Quaternary Science Advances 17 (2025) 100259

Contents lists available at ScienceDirect

Quaternary Science Advances

journal homepage: www.sciencedirect.com/journal/quaternary-science-advances

Reconciling the environmental implications of late Quaternary faunal and pollen records in southern Africa

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ARTICLE INFO

Keywords:
Herbivores
Grass
Grazers
Seasonality
Extinction

ABSTRACT

Across southern Africa, the Pleistocene-Holocene transition was associated with changes in community composition of large mammalian herbivores, which included the extinction and extirpation of numerous grazers. Past research has often linked these changes to the contraction and disappearance of grasslands; however, the relationship between faunal and pollen records spanning this transition has not been systematically analyzed. Here, we investigate changes in fossil ungulate community composition and grass pollen abundance from late Quaternary sites across southern Africa to evaluate the extent to which these communities track paleovegetation change across this interval. Our dataset draws from faunal and pollen records across southern Africa. Results from the comparison of compositional changes in both records suggest a sub-continental-scale decoupling of grass cover and ungulate community composition during the Pleistocene-Holocene transition. Although there is strong evidence for a regional-scale decline in grazers from the Last Glacial-Interglacial Transition to the early Holocene, there is no evidence for regional-scale declines in grassy vegetation. Several potential mechanisms may account for this decoupling of grazers and grass abundance. The possible strengthening of winter rainfall systems during glacial Pleistocene may have played a role by enhancing year-round availability of grasses in the interior and by elevating moisture availability and productivity in the Cape Floristic Region. Alternatively, current paleoecological data allow for the possibility that Pleistocene 'grazers' consumed more dicots, such that their decline at the onset of the Holocene reflects dietary niche contraction rather than vegetation change. These findings contribute to a growing body of evidence challenging the link between grass abundance and grazer diversity and complicate our understanding of the drivers of late Quaternary extinctions in southern Africa.

1. Introduction

Southern Africa's large mammal fossil record features prominently in research on late Quaternary paleoenvironmental change in the region. Classic studies by Klein (1972, 1978, 1983) on fossil mammals from the Cape Floristic Region demonstrated a marked decline in the abundance and diversity of ungulate grazers from the end of the Last Glacial Maximum (LGM; 26.5-19 ka; Clark et al., 2009) to the onset of the Holocene (11.7 ka to present). This was associated with the extinction of several species adapted to foraging in open and grassy environments, such as the long-horn buffalo (*Syncerus antiquus*), giant wildebeest (*Megalotragus priscus*), and Cape zebra (*Equus capensis*) (Faith, 2014; Klein, 1980, 1984). Though the magnitude of faunal turnover observed elsewhere in southern Africa tends to be less pronounced than in the fynbos biome (Klein, 1980), Late Pleistocene fossil assemblages consistently document extinct and extralimital grazers (e.g., Cruz-Uribe, 1983; Klein et al., 1991; Plug and Engela, 1992; Thackeray, 1979), suggesting that the loss of grazer diversity across the Pleistocene-Holocene transition is a regional phenomenon (Brink, 2016).

Researchers have offered various related explanations to account for these changes in faunal community composition. Chief among them is that LGM and Last Glacial-Interglacial Transition (LGIT; 19 to 11.7 ka) environments had more extensive grassy cover relative to today (e.g., Faith, 2013b; Klein, 1972, 1978, 1983; Thackeray, 1979). Although the link between grazers and grasslands is intuitively appealing (but see

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https://doi.org/10.1016/j.qsa.2024.100259
Received 24 October 2024; Received in revised form 2 December 2024; Accepted 4 December 2024
Available online 6 December 2024

Sokolowski et al., 2023), especially in parts of southern Africa where grasses are sparse today, independent evidence for an expansion of grassy cover is mixed at best. Many pollen records, including those from parts of southern Africa with dramatic temporal shifts in faunal composition, fail to show any appreciable increases in grassy cover during the LGM and Late Glacial (e.g., Dupont et al., 2022; Holmgren et al., 2003; Scott, 2002; Zhao et al., 2024). This poses an apparent conflict between environmental interpretations derived from the mammalian fossil record and the empirical evidence for vegetation change. If this mismatch is widespread across southern Africa, it may be that the regional-scale environmental signal provided by the faunal evidence is not reflecting the amount of grass on the landscape (though this may be important at local scales), but rather its seasonal availability and year-round productivity (e.g., Brink and Lee-Thorp, 1992; Faith, 2011b; Thackeray, 1980). It follows that a regional-scale assessment of late Quaternary faunal and floral records is warranted.

With this in mind, we examine late Quaternary faunal and pollen records from across southern Africa to evaluate whether there have been coherent shifts in faunal composition and vegetation structure since the LGM. This two-pronged approach first quantifies the faunal evidence from stratified faunal sequences across southern Africa to evaluate the regional pattern of long-term shifts in ungulate community composition from the LGM through the Holocene. We then synthesize a dataset of late Quaternary pollen records to evaluate whether there are parallel changes in grassy cover. Taken together, these analyses allow us to ask whether regional-scale changes in ungulate community composition are a consequence of changing overall availability of grasses on the landscape.

2. Methods

2.1. *Fauna*

Faunal data were compiled from sites across southern Africa that encompass the Pleistocene-Holocene transition—i.e., those that preserve terminal Pleistocene (LGM to LGIT) and early Holocene deposits. These include Boomplaas Cave, Buffelskloof Rock Shelter, Bushman Rock Shelter, Byneskranskop 1, Elands Bay Cave, Equus Cave, Nelson Bay Cave, Putslaagte 8, Rose Cottage Cave, and Sehonghong (Fig. 1, Table 1, SI Tables 1 and 2). These sites collectively encompass considerable environmental variation across southern Africa today, occurring in different biomes (e.g., fynbos, grassland, and savanna; after Rutherford et al., 2006) and climatic zones (e.g., winter, aseasonal and summer rainfall zones; after Chase and Meadows, 2007).

