77.3	79.3	92.0	79.3	98.3	76.1
Number analysed	*40*	*108*	*92*	*24*	*18*	*107*	*31*	*22*	*29*	*25*	*58*	*58*	*46*

MSA II Upper sample from cave 1A generally had a greater frequency of rounded breaks and etching compared to the other units. Etching was least frequent in cave 1 units while rounding of breaks was confined to the two other caves (Appendix, Tables A4, A5 and A.6).

Burnt elements were unevenly represented in the assemblage. In MSA II Upper the frequency was low at < 2.7% in cave 1 and < 1.0% in cave 1A (Nel, 2013). In MSA II Lower burning was more recurrent, especially in lower levels of cave 1 where 27.8% of limb bones in HHH were burnt, 19.3% in OHO and 22.1% in TSM. In SMB 11.8% were burnt, while frequencies were lower in SSM at 3.6% and in FM 2.3%. In cave 1A limb bones were frequently burnt; 20.0% in Y44 SM5, 45.2% in Y44 CL&BS and 25.8% in Y45 YS1 (Nel, 2013). For MSA I there were burnt elements in all units - RS Gr. C in cave 1B had highest frequency at 8.9%, followed by RS Gr. K at 6.9%, while the remaining units had less than 3.8% (Nel, 2013).

3.2. Taxonomy

The study sample contained 2067 minimum numbers of individuals from 26 different species including golden moles, shrews, mole rats, mice, vlei rats and bats (Table 5). There were two taxa of Chrysochloridae, four species of Soricidae, two Bathyergidae, fourteen species from the Muroidea superfamily and four species of Chiroptera.

The Southern African vlei rat (*Otomys irroratus)* was the best represented species in MSA II Upper (34.1%) and MSA II Lower (19.8%). While in MSA I, forest shrews (*Myosorex varius*) were most abundant (12.7%) closely followed by xeric four striped grass rats (*Rhabdomys pumilio*) (12.2%). There are 26.9% Otomyinae present in MSA I, though identification to species was not possible due to fragmentation. Soricidae and xeric four striped grass rats declined in abundance from MSA I to MSA II Upper, as did golden moles, climbing mice and Verreaux's white-footed rats, while laminate vlei rats increased in abundance (Table 5).

Taxonomic composition was compared by evaluating similarity (Fig. 5). The high rank Jaccard index is 0.54, and the low rank Bray-Curtis is 0.55, indicating equal variations in both species composition and abundance throughout MIS 5. However, species compositions in MSA I and MSA II Lower are more similar to each other than to MSA II Upper. However, percentage representation of species show greater similarity between MSA II Lower and MSA II Upper compared to MSA I.

3.3. Biodiversity

3.3.1. Species richness and diversity

The rarefaction curves for MSA I and MSA II Lower overlap, while MSA II Upper had less species richness (Fig. 6). The rarefaction results were standardised to the smallest sample (based on MNI) and compared statistically by a *t*-test (Hammer and Harper, 2006). Both MSA II Upper (t = 25.2, p < 0.001) and MSA II Lower (t = −2.18, p < 0.004) are statistically different from the smallest sample, MSA I. The results indicate that the observed variation in species

Table 5
Taxonomic percentage representation (relative abundance) for the MSA II Upper, MSA II Lower and MSA I phases.

Chrysochloridae	Common name	MSA II Upper	MSA II Lower	MSA I
Amblysomus hottentotus	Hottentot golden mole	0.8	2.6	4.8
Chlorotalpa duthieae	Duthie's golden mole	–	2.4	3.4
Soricidae				
Crocidura flavescens	Greater red musk shrew	3.9	4.1	7.9
Myosorex varius	Forest shrew	1.8	6.5	12.7
M. varius/C. cyanea	–	0.6	1.2	1.2
Crocidura cyanea	Reddish-grey musk shrew	0.4	0.3	–
Suncus varilla	Lesser dwarf shrew	–	–	0.3
Bathyergidae				
Cryptomys hottentotus	Southern African mole-rat	1.4	1.8	1.4
Georychus capensis	Cape mole-rat	2.2	2.6	1.5
Muroidea				
Mastomys verreauxii	Verreaux's white-footed rat	–	2.4	3.3
Myomyscus natalensis	Natal mastomys	–	0.1	–
M. natalensis/M. verreauxii	–	0.6	0.9	0.9
Dendromus mesomelas	Brant's African climbing mouse	–	0.1	0.6
Dendromus melanotis	Grey African climbing mouse	–	0.3	0.3
Dendromus sp.	–	–	0.5	0.5
Dendromurine sp.	–	–	–	0.6
Mus minutoides	Southern African pygmy mouse	–	0.3	–
Dasymys incomtus	Common dasymys	1.6	0.4	–
Rhabdomys pumilio	Xeric four striped grass rat	8.6	13.5	12.2
Steatomys krebsii	Kreb's African fat mouse	–	0.1	–
Acomys subspinosus	Cape spiny mouse	0.2	0.2	0.3
Micaelamys namaquaensis	Namaqua micaelamys	–	0.4	0.6
Mystromys albicaudatus	African white –tailed rat	–	–	0.2
Otomys irroratus	Southern African vlei rat	34.1	19.8	7.9
Otomys saundersiae	Saunders' vlei rat	0.8	1.7	2.2
O. irroratus/O. saundersiae	–	3.5	3.3	5.9
Otomys laminatus	Laminate vlei rat	28.4	10.0	4.0
Otomys sp.	–	11.0	23.7	26.9
Chiroptera				
Rhinolophus capensis	Cape horseshoe bat	–	0.2	–
Rhinolophus clivosus	Geoffroy's horseshoe bat	0.2	0.1	0.2
Eptesicus hottentotus	Long tailed serotine	–	0.1	–
Neoromicia capensis	Cape serotine	–	–	0.2
MNI:		**510**	**911**	**646**

