Quaternary Dryland Dynamics: perspectives and prospects

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Abstract

Reconstructing Quaternary-timescale environmental change in drylands provides insights into styles and rates of change in response to direct insolation forcing and variations in global temperature, ice-volume and sea-level. Changes to the relatively inhospitable environments presented by drylands is also central to debates about the migration and adaptability of hominin species. This review outlines approaches used for reconstructing past environments, which use dated sequences of environmental proxies - the properties of physical sediments, chemical precipitates and biological materials. In addition, climate model simulations can explore responses to known climatic forcing factors. Advances in both approaches remain situated within conceptual frameworks about dryland responses to: (i) cyclical changes in the Earth's orbit around the sun, either mediated via the global cryosphere during glacial-interglacial cycles (~100 ka periodicity during the last ~0.9 Ma), or mediated via the response of the global monsoon with ~23 ka periodicity (precession) and (ii) millennial-scale climatic shifts, which are thought to originate outside drylands, and in the North Atlantic.

In this review, three examples are outlined to demonstrate areas of emerging consensus and remaining contradictions: (1) speleothem, and tufa, growth records that span hundreds of ka, (2) conditions at the Last Glacial Maximum (LGM), and (3) proxies recording millennial-scale events. Precessional-scale forcing of the monsoon is not always observed, with apparent mediating roles from glacial boundary conditions in parts of the northern-hemisphere (NH) and from interglacial boundary conditions in part of the southern-hemisphere (SH). The LGM in drylands was initially conceptualised as experiencing pluvial (wet) conditions, which shifted to a glacial aridity paradigm, and is again shifting to a pattern of global heterogeneity, in which some drylands were wetter-than-present and others drier. However, there remain contradictions between environmental proxies and model simulations, and spatial heterogeneity observed within many drylands. Dryland proxies that record millennial-scale events demonstrate clearly the importance of climatic teleconnections across the globe in influencing dryland hydroclimate. The records of Quaternary dryland change across a range of timescales are used alongside simulations of ecosystem response through time, hominin habitat and even hominin physiology to better understand likely hominin dispersals through dryland regions.

Impact statement

Dryland environments have undergone significant change during the Quaternary Period (2.58 Ma), offering a crucial long-term perspective on the climatic, environmental and ecological conditions observed today. This period is also central to understanding the large-scale impact of dryland climatic change on hominins, including the drivers for migration and evidence for adaption to aridity. This review paper presents an overview of the approaches taken to reconstruct environmental conditions and to simulate climatic changes. The paper uses three key examples that exemplify advancements in the field, that illustrate evolving interpretations, significant developments in thought, and areas where uncertainty persists. The paper emphasizes the complexity and variability of dryland changes—both across different regions and

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within individual landscapes—evident in both reconstructions and model simulations. In its final section, the review explores recent progress in understanding how hominins responded to climatic and environmental shifts in drylands during the Quaternary. The interplay between environmental change and hominin adaptation, migration, and evolution is currently revitalizing this area of dryland research.

Introduction

Reconstructing the past in drylands is important for three key reasons. First, geomorphological processes operating today are influenced by the landscape features inherited from the past, including the Quaternary-past (~2.58 Ma). For example, the emplacement and migration of dunes during the Quaternary influence modern-day surface hydrology, such as dune damming during flash-flooding as well as groundwater-fed interdune lakes (Al-Masrahy and Moutney, 2015; Liu and Coulthard, 2015), with recent dramatic examples recently observed in southeast Morocco (Egbejule, 2024). Second, it helps us to understanding the range of climatic and environmental conditions drylands can (or have) experience(d), which provides important context for the post-industrial period and changes predicted for the future. Reconstructions using landforms and sediments progress alongside numerical model simulations, which are valuable for exploring the influence of driving forces of past climate change in drylands, although model performance is evaluated using palaeoenvironmental data from reconstructions, reminding us of the need to examine their ability to simulate past climates realistically (e.g. Otto-Bliesner et al., 2017). Thirdly, spatio-temporal changes to aridity are central to endeavours to understand hominin evolutionary transitions (e.g. Timmerman et al., 2022), particularly abilities to tolerate dry conditions. Climate-induced changes to habitat can be simulated in order to test hypotheses about hominin evolution and migration across dryland regions.

Quaternary dryland research is a major sub-topic within drylands science, and this review aims to outline the approaches taken to reconstruct the past. In doing so, it aims to provide some critique of the current state of knowledge production and set out key areas of progress and continued debate, rather than attempt a comprehensive review of Quaternary environmental change for all major dryland regions, which would require an extensive treatment beyond the scope of a short overview. The paper briefly outlines: (1) the range of environmental data used within those reconstructions and some key numerical models used to simulate the past and (2) the dominant frameworks for global climatic change during the Quaternary. These frameworks are organised into different timescales that inherently reflect the climatic drivers, such as periodic variations in the Earth's orbit around the sun and the behaviour of the global cryosphere. I then (3) use illustrative examples to explore the status of understanding of Quaternary dryland environments, which also helps demonstrate how #2 has guided interpretations. A combination of conceptual frameworks, proxy data and model simulations are used by researchers to construct arguments, and therein, whilst we can see examples where some consensus is emerging, interpretations and reasoning often get complicated, and debates remain. The final section (4) examines a major motivation for current Quaternary dryland research, concerned with aridity as a factor likely to constrict hominin migration and/or influence adaptability.