We restricted faunal lists from each site in this analysis to the dominant large mammals, the ungulates, which include artiodactyls, perissodactyls, and proboscideans. Each taxon was assigned to a dietary guild following Gagnon and Chew (2000), who define guilds based on percentage of monocots, dicots, and fruits consumed. We use the following categories: browser (>70% dicots), grazer (>60% monocots), which combines the Gagnon and Chew obligate grazer and variable grazer categories, mixed feeder, for Gagnon and Chew's browser-grazer intermediate and generalist categories. We assign bush pigs (*Potamochoerus*) to an ominivore category outside of Gagnon and Chew's classification scheme (Leslie and Huffman, 2015). We also categorized each taxon by herbivore functional type following Hempson et al. (2015): (A) small, non-social, water independent browser/frugivores (e.g., *Sylvicapra grimmia*), (B) small-medium, social, non-water reliant mixed feeders (e.g., *Antidorcas marsupialis*), (C) large, social, water dependent browsers (e.g., *Tragelaphus strepsiceros*), (D) medium-large, social, water dependent grazers (e.g., *Alcelaphus buselaphus*), and (E) large, water dependent, non-ruminants (e.g., *Equus quagga*). For the extinct species in our dataset, we assign diet and functional type classifications using extant congeners (e.g., *Equus* spp. for extinct *Equus capensis*) or nearest living relatives (e.g., *Connochaetes* spp. for extinct *Megalotragus priscus*) (i.e., taxonomic uniformitarianism). The one exception is Bond's springbok (*Antidorcas bondi*), which is known to have been a grazer (Brink and Lee-Thorp, 1992), unlike extant springbok (*Antidorcas marsupialis*), which are mixed feeders (Gagnon and Chew, 2000). Both Bond's springbok and extant springbok are placed in herbivore functional type B, in which Hempson et al. include other small-medium mixed-feeding to grazing antilopins. Each faunal

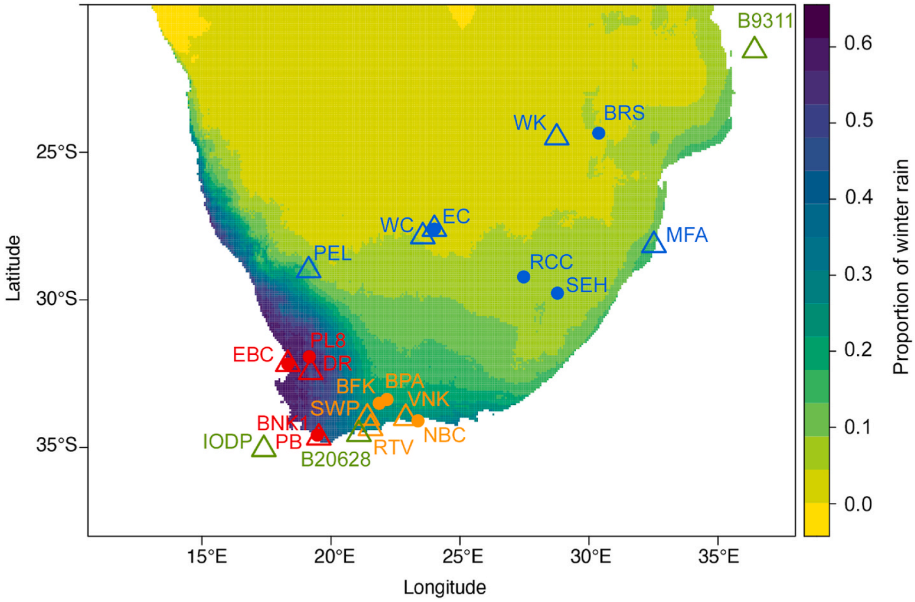

Fig. 1. Map of southern Africa with a color gradient that represents the proportion of winter (June–August) rainfall. Sites in each rainfall zone are color-coded: Winter Rainfall Zone (WRZ) sites are red, Aseasonal Rainfall Zone (ARZ) sites are orange, Summer Rainfall Zone (SRZ) sites are blue, and marine sites are green. Pollen sites are designated by triangles, and faunal sites are designated by circles. Site names are abbreviated as follows: Boomplaas (BPA), Buffelskloof (BFK), Bushman Rock Shelter (BRS), Byneskranskop 1 (BNK1), De Rif (DR), Eland's Bay Cave (EBC), Equus Cave (EC), GeoB20628-1 (B20628), GeoB9311-1 (B9311), IODP Site 361-U1479 (IODP), Mfabeni (MFA), Nelson Bay Cave (NBC), Pearly Beach (PB), Pella 1 (PEL), Putslaagte 8 (PL8), Rietvlei-Still Bay (RTV), Rose Cottage Cave (RCC), Sehonghong (SEH), Seweweekspoort (SWP), Vankervelsvlei (VNK), Wonderkrater (WK) and Wonderwerk Cave (WC). The precipitation base map was generated with data from CRU-TS 4.06 (Harris et al., 2020) downscaled with WorldClim 2.1 (Fick and Hijmans, 2017).