richness is not due to sample size (Hammer and Harper, 2006). Thus, factors causing variation in species richness could link to environmental productivity (Belmaker and Hovers, 2011).

MSA II Upper has the lowest diversity at $H = 1.56$ and the greatest dominance $D = 0.29$ (Table 6). MSA I has the greatest diversity, $H = 2.33$, and a correspondingly lower dominance, $D = 0.12$. Diversity and dominance indices were statistically compared by a diversity permutation test for equality where $p < 0.05$ (Table 6) (Hammer and Harper, 2006). The Shannon-Wiener diversity index is significantly different for MSA II Upper compared to MSA II Lower and MSA I. There is no significant difference in diversity for the MSA II Lower compared to MSA I. All phases are statistically different from each other when comparing the Simpson index for dominance.

A bi-plot (Fig. 7) of diversity and dominance indices illustrates transitional changes in species composition during the MSA I to MSA II Upper. In MSA I diversity indices range from 1.57 (Z44 SCB & SAS) to 2.28 (RS Gr. K), in MSA II Lower from 1.37 (SMB) to 2.29 (TSM) and in MSA II Upper from 1.00 (T51 BS1L) to 1.69 (T51 BS1) (Nel, 2013). Dominance indices range from 0.25 (Z44 SCB & SAS and RS Gr. F) to 0.12 (RS Gr. D and RS Gr. K) in MSA I, 0.33 (SMB) to 0.12 (TSM) in MSA II Lower and 0.41 (T51 BS1L) to 0.22 (B) in MSA II Upper (Nel, 2013). The gradual lower diversity and greater dominance of single taxa from MSA I to MSA II Upper suggests a progressively less diverse range of vegetation from MIS 5 e/d towards MIS 5b/a.

3.3.2. Taxonomic habitat index

The THI comprises categories based on specific habitats of extant micromammals in the study assemblage and characteristics of current vegetation types in the Klasies River area (Table 1). The categories accommodate local vegetation (moist grass, dry grass, bush/forest, shrubland, coastal scrub) and substrate (rocky and sandy). Substrate components were included as they comprise habitats specific for some of the micromammal species recovered (Nel and Henshilwood, 2016). Method of weighting species followed Nel and Henshilwood (2016) and Nel (2013) (Appendix, Table A.7).

Moist grass is associated with damp, thick grass close to reedbeds, streams, vleis and dams (Nel and Henshilwood, 2016). The Cape lowland freshwater wetlands and mesic grasses in Eastern fynbos and renosterveld (Table 1) are examples of existing vegetation at Klasies River.

Dry grass signifies tall grasses similar to savanna type vegetation, grassy dunes associated with Cape seashore vegetation, shrubby grassland and salt-tolerant grass (i.e. *Trachyandra divaricate*) growing on low lying coastal sections (Van Wijk et al., 2017; Nel and Henshilwood, 2016).

Bush/forest is coastal forest margins of the Southern coastal forest that occurs in wind- and fire-protected areas at Klasies River (Van Wijk et al., 2017). It also includes tall and dense thickets of Algoa dune strandveld growing on wind-exposed coastal slopes and other thicket and forest type vegetation currently forming a mosaic structure in the area (Van Wijk et al., 2017) (Table 1).