Sources of evidence and numerical climate model simulations

To appreciate where our understanding of Quaternary environmental change in drylands comes from, we must acknowledge a range of archives (such as marine basin sediments and a range of terrestrial settings) and proxies (sedimentary, chemical and biological properties that have recorded a response to past environmental conditions) (Table 1). Environmental reconstruction uses abductive reasoning (Inkpen and Wilson, 2009), looking at changes in that proxy record through time to infer the past conditions under which it formed. This process is inherently imperfect, and whilst some signals can be statistically transformed into

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quantitative estimates of temperature, precipitation and salinity etc., many give qualitative information about warmer or colder, or higher or lower moisture availability.

[POSITION TABLE 1]

Table 1: Archives and their proxies for past climatic and environmental conditions in drylands, giving an overview of archives and their proxies for past climatic and environmental conditions in drylands, and key modelling simulations from which changes in dryland aridity can be inferred. (abbreviations are used: N – north, N-cen – north central, NW – northwest, S – south, Sn – southern, W – West, Wn – western, Kal – Kalahari).

The study of Quaternary climatic change in drylands is not solely proxy-data driven, with ideas generated from conceptualising how variations in global-scale temperature and circulation patterns may have driven the hydroclimatic conditions in drylands. For example, Jamieson (1863), Passarge (1904) and Flint (1959) argued for dryland "pluvial" conditions during glaciations, based partly on lower temperatures favouring a higher moisture balance, whilst Sarnthein (1977) argued that lower sea-surface temperatures during glacials drove continental aridity, alongside the wind patterns tending to outflow from continental surfaces (Manabe and Hahn, 1977).

Numerical modelling simulations also advance our understanding of Quaternary dryland dynamics, allowing us to explore the how drylands respond to a range of climatic drivers, or boundary conditions, such as the orbital parameters that control Earth's receipt of insolation, greenhouse gas concentrations, global terrestrial ice cover, sea-level and meltwater fluxes. This includes simulations of global aridity (e.g. Greve et al., 2017) and targeted simulations of dryland regions (e.g. Liu et al., 2021). These may be conducted for individual time-slices, such as the global Last Glacial Maximum (LGM) or the mid-Holocene, undertaken as transient simulations through time, or targeted to explore potential climatic teleconnections to a known discrete forcing event (see Table 1).

Frameworks of Quaternary climatic change

Orbital cycles

The influence of changes to Earth's orbit on glacial-interglacial cycles of the Quaternary, linked predominantly to the cryosphere in the Northern Hemisphere (NH), is well established (e.g. Milankovitch, 1920; Hays et al., 1976; Ruddiman, 2006). The varying eccentricity of the elliptical-shaped orbit influences total solar insolation receipt with quasi-regular cycles of ~400 ka and ~100 ka. The other two cycles relate to seasonality of the receipt of insolation: (i) the change in the degree of the title of the Earth (obliquity) influences the intensity of season in both hemispheres (~41 ka), whilst (ii) the direction the Earth's axis points in space, combined with the rotation of the elliptical orbit around the Sun, influences the relative strength of seasons in each hemisphere via the precession of the equinoxes (~23 ka). The pacing of global glacial-interglacial cycles, inferred from marine oxygen isotope stratigraphy (MIS), starts at ~41 ka (e.g. Pisias and Moore, 1981; Ruddiman et al., 1986; Raymo et al., 1990), transitioning during 1.25-0.7 Ma to ~100 ka cyclicity. In MIS even numbers are glacials and odd numbers are interglacials (Fig. 2A). The ~41 ka cyclicity is thought to relate to direct obliquity forcing, involving feedbacks with atmospheric greenhouse gases, whilst the ~100 ka cyclicity cannot be accounted for by the small total insolation variations related to eccentricity (Ruddiman, 2006). Notwithstanding the debates about the nature of the forcing-cryosphere response, and the role of internal forcing and ocean-atmospheric reorganisations in the climate system (e.g. Broecker and Denton, 1989; Berger, 2013), the large change to the Earth's climatic state during these glacial-interglacial cycles is likely to have influenced the terrestrial dryland regions.

The way conditions in drylands have been conceptualised over global glacial-interglacial periods has gone through large changes in thought. There was a widespread shift in the idea of dryland pluvials during glacial periods to dryland aridity, aided by the advent of chronological control for some proxies (e.g. Williams, 1975; Sarnthein, 1977). This 'glacial aridity paradigm' was lent support by the timing of higher volumes of

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dust volumes in the Antarctic ice cores such as Vostok during glacials, and larger particles in the Last Glacial Maximum (LGM) layers (Petit et al., 1999), and back to 800 ka in EPICA DomeC (Lambert et al., 2012) (Fig. 2B), and marine sediments (Fig. 1 s1, Fig. 2C). However, higher dust concentrations do not necessarily require an expansion of drylands, being wind-driven (more turbulent atmospheric circulation) and because of a potential reduction in wet-deposition of dust owing to a globally-averaged lower moisture content during cooler glacials. The marine archives also represent an average of terrestrial material received from a wide spatial area, so that spatial heterogeneity within dryland regions will not be recorded. Therefore, whilst the dryland-derived dust proxy in ice core and marine sediment archives remains an appealing record for terrestrial drylands because they cover a long timescale, capturing multiple glacial-interglacial cycles, they are insufficient for reconstructing conditions in the drylands themselves. This requires terrestrial archives and proxies.