Table 1
Faunal records from southern Africa spanning the Pleistocene-Holocene transition. Rainfall zones are abbreviated as follows: Winter Rainfall Zone (WRZ), Aseasonal Rainfall Zone (ARZ), Summer Rainfall Zone (SRZ).

Site	Lat	Long	Rainfall Zone	Age range [ka]	Fauna Source	Age Source
Boomplaas	-33.38	22.17	ARZ	2.8 - 35.2	Faith (2013a)	Pargeter et al. (2018)
Buffelskloof Rock Shelter	-33.51	21.87	ARZ	3.8 - 19.1	Opperman (1978)	Opperman (1978)
Bushman Rock Shelter	-24.35	30.38	SRZ	12 - 18	Badenhorst and Plug (2012), Plug (1981)	Badenhorst and Plug (2012)
Byneskranskop 1	-34.58	19.47	WRZ	1.8 - 16.6	Schweitzer and Wilson (1982)	Loftus et al. (2016)
Elands Bay Cave	-32.18	18.33	WRZ	9.3 - 15.5	Klein and Cruz-Uribe (2016)	Klein and Cruz-Uribe (2016)
Equus Cave	-27.617	24.633	SRZ	4.9 - 16.3	Klein, Cruz-Uribe, and Beaumont (1991)	Vogel et al. (1986)
Nelson Bay Cave	-34.10	23.37	ARZ	10.4 - 22.2	Klein (1972)	Loftus et al. (2016)
Putslaagte 8	-31.93	19.16	WRZ	12.5 - 23.5	Mackay et al. (2015)	Mackay et al. (2015)
Rose Cottage Cave	-29.22	27.47	SRZ	8.4 - 23.9	Plug and Engela (1992)	Wadley and Vogel (1991)
Sehonghong	-29.77	28.78	SRZ	12.9 - 29.7	Plug and Mitchell (2008); unpublished Plug database	Plug and Mitchell (2008); Pargeter et al. (2017)

assemblage was then sorted into time bins: MIS2/3 (56–26.5 ka), LGM (26.5–19 ka), LGIT (19–11.7 ka), early Holocene (11.7 - 8 ka), mid-Holocene (8–4 ka), and late Holocene (4–0 ka).

We conducted two analyses to identify temporal changes in faunal community composition. To summarize broad changes in the functional makeup of faunal communities, the first analysis employs a detrended correspondence analysis (DCA), using the ‘vegan’ package (Oksanen et al., 2022) in R version 4.3.2 (R. Development Core Team, 2023). To ameliorate noise introduced by small samples, only assemblages with at least three taxa are included ($n = 93$ assemblages). The DCA was conducted on the number of taxa within each functional type for each assemblage (SI Fig. 1), such that assemblages are differentiated from each other based on functional composition as opposed to taxonomic identity. This analysis is sensitive to the relative proportions of taxa across function groups rather than the absolute number of taxa (e.g., an assemblage with four grazers and one browser is identical to an assemblage with eight grazers and two browsers). Functional type C (large, social, water-dependent browsers) was excluded because only one species in our dataset (the greater kudu: *Tragelaphus strepsiceros*) belongs to this type, and singletons in correspondence analysis can disproportionally influence the outcome (Faith and Lyman, 2019). We then used the DCA axis 1 score as a summary measure of faunal composition (Faith and Lyman, 2019). To facilitate the identification of temporal shifts in faunal composition across sites, we scaled the DCA axis 1 score for each assemblage using z-scores. These were calculated using site-specific means (μ) and standard deviations (σ) for the DCA axis 1 score of each assemblage (x), with the following equation: $z = (x-\mu)/\sigma$. The rationale for doing so is that this allows for comparison of sites that may show similar functional trends but have different baselines (e.g., two sites may show a similar loss of type D through time but one may be more dominated by type D taxa than the other). To statistically compare change over time, we then used a Tukey test (Tukey, 1949) to test for significant differences in z-scores between time bins.

Because temporal changes in grazer richness (and abundance) feature prominently in discussion of southern Africa’s late Quaternary faunas, our second analysis directly examines the representation of grazing taxa by comparing the proportion of grazer species across assemblages. In our dataset, the more common grazers include plains zebra (*Equus quagga*), hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*), mountain reedbuck (*Redunca fulvorufula*), and buffalo (*Syncerus caffer*). Once again, only assemblages with at least three taxa are included. Following the same procedure described above, we z-scored the proportion of grazers in each assemblage (on a per site basis) to synthesize temporal trends and again used a Tukey test to identify significant differences between time bin z-scores. Because the relative proportions of different functional types and dietary guilds may be sensitive to sampling artifacts (Faith and Lyman, 2019), we used Spearman’s Correlation Coefficients to examine whether DCA axis 1 scores and grazer proportions are driven by assemblage sample size (minimum number of individuals, MNI).

2.2. Pollen

Pollen data were compiled from both continental and marine cores that encompass the Pleistocene-Holocene transition across southern Africa: De Rif, Elands Bay Cave, Equus Cave, GeoB20628-1, GeoB9311-1, IODP U1479, Mfabeni, Pearly Beach, Pella 1, Rietvlei-Still Bay, Seweweekspoort, Vankervelsvlei, Wonderkrater, and Wonderwerk Cave (Fig. 1, Table 2, SI Table 3). As with the faunal data, the localities from which these cores derive span considerable variability in present-day vegetation (e.g., fynbos, savanna, and succulent karoo biomes) and climate regimes (e.g., winter, aseasonal, and summer rainfall zones).