Shrubland includes low to medium height shrubby vegetation, as associated with *Proteaceae* spp. and *Ericacea* spp. of Tsitsikamma sandstone fynbos and sclerophyllous shrub in Southern Cape dune fynbos. Van Wijk et al. (2017) have noted that Holocene dunes at
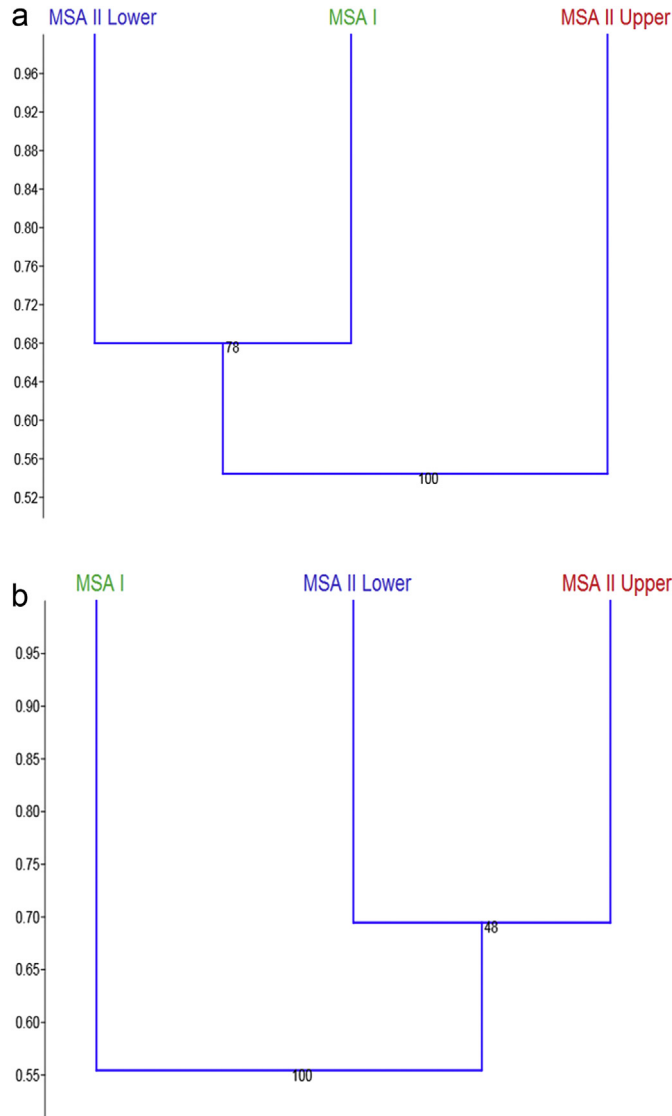
Fig. 5. Species composition assessed by similarity indices. (A) Jaccard similarity illustrated by unconstrained paired groups based on presence-absence of taxa. (B) Bray-Curtis similarity illustrated by unconstrained paired groups based on relative abundance of taxa. The results were bootstrapped (n = 9999).

Table 6
Shannon-Wiener index, H, and Simpson index of dominance, D, compared by phases and by diversity permutation test of equality where p < 0.05.

			Shannon-Wiener		
			MSA II Upper	MSA II Lower	MSA I
		Indices	1.56	2.23	2.33
Simpson Index	MSA II Upper	0.29		*0.0001*	*0.0001*
	MSA II Lower	0.15	*0.0001*		0.10
	MSA I	0.12	*0.0001*	*0.001*	

Klasies River support a mosaic of dune fynbos and thicket. Shrubland also includes low-growing woody elements such as dwarfed vegetation (Van Wijk et al., 2017) and dense, layered vegetation cover similar to heather (Nel and Henshilwood, 2016).

Coastal scrub signifies patchy, sparse vegetation associated with succulent elements in Cape seashore vegetation and xeric low growing vegetation on nutrient poor soil and sandy substrates along the coast (Nel and Henshilwood, 2016). Van Wijk et al. (2017) have associated coastal species with the sea-spray affected littoral and hummock dune vegetation.

The *rocky* component refers to hilly outcrops favoured by some micromammals such as *Acomys subspinosus* (Skinner and Chimimba, 2005). At Klasies River these outcrops are a consistent feature (Singer and Wymer, 1982). The *sandy* category is alluvium dry soil and sandy loams in dune systems with patches of vegetation cover closely associated with the coastal margin (Van Wijk et al., 2017).

THI indicate that there was gradual increase through time in both moist and dry grass cover in the Klasies River area (Table 7 and Fig. 8). The general grass cover, near the site, increase with over 25% during MIS 5, while shrubland, bush/forest and sandy areas declined. Rocky outcrops and coastal scrub seem to have maintained relatively constant proportions.

