


Research Article

Vegetation dynamics in Dhofar, Oman, from the Late Holocene to present inferred from rock hyrax middens

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Abstract

Arid regions are especially vulnerable to climate change and land use. More than one-third of Earth's population relies on these ecosystems. Modern observations lack the temporal depth to determine vegetation responses to climate and human activity, but paleoecological and archaeological records can be used to investigate these relationships. Decreasing rainfall across the Late Holocene provides a case study for vegetation response to changing hydroclimate. Rock hyrax (*Procapra capensis*) middens preserve paleoenvironmental indicators in arid environments where traditional archives are unavailable. Pollen from modern middens collected in Dhofar, Oman, demonstrates the reliability of this archive. Pollen, stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and microcharcoal data from fossil middens reveal changes in vegetation, relative moisture, and fire from 4000 cal yr BP to the present. Trees limited to moister areas (e.g., *Terminalia*) today existed farther inland at ~3100 cal yr BP. After ~2900 cal yr BP, taxa with more xeric affiliations (e.g., *Senegalia*) had increased. Coprophilous fungal spores (*Sporormiella*) and grazing indicator pollen revealed an amplified signal of domesticated grazing at ~1000 cal yr BP. This indicates that trees associated with semiarid environments were maintained in the interior desert during ~3000–4000 yr of decreasing rainfall and that impacts of human activity intensified after the transition to a drier environment.

Keywords: Paleocology, Paleoclimate, Quaternary, Pastoralism, Dryland ecosystems, Pollen, Stable isotopes

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INTRODUCTION

Humans are unprecedented agents of landscape change. Anthropogenic climate change continues to accelerate, and other activities such as urban expansion and animal grazing will likely cause drastic changes in ecosystems (Maestre et al., 2016; Dahinden et al., 2017; IPCC, 2022). Dryland ecosystems comprise 41% of Earth's terrestrial surface, and 38% of the human population relies on them (Maestre et al., 2016). These ecosystems are especially sensitive to ecological change—small decreases in precipitation or increases in domesticated animal grazing can lead to a reduction in vegetation cover, with resultant impacts to water and food security (Asner et al., 2004; Maestre et al., 2016; Ball and Tzanopoulos, 2020). Climate models predict globally increasing temperatures that have the net effect of decreasing relative moisture in arid places (Stavi et al., 2021). However, recent data are too brief to assess natural variability and long-term ecosystem dynamics (Dietl et al., 2015). There is a need for longer-term

records to investigate how changes in climate, particularly water availability, affect vegetation.

Southern Arabia is mainly hyperarid, but also hosts a biodiverse flora with a high level of endemism (Miller and Morris, 1988; Ghazanfar, 1998). The Dhofar Governorate of Oman is home to a unique cloud forest, with trees that intercept fog moisture from the seasonal Indian Ocean monsoon (*khareef*) (Hildebrandt et al., 2007). These conditions make the vegetation of Dhofar particularly sensitive to changes in temperature and precipitation: rainfall is correlated with vegetation cover, which is shown to be declining in the most arid locations in Dhofar (Ramadan et al., 2021). Recent studies have additionally highlighted the threat of overgrazing of native vegetation by domesticated animals due to rapid economic growth over the last few decades, which has led to increased stocking rates of cattle and camels in Dhofar (Ghazanfar, 1998; Galletti et al., 2016; Ball and Tzanopoulos, 2020). The preferential browsing of young shoots compared with adult trees prevents the regeneration of woody taxa, and there has been up to 10% loss of forest land cover in some areas of the cloud forest due to grazing alone (Galletti et al., 2016; Ball and Tzanopoulos, 2020). These changes have only been quantified over the last few decades as stocking rates reached current high levels (Galletti et al., 2016; Ball and

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Tzanopoulos, 2020). It is imperative to understand how both changes in climate and human activity dynamically influence vegetation, as human land use may amplify the effects of projected climate conditions.

One period that provides a case study for determining the vegetation response to increasing aridity is the end of the Holocene Humid Period. The termination of the Holocene Humid Period (~5.5 ka) led to decreased rainfall in southern Arabia and increasingly arid conditions (Morrill et al., 2003; Renssen et al., 2003; Fleitmann et al., 2007, 2011; Lézine et al., 2014; Ivory et al., 2021). Although this period has been well studied in places like North Africa, there are relatively few paleoclimate records from southern Arabia (Burns et al., 1998, 2001; Fleitmann et al., 2004, 2007, 2011; Kröpelin et al., 2008). However, speleothem $\delta^{18}\text{O}$ records preserve changes in precipitation during the last deglaciation from multiple locations in southern Arabia. These records suggest a gradual decline in precipitation beginning at ~8–7 ka (Fleitmann et al., 2007; Lézine et al., 2014). While it is likely that conditions were already semiarid in this region in the Early Holocene, these paleoclimate records indicate conditions became increasingly dry across the Holocene, such that perennial lakes disappeared and surface runoff became more limited (Hoorn and Cremaschi, 2004; Fleitmann et al., 2007; Lézine et al., 2014). The response of vegetation communities to these changes remains somewhat unclear.

To understand how ecosystems responded to decreasing rainfall over the Middle to Late Holocene, several previous paleoecological studies have been conducted in southern Oman and nearby Yemen. Estuarine cores from Oman provide near-continuous records of changes in coastal vegetation in the Middle to Late Holocene that show an increase in more saline- and drought-tolerant taxa (e.g., *Amaranthaceae*). This supports aridification by ~1.7–1.5 ka based on palynological and sedimentological evidence (Lézine et al., 2002, 2017; Hoorn and Cremaschi, 2004). There is also support for more wet phases that punctuated the trend in increasing aridity at ~2700–2300 and ~1700–1500 cal yr BP, when there was increased runoff to the estuaries (Hoorn and Cremaschi, 2004). However, information away from the coasts is patchy in both space and time. In Yemen, paleolakes provide insight into the wetter climate at the last deglaciation into the Early Holocene, as no perennial lakes exist in this region today (Lézine et al., 1998, 2007). Pollen and sedimentological records from these lakes indicate that even during maximum humid conditions, there were seasonal periods of high evaporation that led to a persistence of a semiarid desert vegetation community in inland Yemen (Lézine et al., 2007). However, due to desiccation of most inland lakes by ~7 ka, evidence of vegetation change from sedimentary deposits in these areas after this time does not exist (Lézine et al., 2007). Pollen preserved in hyrax middens provides later records that suggest a semiarid woodland with tropical trees such as *Terminalia* at 5 ka at Wadi Sana, Yemen (Ivory et al., 2021). Little information exists about vegetation changes farther inland in Dhofar as aridification intensified from the mid-Holocene to the present.

Archaeological evidence suggests changes in settlement and mobility in Dhofar during the Holocene, lending some insight into changes in human land use over this time frame (Harrower et al., 2014; McCorrison et al., 2018; McCorrison and Harrower 2020). Nomadic pastoralism has been practiced in this region for at least 7000 yr and continues to be a culturally important lifeway (McCorrison et al., 2018). Archaeological evidence based on the construction of megalithic monuments in the

desert and the lack of permanent habitation sites indicates pastoral groups were highly mobile and grazed their animals far inland (Harrower et al., 2014; McCorrison et al., 2014, 2018). This was during an interval when paleoclimatic records suggest wetter than modern conditions (~7–5 ka) (Fleitmann et al., 2004, 2007). During a period of increased aridity in the Late Holocene (~2–1 ka), pastoralists built more permanent settlements closer to the coast (McCorrison et al., 2014; McCorrison and Harrower 2020). The ecological effects of ancient pastoralism and changes in settlement patterns are not well understood. Modern pastoral activity can have surprising impacts on vegetation in these arid regions that are not always degradational. For example, grazing and browsing can maintain grasslands and domesticate dung increases nutrient input to dry soils (Brierley et al., 2018). Assessing changes in vegetation in this region is important for understanding the persistence, and hopefully the continued sustainability, of pastoralism under changing climate conditions. Moreover, teasing apart climate- and human-driven mechanisms of vegetation change is important for making more accurate predictions about changes to semiarid pastoral landscapes and designing sustainability initiatives to mitigate them.

In this study, we present pollen and bulk stable isotope data from rock hyrax (*Procapra capensis*) middens collected in the Dhofar Governorate of Oman. We use thin (<5 cm) middens that represent individual, temporally averaged samples, with the oldest radiocarbon age at ~4000 cal yr BP. Rock hyrax middens serve as well-established paleoecological archives in arid ecosystems, preserving pollen, macrofossils, and isotopic information for thousands of years (Scott and Cooremans, 1992; Scott and Woodborne, 2007; Chase et al., 2012; Ivory et al., 2021). The records presented here provide paleoecological information after the onset of decreasing precipitation in this region at the end of the Holocene Humid Period to the present. While future conditions in Dhofar are likely to be drier than those seen in the last 4000 yr, this record provides a long-term view of vegetation response to climate change in this unique, biodiverse dryland ecosystem (Dahinden et al., 2017). This can help inform predictions for southern Arabia as well as semiarid drylands that are expected to experience aridification similar to that seen across the Holocene in Dhofar.

Modern setting

The physiography of southern Oman is strongly characterized by the steep south-facing escarpments of the Dhofar Mountains. These mountains are mainly composed of Tertiary limestone, with a karst net that forms caves and rock shelters (Miller and Morris, 1988; Cremaschi et al., 2015). A fault system crosscuts the north-dipping limestone strata, which is mainly oriented east-west (Zerboni et al., 2020). At the highest elevations, approximately 850 m above sea level, the landscape becomes a plateau inset by northward-draining wadi systems (Miller and Morris, 1988; Zerboni et al., 2020). The Tertiary carbonates are incised by these dry riverbeds, which are covered with large gravel alluvium (Al-Mashaikhi et al., 2012). A lack of soil in the desert inland from the coast creates a landscape of large, bare carbonate outcrops that form the wadi walls (Zerboni et al., 2020).

The Dhofar Governorate is predominantly arid. The coastal region receives approximately 120–150 mm of precipitation per year and has a mean annual temperature of 25.7°C based on data from the Salalah airport weather station (1970–1990) (Fleitmann et al., 2004, 2007; Cremaschi et al., 2015). However, hyperarid

conditions prevail farther inland in the Nejd Desert, which receives an average of 30 mm of precipitation per year based on observations from the Thumrait weather station (1980–2015) (Almazroui et al., 2012). These two weather stations are denoted on the map in Figure 1. Most of the precipitation in this region occurs during the northern summer (June–September) (Fleitmann et al., 2007), when the Indian monsoon brings dense fog to the coastal regions of Dhofar, increasing relative humidity to as much as 97% (Patzelt, 2015). This fog forms as moisture-laden air passes over the cool surface waters off the coast (Miller and Morris, 1988). As the fog moves inland, it becomes trapped against the slopes due to a temperature inversion, blanketing the escarpment with thick cloud cover that generally does not extend past the crest of the escarpment (Miller and Morris, 1988).