Assemblages from each core were sorted into the same time bins as the faunal data. Because pollen are often identified at coarse taxonomic resolution (e.g., family level or above), many commonly identified southern African pollen taxa encompass large numbers of species and various growth forms (e.g., herbs, shrubs, trees) (Chevalier et al., 2021b). Rather than attempting a multivariate ordination of pollen functional types, we instead focus on the proportion of grasses (Poaceae)—the variable frequently thought to explain temporal shifts in faunal composition (e.g., Faith, 2013b; Klein, 1972, 1978; Thackeray, 1979). Although both C_3 and C_4 grasses are present in southern Africa, these cannot be differentiated on the basis of pollen. Following the same methods described for the fauna, we calculated the z-scores for proportion Poaceae in each assemblage from each core and conducted parallel Tukey tests.

3. Results

Turning first to the fossil fauna, we note that there are no strong correlations between assemblage sample size and the DCA axis 1 scores (Spearman’s rho $= -0.186$, $p = 0.074$) or the proportion of grazers (Spearman’s rho $= -0.040$, $p = 0.707$). It follows that variation in sample size is not responsible for driving the temporal trends examined here. DCA axis 1 differentiates assemblages based on the proportion of species falling within functional type A (small, non-social, water independent browser/frugivores) versus D (medium-large, social, water dependent grazers) (Fig. 2, Table 3). This confirms that the representation of ruminant grazers (e.g., *Alcelaphus buselaphus*, *Damaliscus pygargus*, *Connochaetes gnou*), especially relative to small-bodied browsers and frugivores (e.g., *Raphicerus melanotis*, *Sylvicapra grimmia*, and *Philantomba monticola*), underpins much of the spatiotemporal variation in assemblage composition across southern Africa’s late Quaternary fossil record. When both DCA axis 1 z-scores and grazer proportion z-scores are plotted over time for each site, similar patterns emerge (Fig. 3). Both metrics indicate peak representation of type D species/grazers during the LGIT, with considerable declines into the early Holocene. Tukey test outputs show significant differences in z-

Table 2

Pollen records from southern Africa spanning the Pleistocene-Holocene transition. Rainfall zones are abbreviated as follows: Winter Rainfall Zone (WRZ), Aseasonal Rainfall Zone (ARZ), Summer Rainfall Zone (SRZ).

Site	Lat	Long	Region	Age Range [ka]	Relevant Citations	Data Source
De Rif (DR2)	−32.45	19.2	WRZ	6–24	Quick et al. (2011); Chase et al. (2011)	Quick et al. (2011)
Elands Bay Cave	−32.2	18.3	WRZ	10.66–40	Meadows and Baxter (1999)	Meadows and Baxter (1999)
Equus Cave	−27.6	24.0	SRZ	0.8–30	Scott (1987)	Scott (1987)
GeoB20628-1	−34.6	21.1	Indian Ocean	0–13.5	Zhao et al. (2024)	Zhao et al. (2024)
GeoB9311-1	−21.6	36.4	Indian Ocean	1–208	Dupont and Kuhlmann (2017)	Dupont and Kuhlmann (2017)
IODP Site 361-U1479	−35.06	17.4	Atlantic Ocean	0–300	Dupont et al. (2022)	Dupont et al. (2022)
Mfabeni	−28.2	32.5	SRZ	0.3–35	Finch and Hill (2008); Baker et al. (2016, 2017); Miller et al. (2019)	Finch and Hill (2008)
Limpopo MD96-2048	−26.2	34.0	Indian Ocean	<342	Dupont et al. (2011)	Dupont et al. (2011)
Pearly Beach	−34.7	19.5	WRZ	0.3–25.3	Quick et al. (2022)	Quick et al. (2022)
Pella 1	−29	19.1	SRZ	0.9–49.4	Lim et al. (2016)	Lim et al. (2016)
Rietvlei-Still Bay	−34.4	21.5	ARZ	0–34.8	Quick et al. (2015)	Herzschuh et al. (2021)
Seweweekspoort	−33.4	21.4	ARZ	0–22.5	Chase et al. (2018)	Chase et al. (2018)
Vankervelsvlei	−34.0	22.9	ARZ	4.4–109	Quick et al. (2016)	Quick et al. (2016)
Wonderkrater borehole 3	−24.5	28.8	SRZ	0–19.89	Scott and Thackeray (1987); Scott et al. (2003, 2008, 2012); Scott (2016), Truc et al. (2013); Chevalier and Chase (2015, 2016).	Sanchez Goñi et al. (2017b)
Wonderkrater borehole 4	−24.5	28.8	SRZ	20–28	Scott and Thackeray (1987); Scott et al. (2003, 2008, 2012); Scott (2016), Truc et al. (2013); Chevalier and Chase (2015, 2016).	Sanchez Goñi et al. (2017a)
Wonderwerk Cave	−27.85	23.6	SRZ	0.3–36.4	Scott and Thackeray (2015)	Scott and Thackeray (2015)