4. Discussion

4.1. Taphonomy

4.1.1. The predator

The incisor digestion frequency varies in the assemblage (Tables 2–4). Digested incisors mainly have light and moderate digestion, with few occurrences of heavy and extreme digestion.
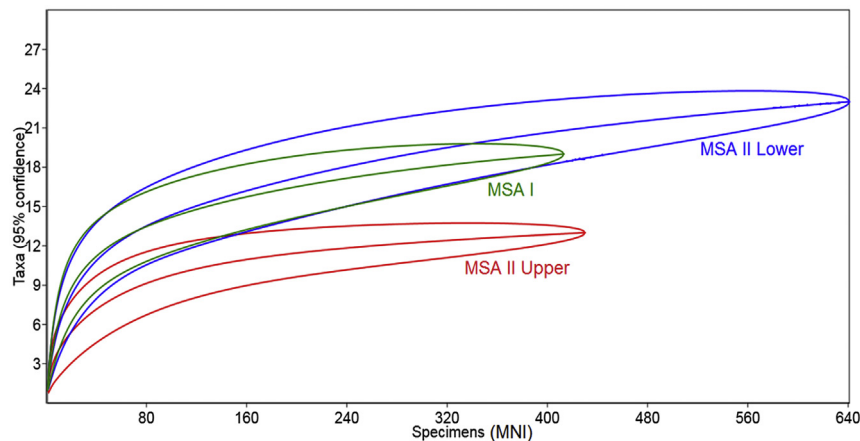
Fig. 6. Point by point individual rarefaction curves with estimated species richness and 95% confidence interval.
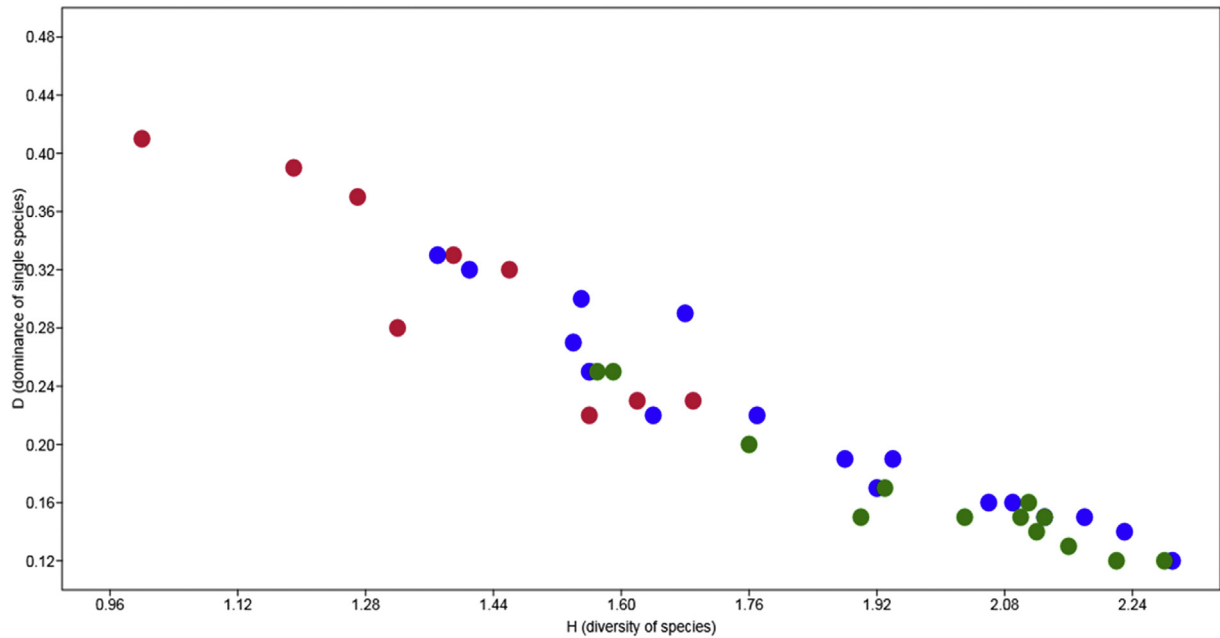
Fig. 7. Bi-plot of Shannon-Weiner index, H, and Simpsons index for dominance, D for each unit in the studied sample (Nel, 2013). MSA I = green, MSA II Lower = blue and MSA II Upper = red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 7
Reconstructed microhabitat at Klasies River during MIS 5e/d, MIS 5c and MIS 5b/a based on taxonomic habitat index. Values expressed as percentage distribution.

	Moist grass	Dry grass	Bush/forest	Shrubland	Coastal scrub	Rocky	Sandy
MSA II Upper	36.3	36.2	2.8	2.0	17.5	1.1	3.9
MSA II Lower	28.6	30.1	6.1	6.7	16.4	1.7	10.0
MSA I	23.4	23.5	9.2	12.3	15.7	3.1	12.5
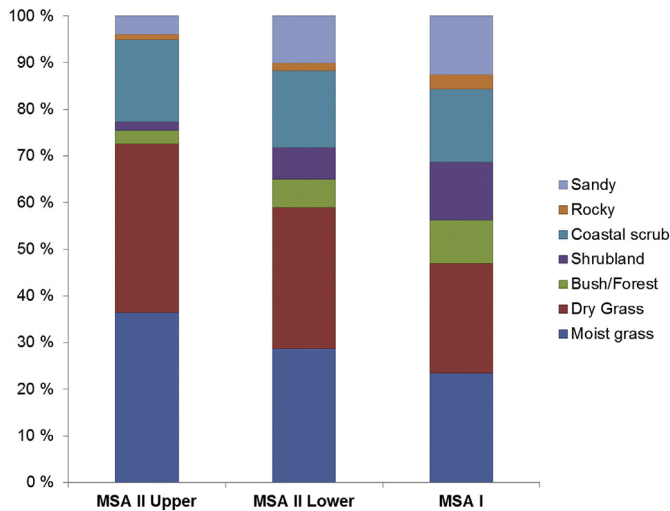
Fig. 8. The percentage representation of vegetation components in MSA I, MSA II Lower and MSA II Upper based on THI.