The modern vegetation can be categorized into four ecological zones from south to north (coastal plain, escarpment, plateau, and Nejd Desert), which encompass changes in elevation and climate conditions, as well as the dominant taxa (Miller and Morris, 1988). The coastal plain is a flat, low-elevation band that stretches from the coast to the foothills of the escarpment. The vegetation in this zone is extremely sparse due to overgrazing and other

human activities, but plants such as *Aerva javanica* and *Heliotropium* spp. can be found on rockier soils (Miller and Morris, 1988). The escarpment is home to the seasonal cloud forests composed of deciduous trees, notably *Terminalia dhofarica* and *Maytenus dhofarensis*, with an understory of grasses (Poaceae) and other herbs (*Merremia* spp., *Heliotropium* spp.) (Patzelt, 2015). These trees, particularly *T. dhofarica*, are reliant on moisture from the monsoon fog. *Terminalia dhofarica* intercepts moisture directly from the air during the khareef to increase net water availability locally (Hildebrandt et al., 2007; Friesen et al., 2018). The plateau is a grassland with isolated trees such as *Ficus vasta* (Miller and Morris, 1988; Buffington and McCorriston, 2019). On the distal reaches of the plateau beyond the monsoonal fog, *Boswellia sacra* (frankincense) is commonly found (Patzelt, 2015). The farthest inland is the Nejd Desert, which is the driest sector in the region (Almazroui et al., 2012). This zone is characterized by isolated trees (*Senegalia* spp., *Boscia*, *Maerua*, *Ficus salicifolia*) and sparse herbaceous cover (*Heliotropium* spp., *Cornulaca*) (Miller and Morris, 1988; Ghazanfar, 2004; Patzelt, 2015). Table 1 highlights the dominant taxa in each of these areas.



Figure 1. Map of Dhofar depicting the four ecological zones. The midden sampling locations are shown by the boxes. Inset shows the geopolitical boundaries of Oman on the Arabian Peninsula.

Table 1. The four ecological zones of Dhofar and their dominant vegetation taxa.

Ecological zone	Description	Dominant vegetation
Coastal plain	Low elevation, highly disturbed and sparsely vegetated	<i>Aerva javanica</i> , <i>Heliotropium</i> spp.
Escarpment	High elevation, mountainous, seasonal cloud forest	<i>Terminalia dhofarica</i> , <i>Maytenus dhofarensis</i> , Poaceae, <i>Merremia</i> spp., <i>Heliotropium</i> spp.
Plateau	High elevation, flat, grassland	Poaceae, <i>Ficus vasta</i> , <i>Boswellia sacra</i> , <i>Dracaena</i>
Nejd	Desert, isolated trees and sparse herbs	<i>Senegalia</i> spp., <i>Boscia</i> , <i>Maerua</i> , <i>Ficus salicifolia</i> , <i>Heliotropium</i> spp., <i>Cornulaca</i>

Hyrax middens as paleoenvironmental archives

Various types of animal middens have been successfully employed for paleoenvironmental analyses. These archives represent different spatial and temporal scales, dictated by the behavior of the animal and the manner in which they are deposited (Cole, 1990; Anderson and Van Devender, 1995; Scott et al., 2004; Chase et al., 2012). In the dry regions of western North America, packrat (*Neotoma*) midden studies have revealed changes in local flora within ~10–100 m of den sites through pollen and macrofossil studies and, more recently, ancient DNA (Cole, 1990; Anderson and Van Devender, 1995; Fisher et al., 2009; Moore et al., 2020). Packrats collect plant matter and other materials, creating “garbage piles” protecting the entrances of their dens (Cole, 1990). Through the defecation and urination of the packrats, this garbage pile will become an indurated mass, or midden (Cole, 1990; Anderson and Van Devender, 1995; Fisher et al., 2009). Analyses of modern packrat middens and local vegetation show high agreement, indicating that fossil middens are a reliable archive of past environments (Cole, 1990; Anderson and Van Devender, 1995; Fisher et al., 2009). These samples are processed through dissolution in water, then a sieving process that separates macrofossil and microfossil fractions (Van Devender et al., 1994; Moore et al., 2020). Each midden is dated and treated as one sample at an individual point in time (Van Devender et al., 1994; Anderson and Van Devender, 1995).

Rock hyrax middens have emerged as a powerful tool for similar paleoecological studies in the arid regions of Africa and Arabia (Scott and Woodborne, 2007; Chase et al., 2012; Ivory et al., 2021). Rock hyraxes are small mammals that resemble rodents but are in fact most closely related to elephants. They can eat a wide variety of plants and tolerate a large range of temperature and precipitation conditions (Sale, 1965; Rübsamen et al., 1982; Chase et al., 2012; Mohamed, 2019). Generally, middens are deposited in caves and rocky overhangs as compacted deposits of crystallized urine (hyraceum) and fecal pellets (Gil-Romera et al., 2010; Chase et al., 2012). Pollen and other paleoenvironmental indicators are brought into the caves on the feet or fur of hyraxes and blown in via eolian deposition, then trapped in the sticky hyraceum (Chase et al., 2012). Plant matter consumed by the hyraxes also passes through their digestive systems and is preserved in their dung (Scott et al., 2004; Scott and Woodborne, 2007; Gil-Romera et al., 2010; Chase et al., 2012). Stable carbon isotope analyses of fecal pellets and hyraceum reflect the input of C₃ and C₄ vegetation, and nitrogen isotope studies can reveal changes in relative moisture (Chase et al., 2012; Ivory et al., 2021). Middens can differ in thickness and the amount of hyraceum versus fecal pellets, and thus can have varying degrees of dietary bias and represent disparate temporal

scales (Scott and Cooremans, 1992; Scott et al., 2004; Gil-Romera et al., 2006; Scott and Woodborne, 2007; Chase et al., 2009, 2012).

In southern Africa, massive middens composed primarily of hyraceum have been discovered, providing paleoenvironmental insight for the late Pleistocene and Holocene (Chase et al., 2009, 2012; Carr et al., 2010). These types of middens can be subsampled for isotope and pollen analyses, much like a sediment core, and the data can be interpreted as a time series (Chase et al., 2012). However, thinner middens consisting of indurated dung material have also proved a useful archive of the same paleoecological indicators (Scott and Cooremans, 1992; Scott et al., 2004; Gil-Romera et al., 2006; Scott and Woodborne, 2007; Ivory et al., 2021). While these contain a higher dietary input from fecal material, analyses of modern dung middens from South Africa illustrate that their pollen spectra are negligibly different from pollen spectra of surface soils (Scott and Cooremans, 1992). Moreover, studies of hyrax diet and behavior from both Africa and Arabia demonstrate that hyraxes are generalists and have few dietary restrictions (Sale, 1965; Mohamed, 2019).

The methodology for processing these samples is also different. Hyraceum middens are typically radiometrically dated, drilled for isotopic analyses, then processed for pollen and other indicators through the midden’s growth axis (Carr et al., 2010; Chase et al., 2012). Processing of thin dung middens follows a protocol similar to the one described for packrat middens: they are first disaggregated in water, then sieved to obtain macrofossil and microfossil fractions (Van Devender et al., 1994; Scott and Woodborne, 2007; Ivory et al., 2021). Because of the differences in material and sampling, thin middens are interpreted as single, variably time-averaged samples. Hyraceum middens can provide long term (10³–10⁴ yr) paleoecological sequences with single data points averaged over ~10¹–10² yr, whereas paleoecological data from dung middens are averaged over the period of midden deposition and include more dietary information (Scott and Cooremans, 1992; Gil-Romera et al., 2006; Scott and Woodborne, 2007; Chase et al., 2012; Ivory et al., 2021).

In this study, we obtained thin (<5 cm) rock hyrax middens consisting of indurated dung pellets cemented with crystallized urine. To process these middens and conduct pollen analysis, we utilized the same approach that has been successful for both packrat middens and other fossil hyrax dung middens in South Africa (Van Devender et al., 1994; Scott and Woodborne, 2007; Ivory et al., 2021). The presence of fecal matter introduces a degree of dietary bias in these samples. However, we conducted a comparison of pollen abundances from modern middens with botanical information from Dhofar and determined that the signal recorded within the middens is a good representation of

local vegetation. To assess the period over which thin middens accumulate, Ivory et al. (2021) obtained multiple radiocarbon dates from the same midden, which resulted in ages that were not significantly different. This analysis was conducted on multiple middens. Based on this analysis from nearby Yemen on similar middens, we assume the middens from our study represent decades to ~100 yr of deposition. As such, we interpret each midden as one sample, and the data as an average of local vegetation over ~100 yr.

METHODS

Pollen analysis was conducted on 13 modern hyrax middens across a large geographic area and spans the four ecological zones (Table 2, Supplementary Material 1). These were determined to be modern through radiocarbon dating or if the samples were not compacted and included fresh dung, as was the case for all middens collected closer to the coast. In these regions, prevailing moist conditions during the monsoon season lead to the disintegration of middens; older middens are not typically preserved. Four samples were taken from the distal plateau (Wadi Ayun), two from a drainage system in the western Nejd (Wadi Ghadun), and three from the east Nejd (Wadi Dhahabun). Two samples were collected from the coastal plain close to the base of the escarpment. Two samples of fresh camel (*Camelus dromedarius*) dung were also collected on the escarpment, where no hyrax middens were found. These samples were then compared with published botanical literature from the Dhofar region as well as vegetation surveys (provided in Supplementary Material 2) to assess the representativity of flora within this archive (Miller and Morris, 1988; Ghazanfar, 1998, 1999, 2004; Raffaelli et al., 2003; Hildebrandt et al., 2007; Patzelt, 2015). The modern samples were also compared with four submodern middens from the east Nejd (110–160 cal yr BP) to assess historic changes in vegetation.

Additionally, pollen analysis was completed on fossil middens in the Nejd Desert to establish a record of vegetation change over the last 4000 yr. To create the fossil pollen record, 26 rock hyrax middens were collected over three field seasons from February 2017 through October 2018 (Table 3). Twenty-two fossil middens and one modern midden were collected from the east Nejd, while three additional modern midden samples from the distal plateau farther to the west were used to compare a wide geographic range of modern vegetation with the recorded fossil vegetation (Fig. 1). Surveying for middens consists of examining small natural caves in cliffs and looking for fecal pellets in and around these sheltered locations. The presence of these pellets helped identify caves that could contain middens. Once discovered, these middens were carefully extracted from the caves using a chisel and hammer, keeping them as intact as possible. The samples were then wrapped in plastic to avoid contamination before shipment. A photograph of a representative midden as well as a midden in situ are shown in Figure 2.