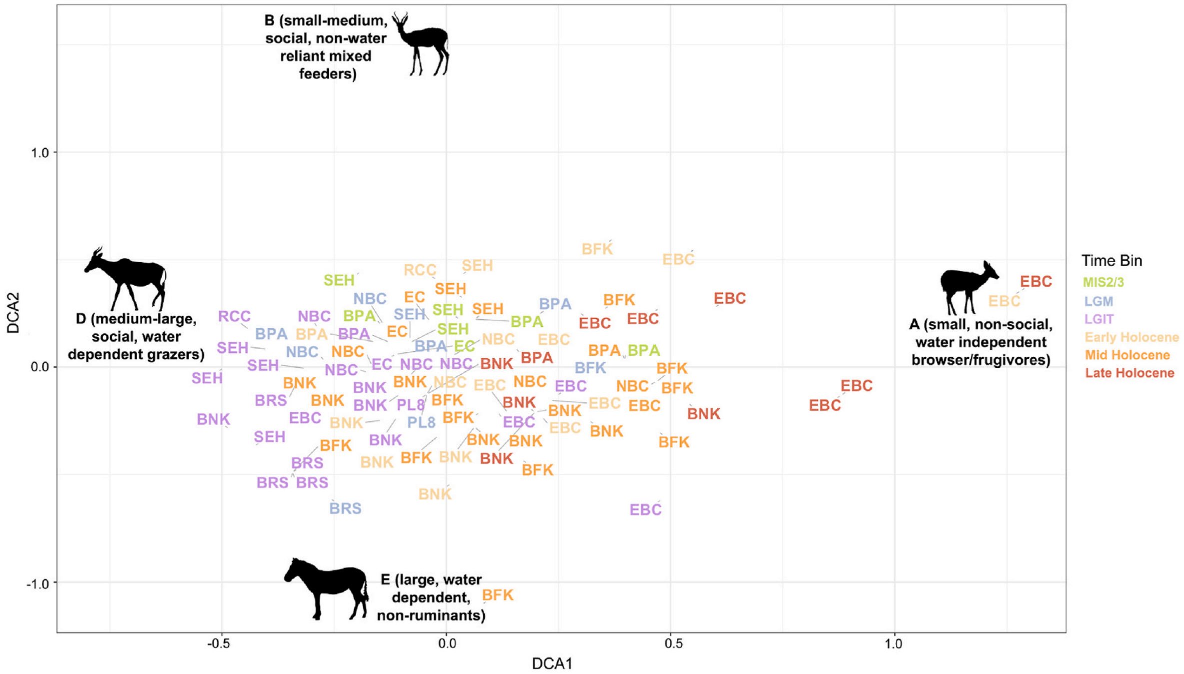

Fig. 2. Detrended Correspondence Analysis (DCA) scores for each herbivore functional type (black silhouettes) and each faunal assemblage, labeled by site and colored by time bin. Site names are abbreviated as Boomplaas (BPA), Buffelskloof (BFK), Bushman Rock Shelter (BRS), Byneskranskop 1 (BNK), Eland's Bay Cave (EBC), Equus Cave (EC), Nelson Bay Cave (NBC), Putslaagte 8 (PL8), Rose Cottage Cave (RCC), and Sehonghong (SEH). Animal silhouettes are from Phylopic (https://www.phylopic.org).

Table 3

DCA Hempson functional type loadings.

Functional type	DCA1	DCA2	DCA3	DCA4
A	1.281	0.354	−0.358	−0.432
B	−0.307	1.554	1.687	0.634
D	−0.766	0.122	−0.787	−0.404
E	0.080	−1.102	0.806	0.728

score distributions for both DCA axis 1 and grazer proportions between the LGIT and the Holocene (Fig. 4). There are no significant differences between the Pleistocene time bins (MIS2/3, LGM, or LGIT) or between the Holocene time bins (early, middle, and late Holocene).

Our analysis of the pollen records shows a very different pattern. When z-scores of percent Poaceae are plotted over time for all assemblages, there is no pattern in shifting grass abundances across southern Africa (Fig. 3). The pollen Tukey test yielded no significant differences in