Variations to the global monsoon system (Wang and Ding, 2008) on ~23 ka (precession) cyclicity is also well established (e.g. Kutzbach, 1981; Cheng et al., 2022). This global-scale system includes the Asian monsoon, North African monsoon, North American monsoon, the Indonesian-Australian Monsson, South African monsoon, South American monsoon (Wang et al., 2017), with a strong influence on the hydroclimate of neighbouring dryland regions. For example, the well-established influence of the North African Monsoon on the hydroclimatic of the Sahara, including recent ‘greening’ during the North African Humid Period (see deMenocal and Tierney (2012) for a brief overview). The global-scale influence of ~23 ka (precession) forcing of insolation is complicated by it occurring in anti-phase between Earth’s two hemispheres. This owes to the hemisphere tilting towards the Earth (experiencing summer) moving in a cycle from a short-pass to a long-pass around the sun in Earth’s elliptical orbit, such that for any year with a NH summer at short pass, the SH summer is at long pass, and vice-versa. Therefore, insolation forcing is calculated and plotted for the hemisphere from which the monsoon-related response is being considered (Fig. 2N shows a NH and SH summer insolation curve).

Millennial-scale variability

Climatic variability with millennial-timescale pacing was initially detected in the ice core proxies covering the last glacial (Dansgaard et al., 1972; 1982; 1993) as well as ice-rafted detritus in marine sediment cores in the North Atlantic (e.g. Heinrich, 1988), with the noticeable coincidence in timing set out by Bond et al. (1993) and Broecker (1994). Hemming (2004) considered evidence for a global climate imprint of these events and started to consider whether a connection (or teleconnection) between events had a physical basis, via ocean and atmospheric circulation. The 21 warming events from 87 to 12 ka have a quasi-periodic spacing of <2,000 years and last for 50 to 100 years (Wolff et al., 2010; Rousseau et al., 2017). Millennial events with a similar 1470 ± 500-year cyclicity have also been observed through in the Holocene (11.7 ka) in the North Atlantic (Bond et al., 1997), although the magnitude of the variations is higher with larger ice sheets. The ‘agitation’ to the climate system provided by millennial-scale variability may have a role in glacial-interglacial transitions (e.g. Hodell and Channell, 2016). In order to explore potential teleconnections between NH high-latitude driven millennial events and low-latitude dryland climatic responses, numerical climate model simulations can be used.

[POSITION FIGURE 1] Fig. 1. Map of current global dryland distribution, alongside the locations of the major proxy records explored in the three key example in this paper and an inset of the TraCE-21 ka simulation for the Last Glacial Maximum from Lui et al. (2021) demonstrating which dryland regions are simulated to be wetter-than-present, or drier-than-present. Site numbers (s) are referred to in the text, and 1) North Atlantic dust records, ODP659 (deMenocal, 1995), MD03-2705 and ODP659 (Skonieczny et al., 2019), 2) Mukalla Cave (Nicholson et al., 2020), 3) Hoti Cave (Nicholson et al., 2020), 4) North Arabian Sea dust record ODP721/722 (deMencoal, 1995), 5) Red Sea dust record K11 (Ehrmann et al., 2024), 6) Gulf of Aden RC09-166 (Tierney et al., 2017), 7) Wadi Dabsa tufa record (Stone et al., 2023), 8) Soreq Cave (Bar-Matthews et al., 1997), 9) Egyptian tufa growth (Kele et al., 2021), 10) Rössing Cave, Namibia (Geyh and Heine, 2014), 11) Tswaing Crater (Partridge et al., 1997), 12) CD15410-06 (Simon et al., 2015), 13) Naracoorte Caves (Weij et al., 2023), 14) Leeuwin-Naturaliste-region caves (Weij et al.,

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2023), 15-17) speleothems on the northwest seaboard of Australia (Denniston et al., 2017), 18) Kati Thanda-Lake Eyre Basin, 19) Murray Darling Basin, 20) Tasman Sea dust record (Hesse, 1994), 21) Native Companion Lagoon, eastern Australia (Petherick et al., 2008), 22) Lake Chilwa, Malawi (Thomas et al., 2009), 23) Pella hydrax midden (Chase et al., 2019), 24) Zizou hyrax midden (Chase et al., 2019), 25) Spitzkoppe midden (Chase et al., 2019), 26) De Rif hyrax midden (Chase et al., 2011).

Example 1: the timing of dryland speleothem (and tufa) growth

Speleothem and tufa growth in drylands are good indicators for reductions in aridity (Table 1), with uranium-series dating allows scientists to constrain their growth records over multiple 100 ka cycles. This makes them a useful archive to explore both glacial-interglacial cycles and precession-forcing of the monsoon as drivers of Quaternary climate change in drylands.

On the Arabian Peninsula, the discontinuous Mukalla and Hoti Cave speleothems (14.917°N, 48.590°E and 23.083°N, 57.350°E) (Fig. 1 s2,3) cover 1.1 Ma, with growth phases only occurring during peak interglacial and warm sub-stages during interglacials, and no growth during glacials (Nicholson et al., 2020). The record is used to delimit South Arabian Humid Periods (SAHPS) (Fig. 2G), which show correspondence with other proxy records for humidity in the region (Nicholson et al., 2020) (Fig. 1 s4-6, Fig. 2D-F), and MIS7 and MIS5 interglacial tufa deposition at Wadi Dabsa (18.307°N, 41.564°) (Stone et al., 2023) (Fig. 1 s7, Fig. 2I). The conceptual explanation for the absence of speleothem growth during glacial periods is that glacial boundary conditions 'dampen' monsoon strength. More specifically, large NH high-latitude ice sheets influenced atmospheric circulation, preventing on-land penetration of the summer monsoon (Burns et al., 2001; Fleitmann et al., 2003). A role for precession-forcing seems less conclusive - there is not a SAHP for every peak in insolation (at 15°N) even during an interglacial (the non-dampened state) (Nicholson et al., 2020).