Palynological analysis

This study involves a sampling protocol for thin (<5 cm) middens. A minimum of 100 g of material, representing the entire vertical thickness of the midden, was disaggregated in 1 L of deionized water. This solution was sieved at 500 µm to remove fecal pellets and separate macrobotanicals. The <500 µm fraction was then used for pollen and microcharcoal analyses. A standard volume (45 mL) from each disaggregated sample was processed using the extraction method of Faegri and Iversen (1989). Hydrochloric acid was used to remove carbonates, and hydrofluoric acid was used to remove silicates. Acetolysis removed most organic material from the samples. The samples were sieved at 180 and 10 µm to remove large particulates and clays, respectively. *Lycopodium* spores were added to each sample to calculate pollen

Table 2. Modern midden sampling locations, accelerator mass spectrometry (AMS) radiocarbon dates, calibrated ages, and bulk stable isotope information.

Sample ID	Ecological zone	Material	Latitude (N)	Longitude (E)	Age (cal yr BP)	δ ¹³ C (‰)	δ ¹⁵ N (‰)
WP19	Coastal plain	Hyrax midden	17°12.804'	55°03.446'	Modern (no date)	-27.54	7.14
WP18	Coastal plain	Hyrax midden	17°12.854'	55°03.761'	Modern (no date)	-27.84	6.03
C1 Camel	Escarpment	Camel pellet	17°4.655	54°27.068'	Modern (no date)	-29.81	6.35
C2 Camel	Escarpment	Camel pellet	17°4.655	54°27.068'	Modern (no date)	-30.07	8.01
ASO6	Distal plateau	Hyrax midden	17°14.612'	53°53.365'	Modern (no date)	-28.31	5.56
ASO3	Distal plateau	Hyrax midden	17°14.618'	53°53.380'	Modern (no date)	-27.05	4
ASO4	Distal plateau	Hyrax midden	17°14.618'	53°53.380'	Modern (no date)	-27.53	5.79
ASO7	Distal plateau	Hyrax midden	17°14.618'	53°53.380'	Modern (no date)	-26.24	4.01
WP79-2c	Nejd—west	Hyrax midden	17°20.987'	53°42.938'	0	-28.2	7.3
WP83-1	Nejd—west	Hyrax midden	17°24.138'	53°41.690'	0	-28.14	5.95
WP61-1	Nejd—east	Hyrax midden	17°24.865'	54°20.822'	0	-27.18	7.38
WP61-2	Nejd—east	Hyrax midden	17°24.865'	54°20.822'	0	-27.83	9.07
WP48-1B	Nejd—east	Hyrax midden	17°25.431'	54°29.385'	0	-28.12	7.98
ASO5	Nejd—east	Hyrax midden	17°23.123'	54°29.767'	110	-25.65	4.37
WP57-4	Nejd—east	Hyrax midden	17°23.210'	54°20.848'	130	-25.8	22.8
ASO1	Nejd—east	Hyrax midden	17°23.110'	54°29.755'	140	-25.96	6.99
WP45-2	Nejd—east	Hyrax midden	17°25.454'	54°29.296'	160	-27.37	4.69

Table 3. Fossil midden sampling locations, accelerator mass spectrometry (AMS) radiocarbon dates, calibrated ages, and bulk stable isotope information.

Sample ID	Latitude (N)	Longitude (E)	UGAMS no. ^a	Material dated	¹⁴ C date (yr BP)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	2 σ range (yr BP)	Median age (cal yr BP)	
WP135-1	17°14.618'	53°53.380'	42490	Fecal pellets	n/a	-27.53	5.79	n/a	n/a	n/a (modern)
WP135-2	17°14.618'	53°53.380'	42491	Fecal pellets	n/a	-27.05	4	n/a	n/a	n/a (modern)
P135-3	17°14.618'	53°53.380'	42492	Fecal pellets	n/a	-26.24	4.01	n/a	n/a	n/a (modern)
WP48-1B	17°25.431'	54°29.385'	32591	Fecal pellets	modern	-28.12	7.98	n/a	n/a	0
WP144-4	17°24.000'	54°30.580'	44358	Fecal pellets	130 ± 20	-24.91	6.58	268	11	107
WP108-1B	17°23.123'	54°29.767'	37185	Fecal pellets	110 ± 20	-25.65	4.37	261	27	109
WP107-2B	17°23.110'	54°29.755'	37187	Fecal pellets	140 ± 20	-25.96	6.99	277	7	114
WP142-B	17°24.007'	54°30.376'	44357	Fecal pellets	100 ± 20	-26.03	8.01	257	32	115
WP45-2	17°25.454'	54°29.296'	32588	Fecal pellets	160 ± 25	-27.37	4.69	283	0	177
WP153-2	17°23.843'	54°30.563'	44360	Fecal pellets	340 ± 20	-26.98	7.51	472	315	384
WP155-2B	17°24.513'	54°30.555'	42501	Fecal pellets	510 ± 20	-26.3	7.45	545	511	529
WP38-3a	17°25.684'	54°28.774'	29897	Fecal pellets	710 ± 25	-21.9	15.4	682	570	665
WP146	17°23.523'	54°31.010'	42500	Fecal pellets	800 ± 20	-24.86	5.88	730	680	706
WP50-2	17°25.694'	54°28.851'	29898	Hyraceum	970 ± 25	-24	20.9	927	793	853
WP155-2C	17°24.513'	54°30.555'	44353	Fecal pellets	1540 ± 20	-25.49	8.36	1514	1356	1403
WP38-2	17°25.684'	54°28.774'	29900	Fecal pellets	1570 ± 25	-23.7	21.3	1521	1390	1461
WP147-1	17°23.331'	54°30.724'	44355	Fecal pellets	1580 ± 20	-26.32	7.41	1522	1404	1466
WP50-3a	17°25.694'	54°28.851'	29896	Hyraceum	1640 ± 25	-24.3	30	1585	1412	1522
WP138	17°23.150'	54°29.825'	42505	Fecal pellets	1680 ± 20	-26.24	10.33	1688	1532	1566
WP151	17°23.305'	54°30.724'	42507	Fecal pellets	1690 ± 20	-26.2	7.4	1689	1535	1574
WP145-4	17°23.733'	54°30.996'	42506	Fecal pellets	1740 ± 20	-25.69	6	1704	1549	1638
WP111-2E	17°23.142'	54°29.869'	44361	Fecal pellets	1760 ± 20	-26.94	9.65	1711	1590	1651
WP155-D	17°24.513'	54°30.555'	44359	Fecal pellets	2820 ± 20	-26.87	9.29	2994	2860	2920
WP103-2C	17°25.338'	54°29.861'	37186	Fecal pellets	2940 ± 20	-24.13	8.22	3167	3004	3103
WP149-2	17°23.298'	54°30.711'	42503	Fecal pellets	3030 ± 20	-25.82	9.68	3336	3167	3233
WP155-F	17°24.513'	54°30.555'	44362	Fecal pellets	3690 ± 20	-25.85	10.85	4140	3932	4038

^aUGAMS, University of Georgia Center for Applied Isotope Studies for Accelerator Mass Spectrometry.



Figure 2. Pictures of representative rock hyrax middens.

concentrations. The pollen residue was suspended in glycerin and mounted on glass slides for microscopy, and an average of 354 pollen grains (including fern spores) per sample were counted. For four samples, pollen counts fell below 300 but were still >250 grains. For two samples, WP107-2B and WP149-2, 44 and 186 grains were counted, respectively, due to issues of preservation. Microcharcoal pieces that were >10 μm were also counted.

Pollen identifications were made using the African Pollen Database (APD; Lézine et al., 2021), the pollen atlas of Bonefille and Riollot (1980), and a collection of reference slides from the Penn State Paleocology Lab. Pollen taxa were categorized by plant habit, with the most predominant types being arboreal, herbs, and indeterminate, with indeterminate indicating there are multiple plant habits represented by that taxon. Taxonomic nomenclature and plant habit follow the APD (Vincens et al., 2007; Lézine et al., 2021). Pollen morphotypes for the genus *Senegalia* were differentiated based on their exine texture. Smooth exines were classified as *Senegalia* I, gemmate as *Senegalia* II, and reticulate as *Senegalia* III (Guinet and Vassal, 1978).

Certain groups of taxa were defined based on their affiliations to wetter or drier areas in Dhofar, as well as whether they are considered grazing indicators. Grazing indicators in this setting are plant taxa that are avoided by domesticated animals, and therefore tend to be in higher abundances relative to other plants in highly grazed areas. Of these taxa, *Dodonaea viscosa*, *Cassia*-type, *Heliotropium*, and *Cornulaca/Aerva*-type are observed in the pollen record (Dereje and Udén, 2005; Brinkmann et al., 2009). Mesic-affiliated taxa are arboreal pollen taxa that are generally found in moister areas of Dhofar, such as the escarpment and plateau; these are identified as *T. dhofarica*, *Boscia/Cadaba*, *Maytenus*, *Ficus*, and *B. sacra* (Miller and Morris, 1988; Patzelt, 2015). Nejd associations are defined here as the most common pollen taxa found today in the dry Nejd: *Amaranthaceae*, *Senegalia* I, *Commiphora*, *Salvadora persica*, and *Senegalia* III (Miller and Morris, 1988; Patzelt, 2015).

Raw pollen counts were converted to relative abundances using a total of pollen grains and fern spores (APD). Concentrations were calculated by first determining the particles per milliliter of disaggregated sample, then using the sample mass that was rehydrated to calculate particles per gram of sample. A pollen diagram based on the relative abundances (%) was generated in Tilia (Grimm, 1987), and pollen zones were quantitatively determined

using the CONISS program (Grimm, 1987). CONISS cluster analysis is stratigraphically constrained and uses the sum of squares (Grimm, 1987). Detrended correspondence analysis (DCA) was conducted using the vegan package in R (ter Braak 1985; Oksanen et al., 2013; RStudio Team, 2020). Taxa with maximum abundances less than 2% within a single sample and taxa with only one occurrence were excluded from the DCA and the CONISS. The relative abundances were Wisconsin-transformed and detrended using 26 segments. The axes were rescaled using four iterations. Sample and taxa scores were plotted on the first two axes, and the samples were assigned colors according to their CONISS cluster membership.