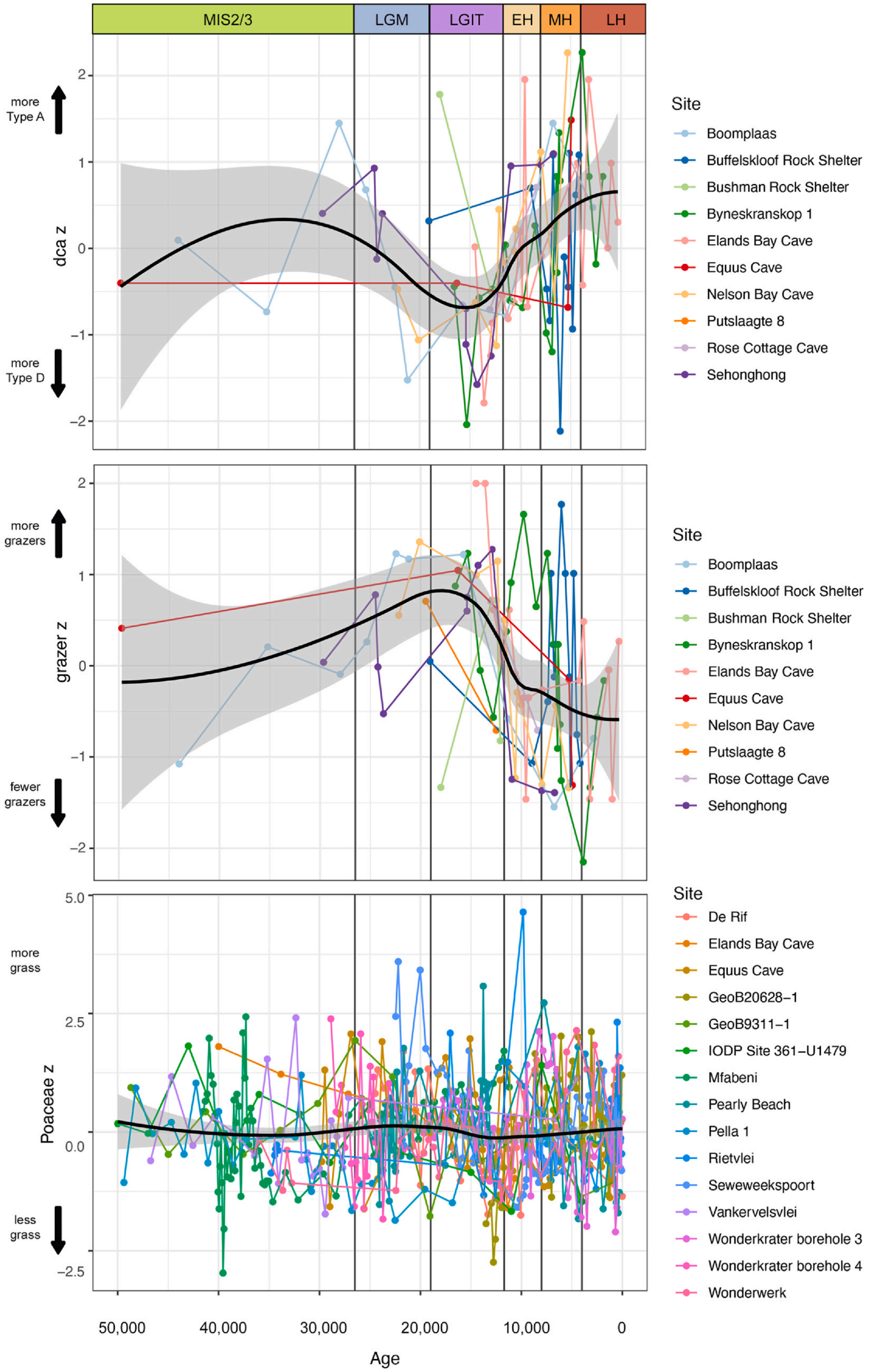

Fig. 3. Z-scores over time for DCA axis 1 scores and grazer proportion for each faunal record and grass (Poaceae) proportions for each pollen record. Time bins are designated by colored bands: MIS2/3 (56–26.5 ka), LGM (26.5–19 ka), LGIT (19–11.7 ka), early Holocene (EH, 11.7 - 8 ka), mid-Holocene (MH, 8–4 ka), and late Holocene (LH, 4–0 ka). Colored lines represent each individual record. The black lines are loess curves that summarize the trends of their entire respective data sets, calculated as a moving average of 75% of the data. The dark grey area around each loess line indicates a 95% confidence interval. Expanded confidence intervals during MIS 2/3 for faunal records are a consequence of low sample size.

