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Research Article

A ca. 39,000-year record of vegetation and climate change from the margin of the Namib Sand Sea

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Abstract

This paper presents the first continuous multi-proxy record of climate and vegetation change from the central Namib Desert extending over much of the last ca. 39,000 years. Derived from rock hyrax middens, evidence from stable carbon and nitrogen isotopes, pollen, and microcharcoal reveals significant differences between glacial-age and Holocene climates and vegetation types. Although still arid to semi-arid, conditions during Marine Oxygen Isotope Stages (MIS) 2–3 were significantly more humid than in the Late Holocene. Considerable associated vegetation change is apparent, with cooler temperatures and higher/more-regular rainfall promoting the westward expansion of relatively mesic shrubby karroid vegetation during MIS 2–3. With the last glacial–interglacial transition, increasing temperatures and less/less-regular rainfall resulted in marked vegetation changes and the establishment of current xeric grasslands. The inter-plant spacing of the karroid vegetation promoted by wetter conditions does not carry fire effectively, and the microcharcoal record indicates that more extensive fires may develop only with the development of grassier vegetation under drier conditions. As with other terrestrial records from the Namib Desert and environs, no Cape flora elements were found to support previously hypothesised expansion of the Fynbos Biome during the last glacial period.

Keywords: Pleistocene, Rock hyrax midden, Namib Desert, Southern Africa, Paleoenvironment, Pollen, Stable isotopes

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INTRODUCTION

Reliable information regarding past climate and vegetation change in the Namib Desert region is extremely difficult to obtain because the arid environment is not conducive to preservation of organic material and associated proxies (see Lancaster, 2002; Chase and Meadows, 2007). Indirect evidence from marine sediments has thus been drawn upon extensively to compensate for this lack of terrestrial archives (e.g., Shi et al., 2001; Stuut et al., 2002; Collins et al., 2014). However, the influences on such marine records of the region's complex circulation and taphonomic dynamics are difficult to assess, and clear discrepancies exist with those terrestrial records that do exist (Scott et al., 2004, 2018; Lim et al., 2016; Chase et al., 2019). As a result, a clear understanding of long-term vegetation change in the Namib Desert region remains to be established.

As an iconic feature of southern Africa's diverse geography, the Namib Desert, which extends over 2000 km along the southwestern coast of Africa, has long been a focus of paleoenvironmental study. Arid conditions in the region likely date to at least the late Cretaceous (ca. 80 Ma) (Ward et al., 1983), while intensification of the South Atlantic Anticyclone and the Benguela upwelling system since the Eocene (ca. 34 Ma) is likely to have induced increasingly arid conditions through higher atmospheric pressure and cooler coastal waters (van Zinderen Bakker, 1975; Tankard and Rodgers, 1978; Etourneau et al., 2009). Within this context and based on these mechanisms, it has been suggested that the last glacial period, particularly Marine Oxygen Isotope Stages (MIS) 2–4 (12–70 ka), which experienced marked increases in anticyclonic intensity and coastal upwelling (Little et al., 1997; Stuut et al., 2002; Farmer et al., 2005; Pichevin et al., 2005), would have been a period of increased aridity in the Namib Desert (van Zinderen Bakker, 1975). However, studies of relict lacustrine deposits from across the Namib, including sites such as Kannikwa (Beaumont, 1986), Koichab Pan (Lancaster, 1984), Narabeb (Teller and Lancaster, 1986), Khommabes (Teller and Lancaster, 1985), and Gobabeb (Vogel and Visser, 1981) indicate periods of more/more-effective precipitation (Δprecipitation:potential evapotranspiration) during much of MIS 2–3 (37–31 cal ka BP, 30–24 cal ka BP), as well as the during the late glacial and earliest Holocene (14–10 cal ka BP) (Lancaster, 2002). Much of these early data are derived from paleolacustrine and paleofluvial (Marker and Müller, 1978; Vogel, 1982; Ward, 1982; Heine and Heine, 2002) archives associated with hydrologic networks sourced in the relatively mesic uplands of the Great Escarpment, to the east of the Namib Desert. Thus, an often-posed question has been to what extent does evidence from these archives reflect changes in the uplands or in the desert itself (Ward et al., 1983; Heine, 1998; Lancaster, 2002)?

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Questions regarding (1) the significance of phases of increased humidity inferred from discrete lacustrine deposits, and (2) the loci of the rainfall that fostered development of the region's lacustrine and fluvial features are being addressed via a wider network of new paleoenvironmental archives. In recent years, it has been shown that rock hyrax middens (Chase et al., 2012) can provide such valuable archives. Several continuous high-resolution records from rock hyrax middens from the Namib Desert have indicated that the last glacial period was indeed relatively humid compared to the Holocene (Lim et al., 2016; Chase et al., 2019), adding significant detail to our understanding of regional climate change over the last 50,000 years. While some middens, such as those from Pella (Lim et al., 2016), are located at the margins of the Namib Desert, and may be considered to reflect conditions in the Great Escarpment, others, such those recovered from Spitzkoppe (Chase et al., 2009, 2019) and, particularly, Mirabib (Scott et al., 2018), are located to the west and lie within the arid core of the desert. In contrast to the region's fluvio-lacustrine archives, it is generally considered that rock hyrax middens preserve a predominantly local signal that reflects the foraging range of the animals (less than ∼60 m from the midden/shelter site) (Sale, 1965; Chase et al., 2012) and that, accordingly, the indications of increased glacial-age humidity at Spitzkoppe and Mirabib can be interpreted to reflect conditions within the desert itself.

Strong similarities are evident in the stable nitrogen isotope records (interpreted as a reflection of water availability) from middens recovered from Aba Huab/Austerlitz (Chase et al., 2010), Spitzkoppe (Chase et al., 2009, 2019), Zizou (Chase et al., 2019), and Pella (Chase et al., 2019), indicating a generally common climate response signal across a 900-km transect of the Namib Desert (Fig. 1). Evidence of associated changes in vegetation, however, is often restricted to the Holocene (Scott et al., 1991, 2022; Scott, 1996; Gil-Romera et al., 2006, 2007), with the only indications of glacial-age vegetation coming from the continuous 50-kyr record from Pella (Lim et al., 2016), and shorter MIS 2–3 time slices from the Brandberg (Scott et al., 2004) and Mirabib (Scott et al., 2018). While each record expresses changes specific to its environmental context, evidence from all of these sites contrasts markedly with pollen records recovered from marine cores off the coast of Namibia (Shi et al., 2000, 2001; Urrego et al., 2015). A distinctive component in these marine records—both in terms of their content and the associated proxy interpretations—is the prevalence of pollen types associated with the Cape Floristic Region during the Pleistocene. This is evinced in levels of Restionaceae pollen as high as 14–20% during MIS 2–3 (Shi et al., 2000, 2001; Urrego et al., 2015). In some cases, the addition of other pollen types, such as *Anthospermum*, *Stoebe*-type, and *Artemisia* pollen, that are found in, but are not specific to, fynbos augments the percentage of pollen from "fynbos taxa" to as much as 40% of the pollen sum (e.g., Urrego et al., 2015). Such conclusions have played a significant role in theories regarding expansions of the southwest African winter rainfall zone and Fynbos Biome to the north during glacial periods (Chase and Meadows, 2007; Shi et al., 2000, 2001; Urrego et al., 2015).