Radiocarbon dating and stable isotopes

After the middens had been disaggregated, the sieved >500-micron fraction was separated and dried. This fraction included plant macrobotanicals and fecal pellets. Ten fecal pellets were randomly selected from the sieved material and homogenized, then sent to the University of Georgia Center for Applied Isotope Studies for Accelerator Mass Spectrometry (AMS) radiocarbon dating. More than one pellet was used to obtain an average age for the sample. There is the possibility that these pellets were deposited and not cemented by hyraceum for a period of time, and thus have ages not directly representative of fossil pollen in the hyraceum fraction. However, given the nature of the middens as thin, dung-rich accumulations, it is likely they formed within a relatively brief amount of time (10^1 – 10^2 yr). Because of this, we interpret the data as averaged across this time frame (Scott and Woodborne, 2007; Ivory et al., 2021). For two samples (WP38-3a 4-6 and WP50-2 0.5-2), radiocarbon dates were obtained on hyraceum drilled out of the solid sample before disaggregation. Calibrated ages were determined using Calib 8.20 (Stuiver and Reimer, 1993) and the Intcal20 calibration curve (Reimer et al., 2020).

Bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were also measured on the same homogenized samples at the same laboratory using gas chromatography isotope ratio mass spectrometry (Table 3). Bulk $\delta^{13}\text{C}$ values measured on fecal pellets should be largely reflective of the carbon isotopes of undigested plant material and can be used to infer changes in C_3 and C_4 vegetation (Ehleringer et al., 1997; Chase et al., 2012). Analyses of rock hyrax middens in southern Africa

and Yemen have demonstrated a link between bulk $\delta^{15}\text{N}$ and relative moisture, wherein the nitrogen isotope composition in the feces reflects that of the consumed plant tissue, which is absorbed from the pool of nitrogen in the soil (Chase et al., 2012; Craine et al., 2015; Ivory et al., 2021). This relationship has also been observed in feces from other herbivores (Díaz et al., 2016). Generally, $\delta^{15}\text{N}$ is negatively correlated with mean annual precipitation (MAP) on a global scale, and thus has an inverse relationship with soil moisture (Chase et al., 2012; Wang et al., 2014). However, nitrogen cycling in soils is a complicated process that may be driven by other mechanisms in arid regions (Wang et al., 2014; Craine et al., 2015; Díaz et al., 2016).

To evaluate the relationship between $\delta^{15}\text{N}$ and moisture in the middens, we compared the bulk $\delta^{15}\text{N}$ with speleothem records of $\delta^{18}\text{O}$ from the Qunf and Defore Caves (Fleitmann et al., 2004, 2007). While these indicators reflect different aspects of hydroclimate, speleothem $\delta^{18}\text{O}$ can be used as a proxy for precipitation, specifically monsoon rainfall, which represents most of the MAP in this region (Fleitmann et al., 2007). Values of $\delta^{15}\text{N}$ traditionally have an inverse relationship with MAP, but this correlation may change in very arid places (Chase et al., 2012; Wang et al., 2014; Díaz et al., 2016). The Qunf Cave (17°10'N, 54°18'E) $\delta^{18}\text{O}$ data were sourced from the National Oceanographic and Atmospheric Administration paleoclimatology database. To obtain submodern (~200–50 BP) $\delta^{18}\text{O}$ values, which are missing due to a hiatus at Qunf Cave, data were extracted from a speleothem from nearby Defore Cave (17°07'N, 54°05'E) that covers this interval (Fleitmann et al., 2004).

The temporal resolution of the Qunf Cave speleothem record was much higher than that of the middens, which were temporally averaged (Fleitmann et al., 2004, 2007; Ivory et al., 2021). To help account for this, the 1 σ range (68.3% probability) of the calibrated ages for the midden samples was used to determine an age range over which to average the $\delta^{18}\text{O}$ data from the speleothem record. A set of three samples (WP38-3a 4-6, 665 cal yr BP; WP50-2 0.5-2, 853 cal yr BP; WP38-2B, 1461 cal yr BP) with particularly high measured values of $\delta^{15}\text{N}$ (6.7–12.6‰ above the average of 9.5‰) were not included in this analysis. Two of

these (WP38-3a 4-6 and WP50-2 0.5-2) were measured on hyrax feces rather than fecal pellets. Rock hyraxes concentrate their urine to preserve water as an adaptation to their arid environment, which likely affects the $\delta^{15}\text{N}$ value (Rübsamen et al., 1982; Chase et al., 2012). The third sample (WP38-3a 4-6, 21.3‰) was removed, as it fell far beyond the calculated standard deviation ($7.90 \pm 3.43\%$). Modern samples and five samples with median ages 1922–1566 cal yr BP were also excluded due to a lack of coverage in the speleothem $\delta^{18}\text{O}$ data. The averaged speleothem $\delta^{18}\text{O}$ values were then plotted against the bulk $\delta^{15}\text{N}$ from each midden. For samples with overlapping 1 σ ranges, each $\delta^{15}\text{N}$ value was plotted individually. Error bars representing the 95% confidence interval were added for the $\delta^{18}\text{O}$ averages, then a linear regression was conducted.

RESULTS

Modern pollen

On the coastal plain near the base of the escarpment, the samples are dominated by *Dracaena* (31.0%), Poaceae (17.6%), and *Senegalia* III (6.8%). The pollen taxa in highest abundance from the camel dung collected in the escarpment mountains were Poaceae (67.6%), *T. dhofarica* (7.4%), and *Suaeda* (6.3%). In the distal plateau samples, the most abundant taxa are *S. persica* (17.7%), Poaceae (9.2%), *D. viscosa* (8.3%), *Cocculus pendulus* (7.9%), and *Senegalia* III (7.3%). Here, the abundance of *B. sacra* is highest (6.5%). In the western Nejd, *S. persica* (19.0%), *Ficus* (14.0%), Poaceae (10.3%), *Senegalia* III (9.5%), and *Ziziphus*-type (8.9%) are all relatively abundant. Cyperaceae pollen also occurs in a relatively higher proportion (7.8%). Modern east Nejd samples are characterized by *Polycarpon*-type (*Reseda*) (39.2%), *Kohautia* (12.9%), Poaceae (8.7%), and *Senegalia* III (7.2%). The submodern samples from east Nejd have a lower pollen abundance of *Polycarpon*-type (*Reseda*) (12.0%) and *Kohautia* (1.7%). *Senegalia* III (9.7%) is higher in abundance. The samples contain higher percentages of *Ficus* (8.2%) and Poaceae (15.2%) (Fig. 3).

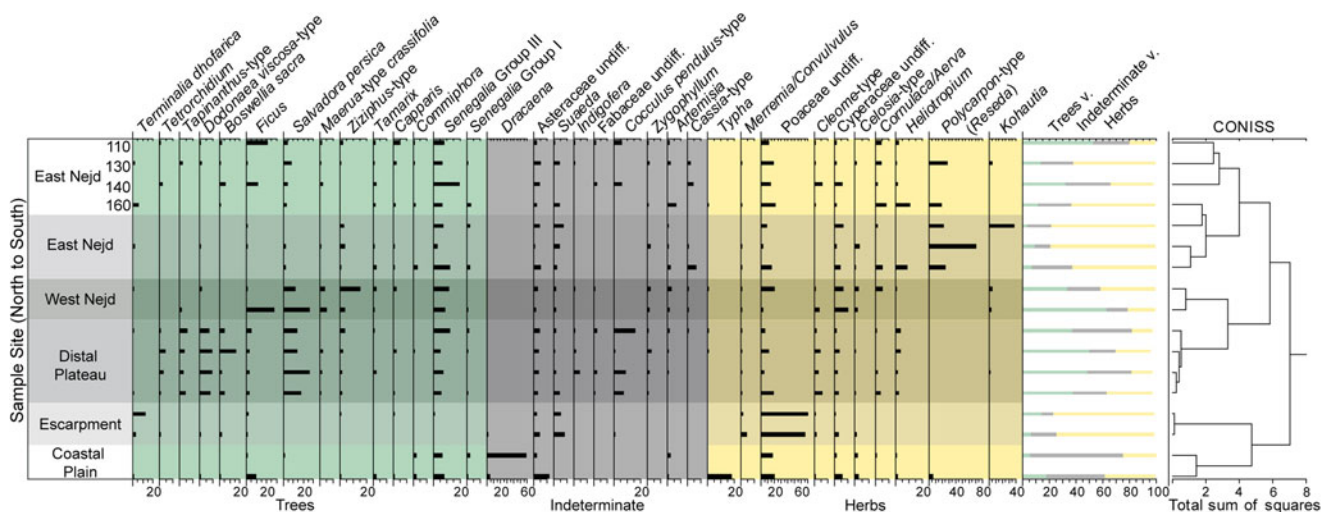


Figure 3. Pollen diagram of modern hyrax middens and two camel dung samples, in order from north to south. The middens are grouped by their ecological zone (east Nejd, west Nejd, distal plateau, escarpment, coastal plain). The two escarpment samples are camel dung specimens. Submodern hyrax middens are included with their median calibrated ages. Pollen abundances are on the x-axis. The green shade indicates tree pollen habits, gray, indeterminate habits, and yellow, herbaceous pollen habits. The CONISS dendrogram is plotted on the right.

CONISS cluster analysis reveals two compositionally distinct groups of samples; those collected from the escarpment and coastal plain ecological zones cluster as one group, and samples from the Nejd and distal plateau locations cluster as the other (Fig. 3). In the DCA, Nejd samples cluster with common modern taxa observed within 100 m of the midden caves such as *Senegalia* (4.3%) and *S. persica* (12.6%) (Fig. 4). Two samples of fresh camel dung collected from the escarpment region have pollen representative of modern cloud forest taxa, notably *T. dhofarica* (7.4%). Grazing indicator pollen taxa are in highest abundance today in samples from the distal plateau (13.2%). Submodern (160–110 cal yr BP) samples in the east Nejd reveal higher abundances (10.7%) of grazing indicators compared with modern abundances in this region (7.9%).

Fossil pollen zones

Pollen analysis of the fossil middens revealed a diverse flora, with 134 total pollen taxa identified. Preservation was variable among the samples, with a range of percent broken grains of 0–11.9%. Most samples (23) had good preservation (broken grains <10%), while three had higher abundances of broken pollen grains (WP45-2, WP153-2, and WP38-3a 4-6). The average pollen concentration of the samples was 12,825.13 particles/g. Zonation of the pollen stratigraphy was determined using the CONISS dendrogram, which splits the assemblages into two distinct sets of samples, the fossil samples and the modern. The fossil samples are then subdivided into groups A and B, then again into A1, A2, B1, and B2. These subzones were based on the two next-highest branch heights in the dendrogram. The percentages given are zonal average abundances, except for those that refer to a single sample and are specified as such. Pollen taxa were grouped within the pollen diagram by plant habit (APD; Vincens et al., 2007; Lézine et al., 2021). The trends described in this section refer to the pollen diagram in Figure 5.