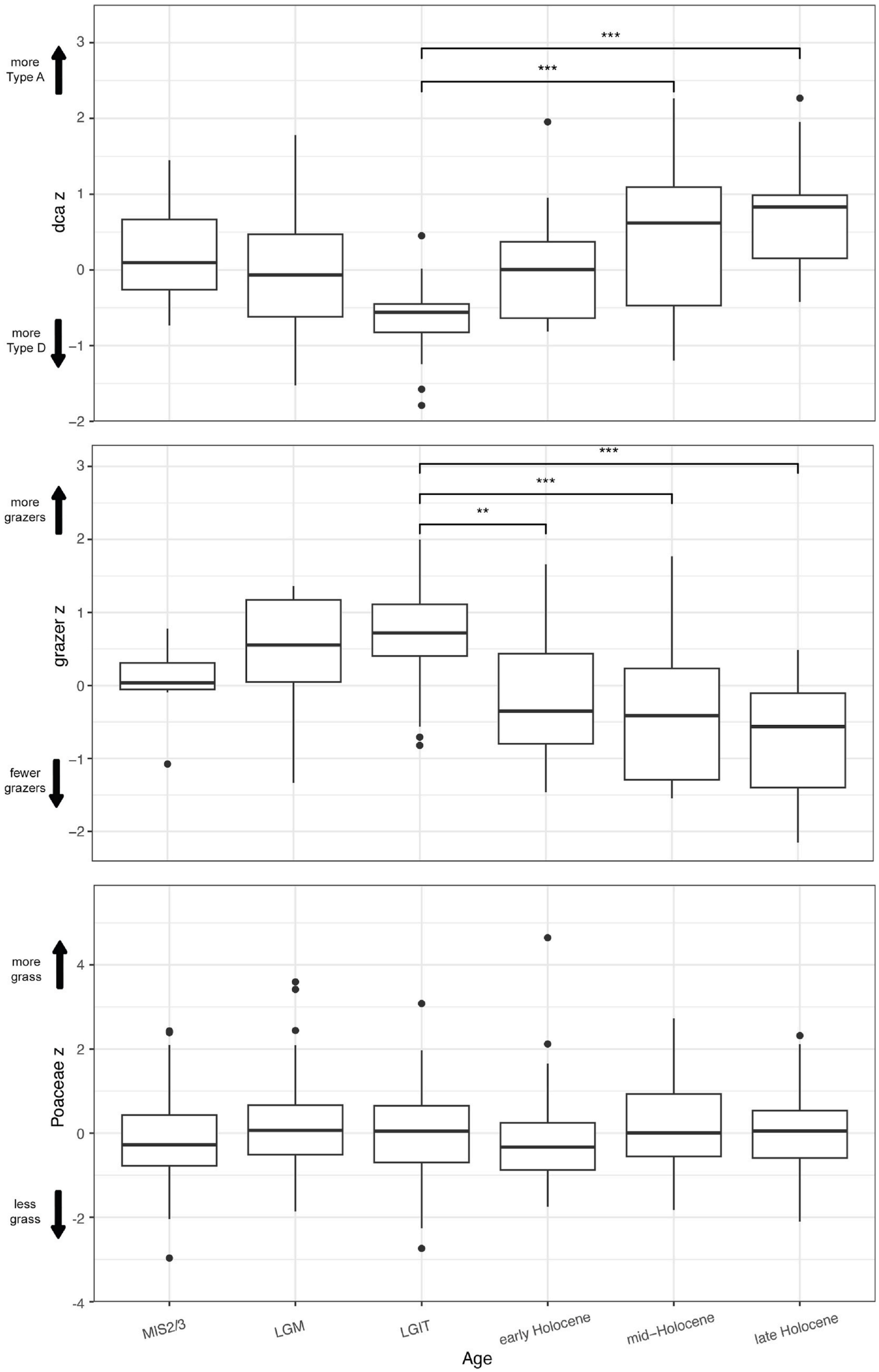

Fig. 4. The distribution of z-scores for faunal DCA axis 1, grazer proportion, and Poaceae proportion in each time bin: MIS2/3 (56–26.5 ka), LGM (26.5–19 ka), LGIT (19–11.7 ka), early Holocene (11.7 - 8 ka), mid-Holocene (8–4 ka), and late Holocene (4–0 ka). Pairs with significant differences are labeled where ** indicates $p \leq 0.01$ and *** indicates $p \leq 0.001$.

Poaceae z scores over time (Fig. 4).

4. Discussion

Our analysis shows that there is a coherent regional-scale decline in grazers and relatedly in Hempson's herbivore functional type D (medium-large, social, water dependent grazers) from the LGIT to the Holocene (Figs. 2 and 3). This trend is present at sites in the southern Cape (Faith, 2013a; Klein, 1972), the southwestern Cape (Klein and Cruz-Uribe, 2016; Mackay et al., 2015), in the interior at Equus Cave (Klein et al., 1991), in the highlands around Lesotho (Plug and Engela, 1992; Plug and Mitchell, 2008), and in the lowveld at Bushman Rock Shelter (Badenhorst and Plug, 2012; Plug, 1981). At nearly all of the sites in our sample, the change in functional composition is associated with extirpations (e.g., disappearance of black wildebeest from the southern Cape) and extinctions (e.g., *Equus capensis*, *Syncerus antiquus*, *Antidorcas bondi*) (SI Table 1) of grazing ungulates (i.e., temporal changes in community composition are not a consequence of increased diversity among browsers or mixed feeders; see Faith, 2011b). Our analyses reinforce the long-standing focus on turnover among grazers and imply a regional-scale phenomenon that likely resulted from regional-scale (or larger) forcing mechanisms. Significantly, the coherence in southern Africa's late Quaternary faunal records contrasts with observations of oftentimes considerable paleoclimatic variability at finer spatial scales (e.g., Chase et al., 2017; Chase and Meadows, 2007; Chase and Quick, 2018).

Though researchers have linked changes in faunal composition to the extent of grassy vegetation (e.g., Faith, 2013b; Klein, 1972, 1978, 1983; Thackeray, 1979), our analysis of the pollen record fails to detect a complementary regional-scale decline in the abundance of grasses (Figs. 2 and 3). Importantly, the pollen records examined here encompass a comparable spatial scale as the fossil mammal records, spanning a broad swathe of southern Africa (Fig. 1). From the regional-scale perspective provided by this analysis, the expectation is that both the mammal and pollen records should show parallel trends if temporal changes in the former (e.g., decline of grazers) are a consequence of changes in the latter (e.g., loss of grass). In contrast to this expectation, we see little evidence that the strong regional-scale faunal signal is linked to a regional-scale decline of grassy vegetation (Figs. 2 and 3). A small number of individual pollen records demonstrate declines in grass from the LGM through the Holocene (e.g., Seweweekspoort and Elands Bay Cave) (Chase et al., 2018; Meadows and Baxter, 1999; Parkington et al., 2000), implying some local-scale losses of grass, but in the majority of pollen records across southern Africa, there is no appreciable decline in grass pollen abundance over time. The regional-scale signal is one of muted change — and no significant changes from the LGIT into the Holocene, precisely when we observe the most dramatic changes in faunal community composition. This is perhaps best exemplified in the Cape Floristic Region, which shows some of the most dramatic changes in ungulate community composition across the Pleistocene-Holocene Transition (P-HT) (Klein, 1972, 1978, 1983; Klein and Cruz-Uribe, 2016), yet the marine core records that sample the region (IODP U1479 and GeoB20628-1) fail to demonstrate major declines in Poaceae abundance across this interval (Dupont et al., 2022; Zhao et al., 2024).

Our analyses do not rule out the possibility of important local-scale changes in grass extent across the P-HT, as demonstrated at a few sites (e.g., Chase et al., 2018; Parkington et al., 2000), but the lack of a region-wide decline in grasses implies that the extent of grasses on the landscape cannot account for regional-scale faunal shifts. We can reasonably reject the possibility that this apparent mismatch is due to sampling bias, as this would require a highly improbable scenario—i.e., that the faunal records consistently sample environments where grass declined whereas the pollen records do not. From an ecological perspective, the apparent mismatch between the faunal and pollen records is perhaps not surprising. With the exception of the faunal records from the Cape Floristic Region, those from the interior of southern Africa occur in places where there is still a considerable amount of grass today, and presumably through much of the Holocene. A decline in the extent of grassy vegetation seems unlikely to account for the loss of grazing fauna across diverse and variably grassy biomes. This is reinforced by observations from Sokolowski et al. (2023), who show that grazers, browsers, and mixed feeders have a very broad, and frequently overlapping, tolerance for variation in vegetation composition.