As early as 2004 the reliability of interpretations of marine pollen records in the region was questioned, based on an absence of Restionaceae and Ericaceae pollen in glacial-age samples from the Brandberg hyrax middens (Scott et al., 2004). As a single site, this could not provide definitive refutation (see Chase and Meadows, 2007), but the absences of these taxa in subsequent records (Scott et al., 2018), including sites on the southern boundary of the Namib (Lim et al., 2016), implies that the microfossils from marine cores in the Benguela system may be significantly influenced by long-distance transport. As such, they cannot therefore be considered a direct reflection of environmental change on the adjacent continent (Scott et al., 2004, 2018; Lim et al., 2016; Chase et al., 2019).

To characterise the nature of environmental and vegetation change in the Namib Desert, and to further test the hypothesis of substantial expansions of the Fynbos Biome during the last glacial period, we present new pollen, microcharcoal, and stable isotope records from the Zizou rock hyrax midden site. Located on the plains below the Great Escarpment on the eastern margin of the Namib Sand Sea (Figs. 1, 2), the Zizou rock hyrax midden site encompasses much of the last 39,000 years and allows an analysis of changes in vegetation and fire regimes within the context of an independent perspective (via stable isotope data) on climate variability.

Regional setting

The Zizou rock hyrax midden site is located on the eastern margin of the northern Namib Sand Sea, 20 km SSW of the town of Solitaire (24.07°S, 15.97°E, 1120 m asl) (Figs. 1, 2). Situated at the base of the western flank of the Great Escarpment, the site lies within the steep environmental gradient between the hyper-arid regions of the Namib Desert and the semi-arid interior (Fig. 2). The limited precipitation received at the site (130 mm/yr on average, but with a high degree of interannual variability) falls almost exclusively during the austral summer (Fick and Hijmans, 2017). Vegetation at the site is classified as xeric Namibian Savanna Woodland (Fig. 2), characterised by sparse C_4 grass cover on the plains surrounding the site, with sporadic shrubs of the Capparaceae family (*Boscia*, *Maerua*) and isolated small trees (*Vachellia* and *Searsia*) along drainage lines (Fig. 1). Shrubs and arboreal taxa are more common on the rocky slopes surrounding the midden site, including the occurrence of *Commiphora*. To the west, the Namib Desert ecoregion is characterised by sparse cover of xeric grasses, particularly *Stipagrostis*, if vegetation is present at all. Here, the water table is generally too low to support even deep-rooting arboreal taxa, and only plants capable of exploiting the region's extremely sporadic rainfall occur. To the east, the uplands of the Great Escarpment and interior plateau support the low-shrub vegetation of the Gariep Karoo ecoregion. Shrubs of the Asteraceae and Aizoaceae families are most common, including *Eriocephalus*, *Pentzia*, and *Ruschia*, as are arid-adapted C_4 grasses such as *Aristida* and *Stipagrostis*.

Material and methods

The middens considered in this study were collected and analyzed according to the techniques described by Chase et al. (2012, 2019). Depending on the architecture of the shelter in which a midden is found, the accumulation may have varying proportions of faecal pellets to urine (known as hyraceum). At Zizou, two midden sections (ZIZ-1-1 and ZIZ-1-3) were found in close proximity (∼2 m) as part of the same midden complex. They were selected for analysis because they are composed primarily of hyraceum, and thus have superior stratigraphic integrity compared to more pellet-rich (and thus coarser) middens (Chase et al., 2012). Representative portions of the middens (measuring 227 mm and 145 mm in depth for ZIZ-1-1 and ZIZ-1-3, respectively) were