[POSITION FIGURE 2] Fig. 2. Key proxy records globally and for drylands, where: (A) the LR04 oxygen isotope record, with Marine Oxygen Isotope Stages (MIS) above (Lisicki and Raymo, 2005), (B) Antarctica Vostok (Petit et al., 1999) and EPICA DomeC (Lambert et al., 2012) dust records, (C) North Atlantic dust records, ODP659 (deMenocal, 1995) and ^{230}Th corrected MD03-2705 and ODP659 (Skonieczny et al., 2019) (sites near 1), (D) North Arabian Sea dust record ODP721/722 (deMencoal, 1995) (site 4), (E) Red Sea dust record K11 (Ehrmann et al., 2024) (site 5), (F) Gulf of Aden RC09-166 terrestrial leaf wax δD (Tierney et al., 2017) (site 6), (G) speleothem-growth record derived South Arabian Humid Periods (SAHPS) (Nicholson et al., 2020) (sites 2 and 3), (H) Soreq Cave δ^{18}O record (Bar-Matthews et al., 1997) (site 8), (I) Tufa growth records from Wadi Dabsa, SW Arabia (Stone et al., 2023) (site 7) and N Africa (summarised in Kele et al., 2021) (within box 9), (J) Rössing Cave speleothem growth record (Geyh and Heine, 2014) (site 10), (K) Tswaing Crater rainfall proxy (Partridge et al., 1997) (site 11), (L) CD154-10-06P southwest Africa humidity record derived from Fe/K ratios for highly eroded terrestrial sediment (Simon et al., 2015) (site 12), (M) KDE (Kernel Density Estimates) for speleothem U-Th ages using 5 ka bandwidth for Naracoorte (east) (site 13) and Leeuwin-Naturliste region (west) (site 14) speleothems in southern Australia (Weij et al., 2024), and (N) insolation curves for summer in each hemisphere to demonstrate precession-paced forcing, where solid orange line is 30°N June and dashed red line is 30°S December (from Laskar et al., 2004).

Records of speleothem growth in the Negev Desert, adjacent to the Arabian Peninsula, do not align strictly with interglacials, suggesting glacial-interglacial forcing of aridity-humidity may not be widespread across NH drylands. The ~200 ka Soreq Cave (31.754°N, 35.021°E) δ^{18}O record (Bar-Matthews et al., 1997) (Fig 1 s8, Fig. 2H), along with dated fragments across seven other caves, indicate four Negev Humid Periods (NHPs) (Vaks et al., 2010), which do not align strictly with interglacials: NHP-4 (MIS10 into MIS9), NHP-3 (MIS8), NHP-2 (MIS7), and NHP-1 (late MIS6 into MIS5). In examining a role for precession-paced forcing, Vaks et al. (2010) find NHPs lead NH insolation peaks by several 1,000 years, with no clear explanation. The conceptual mechanism to explain monsoon-forcing of NHPs is complicated, involving a Mediterranean Sea moisture source from synoptic cyclones and an Atlantic moisture source. For the latter, a sea-surface temperature driven reduction of the Azores high pressure might allow the North African summer Monsoon (Atlantic-source) to reach as far east as the Negev (deMenocal, 1995; 2004; Bar Matthews et al., 1997).

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Further west into northeast Africa, Egyptian tufa growth records also record deposition in glacial periods (MIS2 to MIS12), in addition to peak interglacials, but not with precession-pacing (Kele et al., 2021) (Fig. 1 s9, Fig. 2I). Kele et al. (2021) propose a mechanism for 'glacial enhancement' of moisture in Egypt rather than the 'dampening' experienced in southern Arabia. When the Sunda and Sahul shelves (Indonesia and north of Australia) are exposed as landmass during glacial lowering of sea level, reduced oceanic Indonesian throughflow leads to atmospheric circulation changes that increased rainfall over east Africa. However, whilst Kele et al. (2021) draw on the CESM1 simulation of response to that glacial sea level change to support this idea (Di Nezio et al., 2016), the simulation only demonstrates an increase in rainfall over eastern equatorial Africa, not over Egypt.

In the SH, stalagmite and flowstone growth records from Rössing Cave, Namibia (22.531^{o}S, 14.798^{o}) (Fig. 1 s10) date to interglacials MIS5e, MIS7 and MIS11, but also extend through the MIS10 glacial (Geyh and Heine, 2014) (Fig. 2J). The proposed moisture source is a summer rainfall expansion over to the west coast of southern Africa, bringing Indian Ocean monsoon moisture, although it is not clear why Geyh and Heine (2014) do not consider precession-paces forcing. Two key long proxy records for eastern southern Africa do reveal some precession-pacing: (i) Tswaing Crater sedimentary proxy record (25.416 ^{o}S, 28.101 ^{o}E) (Fig. 1 s11, Fig 2K) (Partridge et al., 1997) and (ii) CD15410-06 (31.177°S, 32.159°E) (Fig. 1 s12) humidity proxy based on Fe/K ratios for highly-weathered terrestrial sediment delivered to the ocean (Fig. 2L) (Simon et al., 2015). This example clearly illustrates the practice of different authors with respect to using the frameworks for Quaternary climatic change - Geyh and Heine (2014, p381) frame their studying by asking "whether the speleothems of the cave formed during glacial or interglacial periods".