For the majority of units the degree, intensity and frequency of digestion are within the range of modern comparative samples of spotted eagle owls (*Bubo africanus*) (Andrews, 1990; Reed, 2005; Matthews, 2008; Matthews et al., 2011; Fernandez-Jalvo and Avery, 2015). However, modern samples from spotted eagle owls contain 25—26% of moderately digested incisors (Matthews et al., 2011), while the study assemblage has lower ranges from zero to

14%. Thus, the variation in digestion frequency and intensity suggests that a predator with lighter digestion traits cannot be excluded as a contributor to the assemblage. The likely predator associated with lighter digestion is the African barn owl (*Tyto alba*), as it is known to occupy and live in similar habitats as the spotted eagle owls (Reed, 2005; Steyn, 2009; Matthews et al., 2011). The presence of both spotted eagle owls and African barn owls as predators are also found elsewhere on the Cape coast at Pinnacle Point Cave 9 during the MIS 6 to 5 transition (Fig. 1) (Matthews et al., 2011).

Spotted eagle owls and African barn owls mainly inhabit open areas, cliffs and rocks (Reed, 2005), but may also roost in caves. Both species are opportunistic, adapting to different prey in different habitats, hunting over open country and selecting the most abundant prey species (Fernandez-Jalvo and Avery, 2015; Fernandez-Jalvo et al., 2016). Potential biases include a preference for open vegetation and avoidance of closed woodland or forest (Fernandez-Jalvo and Avery, 2015), although spotted eagle owls may have a more likely presence in woodland than African barn owls (Reed, 2005). Opportunistic behaviour may result in overemphasising abundant prey species whilst rare or cryptic species are underrepresented (Fernandez-Jalvo and Avery, 2015).

Concerning assessment of predator species by breakage, the SEA patterns (Fig. 2) are obscured by post-depositional breakage, erasing the signature of the original predators. The SEA had low representation of fragile elements and greater percentages of robust limb bones and incisors similar to modern samples from mammalian carnivores (Andrews, 1990; Matthews, 2008). However, zygomatic processes of maxillae were present in all units

except for FM, SSM and SMB in MSA II Lower (Nel, 2013). A mammalian carnivore chews bones during ingestion and causes damage (Andrews, 1990), making it unlikely that these delicate elements would be preserved. Their presence suggests that maxillae or skulls were complete before deposition, and the SEA pattern is indicative of extensive post-depositional breakage (Nel, 2013). It is reasonable to assume that SEA displays a 'site-specific' pattern caused by post-depositional breakage, a known quandary common for cave sites (Andrews, 1990; Matthews, 2004; Fernandez-Jalvo et al., 2016; Nel and Henshilwood, 2016).

4.1.2. Post-depositional damages and site formation

Type, frequency and intensity of post-depositional damages varied in different areas of the site, likely reflecting specific sediment characteristics and site utilization. There was distinct variation in breakage of elements in cave 1, where the lower units (TSM, OHO and HHH) had greater fragmentation of elements and rounding of breaks than the overlying units. Deacon and Geleijnse (1988) argued that the SAS (W) assemblage was talus material and thus not in primary context nor being subject to trampling (Appendix, Table A2). Our analysis show that the upper units in SAS (U) (FM, SSM and SMB) in MSA II Lower also had less fragmentation of limb bones and maxillae when compared to the lower SAS (U) units (Figs. 2 and 3). The lower units were trampled, while the overlying units may not have been (Deacon and Geleijnse, 1988), accounting for variation in fragmentation. Human occupation was likely not possible in cave 1 when cave 1A filled up with material (Fig. 2). Further indications are greater amounts of burnt elements in the lower SAS (U) units. The elements were possibly burnt accidentally when human occupants made fire. Fewer burnt elements in the upper levels of SAS (U) and SAS (W) indicate that this area was no longer in use for human occupation.

Rounding of breaks and etching on elements was most frequent in cave 1A. Damages observed are associated with post-depositional processes, as they occur in specific areas of the site and the rounding is associated with post-deposition (see 2.2.1). Similarly, the observed etching is associated with micro-morphological features of soil affecting bones post deposition (Nel, 2013). Variations in post-depositional modification may be caused by preservation conditions within the site (Deacon and Geleijnse, 1988). Degradation of organic matter causes soil to be acidic (Shahack-Gross et al., 2004), and would be more frequent in high intensity deposits associated with human occupants. Such deposits likely contained plant material, faeces, unutilised animal remains etc. resulting in greater soil acidity in areas of high occupation intensity (Shahack-Gross et al., 2004; Nel, 2013; Nel and Henshilwood, 2016). As inferred from post-depositional processes, cave 1A was most likely an area of high intensity deposits, and to some extent the lower units (TSM, OHO and HHH) in cave 1. There was less post-depositional damage in cave 1B which suggests that this area was probably not utilized as intensively for human occupation. These tentative observations should be viewed in relation to other intra-site spatial analysis and soil micromorphology.