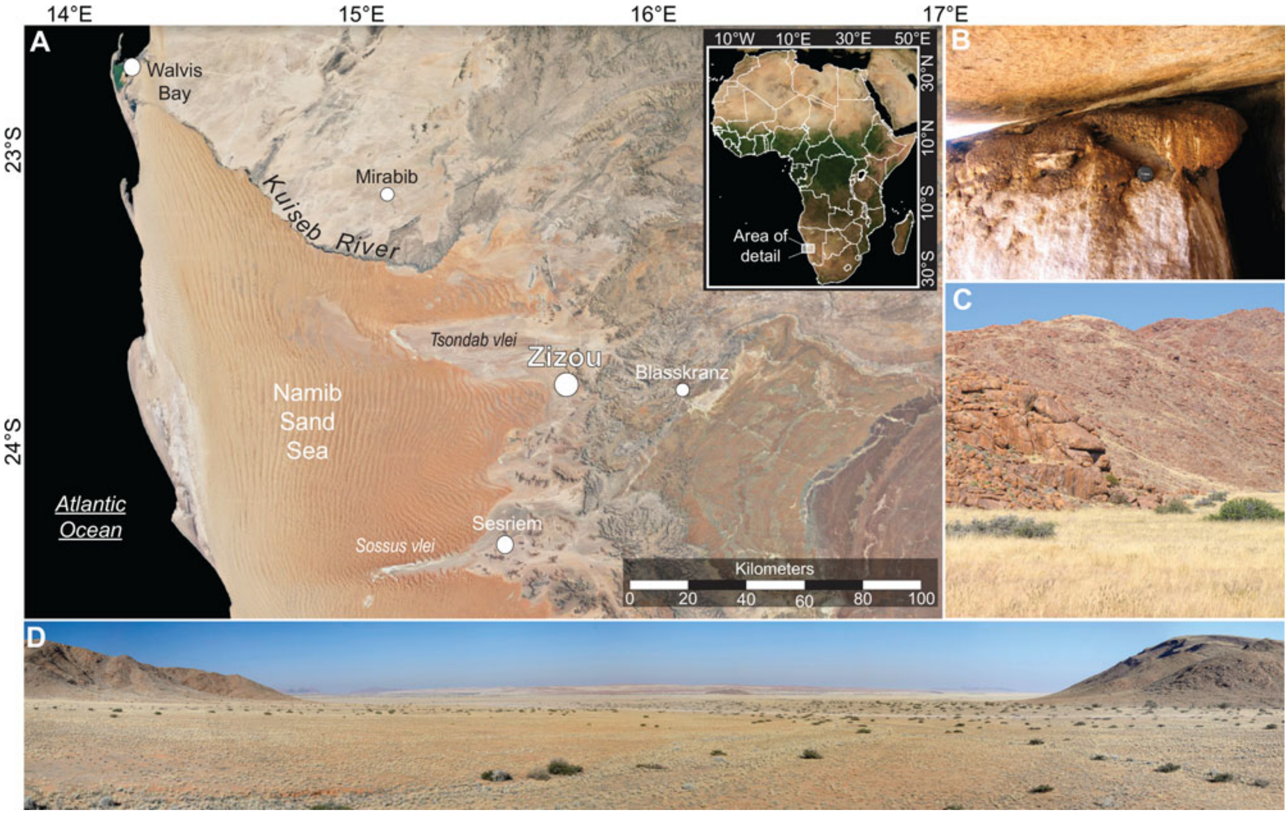

Figure 1. (**A**) Map of study region, indicating location of the Zizou rock hyrax midden site. (**B**) The Zizou-1 rock hyrax midden (21.3 cm thick), with view of local landscape and vegetation (**C**) and (**D**) view eastward from the site towards the Namib Sand Sea (visible in distance).

extracted using an angle grinder and transported back to the laboratory, where the sections were cleaned using progressively finer grades of sandpaper prior to sub-sampling for radiocarbon, microfossil, and stable isotope samples.

Radiocarbon dating

Radiocarbon age determinations for the ZIZ-1-1 (n = 14) and ZIZ-1-3b (n = 13) middens were processed at the ^{14}CHRONO Centre, Queen's University Belfast using accelerator mass spectrometry (AMS) (Table 1; Fig. 3). Samples were pre-treated with 2% HCl for one hour at room temperature to remove carbonates and dried at 60°C. They were then weighed into quartz tubes with an excess of CuO, sealed under vacuum, and combusted to CO_2. The CO_2 was converted to graphite on an iron catalyst using the zinc reduction method (Slota et al., 1987). The radiocarbon ages were corrected for isotope fractionation using the AMS measured $\delta^{13}C$. The ages were calibrated using SHCal20 calibration data (Hogg et al., 2020), and rbacon v.2.5.8 software package (Blaauw and Christen, 2011, 2020) was used to generate the age-depth models for each midden, employing in each case calculated mean accumulation rate of 100 yr/mm (Fig. 3).

Stable carbon and nitrogen isotopes

Following the previous works of Chase et al. (2012, 2019), the stable carbon and nitrogen isotope composition of 271 hyraceum samples (~2 mg) was determined at the School of Geography, Geology and the Environment, University of Leicester, with contiguous/overlapping samples obtained from two offset tracks using a 1-mm drill. Isotope ratios were measured on a Sercon 20-20 continuous flow isotope ratio mass spectrometer. For the stable isotope analyses, the standard deviation derived from replicate analyses of homogeneous reference material (Casein protein CatNo.B2155 Batch no. 114859 Elemental Microanalysis Ltd UK) was better than 0.2‰ for both carbon and nitrogen. Carbon isotope results are expressed relative to Vienna PDB, and nitrogen isotope results are expressed relative to atmospheric nitrogen (Fig. 5).

Pollen and microcharcoal

Following the protocol of Lim et al. (2016), pollen samples were prepared with standard physical (600-μm sieving and decanting) and chemical (HCl, KOH, HF, and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets (Batch 1031, containing ~20,848 spores/tablet) were added to the weighed sample to estimate pollen concentrations (Stockmarr, 1971). A minimum pollen sum of 400 grains was counted at a magnification of ×400 under a light microscope, and identified using (1) the literature (van Zinderen Bakker, 1953, 1956; van Zinderen Bakker and Coetzee, 1959; Scott, 1982); (2) the photographic and slide reference collections of the University of the Free State, University of Cape Town, and University of Montpellier, and (3) the atlas of southern African pollen types and their climatic affinities (Chevalier et al., 2021).

Microcharcoal particles were identified as black, completely opaque, angular fragments that occurred in the pollen slides (Clark, 1988). Only charcoal particles >75 μm^2 (or longer than 10 μm) were counted under a light microscope at ×400 magnification (Patterson et al., 1987; Mooney and Tinner, 2011). A