In Australia, speleothem growth records covering ~350 ka for Naracoorte Caves (~36.95^{o}S, 140.75^{o}E) (Fig 1, s13) and Leeuwin-Naturaliste-region caves (~33.54 ^{o}S, 115.02 ^{o}E) (Fig. 1 s14) in the southern dryland margin, are derived from speleothem 'rubble' pieces combined into an age-frequency plot smoothed with a kernel density estimator (KDE) (Weij et al., 2023) (Fig. 2M). The KDE plots demonstrate a precessional rhythm of speleothem deposition for both caves, with good coherence with the 30^{o}S summer (Dec 21st) insolation curve (Weij et al., 2024). The absence of growth peaks in the warmest part of the last three interglacials interrupts the precession-paced pattern, which leads Weij et al. (2024) to suggest a threshold of warmth might be crossed during peak interglacials, leading to a drop in moisture availability. We could term this an 'interglacial dampening' of moisture availability, in contrast to the 'glacial dampening' observed in the southern Arabian Peninsula. However, there is an absence of large KDE peaks in some of the glacial periods (e.g. during the two precession peaks later in MIS8 and the final precession peak in late MIS6 for Naracoorte and all of the precession peaks in MIS 8 for Leeuwin-Naturaliste) (Fig. 2M), which requires further explanation.

Overall, the speleothem and tufa records from drylands and their margins do not straightforwardly show an anti-phased NH and SH moisture availability response predicted from precession-paced forcing of monsoons. Feasible mediating roles have emerged for either glacial, or interglacial, end-member boundary conditions, with: a glacial dampening in southern Arabia, a glacial enhancement in north-east Africa and an interglacial dampening in Australia.

Example 2: (Re)assessing Last Glacial Maximum (LGM) aridity

The Australian dryland margin speleothem record (Weij et al., 2024), is one line of evidence that challenges the 'glacial aridity paradigm' for the continent (e.g. Hesse, 1994; Miller et al., 1997; Magee and Miller, 1998). Alongside other speleothems on the northwest seaboard (Denniston et al., 2017) (Fig. 1 s15-17), and proxy evidence in the Kati Thanda-Lake Eyre and Murray Darling Basins (LEB, Fig. 1 s18 and MDB Fig. 1 s19) a continental-wide picture of an LGM without a substantial decrease in moisture balance emerges (Cadd et al., 2024). Earlier LGM proxy data syntheses have variably excluded the arid interior in their treatment (e.g. Petherick et al.'s (2013) temperate zone review), included it (e.g. De Deckker et al., 2020), or focussed

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solely on it (e.g. Fitzsimmons et al., 2013), demonstrating different conceptualisations of spatial heterogeneity from the point of synthesis design. Key records from which arid (and cool) conditions have been inferred include: (i) low lake levels (e.g. Harrison, 1993), (ii) wind-derived terrestrial sediment in the Tasman Sea (Hesse, 1994) (Fig. 1 s20) and in lagoonal sediments (Petherick et al., 2008) (Fig. 1 s21), (iii) an increased rate of dune accumulation across major desert dunefields (Hesse, 2016), and (iv) shifts in vegetation from trees to herbs and grasses (e.g. Dodson, 1975; Harle, 1997; Colhoun et al., 1999). The emerging consensus for a positive moisture balance during the LGM (De Deckker et al., 2020; Weij et al., 2024; Cadd et al., 2024) is motivation to re-examine these proxies.

Terrestrial dust has been critiqued as an aridity indicator (see section 1). For the LGM dune accumulation record, even before questioning whether definitive link to aridity (and not primarily to windiness), there is a notable lack of spatial homogeneity. Whilst LGM accumulation rates are increased the Malee (Lomax et al., 2011), the wider Simpson-Strzelecki contains mixed rates, suggesting "a mosaic of bare patches of sand… and large areas of vegetated, stable surface" (Hesse, 2016, p 26). In the case of the vegetation records, there is a growing argument that lower CO_2 during the LGM had a greater influence on than any inferred changes in moisture availability (e.g. Prentice et al., 2022; Scheff et al., 2017). The lake and fluvial geomorphic records remain more enigmatic. First, there are potential spatial contrasts. In the LEB region, shorelines and basin floor sediment from Lake Callabonna-Frome and Kati Thanda-Lake Eyre indicate low or desiccated conditions respectively, in contrast to oscillating-or-full lake conditions in the MDB region (see review by Fitzsimmons et al., 2013). Furthermore, LEB fluvial proxies (dated channel sediments and overbank sediments) yield a different hydrological record than the lake shorelines, with no discernible decrease in hydrological activity during the LGM observed in a KDE probability density curve (see Cadd et al. (2024)). It is, however, sensible to apply caution to using probability-density estimates on age databases from discontinuous sedimentary archives, particularly when they are not sampled using the same vertical resolution across space (e.g. Stone and Larsen, 2011). Cadd et al. (2024) also explore precipitation minus evaporation in the transient iTRACE simulation (21 to 11 ka), which shows LGM conditions had at least as great (or greater) moisture availability than the Holocene across the whole continent. This simulation contrasts with the Fast Ocean Atmospheric Model (FOAM) time-slice simulation of reduced strength Indo-Australian summer monsoon during the LGM (Marshall and Lynch, 2006) but is similar to the transient TraCE-21 ka simulation of a wetter LGM (~30% reduction in the aridity index) at the continental scale (Liu et al., 2021).