4.2. Palaeoenvironmental implications

4.2.1. Biodiversity

Rarefaction analyses and t-tests suggests that variations in species richness is a function of changing environments (Fig. 6) (Hammer and Harper, 2006; Belmaker and Hovers, 2011). There was more diverse vegetation in MSA I and MSA II Lower compared to MSA II Upper. Following Andrews and O'Brien, (2000) correlation of small mammal species richness and seasonal variation in precipitation, the decline in species richness observed in MSA II Upper

may suggest greater seasonal fluctuation in precipitation in MIS 5b/a.

Lower diversity in MSA II Upper point to alterations in environmental conditions compared to earlier in MIS 5 as diversity has been used as a measure of environmental stability (Table 6). The biplot of the Shannon-Wiener and Simpson indices (Fig. 7) show a transitional decline in diversity from MSA I to MSA II Upper. The decline may reflect a reduction in vegetation diversity at Klasies River in latter MIS 5.

4.2.2. Taxonomic composition

Spotted eagle owls and African barn owls both exploit a wide range of terrain and return to the same roosting site (Levinson, 1982; Reed, 2005). They are two of the most common accumulators of micromammal assemblages, and create assemblages corresponding to live communities (Reed, 2005; Matthews et al., 2011; Belmaker et al., 2016). Reed (2005) and Matthews (2008) found similar ranges of micromammal species when comparing modern spotted eagle owl and African barn owl pellets. Both species are claimed to be nocturnal (Andrews, 1990), however modern pellet samples show that they hunt species such as Otomyinae (diurnal) and *R. pumilio* (crepuscular) (Avery et al., 2005; Matthews, 2008; Matthews et al., 2011). Certain micromammal taxa are found in relatively high frequencies in spotted eagle owl and African barn owl pellets. Species typical for the south coast are Otomyinae, Gerbillinae and Soricids (Avery et al., 2005; Matthews, 2008; Matthews et al., 2011).

Otomys irroratus increase noticeably in abundance from MSA I to MSA II Upper (Table 5). Engelbrecht et al. (2011) have used niche modelling and maximum-entropy when analysing modern *O. irroratus* samples. The greatest relative contribution to their maximum-entropy model was precipitation of the driest month (variable contribution was 73%) for Clade A, with which the Klasies River specimens are associated (Engelbrecht et al., 2011). They found that the localities assigned to Clade A are in areas with relatively high precipitation in the driest month of the year (Engelbrecht et al., 2011). Though *O. irroratus* is a favoured prey of the established predators, greater *O. irroratus* abundances in the latter part of MIS 5 could suggest changes in rainfall distribution due to increased precipitation in the drier months at Klasies River. A possible increase in moisture compared to MIS e/d is supported by *Dasymys incomtus*' presence only in MSA II Lower and Upper. The species is associated with wet habitats (reed-beds and semi-aquatic grasses) (Skinner and Chimimba, 2005) (Table 5).

Myosorex varius decline in abundance from MSA I through to MSA II Upper. It is considered a generalist species, able to adjust its reproductive cycle to suit different environmental conditions, particularly rainfall (Baxter, 2005). Willows-Munro and Matthee (2011) tested this hypothesis by analysis of phylogeography, and found that the *M. varius* population could be divided in two major groups. A northern group associated with grassland and savanna biomes and summer rainfall, and a southern group associated with the Cape Floristic Region, though further subdivided into a western clade (winter rainfall) and a eastern clade (aseasonal rainfall). In the Port Elizabeth area (Fig. 1), approximately 100 km east from Klasies River, they found specimens that could be associated both with the northern and eastern clade. Provided a possible shift towards more aseasonal rainfall in MSA II Upper, it could be likely that *M. varius* at Klasies River belonged to the northern clade associated with summer rainfall. This needs to be further investigated.

The relative abundance of *Rhabdomys pumilio* is consistent in MSA I and MSA II Lower, but decline in MSA II Upper (Table 5). Du Toit et al. (2012) analysed biome specificity of distinct genetic lineages within *R. pumilio* in southern Africa. Their study indicates the presence of two *R. pumilio* clades on the southern coast. The coastal

clade is associated with fynbos and succulent Karoo biomes and winter rainfall and the central clade is affined to the arid Nama-Karoo biome with mostly late summer rainfall (Du Toit et al., 2012). Their niche model indicates that the coastal clade's occurrence probability declines with increased rainfall outside of the winter season (Du Toit et al., 2012). Thus *R. pumilio's* decline may be further indication of more aseasonal rainfall in MIS 5 b/a compared to earlier in the stage.

Acomys subspinosus is fynbos endemic (Skinner and Chimimba, 2005) and although it is of the least well-represented species, its presence indicates a persistent fynbos component in MIS 5. Ground *proteas* are dependent on *M. verreauxii* for pollination (Matthews et al., 2005) and confirms the presence of fynbos, albeit with possibly less Proteoids available in MSA II Upper (Table 5).