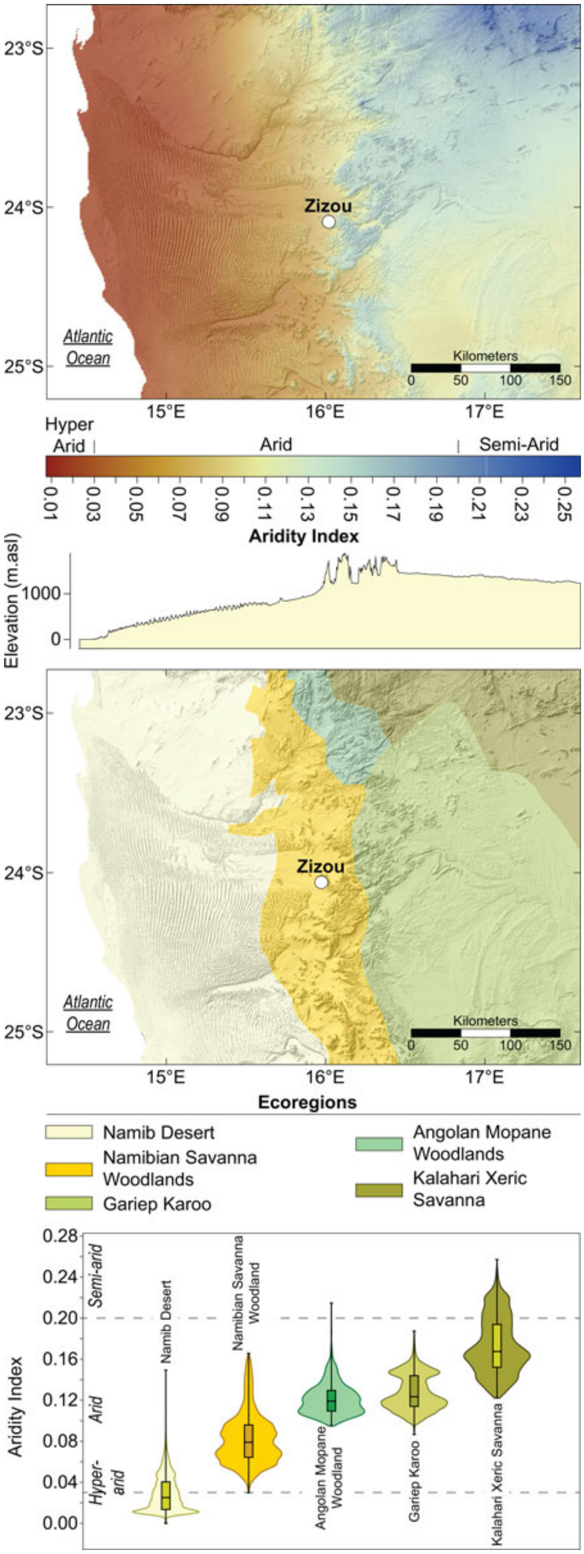

Figure 2. Maps of study region showing Aridity Index gradients (data from Trabucco and Zomer, 2019), an elevation transect across the map at the latitude of the Zizou hyrax midden site, the distribution of ecoregions (from Dinerstein et al., 2017), and the association of each vegetation type in the region with aridity.

minimum count of 200 items (given by the sum of charcoal particles and exotic marker grains) was used. Charcoal particles that exceed the mesh-width size of 600 µm are missing from the microscopic charcoal record and particles of less than ∼10 µm were not counted in order to ensure correct identification (Mooney and Tinner, 2011). Accordingly, the charcoal signal is related primarily to the regional fire signal, specifically with local fires (large particles) and remote, extra-regional fires (<10 µm particles) being excluded. The TILIA program was used to construct the pollen diagrams, and pollen zones were determined by CONISS cluster analysis (Grimm, 2011).

In comparing the stable-isotope and pollen data from middens, differences in sample sizes should be considered since the stable isotope record is based on 1-mm overlapping samples, while pollen samples from the Zizou middens, limited by the brittleness and density of the hyraceum and the larger sample sizes required for pollen analysis, vary in width from 3.15–12.54 mm.

RESULTS

Chronology

The radiocarbon and age-depth modeling results suggest continuous midden accumulation despite changes in accumulation rates. Midden structure and sampling constraints have provided a stable isotope record extending from 2500–37,100 cal yr BP and pollen and microcharcoal records extending from 6000–39,000 cal yr BP (average age of microfossil samples, which measure 6 ± 2 mm in thickness). Notable in the ZIZ-1-1 midden, which extends into the Holocene, is the substantial decrease in accumulation rate, which renders the Holocene record from the middens of significantly lower resolution (two samples comprising 8100 years of accumulated hyraceum) (Fig. 3).

Stable isotopes

The δ^{13}C and δ^{15}N records from the ZIZ-1-1 and ZIZ-1-3b middens have each been integrated into single records based on sample age. The δ^{13}C values of the Zizou middens vary from −18.6 to −24.3‰ (Fig. 5), with the highest values occurring during the Holocene, while the last glacial period is generally characterised by lower values. The δ^{15}N values range from 7.2–13.6‰ (Fig. 5) with Holocene and glacial periods being characterised by generally higher (mean 12.1‰) and lower (mean 10.9‰ values) respectively. The δ^{13}C and δ^{15}N records exhibit a degree of covariance at centennial–millennial timescales, with higher δ^{13}C values occurring, broadly, when δ^{15}N values are elevated. The lowest δ^{13}C and δ^{15}N values occur around 30,000 cal yr BP and at the end of the Last Glacial Maximum (LGM)/earliest glacial-interglacial transition, ca. 16,000–18,000 cal yr BP, with relatively higher values during the LGM (especially 20,000–23,000 cal yr BP) and most notably during the Holocene after 7000 cal yr BP.

Pollen and microcharcoal

As with the stable isotope records, the pollen and microcharcoal records from the ZIZ-1-1 and ZIZ-1-3b middens were integrated into single records based on sample age. Fifty pollen taxa were identified, which then were clustered into four statistically significant pollen assemblage zones (ZIZ 1–ZIZ 4) spanning much of the last 39,000 years (Fig. 4). Poaceae, Asteraceae, Capparaceae, and *Zygophyllum* are the most common pollen types, with much greater pollen diversity in the Pleistocene. The Holocene pollen spectra are dominated by grass (Poaceae) pollen. This Pleistocene–Holocene dichotomy is less evident in the

Table 1. Radiocarbon ages and calibration information for the Zizou-1-1 and Zizou-1-3b rock hyrax middens.

Sample	Depth range (mm)	^{14}C age yr BP	1σ error	calibration data	95.4% (2σ) lower cal yr range BP	95.4% (2σ) upper cal yr range BP	relative area under distribution	median probability (cal yr BP)
Zizou-1-1 midden section								
UBA-24433	3.7288–7.3729	3099	21	SHCal20	3174	3197	5.8%	3275
					3205	3360	94.2%	
UBA-31653	12.0339–15.3390	6985	36	SHCal20	7682	7862	94.9%	7775
					7900	7920	5.1%	
UBA-31654	20.1694–23.0508	13930	65	SHCal20	16630	17059	100.0%	16881
UBA-31655	27.9661–31.3559	14167	59	SHCal20	17043	17364	100.0%	17198
UBA-24434	36.6949–40.6779	14626	50	SHCal20	17529	18116	100.0%	17873
UBA-24435	64.8305–68.2203	16081	53	SHCal20	19184	19522	100.0%	19374
UBA-24436	89.6610–93.0508	17059	58	SHCal20	20424	20784	100.0%	20561
UBA-31656	106.7797–109.8305	17679	81	SHCal20	21008	21719	100.0%	21317
UBA-24437	121.7797–125.3390	18670	82	SHCal20	22374	22868	100.0%	22543
UBA-31657	138.3898–141.6102	19876	102	SHCal20	23458	23500	1.5%	23870
					23730	24190	98.5%	
UBA-24438	153.7288–157.0339	20942	104	SHCal20	24967	25590	100.0%	25208
UBA-24439	174.6610–178.1356	23594	135	SHCal20	27393	27903	100.0%	27721
UBA-24440	189.2373–192.7119	29929	287	SHCal20	33793	34923	99.4%	34380
					34993	35038	0.6%	
UBA-24441	214.2373–217.7119	33763	447	SHCal20	37240	39667	100.0%	38571
Zizou-1-3b midden section								
Pta-9680	0–6.6239	15030	341	SHCal20	17383	18917	100.0%	18268
UBA-24442	10.5013–11.8746	17985	78	SHCal20	21461	22061	100.0%	21855
UBA-9433	12.5208–14.78260	19230	70	SHCal20	22937	23317	99.4%	23086
					23639	23653	0.6%	
UBA-24444	26.3340–27.8688	22034	118	SHCal20	25942	26449	100.0%	26202
UBA-9208	31.1000–33.7657	22062	77	SHCal20	25983	26426	100.0%	26218
UBA-24445	48.8714–50.3255	24777	155	SHCal20	28706	29210	100.0%	28972
UBA-9209	58.3226–61.3922	25073	99	SHCal20	29050	29687	100.0%	29232
UBA-24446	77.0634–78.7598	29339	263	SHCal20	33196	34365	100.0%	33849
UBA-24447	99.6816–101.2164	30173	259	SHCal20	34186	35181	100.0%	34573
UBA-24448	127.0657–128.8429	32063	386	SHCal20	35499	37153	100.0%	36383
UBA-9211	136.6785–140.0712	32358	159	SHCal20	36274	36982	100.0%	36623
UBA-24449	152.6728–155.9039	33703	570	SHCal20	36935	39844	100.0%	38464
Pta-9686	154.8538–160.2660	34250	1600	SHCal20	35811	41895	100.0%	38908