The 'glacial aridity paradigm' is also challenged in southern Africa. Two proxy syntheses indicate an area wetter than present west of ~27^{o}E and south of ~17^{o}S (covering the Namib Desert and most of the Kalahari), whilst the rest of the subcontinent was drier, including the eastern fringes of the Kalahari (Chase and Meadows, 2007; Gasse et al., 2008). There is no clear peak in Kalahari dune building at the LGM for any part of the last ~120 ka (Stone and Thomas, 2008), and southern Africa is the testing ground for a strong critique of dune accumulation as a proxy for inferring dryland aridity (Chase, 2009). Model simulations of LGM precipitation over southern Africa are variable and indicate either drier or wetter conditions (e.g. see Stone's (2014) discussion of outputs from HadAM3, UGAMP, PMIP2 ensemble mean and NCAR-CCM3). TraCE-21 ka simulates an ~8% higher LGM aridity index than pre-industrial conditions for Southern Africa (Liu et al., 2021). In contrast, LOVECLIM transient simulations reveals a spatial contrast, with wetter-than-present conditions in the southwest (30^{o}S, 17^{o}E) and drier-than-present conditions in the central-Kalahari (20^{o}S, 22^{o}E), which is similar in nature, but not spatial boundaries, to the proxy syntheses.

The TraCE-21 ka model provides a global-scale perspective on dryland LGM conditions, simulating wetter conditions (16% lower aridity index) compared to present, as driven by lower gas concentrations (GHG) (Liu et al., 2021). However, there is spatial heterogeneity in the simulations: (i) wetter-than present in northern American drylands, The Mediterranean, inner Asia, northeast Brazil, southern South America, and Australia, and (ii) drier-than-present in eastern Africa, the Sahel, (very slightly in north Africa), west and south Asia and southern Africa (Fig. 1 inset). By separating out driving factors (orbitally-driven insolation (ORB), GHG,

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global ice-sheets (ICE) and meltwater forcing) using multiple simulation runs (Liu et al., 2021), explanations for the regional trends can be extracted: (1) NH mid-latitude drylands (northern America, inner Asia, the Mediterranean) respond most strongly to GHG and ICE; (2) NH subtropics respond mostly to ORB (the Sahel, north Africa, west and south Asia), with LGM-dryness roughly one precession-cycle ago; (3) SH mid-latitudes (Australia, southern South America) are in tandem with the NH mid-latitudes and only increase in aridity post-LGM with reduced ICE and (4) tropical drylands (eastern Africa, northeast Brazil) are also largely driven by ICE, with lower sensitivity to ORB. Southern Africa stands out from the rest of the SH in terms of a drier LGM, and with no dominant driver. Liu et al.'s (2021) study is also a good demonstration of our current limitations in palaeomodel-proxy data comparisons. There are just 17 available hydroclimate proxies for (within, or near) nine of the eleven dryland regions, with a maximum of two per region, and none for Australia. This greatly limits the conclusions we can draw from model-data comparisons and masks the spatial heterogeneity that is revealed in more complete proxy-data syntheses (e.g. Thomas and Burrough, 2012; Stone, 2021).

Overall, this example demonstrates a revision of the LGM aridity paradigm for both Australia and southern Africa back, although this is not necessarily a reversion to the idea of pluvial conditions, rather conditions as wet, or slightly wetter than present. It also reveals complications and contradictions within the proxy record, and between model simulations. Quaternary scientists approach these contradictions in different ways. For some this represents a motivation to re-examine how some of the proxy records are interpreted in terms of the abductive reasoning back to climatic conditions (e.g. Chase and Meadows, 2008; Cadd et al., 2024). For others, the conclusion is that the LGM was spatially heterogeneous within dryland regions (e.g. Thomas and Burrough, 2012; Fitzsimmons et al., 2013; Stone, 2014; 2021).

Example 3: millennial-scale hydroclimatic shifts in African drylands

Luminescence-dated shorelines of Lake Chilwa in the savannah to semi-arid climatic region of Malawi, ~15°30'S (Fig. 1 s22), revealed lake highstands at 38.4-35.5, 24.3–22.3, 16.2-15.1, 13.5-12.7, 11.01 ± 0.76 and 8.52 ± 0.56 ka, (Thomas et al., 2009) (Fig. 3A). The first three have a coincidence of timing with North Atlantic Heinrich Events/Stadials (HS) 4, 2 and 1, and the ~11 ka highstand with the Younger Dryas (Fig. 3A). A HadCM3 climate model simulation was used to explore a potential teleconnection. It showed that a reduction of the Atlantic meridional overturning circulation in response to a North Atlantic Heinrich iceberg discharge event has atmospheric teleconnections, with increases the moisture balance at Lake Chilwa (Thomas et al., 2009) (Fig. 3B). The spatial pattern in the simulation is for increased moisture balance over much of southern Africa (south of 15°S) but drier conditions north of the equator (Fig. 3B). This invites future model-proxy comparisons for the African continent in response to millennial-scale climatic forcing.