Zone A1 (4038–3233 cal yr BP)

This pollen zone includes the two oldest samples. Herbaceous pollen comprised 4.0–17.0% of total pollen in each sample,

while arboreal pollen was 27.0–57.0% of the total pollen. The most abundant herbaceous taxa were Poaceae (3.0%) and *Kohautia* (1.7%), but these were fairly low in abundance compared with the rest of the pollen record. *Boswellia sacra* (10.8%), *Ficus* (17.9%), and *Boscia/Cadaba* (5.2%) pollen were the most dominant tree taxa. The liana *Cocculus pendulus* was also a dominant pollen taxon (10.8%) in this zone.

Zone A2 (3103–1466 cal yr BP)

There are eight samples within this zone, which bracket an 1100-yr gap from 2920 to 1651 cal yr BP. The oldest sample (3103 cal yr BP) contained notably high abundances of Combretaceae pollen (31.2%), which mainly consisted of *T. dhofarica* (30.9%). The third sample occurred after the gap in the record, and at this time there was a transition to increased abundances of herbaceous pollen taxa (21.2%) on average in the rest of the samples. There was a pronounced increase in *Kohautia* pollen (10.3%), as well as an increase in pollen from Poaceae (8.2%) in the younger six samples. Tree pollen (30.7%) decreased from the previous zone but remained abundant. *Ficus* (7.7%) decreased in this zone.

Zone B1 (1461–115 cal yr BP)

This zone contains nine samples. Herbaceous pollen taxa (21.8%) remained similarly abundant from the prior zone, while tree pollen (18.7%) decreased further in abundance. The transition to this zone was dominated by pronounced increases in *Commiphora* (11.3%) and Cyperaceae (22.3%) pollen in the oldest sample. Pollen from the Amaranthaceae family (12.0%) also increased during this interval.

Zone B2 (114–107 cal yr BP)

This pollen zone consists of three submodern samples. Herbaceous pollen taxa (22.9%) were still abundant, but there was also a significant increase in tree pollen (29.1%). *Ficus* pollen (12.0%) was the most abundant tree taxon. Poaceae pollen (10.6%) became more abundant than in previous intervals, while Amaranthaceae pollen (5.3%) decreased.

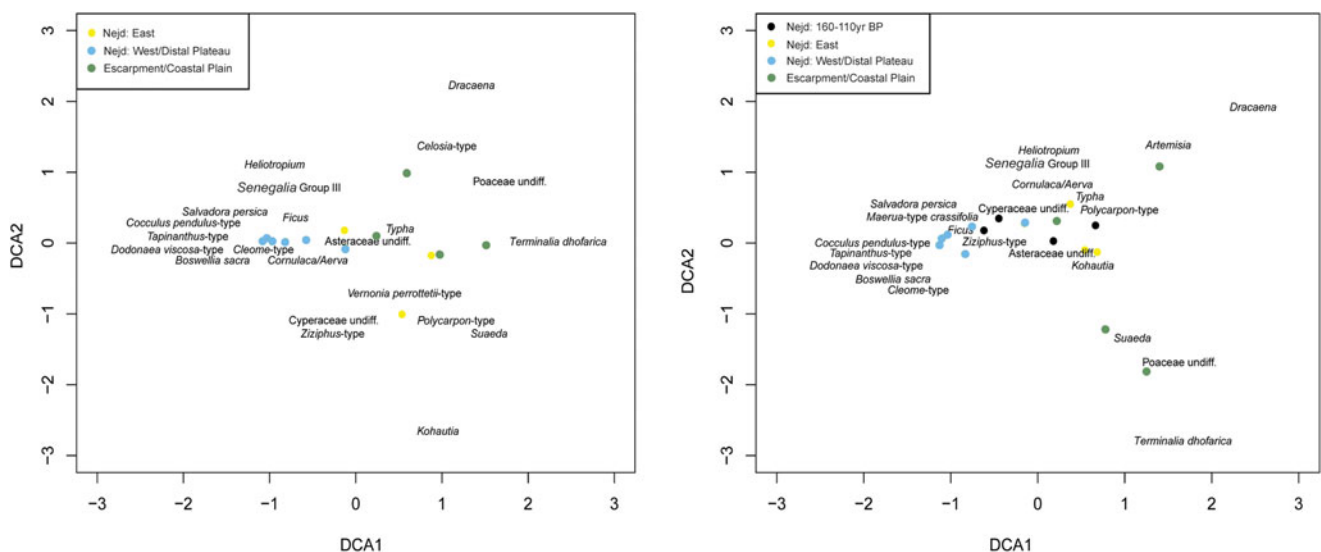


Figure 4. Detrended correspondence analysis (DCA) of all modern samples (right), and including submodern samples (left). Samples are color coded by ecological zone.

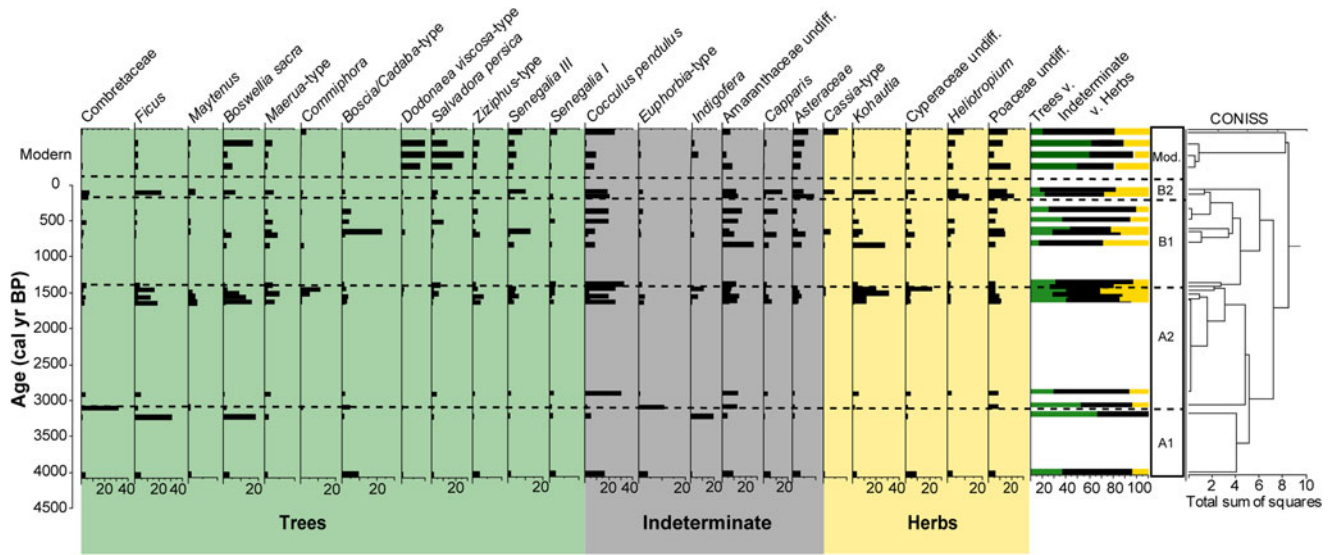


Figure 5. Pollen diagram of selected taxa from east Nejd fossil middens. Abundances are plotted on the x-axis and age in calibrated years BP on the y-axis. The four modern samples are plotted individually. The green shade indicates tree pollen habits, gray, indeterminate habits, and yellow, taxa with herbaceous pollen habits. Pollen zones determined via CONISS cluster analysis are represented by the column on the right.

Modern

This zone consists of all the modern samples from both the east Nejd and the distal plateau. These samples were characterized by high abundances of tree pollen (37.9%). Herbaceous pollen (22.5%) remained at an abundance consistent with the previous zone. There was a marked increase in pollen from the trees such as *S. persica* (15.1%) and *D. viscosa* (6.7%), as well as an increase in *Senegalia* III (4.4%). Poaceae pollen (12.2%) increased

from the previous zone, while Cyperaceae pollen (2.9%) decreased.

Fossil midden DCA

The first two axes of the DCA performed on the fossil midden samples is shown in Figure 6. The first DCA axis had an eigenvalue of 0.3129, and a length of 2.3642 SD. The second DCA

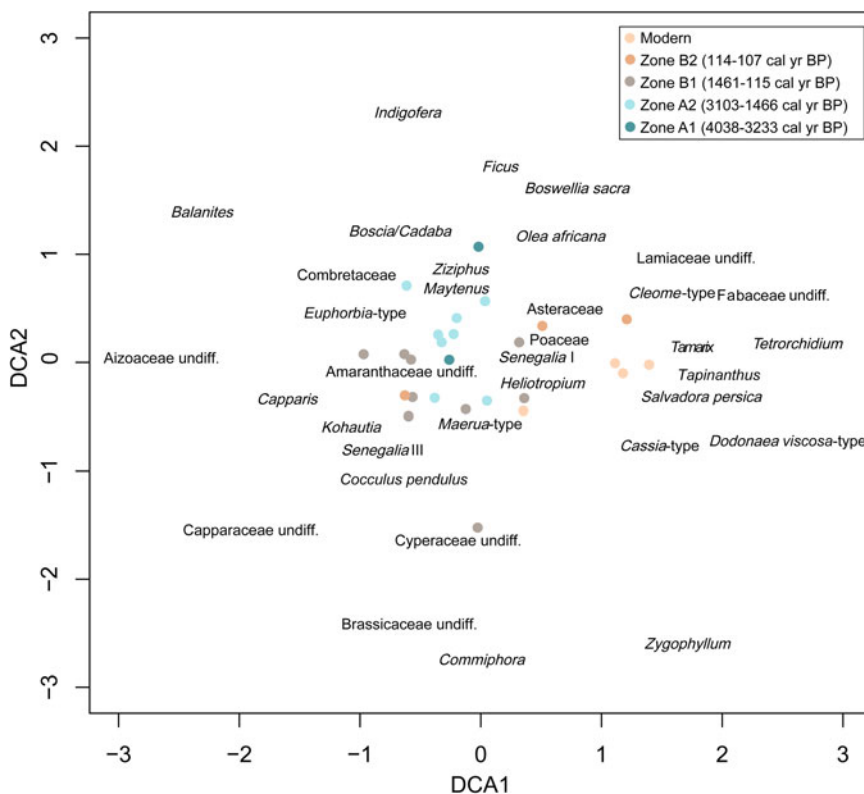


Figure 6. Detrended correspondence analysis (DCA) of fossil middens. Samples are coded by quantitatively determined pollen zone.

axis had an eigenvalue of 0.2203, and the axis length was 2.5927 SD. Modern samples and submodern samples (114–107 cal yr BP) from Zone B2 clustered together near positive values on DCA axis 1. The older samples (Zones A2, A1, and B1) clustered near negative values on DCA axis 1.