microcharcoal record, but charcoal concentrations are highest in Pleistocene zones 1 and 3.

The lowermost pollen Zone (Zone 1; ca. 39,000 to ca. 35,800 cal yr BP) is characterised by early peaks in *Searsia*-type and Moraceae pollen among the arboreal taxa but is primarily defined by elevated levels of Capparaceae and *Zygophyllum* pollen (Fig. 4). Asteraceae pollen is relatively rare (average 10%) and Poaceae pollen is at its lowest levels in the sequence (average 31%).

Pollen Zone 2 (ca. 35,800 to ca. 23,900 cal yr BP) is defined by a strong increase in Asteraceae pollen (average 22%) at the expense of arboreal taxa. Poaceae pollen increases slightly (average 36%) but fluctuates around this mean value. Microcharcoal concentrations decrease slightly in Zone 2, from averages of 913 to 704 fragments/gram.

Subsequently, Pollen Zone 3 (ca. 23,900 to ca. 18,000 cal yr BP) sees a strong increase in microcharcoal, while Asteraceae pollen, particularly *Felicia*, declines. *Zygophyllum* pollen also declines in this zone, while Capparaceae again becomes a dominant element in the pollen assemblage (average 15%). Poaceae pollen increases again (average 42%) and stabilises around this mean.

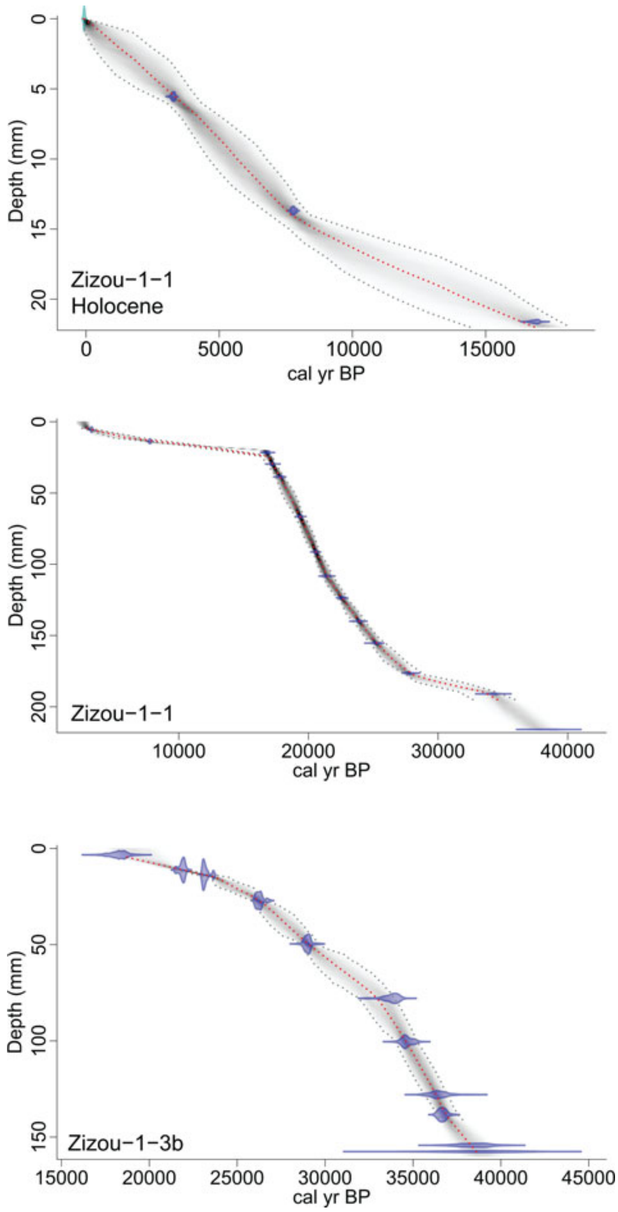

Figure 3. Distribution in time and depth of ^{14}C ages for the Zizou rock hyrax middens with age-depth model (grey), overlying the calibrated distributions of the individual dates calculated using Bacon v2.5.8 (Blaauw and Christen, 2011). Red dotted lines indicate the 'best' model based on the mean age. The Holocene section of the ZIZ-1-1 age model was calculated in isolation (upper panel) to better constrain the marked post-Pleistocene change in accumulation rate.