Golden moles decline in abundance from MSA I to MSA II Upper (Table 5). However, Avery (1987) recorded both *Chlorotalpa duthieae* and *Amblysomus hottentotus* in MSA II Upper units in cave 1A (relative abundances <6%). *C. duthieae* prefer sandy loams within coastal forests of the fynbos biome and likely breed during wet summer months (Skinner and Chimimba, 2005). Fewer *C. duthieae* in MSA II Upper may indicate less sandy substrate and possibly also summer rainfall in MSA II Upper. Lower *M. varius* abundances and increase of *O. irroratus* could support the latter assumption and reflect shifts in rainfall seasonality in MIS 5.

MSA I and MSA II Lower are more similar on a high rank level compared to the MSA II Upper while the MSA II phases have greatest similarity based on relative abundances (Fig. 5). Both phases have high proportions of vlei rats in particular, while MSA I has more evenly distributed relative abundance of species, however with greater percentage of shrews. The results indicate changes in vegetation and/or rainfall regimes during MIS 5, which affected micromammals to such an extent that species disappeared and relative abundances of taxa changed significantly. In this regard, MSA II Lower (MIS 5c) seems to be a transitional phase between the MIS 5 e/d and MIS 5 b/a.

4.2.3. Taxonomic habitat index

THI provides information of general climatic conditions, as optimal conditions result in complex vegetation structures while dominance of a single vegetation type suggest stressed environmental conditions (Cuenca-Bescós et al., 2009). The increasing dominance of grass cover in the latter part of MIS 5 may indicate locally stressed environmental conditions at this time.

In accordance with the biodiversity indices, MSA I (MIS 5 e/d), had a balanced mosaic of vegetation habitats. Although grasses were abundant, they were more equally represented compared to other vegetation components. The greater percentage of shrubland may indicate drier conditions than later in MIS 5.

In MSA II Lower (MIS 5c) moist and dry grass expanded, while shrubland declined. This could reflect fewer patches of schlerophyllous shrub and dwarfed wood elements. Increase in moist grass reflects seasonally waterlogged grassland. This is associated with both dune fynbos and mesic grassy fynbos (Avery, 1987) and implies increased moisture compared to MSA I. A decline in sandy substrate (dune systems), and increase of dry grass, may suggest greater vegetation cover of dunes possibly by pioneering grass species as associated with Cape seashore vegetation. In MSA II Lower, there may thus have been presence of small lakes with reed-beds and dense grasses, separated by herbaceous and grass covered dunes with thicket components in vicinity of the site, as Avery (1987) also have suggested.

Particularly moist grass, but also dry grass, continued to expand in MSA II Upper, while sandy substrate declined further. It is likely that increased or perhaps continuous supply of moisture throughout the year provided sufficient conditions for further grass expansion on old dunes creating habitats for grasses associated with reed-beds and freshwater wetlands. Low diversity of species and dominance of *O. irroratus* and *O. laminatus* are reflected in the THI for the MSA II Upper. As the established predators go for the most abundant prey (Matthews et al., 2011; Fernandez-Jalvo and Avery, 2015), it is likely that there may have been a spur in *O. irroratus* and *O. laminatus* populations at the time. This could also lead to a skewed picture with underrepresentation of other taxa available in lower frequencies in the area.

4.3. A comparison to other palaeoenvironmental proxies from Klasies River

We have used non-metric multidimensional scaling (NMDS) to visualize trends and groupings of our multivariate dataset (Fig. 9) (Hammer and Harper, 2006; Nel, 2013).

Rainfall seasonality is reflected on the horizontal scale, where positive values correlate with more summer rainfall and negative values indicate more aseasonal rainfall patterns (Fig. 9) (Nel, 2013). Vegetation cover density in relation to moisture is the main factor along the vertical scale (Nel, 2013). The inferred moister conditions in MSA II are supported by great species richness of frogs (Van Dijk, 2006). Frogs are particularly sensitive to changes in rainfall regimes and analysis of specimens from the SAS Member in cave 1 shows almost unparalleled species richness in a Quaternary context (Van Dijk, 2006). The presence of Pipidae indicates fresh water, or mildly brackish water, close to the site in MSA II (Van Dijk, 2006). There were sufficient amounts of water to support the same range and diversity of frog species as today.

Our study supports Avery (1987) who suggested that aseasonal rainfall encouraged expansion of grasses associated with dune fynbos and mesic grassy fynbos and she found this to be likely in MSA II. Both MSA II Lower and Upper had more extensive grass cover than the mosaic of grass, shrubs and bush primarily associated with MSA I (Fig. 8). The change from mosaic shrub towards grassland was also noted by Avery (1987) in the later phases (Howiesons Poort and MSA III, c. 80-57 ka), and could represent a cyclical change in vegetation throughout MIS 5 and MIS 4.

Furthermore, the small antelope blue duiker (*Philantomba monticola*), associated with forest fringes, is only present in MSA II Upper (Van Pletzen, 2000; pers. comm.). Similar to our study, Avery (1987) found *O. irroratus* increasingly abundant in MSA II. Modern microfaunal samples from Glentyre (Fig. 1), an area associated with relative moist areas flanked by afromontane forest, *O. irroratus* dominate (Avery, 1987). The domination of *O. irroratus* and occurrence of forest duiker is thus suggestive of afromontane forest being close to the site in MSA II Upper.