Fossil midden stable isotopes

Bulk $\delta^{15}\text{N}$ values showed a gradual depletion over time ($r = -0.7210$) from 4038 cal yr BP (10.9‰) to present (5.4‰ average). In contrast, bulk $\delta^{13}\text{C}$ values did not show a clear trend. Averages of bulk $\delta^{13}\text{C}$ in each pollen zone show they remained relatively consistent (-26.2 to -25.5 ‰), until an approximately 2‰ depletion in the modern samples (-27.2 ‰). $\delta^{18}\text{O}$ from the speleothem records versus $\delta^{15}\text{N}$ from the middens demonstrated a negative correlation ($r = -0.7051$), wherein more depleted values of $\delta^{18}\text{O}$ (-1.1 ‰) corresponded with more enriched values of $\delta^{15}\text{N}$ (10.9‰). The linear regression explained 49.71% of the variance in the $\delta^{15}\text{N}$ data (Fig. 7).

DISCUSSION

Hyrax midden pollen and modern vegetation

The pollen data from the modern hyrax middens were closely aligned with documented vegetation in each ecological zone and thus captured a local signal of vegetation (Table 1). On the coastal plain, *Poaceae* (18.92%), *Dracaena* (31.01%), and *Senegalia* III (6.81%) are most abundant. The vegetation in this region has been significantly reduced due to overgrazing by domesticated animals and other human activity, resulting in a desert grassland with sparse *Senegalia tortilis* trees (Miller and Morris, 1988). In the escarpment samples, *Poaceae* (67.6%) and *T. dhofarica* (7.4%) were found in high pollen abundance. *Suaeda* (6.3%) is common among coastal vegetation communities, and the escarpment samples come from the southernmost area nearest the coastal plain (Miller and Morris, 1988; Patzelt, 2015; Fig. 1). One of these samples contained 12.1% *T. dhofarica* pollen. These samples were camel dung and therefore indicate direct consumption, introducing a dietary bias that created larger pollen

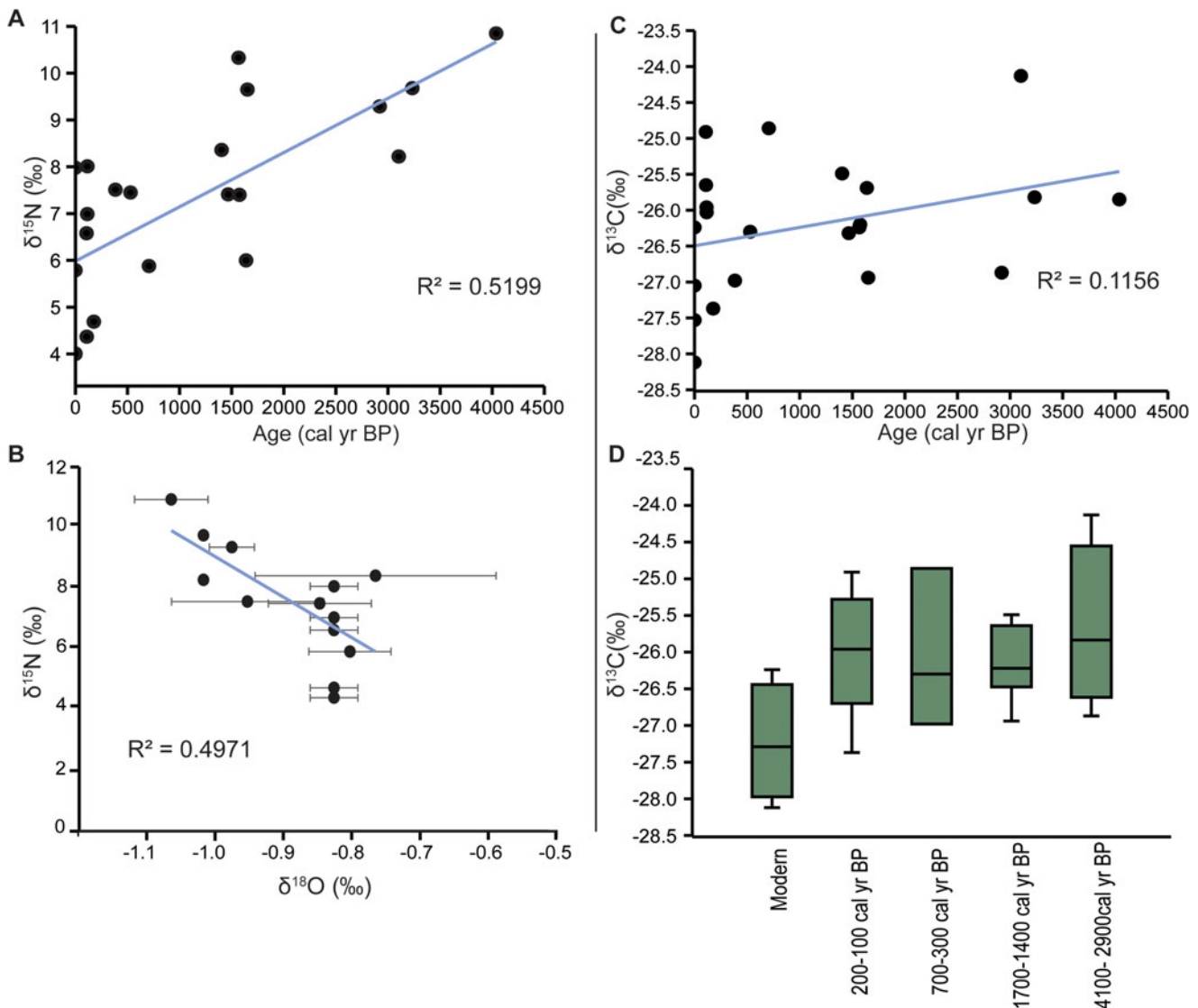


Figure 7. (A) The $\delta^{15}\text{N}$ values of the middens plotted by age in calibrated years BP. (B) The average speleothem $\delta^{18}\text{O}$ plotted against midden N. (C) A plot of the bulk $\delta^{13}\text{C}$ values by midden age in calibrated years BP. (D) A box plot of midden $\delta^{13}\text{C}$ values by age bin.

abundances than those that result from eolian deposition (Scott and Cooremans, 1992). While there is likely dietary contribution of pollen into the hyrax middens, this camel dung was collected from an animal actively browsing on the escarpment and on *T. dhofarica* plants. The pollen abundances in these samples can be used as a tentative benchmark for what could be expected for high dietary input of *T. dhofarica* pollen in the hyrax middens (Scott and Cooremans, 1992; Gil-Romera et al., 2010; Chase et al., 2012). *Terminalia dhofarica* is limited to the escarpment woodlands today (Miller and Morris, 1988; Hildebrandt et al., 2007 Patzelt, 2015).

The distal plateau samples are dominated by the tree taxa *S. persica* (17.7%) as well as Poaceae (9.2%) pollen. The plateau ecological zone is a grassland with sparse trees (Miller and Morris, 1988). *Salvadora persica* is found along wadi drainage systems, preferring wetter soils (Miller and Morris, 1988). *Boswellia sacra* (frankincense) is higher in abundance in the distal plateau samples (6.5%), which is this plant's preferred habitat (Miller and Morris, 1988; Patzelt, 2015). All the Nejd samples contain high abundances of *Senegalia* III (7.2–9.7%). *Senegalia* vegetation communities are prolific throughout the desert of Dhofar (Miller and Morris, 1988; Ghazanfar, 2004). Modern samples from east Nejd have a significant contribution from the pollen taxa *Polycarpon-type* (*Reseda*) (39.2%). A member of the genus *Reseda*, *R. sphenocleoides*, is common in the dry wadi drainage systems of the Nejd (Raffaelli et al., 2003). Cyperaceae pollen is found in a higher proportion in the west Nejd (7.8%). Generally, sedges found in the inland desert are members of the genus *Cyperus*, particularly *Cyperus conglomeratus*, which is found even among the sand dunes of the Rub al' Khali Desert, or the Empty Quarter (Miller and Morris, 1988). Semi-aquatic varieties of Cyperaceae are found on the coast, typically near estuaries (Miller and Morris, 1988; Hoorn and Cremaschi, 2004).

The CONISS results for the samples presented distinguished all the modern Nejd samples, which cover a wide geographic area, from the submodern samples (160–110 cal yr BP). Additionally, the CONISS results distinguished all other samples by geographic location (and ecological zone). The DCA of the modern samples illustrates this ecological gradient, where samples cluster near taxa that today are abundant in their respective ecological zones. These statistical analyses suggest that middens preserve a pollen signal of the local vegetation within a reasonable degree of reliability (Figs. 3 and 4).

Fossil pollen interpretation

We interpret the dated middens as averaged time slices representing approximately decades to ~100 yr of deposition. The fossil pollen record reveals variability between samples of similar ages. While the samples come from the same wadi drainage system, there is still some geographic distance between sample sites (~0.25–4.4 km). Variability in their pollen compositions may reflect the vegetation in the immediate vicinity outside the caves as well as dietary biases from hyrax foraging (Scott and Woodborne, 2007; Chase et al., 2012; Ivory et al., 2021). Having a higher sample density of middens with similar ages but from slightly disparate locations thus gives a broader picture of the vegetation in the east Nejd at a particular time. Moreover, it is important to note that despite the dissimilarities between samples of similar ages, the CONISS statistical analysis reveals that their overall compositions are most similar to one another in comparison to all other samples.

The fossil pollen record demonstrates a change in the vegetation communities such that arboreal taxa with mesic affiliations on the modern landscape (i.e., Combretaceae, *Maytenus*) were more prevalent ~4000–3000 cal yr BP. After 1500 cal yr BP, more xeric taxa (i.e., *Senegalia*, *Kohautia*) became more abundant, and the density of vegetation was much sparser (Figs. 5 and 8). In the DCA, samples grouped near pollen taxa that characterized their composition, which captured this ecological gradient through time along the first axis (McCune and Grace, 2002; Fig. 6). Taxa associated with the Nejd today, such as *Senegalia* III, *S. persica*, and Poaceae were on the positive side of DCA axis 1 near the modern and submodern samples (~120–100 cal yr BP). Emblematic taxa of the older groups were *Boscia/Cadaba* and the Combretaceae family (mainly *Terminalia*), neither of which exist in the Nejd today (Patzelt, 2015).