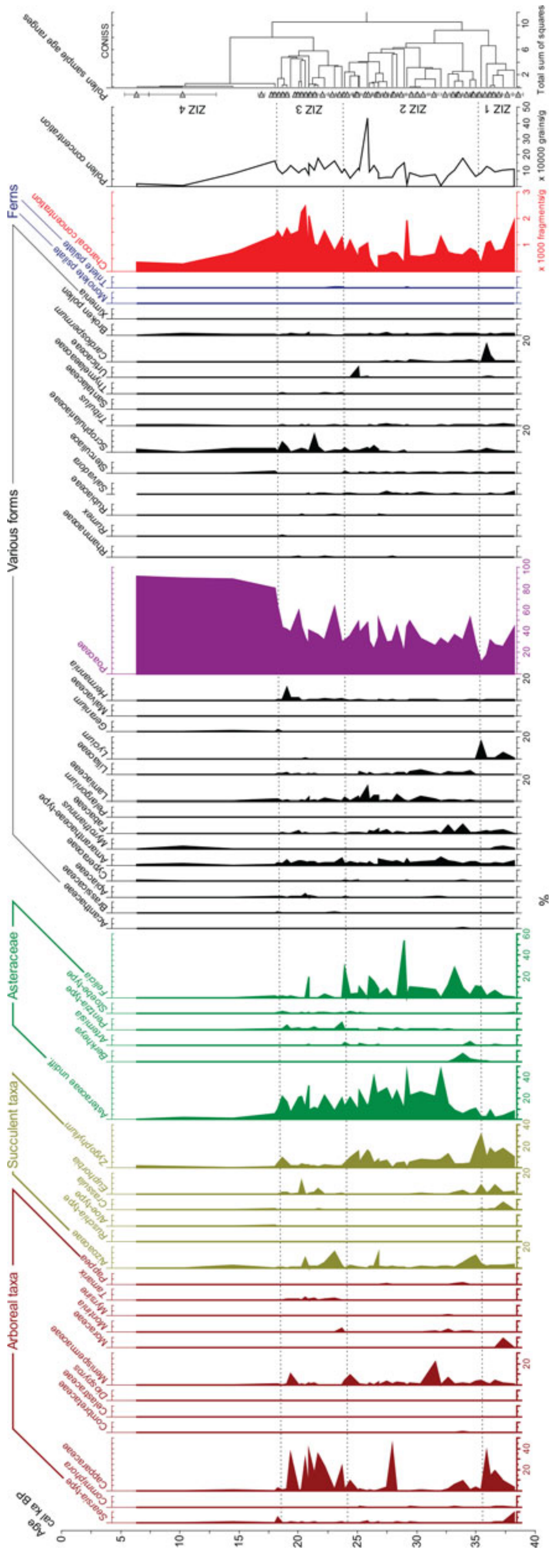

Figure 4. Diagram of pollen and microcharcoal from the Zizou rock hyrax middens, including taxa > 2% of composition. Mean ages for samples, including minimum and maximum depths, are provided.

Pollen Zone 4 (ca. 18,000 to ca. 5300 cal yr BP) reflects a fundamentally different vegetation that the Pleistocene assemblages. Poaceae pollen is totally dominant, representing 92% of the pollen recovered, with only very low percentages of drought-resistant taxa such as Aizoaceae, Amaranthaceae-type, and *Myrothamnus* comprising the other apparent elements. Asteraceae and arboreal pollen are found in trace amounts (<2%).

DISCUSSION

Combining stable carbon and nitrogen data with pollen and microcharcoal data from the same archives provides the opportunity to evaluate vegetation and fire dynamics within the context of an independent climate record derived from midden stable isotope content. As described by Chase et al. (2012, 2019), rock hyrax δ^{15}N records are interpreted as a proxy for water availability,

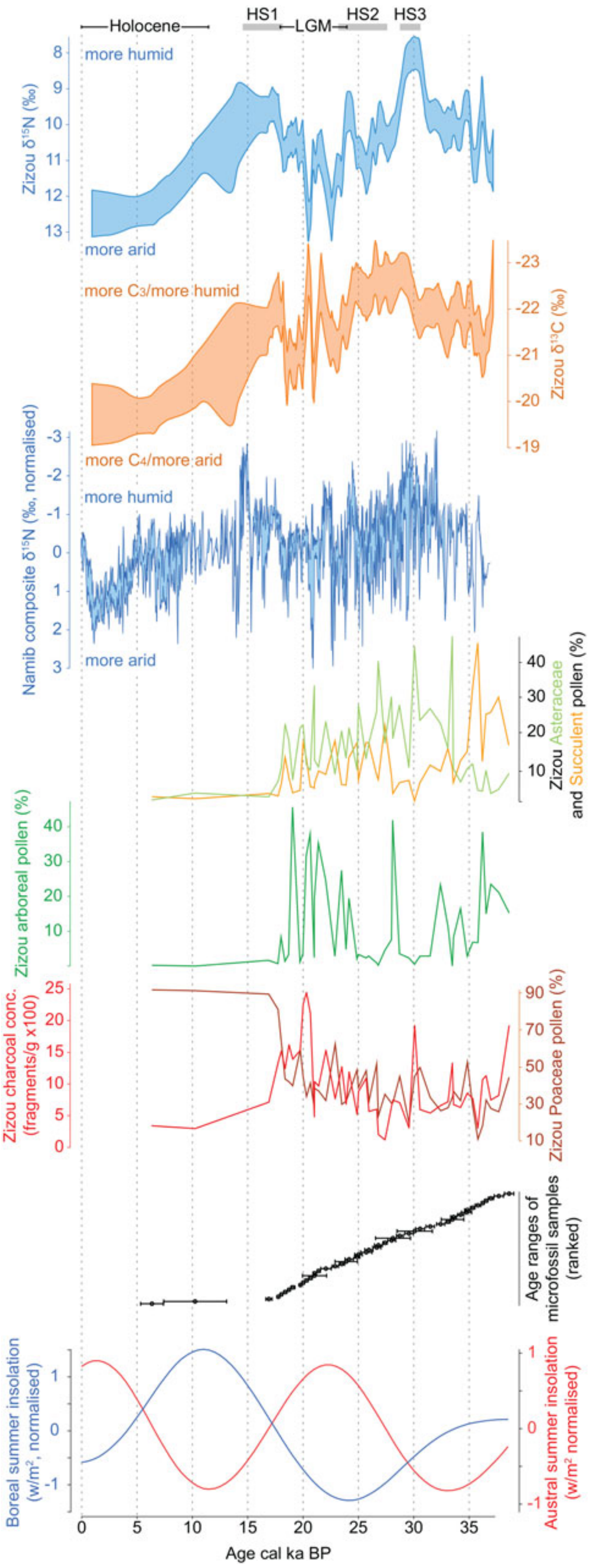

Figure 5. δ^{15}N, δ^{13}C, microcharcoal concentration, and select pollen data from the Zizou rock hyrax middens illustrated along with the Namib composite δ^{15}N record from Chase et al., 2019, and high latitude boreal and low latitude austral summer insolation (Laskar et al., 2004). Holocene, Last Glacial Maximum (LGM), and Heinrich stadial (HS1, HS2, HS3; grey bars) chronozones are indicated.

with higher δ^{15}N indicating drier conditions. As described in several previous studies, and supported by strong correlations with a diverse range of proxy climate records (Chase et al., 2009, 2015a, 2019), drier conditions induce more N flow to inorganic soil nitrogen pools that are subject to gaseous loss of ^{15}N-depleted products (Austin and Vitousek, 1998; Handley et al., 1999; Murphy and Bowman, 2009). Plants growing in the resulting ^{15}N-enriched soils exhibit higher δ^{15}N values (Craine et al., 2009; Hartman and Danin, 2010), a signal that is transmitted to the tissues (and excreta) of animals that consume them (Murphy and Bowman, 2006; Hartman, 2011; Carr et al., 2016).