[POSITION FIGURE 3] Fig. 3 (A) Timing of highstands of Lake Chilwa from luminescence dating of shorelines, compared to the timing of Heinrich Events, (B) HadCM3 simulation of terrestrial moisture balance over Africa caused by a "freshwater hosing" 50-70°N to simulate a North Atlantic Heinrich Event, displayed as an anomaly (modelled years 275-300 minus the average of 0-100 years), where the inset shows modelled reduction in Atlantic Meridional Overturning Circulation (modified from Thomas et al., 2009).

Millennial-timescale change can also be examined using high-resolution (~20-30 μm/y) banded hyraceum (fossilised urine) in hyrax middens on the western margin of southern Africa. The midden record composite $\delta^{15}N$ from three dryland-zone middens (Pella, South Africa: 29.00°S, 19.14°E; Zizou: 24.07°S, 15.97°E and Spitzkoppe: 21.83°S, 15.20°E, Namibia) (Fig. 1 s23-25) contain evidence of phases of increased humidity, which Chase et al. (2019) correlate with HS3, 2 and 1. De Rif midden, just south of the current dryland zone (32.446°S, 19.221°E) (Fig. 1, s26), is also characterised by humid conditions during HS1 (Chase et al., 2011). Although not considered using a simulation experiment, the driving mechanism explored is an oceanic teleconnection with NH millennial events, via their influence on the southern Atlantic (Benguela upwelling zone) sea-surface temperatures (SST), and in turn the influence SSTs have on rainfall over Southern Africa's western margin. This draws on the good temporal correspondence between SST records in the South

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Atlantic Benguela upwelling zone (Farmer et al., 2005; Kim and Schneider, 2003) and the hyrax aridity proxies (Chase et al., 2011). However, unlike for the Chilwa Lake example, the hydroclimatic response of the De Rif midden during the YD (which also involves a North Atlantic meltwater event) is markedly different than for the HS events, with an abrupt drying signal. Chase et al. (2011) invoke an immediate atmospheric interhemispheric teleconnection, as opposed to the oceanic teleconnection with Benguela SST-driven hydroclimatic control for the HS events. These nuances are complex, and a paucity of continuous and high-resolution proxies in African drylands restricts the possibility to test and refine these interpretations, although transient numerical model simulations for discrete spatial locations may provide further insights.

Approaches to understanding hominin response to Quaternary climate change

Understanding Quaternary climatic conditions in drylands is central to ongoing debates around which species in the *Homo* genus first possessed the adaptive capabilities to occupy hyper-arid regions. For example, Mercader et al.'s (2025) assertion that *H. erectus* adapted to a steppe-desert environment in Tanzania by utilising fluvial resources, challenging the dominant narrative that only *H. sapiens* were capable of sustained adaptations (e.g. Roberts and Stewart, 2018). Assessing the large-scale impact of dryland climatic change on hominins is made challenging by the spatially patchy and temporally punctuated nature of both the archaeological record and the terrestrial palaeoenvironmental record. Improving our understanding requires continued efforts to provide environmental reconstructions with robust chronological control at the site of the archaeological evidence, in order to provide the local environmental context for those finds. Model simulations of past climates also offer an opportunity to revolutionise understanding (Timmerman et al., 2024). Early simulation attempts used multiple snapshot simulations. For example, Eriksson et al. (2012) used intervals increasing from 1 to 4 ka through the last 120 ka using the Hadley Centre model (HadCM3) to relate to the record of genetic variation in modern human populations. Increases in computational power now enable transient simulations for 120 ka (e.g. Timmerman and Friedrich (2016) using the Earth system model LOVECLIMv1.1) and even through to 3 Ma (e.g. Zeller et al. (2023) using the Community Earth System Model v1.2 (CESM1.2)) (Table 1).

Timmerman et al. (2022) use the CESM1.2 transient model simulation of the last 2 Ma, linked to a climate envelope model (CEM), to explore how changes in temperature (annual mean), precipitation (annual means and minimums) and terrestrial net primary productivity influenced the species distributions we observe in the fossil record. The CEM used topographically-downscaled (1° x 1° grid) average climate data for 1,000-year time windows and a species database of dated hominin fossils and lithic records (from Raia et al. (2020) and Mondanara et al. (2020)), from which species-presence locations and their associated ages were extracted. The second step derived a habitat suitability model for each species (*H. ergaster + H. habilis, H. erectus, H. heidelbergensis, H. neanderthalensis and H. sapiens*) (Fig. 4), employing the Mahalonobis distance (a statistical approach applicable to a correlation matrix of data for the climatic variables chosen here, rather than pairs of climatic variables (Farber and Kadmon, 2003)).

The habitat suitability model reveals "patchworks of habitable areas" (Timmerman et al., 2022 p.500) within Earth's drylands, and demonstrates that *H. sapiens* is the most tolerant species, or "best equipped to cope with dry conditions" (p.497) (Fig. 4). This supports the idea that *H. sapiens* migrated along 'green corridors' in the dryland Saharo-Arabian belt (Larrasoaña et al., 2013; Breeze et al., 2016; Beyer et al., 2021; Groucutt et al., 2021), and supports the idea of a multi-regional, or polycentric, origin for *H. sapiens* (Scerri et al., 2018). Furthermore, these habitable areas appear likely to have been long-term refugia for a variety of hominins within Africa (Timmerman, 2022), and their locations include dryland regions in both the south and north of the continent (Fig. 4). Timmerman et al. (2022) also observe an orbital-timescale shift in the position of these refugia, which supports the idea that orbital forcing of the global climate was a major driving factor for hominin species distributions, and therefore also dispersal and likely also speciation (e.g. Hua and Wiens, 2013). Climatic change can also be investigated as a driver of *Homo* species extinction, for example Raia et al. (2020), use a statistical approach for the quantification of species vulnerability to climate

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change (climatic niche factor analysis), based on using the Planet Simulator–Grid-Enabled Integrated Earth system model emulator (PALEO-PGEM) of Holden et al. (2019). Their niche analysis demonstrates a significant reduction in climatic niche space just before extinction (disappearance in the fossil record).