In the early part of the pollen record (4038–2920 cal yr BP), there was a higher proportion of tree pollen taxa (~20–57%) on the landscape relative to herbaceous taxa (0–16%). Trees such as *Boscia/Cadaba* and *Ficus* were more abundant on average until approximately 3000 cal yr BP. These trees are common on the landscape today but are typically found in moister places (Miller and Morris, 1988; Patzelt, 2015). There was also a high abundance of Combretaceae pollen in the sample dated to 3100 cal yr BP. Although multiple members of this family are found throughout the Afrotropics, only *T. dhofarica* is native to Dhofar (Miller and Morris, 1988; Patzelt, 2015). This makes *T. dhofarica* the most likely candidate to have been present during this interval. *Terminalia dhofarica* is an insect-pollinated plant group often underrepresented in pollen spectra. Although no modern middens were found in *Terminalia* woodland, limiting our ability to examine the representativity of its pollen in middens, abundances of *T. dhofarica* from within fresh camel dung collected during browsing on an individual tree resulted in values of 12.1%. To the extent that these samples can be used to benchmark the data from the hyrax middens, we tentatively interpret the even higher values in this fossil sample of >30% to indicate a local presence of this tree in the east Nejd at ~3100 cal yr BP (Miller and Morris, 1988; Lippi et al., 2007; Oberprieler et al., 2009; Chase et al., 2012).

The sample at 3100 cal yr BP also contained high abundances (39.9%) of other mesic tree taxa, including *Boscia/Cadaba*-type. This supports the idea that during the period of deposition of this sample, woodlands more like those currently growing in the modern escarpment were supported in the Nejd. Further, this sample had a high concentration of microcharcoal (36,605 particles/g) (Fig. 8). Modern vegetation in the Nejd is severely fuel-limited due to the sparseness of the vegetation. The presence of increased charcoal suggests that vegetation during this interval was continuous enough to be more conducive to burning (Blackford, 2000; Chase et al., 2009; Genet et al., 2021).

Though paleoecological records in this region are fragmentary, several suggest wetter conditions in coastal southern Arabia and more pervasive woodlands in the desert of Yemen ~10–4 ka (Lézine et al., 2002; Parker et al., 2006; Fleitmann et al., 2007; Ivory et al., 2021). Speleothem $\delta^{18}\text{O}$ from Qunf Cave indicates higher precipitation starting at ~10 ka, which then began to decrease around 8–7 ka until the present (Fleitmann et al., 2007). Sedimentological and pollen evidence from the United Arab Emirates illustrates the presence of interdunal lakes during a wetter Early Holocene, which became desiccated by the Late Holocene at ~4000 cal yr BP and a C4 dominated plant community became established (Parker et al., 2004, 2006). Pollen records from coastal

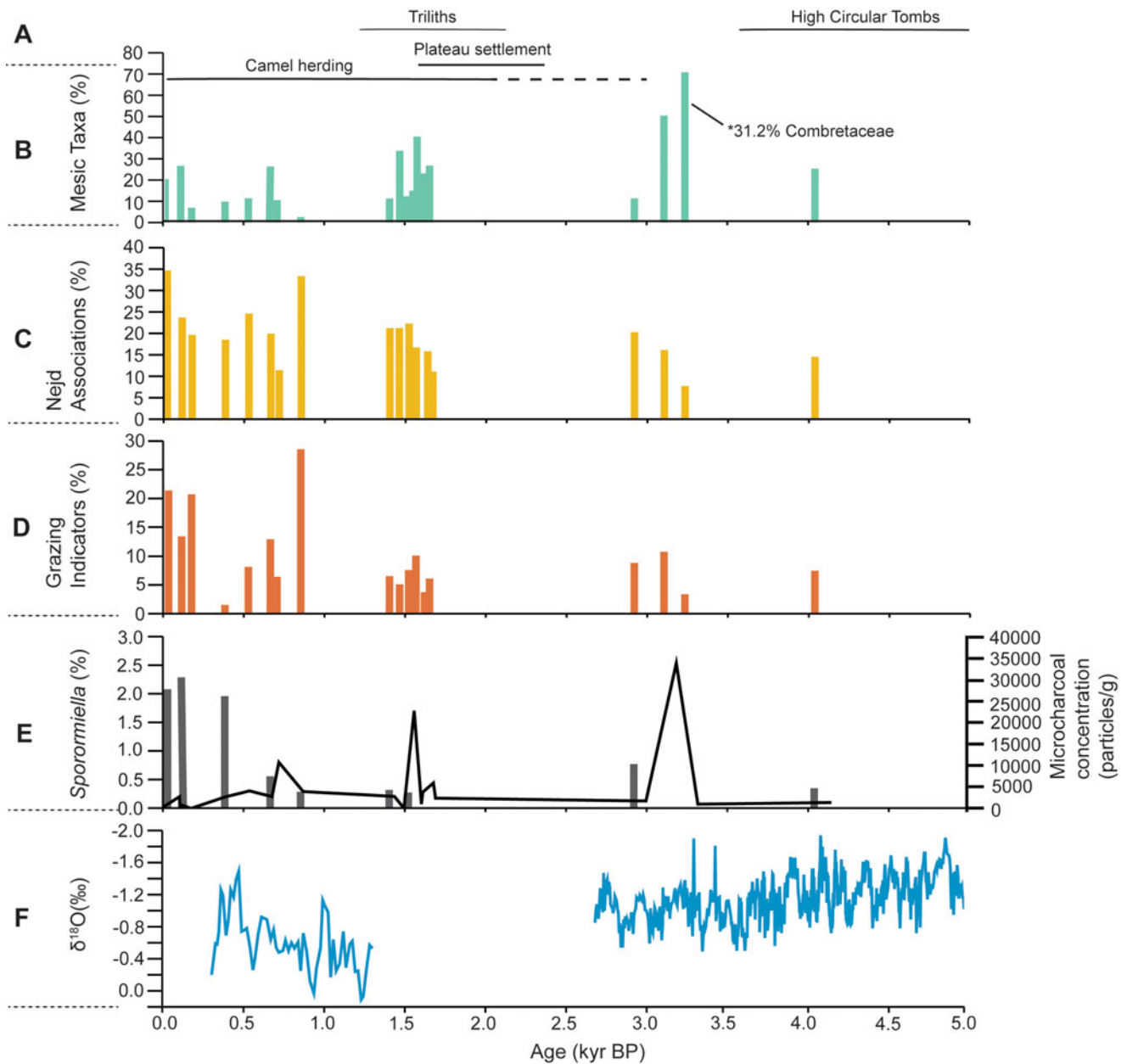


Figure 8. (A) Archaeological periods of monument building and settlement, along with the earliest evidence for the introduction of domesticated camels in Dhofar (2000 yr BP) and elsewhere in Arabia (3000 yr BP). (B) Mesic taxa relative abundances (%): *Ficus*, *Boswellia sacra*, *Boscia/Cadaba*, *Maytenus*. (C) Nejd association relative abundances (%): *Amaranthaceae*, *Salvadora persica*, *Senegalia* I, *Senegalia* III, *Commiphora*. (D) Grazing indicator relative abundances (%): *Dodonaea viscosa*-type, *Cornulaca/Aerva*, *Cassia*-type, *Heliotropium*. (E) Gray bars showing *Sporormiella* relative abundance (%) and black line indicating microcharcoal concentrations (particles/g). (F) Speleothem $\delta^{18}\text{O}$ from Fleitmann et al. (2007).

estuaries demonstrate changes mainly in wetland and mangrove taxa; however, they provide some evidence that communities farther inland included tropical taxa from ~6000 to 4500 cal yr BP (Lézine et al., 2002). Pollen from hyrax middens in Yemen indicate a diverse, semiarid woodland farther inland in the modern-day desert at Wadi Sana during the mid-Holocene (6–4.7 ka), with high local abundances of *Terminalia* (Ivory et al., 2021). The pollen data presented here complement these records, suggesting a denser arboreal community was present in the Nejd in Dhofar from ~4000 to 3000 cal yr BP.

After the gap in the hyrax midden record (~1500 cal yr BP), the composition of the vegetation communities was much different. Between ~2900 and 1500 cal yr BP, there was a taxonomic

turnover characterized by a pronounced increase in herbaceous pollen taxa (*Amaranthaceae* and *Poaceae*) and tree pollen taxa (*Senegalia* III and *S. persica*) indicative of modern Nejd communities (Fig. 8). Species of *Senegalia* are widespread in Dhofar but are most common in the Nejd and make up most of the trees in this zone (Miller and Morris, 1988). The herbaceous *Amaranthaceae* family is also dominant in this part of the record. Many of the species of *Amaranthaceae* in Dhofar are weeds in cultivated areas or grow on disturbed ground, as well as in xeric environments (Miller and Morris, 1988). Additionally, after 1500 cal yr BP, microcharcoal concentrations were much lower (94.9 particles/g). This decrease in charcoal in combination with indications of xeric vegetation suggests a change in fire dynamics to a

regime more like the modern day with less fuel for natural wildfires (Fig. 8).

Monsoon dynamics and aridity

Regional paleoclimate records suggest a gradual decrease in rainfall across the Holocene in southern Arabia. The mechanism behind this decline has traditionally been interpreted as the southward migration of the Intertropical Convergence Zone (ITCZ) following decreasing Northern Hemisphere summer insolation during the mid-Holocene (Fleitmann et al., 2007; Lézine et al., 2014; Nicholson, 2018). More recently, climatologists suggest that this latitudinal shift in the rain belt is driven by the development of the African Westerly Jet and subsequent movement of the African Easterly Jet (Nicholson, 2009). Moreover, the vertical rising of the ITCZ over the ocean amplifies this effect by widening the rain belt and increasing the duration of the rainy season (Nicholson, 2009). These two processes lead to the intensification of the summer monsoon over land. The speleothem $\delta^{18}\text{O}$ records from Dhofar suggest the variation in rainfall over this time are related to changes in Northern Hemisphere insolation (Fleitmann et al., 2007).