Hyrax midden δ^{13}C reflects animal diet and, in turn, two aspects of the response of vegetation to climate change: (1) plant photosynthetic pathway of C_3 (approximately −34 to −24‰), C_4 (approximately −16 to −10‰), and CAM (typically within the range −20 to −10‰) plants (Smith and Epstein, 1971; Smith, 1972; Werger and Ellis, 1981; Rundel et al., 1999; Boom et al., 2014); and (2) changes in C_3 plant water-use efficiency (Farquhar and Richards, 1984; Ehleringer and Cooper, 1988; Farquhar et al., 1989a). Pollen data from Zizou indicate that C_3 vegetation in the form of trees and shrubs, was at times abundant during the Pleistocene. Today, C_4 grasses are the most dominant vegetation, and these data show this has likely been the case throughout much of the Holocene. Although it is possible that C_3 grasses occurred at the site during the Pleistocene, midden δ^{13}C values suggest that C_4 grasses were still present. CAM plants also have been abundant at the site (Fig. 5), and as generalist feeders (Hoeck, 1975; Fourie, 1990) these may have formed part of the hyraxes' diet, although perhaps not in significant quantities (Fourie, 1983; Carr et al., 2010, 2016).

The Zizou δ^{15}N record (Fig. 5) exhibits a pattern of climate variability that is similar to that observed across the Namib Desert region (Chase et al., 2019). Locally and regionally, these data indicate that the last glacial period was generally more humid than in the Late Holocene. Considering data from a 900 km north-south transect of hyrax middens from the Namib Desert, Chase et al. (2019) ascribed these changes in humidity to: (1) changes in high latitude boreal and low latitude austral summer insolation, which operate in concert to modify land-sea pressure gradients and the advection of cold air from the Benguela Upwelling System; and 2) mediation of the response to these orbital parameters by Heinrich events and related stadials, which warm the SE Atlantic and result in more humid conditions in the Namib region.

The observed changes in vegetation are largely consistent with changes in climate inferred from the midden δ^{15}N record. Considered within the context of regional ecosystems, wetter conditions may be expected to favor the development of vegetation types similar to either the Angolan Mopane Woodlands or the Gariep Karoo (Fig. 2). Notably, *Colophospermum* (Mopane) pollen was not recorded in the Zizou middens, while the proportions of pollen from Asteraceae and succulent taxa, the primary plant types of the Gariep and Nama-Karoo ecoregions (sensu Dinerstein et al., 2017), dominated the glacial-age pollen spectra (pollen zones 1–3) (Fig. 4). Pollen zone 1 (ca. 39,000 to ca. 32,900 cal yr BP), pre-dates the phase of peak humidity from 30,700–28,800 cal yr BP and has an assemblage suggesting a dry karroid vegetation dominated by succulents, with arboreal taxa also being well represented. As conditions became wetter, pollen zone 2 (ca. 32,900 to ca. 22,500 cal yr BP) exhibits a marked decline in succulent pollen, concurrent with peak humidity, and a clear increase in Asteraceae pollen. We interpret these changes as indicating a shift to more mesic Karoo vegetation, comprising grasses and asteraceous shrubs, with a reduced succulent component. Based on the climatic affinities of vegetation types in the region today (Fig. 2), humidity may have been 50–100% higher than the modern situation (e.g., aridity index values increasing from ~0.08 to 0.12–0.16).

A similar sequence of vegetation changes is observed in hyrax middens at Mirabib (Scott et al., 2018), on the now grass-dominated plains of the Namib Desert to the north of the Kuiseb River (Fig. 1). As at Zizou, MIS-2–MIS-3 pollen assemblages indicate much higher percentages of Asteraceae, Aizoaceae, and arboreal taxa (particularly *Searsia*, *Euclea*, and Capparaceae). These changes in vegetation observed in both the eastern and central Namib Desert, along with the stable isotope data presented here and elsewhere (Chase et al., 2009, 2019), modify the conclusion of Lancaster's (2002) review of Namib Desert paleoclimates, in which it was suggested that there was little evidence for significantly increased rainfall in the Namib Desert during the last glacial period. Our findings are not inconsistent with the view that conditions during this time remained "arid," since even if humidity at Zizou was doubled, it would still leave the region below the threshold for "semi-arid" conditions (aridity index values of 0.2–0.5; UNEP, 1997). A shift towards drier conditions after ca. 29,000 cal yr BP saw a decline in Asteraceae pollen and an increase in succulent pollen, indicating drier karroid vegetation (Fig. 5).

Pollen zone 3 (ca. 22,500 to ca. 17,700 cal yr BP) spans much of the LGM, which is marked by an abrupt decrease in humidity at Zizou at ca. 24,000 cal yr BP. Vegetation responded to this aridification with a decline in Asteraceae pollen and notable increase in the abundance of Poaceae and arboreal pollen. We interpret this as reflecting a lowering water table, and a change in relative competitive advantage associated with plant rooting depth. As conditions became drier, plant-available water in the near-surface sediments would have been reduced, limiting the occurrence of shallower rooting shrubs. However, arboreal taxa, with their deeper root systems, were able to persist through accessing groundwater resources, while grasses were able to thrive, as they do in the present day, by exploiting superficial soil moisture following occasional rainfall events.

Pollen zone 4 (ca. 17,700 to ca. 5300 cal yr BP) represents the most dramatic shift in the vegetation at Zizou. The regional Namib climate record (Chase et al., 2019) indicates that conditions became more humid after ca. 18,000 cal yr BP, culminating in a period of particularly wet conditions from ca. 15,100–14,400 cal yr BP. This is consistent with a slowing of Atlantic Meridional Overturning Circulation and progressive build-up of heat in the South Atlantic associated with Heinrich stadial 1 (Broecker, 1998; Stocker, 1998; Stocker and Johnsen, 2003; Chase et al., 2015b, 2019). The pollen record from Zizou is of insufficient temporal resolution to address this point but does suggest that after the LGM karroid vegetation and arboreal taxa were largely absent, and opportunistic grasses were the only plants able to persist under the warm, dry conditions that became established. This is inferred to reflect lowering of groundwater resources and dominance of growth forms that were capable of exploiting limited and sporadic rainfall. The better-resolved $\delta^{15}N$ values from the Zizou middens vary consistently with other regional records (Stute and Talma, 1998; Chase et al., 2009, 2010; Carr et al., 2010) that suggest a relatively mesic Early Holocene. The decreased midden accumulation rate and the pollen assemblages suggest a decrease in plant biomass and a decline in the population of the hyrax colony at the site during the Holocene. In the absence of any significantly better-resolved Holocene pollen sequences from the western slope of the Escarpment to facilitate comparison (Scott, 1996; Scott et al., 2022), the samples from Zizou presently can provide only an initial indication of vegetation at the site in the post-glacial period.