[POSITION OF FIGURE 4] Fig. 4. Hominin species distributions, expressed as time-averaged habitat suitability (intensity of blue shading) over 2 million years from Timmerman et al. (2022), also showing (with coloured circles) the locations of fossil and/or archaeological artefact evidence associated with each of the five hominin groups, collated by Timmerman et al. (2022).

Conclusions

Reconstructing Quaternary conditions in drylands allows us to understand how these environments change in response to climatic forcing over a range of timescales, from the changes to Earth's orbit around the sun to the more abrupt millennial-scale cryosphere-oceanic reorganisations. This major sub-topic in dryland science progresses via environmental reconstruction and model simulation approaches, both of which are guided by conceptual frameworks for global climatic change during the Quaternary. In the former, proxy records are interpreted within the frameworks of (i) comparing hydroclimatic conditions during glacials and interglacials, (ii) looking for precession-pacing in responses and (iii) examining any coincidences in timing with millennial-scale events that originate in the North Atlantic region along with potential teleconnections. In the latter, model simulation experiments are set up to explore the role of orbital forcing, long and short-term changes to the Earth's cryosphere with associated changes to sea levels and oceanic circulation, as well as greenhouse gas concentrations. A major motivation for Quaternary dryland research is the desire to understand how environmental changes in drylands relate to habitability limits for hominins and likely routes for migration and dispersal. After setting out approaches taken in reconstructing the Quaternary past in drylands, this review used three key examples to examine and critique progress in understanding, before outlining current and future prospects for understanding the hominin response(s) to Quaternary dryland changes.

The first example of dryland speleothem (and tufa) growth, reveals records of moisture availability that are more complicated than a precession-paced (~23 ka) control on summer monsoon rainfall, which would be antiphased between the NH and SH. Instead, there is strong glacial-interglacial overprinting with regional contrasts in its nature. In the NH, southern Arabia experienced glacial dampening of monsoon rainfall from the Indian Ocean, whilst north-east Africa experienced enhanced rainfall during glacials. In the SH the southern Australian speleothems record is of reduced moisture availability in interglacials, likely representing a temperature threshold, whilst the Namibian record on the west coast of southern Africa shows higher moisture balance during interglacials. In the second example, a combination of proxy data (reconstructions) and model simulations demonstrate a revision of the paradigm of high aridity during the LGM in drylands. The LGM is shown to be wet, or wetter-than-present, across Australia and the west of southern Africa. However, a global-scale simulation reveals heterogeneity across space with six dryland regions wetter-than-present at the LGM, and five drier. Potential explanations for the simulated spatial patterns include different strengths of response to different climatic forcing factors (orbital parameters, the size of the global cryosphere, concentrations of greenhouse gases) in different regions, although southern Africa emerges as an outlier without a dominant driver. The LGM example also reveals that when environmental reconstructions at many sites are considered, spatial heterogeneity of environmental change within that dryland emerges. This requires us to question the usefulness of model-proxy comparisons that are based upon only one or two records of environmental change. The spatial patterns within that heterogeneity require more investigation. For example, the contrast between moisture availability in north-east Africa and Arabia over glacial-interglacial timescales and the reason for the west-east pattern of wetter versus drier for the LGM in southern Africa. It is also important to continue to critique the hydroclimatic inferences that can be made from proxies. For example, deposited dust and dune accumulation relate as much to wind regime as they do to moisture balance. The third example of millennial-scale hydroclimatic shifts in high-resolution archives in southern Africa, provide an excellent

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demonstration of the likely teleconnections between dryland climates and the North Atlantic during high magnitude chances to the cryosphere-ocean-atmosphere system.

All three examples demonstrate a complexity of regional and local patterns of Quaternary environmental change within drylands, of which many details remain to be fully understood. The heterogeneity revealed across space from terrestrial proxy records, is a reminder of the importance of moving beyond marine archives for terrestrial dryland environmental conditions that accumulate a spatially-averaged record of sediments derived from the neighbouring continental land mass. Therefore, site-specific studies of past environmental conditions are central to refining our understanding and importantly are at the heart of understanding the environmental conditions experienced by hominins in the landscapes they were inhabiting. Approaches to understanding hominin interactions with dryland environmental change are also driven forward by model simulation approaches, including simulations of habitat suitability. These suggest that it is likely *H. sapiens* were the most tolerant to dry conditions and able to utilise patchworks of habitable areas, with some habitable areas operating as long-term refugia and others as shorter-lived "green corridors" for migration and dispersal (Timmerman et al., 2022). However, recent environmental reconstructions in Tanzania suggest that earlier members of the *Homo* genus may have also possessed ecological flexibility, such as *H. erectus* utilising dryland water sources and demonstrating adaption to steppe-desert conditions (Mercader et al., 2025). Quaternary dryland research has a rich history and an exciting future.

Data Availability statement

Not applicable (this is a review paper).

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Competing interest

None.

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