The presence of large mammals such as grazers, equids, wildebeest, and hartebeest indicate an open grassland environment during MSA I (Klein, 1976; Van Pletzen, 2000). Our analysis do support grasses as main vegetation component in MSA I (Fig. 9), however with drier conditions and more mosaic vegetation than later in MIS 5. In the large mammal fauna an ecological shift from MSA I to the MSA II is indicated by the increased relative frequencies of browsers and mixed feeders such as grysbok (*Raphicerus* sp.) and tragelaphines, which prefer closed vegetation such as forests and thicket (Wurz, 2010). This does not correlate to the assumed greater grass vegetation cover at Klasies River as inferred from the micromammals. The discrepancy may be due to the variation in territorial ranges of small and large mammals or a result of biased assemblages due to variations in hunting techniques. Furthermore, the mosaic of vegetation as inferred from our study in the immediate vicinity of Klasies River may also reflect climatic fluctuations at a more detailed scale and faster pace than ecological implications derived from large mammals.
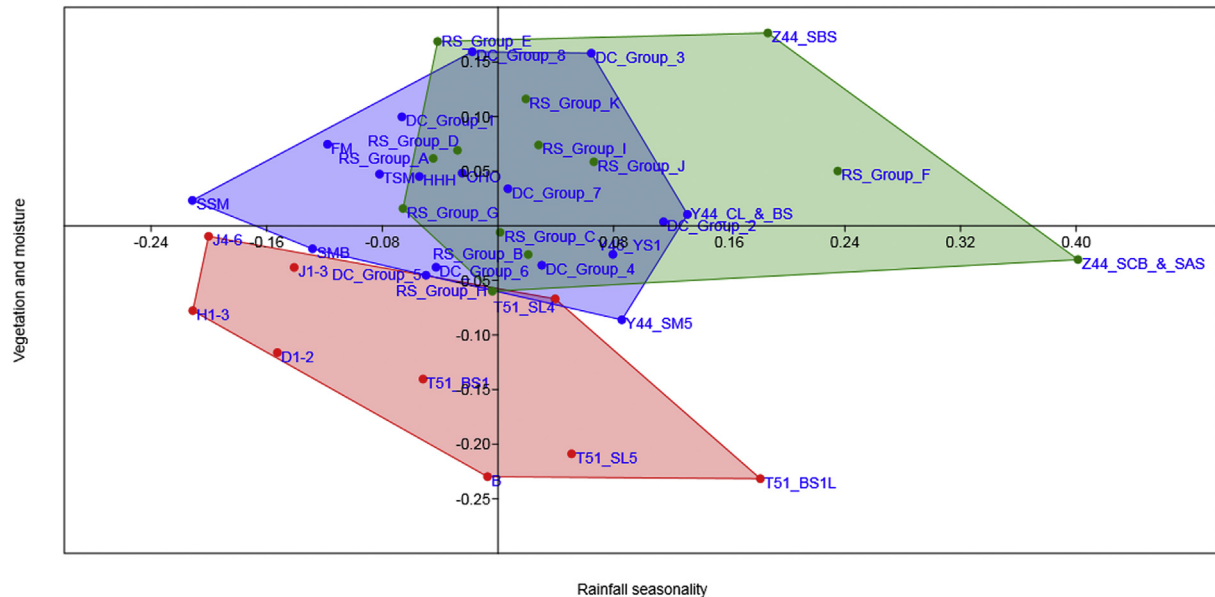
Fig. 9. **Non-metric multidimensional scaling of the units in MSA I (green), MSA II Lower (blue) and MSA II Upper (red) based on binary data (presence/absence of taxa) and by use of the Dice similarity index.** Stress value is 0.22 (Nel, 2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

Our study establishes spotted eagle owls as the main accumulators, though African barn owls likely contributed to accumulation in all three phases. We have demonstrated that taphonomic analysis aids in understanding site formation and utilisation, however further analysis of soil micromorphology is needed to fully comprehend spatial use at this depositionally complex site.

It is likely that Klasies River, due to the vegetation mosaic, could have been sensitive to moderate climatic change. Our results suggest that there may have been shifts in rainfall seasonality during MIS 5. In MIS 5e/d there seems to have been more seasonal precipitation perhaps to a greater degree confined to summer months, as opposed to MIS 5c and MIS 5b/a where rainfall was more aseasonal. It is plausible that moderate changes in rainfall seasonality during MIS 5 c and MIS 5b/a promoted expansion of primarily grasses in the immediate vicinity of Klasies River, which led to less diverse taxonomic assemblage, and dominance of vlei rats, particularly during MSA II Upper. Generally, climatic conditions seem to have supported a greater range of micromammal species in MSA I compared to MSA II Upper and it is assumed that there was decrease in productivity as MIS 5 progressed. This may reflect a cyclical variation in the local extent of grasses and vegetation cover of exposed dune systems close to the site.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quaint.2017.08.074.

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