Throughout the record, changes in vegetation are reflected in the midden $\delta^{13}C$ values, which track variations in Poaceae (predominantly C_4) and to a lesser degree succulent (predominantly CAM) pollen percentages (Figs 4, 5), supporting the evidence that woody/arboreal (C_3) vegetation was dominant during a more humid last glacial period. Together with the observation that grass dominated the Holocene vegetation, our observations indicate a limited role of atmospheric CO_2 concentrations as a driver of glacial–interglacial vegetation dynamics in the Namib Desert. This differs from observations and interpretations in other contexts, where atmospheric CO_2 concentration is thought to play a central role in vegetation change (Bond and Midgley, 2000; Bragg et al., 2013; Prentice et al., 2017; Dupont et al., 2019) through the competitive advantage that C_3 woody plants have under augmented CO_2 conditions (Farquhar et al., 1989a, b; Bond and Midgley, 2000; Donohue et al., 2013). The evidence here suggests that Holocene high-CO_2 conditions were accompanied by the expansion of C_4 grasses and a virtual absence of woody C_3 taxa. This pattern of vegetation change has been observed elsewhere, for example in the southern Namib at Pella (Lim et al., 2016), and in other dryland regions such as the North American southwest (Holmgren et al., 2014). In summary, this evidence suggests that, while variation in CO_2 may influence C_3/C_4 vegetation dynamics, it is not necessarily the dominant driver in some contexts over glacial-interglacial timescales (see Nolan et al., 2018).

The microcharcoal content of the Zizou middens facilitates consideration of the region's fire history and ecology. Generally speaking, arid and semi-arid regions are considered to have fire regimes that are biomass limited (Marlon et al., 2013). As a result, charcoal concentrations may be expected to increase in these environments under wetter conditions, with denser vegetation providing more biomass, allowing fire to travel more effectively and thereby producing more charcoal. At Zizou, the relationships between climate, vegetation, and fire indicate that this nexus may be more complex. During the last glacial period, phases of relatively wet conditions are shown here to be associated with reduced microcharcoal concentrations (Fig. 5), an apparent anomaly that may be explained by the relative ability of different vegetation types to carry fire due to spacing of individual plants. For example, the relatively wide spacing between plants in karroid vegetation limits its potential to carry fire (Mucina et al., 2006; Hebbelmann et al., 2022). At Zizou, increased charcoal concentrations correspond to phases with higher percentages of grass pollen, implying either that grass expansion increased charcoal concentrations as a function of increased biomass, or that it may play an important role in carrying fire in such environments (Rahlao et al., 2009). Elevated percentages of arboreal pollen during these phases likely indicates the presence of an important fuel source, further augmenting charcoal concentrations in what may have been more extensive fires. In contrast, the terminal Pleistocene shift to sparse xeric grassland was accompanied by a decline in microcharcoal concentrations, conforming to predictions based on a marked decreased in biomass.

The Zizou pollen record provides further confirmation of the concerns raised by Scott et al. (2004) regarding the interpretation of pollen and other terrestrial material (e.g., microcharcoal and leaf waxes) recovered from marine cores in the Benguela Upwelling System. For example, whereas abundant Restionaceae pollen is evident in regional marine cores during MIS 2–3, including evidence used to infer significant expansions of the Fynbos Biome and winter rainfall zone (Shi et al., 2000, 2001; Urrego et al., 2015), no similar evidence has been recovered from the Namib Desert (Scott et al., 2004, 2018; Lim et al., 2016; this paper).

Modeling studies of wind trajectories indicate the primary source area for terrestrial components in marine cores GeoB 1710 (Dupont and Wyputta, 2003), GeoB 1712, (Shi et al., 2001), MD96-2098 (Urrego et al., 2015), and MD08-3016 (Collins et al., 2014) lies directly to the east of the core sites (Dupont and Wyputta, 2003). This observation, combined with finding that aeolian transport trajectories deviated little during the LGM (Dupont and Wyputta, 2003), has been used to support the use of marine records as evidence of environmental change on adjacent continental regions (Dupont and Wyputta, 2003; Urrego et al., 2015). However, there are no terrestrial records from this putative source region that support this interpretation (Scott et al., 2004, 2018; Lim et al., 2016; this paper). Records of terrestrial material preserved in marine sediments from this region, for example pollen (Urrego et al., 2015), leaf waxes (Collins et al., 2014), or charcoal (Daniau et al., 2013), require further confirmation of their possible sources. Without such information, reliable reconstructions of the adjacent terrestrial environments are questionable. Possible alternative hypotheses to explain the anomaly between marine and terrestrial records, such as changes in source area driven by demonstrated changes in wind strength (Chase et al., 2019), warrant further consideration.

CONCLUSIONS

- The stable carbon and nitrogen isotope, pollen, and microcharcoal data from the Zizou rock hyrax middens provide evidence for significant differences between MIS 2–3 and Holocene climates and vegetation types in the central Namib Desert.
- While Pleistocene conditions were likely still arid to semi-arid, they were significantly more humid than in the later Holocene.
- During MIS 2–3, shrubby karroid vegetation developed under the most humid conditions, while deeper-rooting arboreal taxa were relatively more abundant under intermediate conditions, in a response to lowering water table. The modern xeric grass-dominant vegetation, an opportunistic vegetation that is capable of exploiting sporadic rains, was established after the last glacial period.
- The Zizou microcharcoal record is most strongly correlated with percentages of grass and arboreal pollen, rather than with humidity. The karroid vegetation that characterises the most humid periods is not conducive to extensive fires because inter-plant spacing does not carry fire well. Under drier conditions, a better-developed grass component carries fire more effectively and the persistence of a significant arboreal component provides fuel, raising charcoal concentrations. This fuel source apparently was absent during the period reflected in our Holocene samples, and charcoal concentrations declined.
- Evolution of the vegetation composition at Zizou does not indicate that changes in atmospheric CO_2 played a dominant role in determining plant functional type. The dominance of grasses (primarily C_4) during the Holocene and shrubs and arboreal (C_3) taxa during the Pleistocene indicates that climate is the primary driver of vegetation composition.
- As at other terrestrial sites from the Namib Desert, no elements of the Cape flora (e.g., Restionaceae) were found in the Zizou pollen assemblages. These results differ markedly from pollen records obtained from marine sediment cores, requiring a fundamental reconsideration of interpretations of environmental change in the region based on marine records.

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