The presence of *T. dhofarica* in the Nejd at 3100 cal yr BP and the high abundances of other relatively mesic taxa (e.g., *Boscia/Cadaba*) suggest that the range of semiarid woodlands was more expansive in the early part of the Late Holocene (4000–3000 cal yr BP). These taxa were locally abundant in the Nejd at this time, at least 25–30 km farther inland than their modern extent. A stronger monsoon during this interval would have brought increased precipitation and/or fog and likely supported more arboreal vegetation farther inland than today (Ivory et al., 2021). While fog is an important climatic factor for modern woodland vegetation in the region, speleothem oxygen isotopes provide a record of rainfall; they do not provide direct information about fog (Fleitmann et al., 2004, 2007). Speleothem growth occurs when water seeps into a cave, and in Dhofar this is strongly tied to the summer monsoon, which brings in both fog and rainfall (Fleitmann et al., 2007). Thus, speleothem $\delta^{18}\text{O}$ is an indicator of this moisture source rather than rainfall or fog alone. Regardless, pollen evidence suggests more expansive semiarid woodlands than seen today.

Additionally, although the hyrax midden record only provides snapshots of vegetation from collected intervals, there is evidence of some level of resilience of woodland taxa to increasing aridification during the Late Holocene. For example, *T. dhofarica* was locally present in the desert at 3100 cal yr BP, ~3000–4000 yr after the onset of decreasing precipitation regionally (Fleitmann et al., 2004; Lézine et al., 2007). Transient climate model simulations indicate that there were abrupt changes in rainfall as the ITCZ retreated southward and the monsoon weakened (Lézine et al., 2017). These model results, compared with mangrove pollen data from the coast, suggest an abrupt decrease in rainfall at 4000 cal yr BP (Lézine et al., 2002, 2017). In the early part of the record, the mangroves contained pollen of *Rhizophora*, a coastal, brackish taxon that requires some freshwater input (Lézine et al., 2017), which became extremely rare after ~4000 cal yr BP and was replaced by more saline- and drought-tolerant species (Lézine et al., 2002). This suggests a transition to more arid conditions in Oman (Lézine et al., 2017). However, the arboreal community farther north in the east Nejd persisted for another ~1000 yr after this transition, suggesting a resilience to increasing aridity in the Late Holocene.

The gap in the hyrax midden record from 2920 cal yr BP to 1651 cal yr BP is coeval with a hiatus in the Qunf Cave speleothem record (Fleitmann et al., 2004). Regional paleoclimate records from Arabia, Africa, and western Asia indicate this was an especially dry period, and it may be that the interior Nejd did not have enough food and water resources to sustain a hyrax population during this period (Gasse and Van Campo, 1994; Fleitmann et al., 2004; Ivory and Lézine, 2009; Gil-Romera et al., 2010). Hyraxes obtain most of their water from foraged vegetation, especially in arid regions (Sale, 1965; Chase et al., 2012; Mohamed, 2019). When drought conditions occur and herbaceous plants do not grow or desiccate on the landscape, the trees become a critical source of both food and water (Sale, 1965). Hyraxes have even been observed stripping bark from trees such as *Senegalia* in southern Africa when under severe drought stress (Sale, 1965). The reduction of the trees during this interval, as seen in the shift in vegetation once middens are again deposited, suggests that hyraxes may have lacked these necessary resources during this arid interval. The alternative hypothesis would be that this gap is simply the result of insufficient sampling. While this is certainly possible, there are many independent lines of evidence indicating that the Nejd may have been too dry and resource depleted during this interval. Additionally, the middens that are dated to ~1500 cal yr BP after this hiatus co-occur with the redeposition of speleothems at Qunf Cave as well as an observed wet phase in the coastal estuaries (Hoorn and Cremaschi, 2004; Fleitmann et al., 2007).

Bulk $\delta^{15}\text{N}$ data from hyrax middens have previously been interpreted to indicate local changes in moisture availability. Soil and plant foliar $\delta^{15}\text{N}$ have an established inverse relationship with water availability that has also been demonstrated in herbivore feces (Chase et al., 2012; Wang et al., 2014; Carr et al., 2016; Díaz et al., 2016). $\delta^{15}\text{N}$ is also negatively correlated with MAP globally (Wang et al., 2014). In our record, $\delta^{15}\text{N}$ became more depleted over time, which would counterintuitively suggest increasing water availability over this study interval. In contrast, all other evidence, from regional precipitation records to the change in vegetation in this area, strongly indicates drying (deMenocal et al., 2000; Fleitmann et al., 2007; Lézine et al., 2017; Ivory et al., 2021). However, the inverse relationship between water availability and $\delta^{15}\text{N}$ observed in previous studies may not apply in hyperarid regions.

A study by Díaz et al. (2016) looked at plants and herbivore feces $\delta^{15}\text{N}$ across an aridity gradient in the Atacama Desert. They observed a unimodal relationship between herbivore fecal $\delta^{15}\text{N}$ and moisture availability. Wang et al. (2014) observed this same curve across an aridity gradient in savannah grassland in both soil $\delta^{15}\text{N}$ and plant foliar $\delta^{15}\text{N}$. Likewise, this study demonstrated a positive correlation between soil and plant $\delta^{15}\text{N}$ and MAP at an arid location. This suggests that after a certain threshold, different controls on the nitrogen cycle become more dominant, such as loss of gaseous nitrogen or nitrogen fixation by bacteria (Wang et al., 2014). The inverse relationship between hyrax midden bulk $\delta^{15}\text{N}$ and speleothem $\delta^{18}\text{O}$ from this study implies a positive correlation between bulk $\delta^{15}\text{N}$ and MAP in Dhofar, and thus continued aridification, over the last 4000 yr (Fig. 7).

Human–environment interactions

Archaeological evidence attests to the movement of ancient pastoralists across the Dhofar region (Harrower et al., 2014;

McCorrison et al., 2014, 2018, 2020). Generally, there is sparse evidence for prolonged habitation in any one spot, suggesting pastoralists were highly mobile (McCorrison et al., 2018). Small monuments were constructed across Dhofar over the last 7000 yr (McCorrison et al., 2014, 2018). This was punctuated by one period of visible settlement by cattle herders on the plateau at ~2 ka, where there are permanent structures documenting ~200 yr of abandonment and reoccupation (McCorrison et al., 2018, 2020). These sites were near more stable water sources, but there is no evidence for the development of settled agriculture (McCorrison et al., 2020).

Historically, there has been a lack of understanding regarding how pastoralist practices impact vegetation, and past theoretical frameworks often focused on exploitation and depletion of habitat resources (i.e., the “tragedy of the commons”) (Hardin, 1968; Warren, 1995). However, recent studies have demonstrated the sustainability of pastoralism even under increasing aridity (Brierley et al., 2018). Linking paleoecological records with archaeological data allows for an increased understanding of long-term human–environment interactions in pastoralist systems. In the early part of the hyrax midden pollen record, there is evidence for more continuous arboreal vegetation cover, and archaeological evidence suggests mobility of pastoralist groups until ~2350 cal yr BP (Harrower et al., 2014; McCorrison et al., 2018). Mesic trees were present farther inland in the Nejd even after 3000–4000 cal yr BP of drying and 4000 yr of a mobile herding practice in Dhofar. This suggests that pastoralists did not degrade woodland vegetation at this time.

Beginning around 1000 cal yr BP, there was a pronounced increase in grazing indicator pollen taxa (12.5%). Likewise, at approximately 500 cal yr BP, there was an increase in the abundance of *Sporormiella* (1.9–2.3%), a fungus found in the dung of large herbivores, which in Dhofar is found abundantly in camel dung (Ivory et al., 2021). The observation of *Sporormiella* in the middens likely occurs through hyraxes walking across soil where camels are present, as the fungus would be trapped in the dung that is on the ground, as well as eolian transport. The increase in grazing indicator taxa and *Sporormiella* may indicate an intensification of land use in the inland desert, particularly camel herding, beginning at 1000–500 cal yr BP. While the distribution of grazing indicator taxa would have also been influenced independently by other ecological or climatic controls, the combination of the higher abundances of these particular pollen taxa and *Sporormiella* point to an increase in domesticated herbivores on the landscape. These pollen taxa are low in abundance in the earlier part of the record (6.6%), suggesting that animal grazing on the vegetation would have been relatively low until ~1000 cal yr BP.

In the modern cloud forests on the escarpment, higher stocking rates of camels increase the abundance of unpalatable plant species, or grazing indicators, and decrease plant diversity (Ball and Tzanopoulos, 2020). Preferential grazing of the softer shoots and saplings of *T. dhofarica* by camels is already being shown to affect the regeneration of these key trees (Ball and Tzanopoulos, 2020). Maintaining these high browsing pressures under anthropogenic climate change may ultimately lead to the degradation of the cloud forest (El-Sheikh, 2013; Ball and Tzanopoulos, 2020). However, it is important to note the long-term sustainability of pastoralism under lower stocking rates, as shown through the archaeological record and the paleoecological evidence presented here. The earliest evidence for domesticated camel herding

in Dhofar is from 2 ka, but there is no observable increase in grazing indicators or *Sporormiella* for another 500 to 1000 yr in the collection region of our samples (McCorrison et al., 2018).

CONCLUSION

The pollen data from the rock hyrax midden record demonstrate a turnover from a more mesic, arboreal vegetation community to the more xeric community that characterizes the Nejd today. While the nature of the termination of the Holocene Humid Period is debated, an arboreal community persisted in the Nejd for approximately 4000–3000 cal yr BP after the onset of decreasing rainfall (Fleitmann et al., 2007). Bulk stable isotope data from the middens indicate a transition to hyperaridity over this time frame. These combined data suggest some resilience of this biodiverse dryland community under increasingly arid conditions. The end of the hiatus in the midden record and its co-occurrence with the renewal of speleothem growth and increased runoff at the coast suggest this overall trend was perhaps punctuated by a wetter phase beginning at ~1500 cal yr BP (Hoorn and Cremaschi, 2004; Fleitmann et al., 2007).

Modern human land use enhances the risk of vegetation degradation, and anthropogenic climate change is likely to push this region into novel climate spaces (Dahinden et al., 2017; Ball and Tzanopoulos, 2020). There is an outstanding need to mitigate the effects of global climate change and reduce degradational impacts from human land use to help maintain this biodiverse and vulnerable vegetation community. Evidence for the practice of nomadic pastoralism in southern Arabia dates to at least 7000 cal yr BP (Martin and Roe, 2020). Indicators of more intense human landscape use do not appear in the paleoecological record generated from the middens until 1000–500 yr BP. The lack of evidence for human impacts on vegetation for the bulk of the record highlights continued sustainability of pastoralism in this region under changing climate conditions. In terms of vegetation composition, the modern samples were considerably different compared with the fossil samples, indicating the recent economic growth and substantially higher stocking rates are an unprecedented driver of vegetation change in Dhofar. It is important to consider the context provided by these long-term records when discussing human activity and impacts to the landscape: although animal grazing may be degradational to the modern vegetation, it has not always been in the past, and there may be conservation options that preserve the practice of nomadic pastoralism in Dhofar and other drylands.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/qua.2023.42>

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