If the temporal shift in faunal composition is not a consequence of the amount of grass on the landscape, then what is the likely driver? Based on inferences about the ecology of the extinct Bond's springbok (*Antidorcas bondi*), Brink and Lee-Thorp (1992) propose that a key factor is year-round availability of grassy forage. Bond's springbok was a small-bodied (~30 kg) grazer that is commonly found in Pleistocene and earliest Holocene fossil assemblages from the interior of southern Africa (Brink, 2016; Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018). Unlike the extant springbok (*Antidorcas marsupialis*), which consume grasses in the wet season and switch to dicots when the grasses cure during the dry season (Gagnon and Chew, 2000; Kingdon, 2015; Skinner and Louw, 1996), isotopic analysis demonstrates that Bond's springbok consumed a greater amount of C_4 grasses (Brink and Lee-Thorp, 1992; Ecker and Lee-Thorp, 2018). This is atypical of extant smaller-bodied antelopes, which are limited by forage quality rather than quantity and are unable to meet their energetic demands by consuming low-quality cured grasses in the dry season (e.g., Bell, 1971). The dominance of grass in the diet of Bond's springbok strongly suggests that there was year-round availability of high-quality grasses (Brink and Lee-Thorp, 1992). Thus, Brink proposes that Middle-to-Late Pleistocene faunas in southern Africa are signaling grassy ecosystems that were productive throughout the year and able to sustain a grazing succession unlike that seen today—e.g., from enormous grazers like the giant long-horn buffalo (*Syncerus antiquus*) to small-bodied grazers like Bond's springbok (Brink, 1987, 1994, 2016; Brink and Lee-Thorp, 1992).

Two mechanisms could be important in promoting year-round availability of palatable grassy forage in southern Africa's interior. First, lower temperatures during glacial Pleistocene (e.g., Chevalier et al., 2021a; Talma and Vogel, 1992) implies a reduction in evapotranspiration, which should prolong the palatability of grasses during the drier parts of the year. Second, there is growing evidence from paleoecological records (Ecker et al., 2018a; Lee-Thorp and Beaumont, 1995) and climate models (Engelbrecht et al., 2019) that southern Africa's winter rainfall systems were intensified and penetrated deeper into the interior during glacial phases of the Pleistocene. The majority of grass available to grazing ungulates in southern Africa today is C_4 grass, which favors a warm growing season and is relatively abundant in the SRZ. C_3 grass, which tolerates a cold growing season, is found primarily in the WRZ, in smaller proportions in the ARZ, and at high elevations in the Drakensberg region (Vogel, 1978). Whereas winter rains today are primarily restricted to the southern and western margins of southern Africa, the potential expansion of winter rains into the interior (where most rainfall presently occurs in the summer) would enhance moisture availability during the dry season and promote growth of some C_3 grasses in the winter (Lee-Thorp and Beaumont, 1995). Stable carbon isotope analysis of grazer tooth enamel from Equus Cave and Wonderwerk Cave is consistent with the consumption of more C_3 forage during the Late Pleistocene relative to the Holocene (Ecker et al., 2018a; Lee-Thorp and Beaumont, 1995). The availability of fresh grass in both the summer (C_4 grass) and winter (C_3 grass) could result in the kind of year-round access to grasses envisioned by Brink for the southern African interior (Brink, 1987, 1994, 2016; Brink and Lee-Thorp, 1992). If this hypothesis is correct, then it should be testable through evaluation of temporal changes in proxy records that document seasonality (e.g., isotopic records of seasonality in herbivore tooth enamel; Blumenthal et al., 2019; Norwood et al., 2023).

Several related factors may be important in explaining the high diversity of ungulate grazers in the Cape Floristic Region. Paleoecological records show that high grazer diversity during the LGM and LGIT occurs in environments where the dominant grasses were C_3 or a mixture of C_3 and C_4 species (e.g., Sealy et al., 2016, 2020; Stowe and Sealy, 2016). As in the interior of southern Africa, strengthening of the winter rainfall systems during glacial Pleistocene is likely to have played a key role in promoting grazer diversity. Intensification of winter rainfall is broadly linked to wetter conditions across much of the Cape Floristic Region (e.g., Chase et al., 2017; Chase and Meadows, 2007; Faith et al., 2019, 2020). Especially in the arid-to-semi-arid parts of the region, the associated increase in primary productivity should favor greater diversity and biomass among mid-sized grazers relative to small browsers (e.g., Faith et al., 2024; Hempson et al., 2015). At the same time, biogeographic processes should interact to enhance grazer diversity within the regional species pool. The combination of wetter conditions and lower sea levels means that important dispersal barriers were eliminated, facilitating ungulate dispersals from the interior (Compton, 2011; Faith and Behrensmeyer, 2013). Moreover, due to the increase in species richness as a consequence of geographic area (i.e., the species-area relationship; MacArthur and Wilson, 1967), the added landmass created by the exposure of the Paleo-Agulhas Plain during marine regressions (de Wet and Compton, 2021) is predicted to enhance regional diversity. The combination of these climatic and biogeographic factors could explain the frequent occurrence of extralimital grazers that are presently restricted to southern Africa's interior (e.g., *Connochaetes gnou*, *Redunca arundinum*) as well as extinct species in the late Pleistocene fossil record from the Cape Floristic Region.

The decoupling of floral and pollen records across southern Africa also warrants a reconsideration of a fundamental assumption—that Pleistocene grazers were dependent on access to grassy forage. Many of the taxa identified as grazers in South Africa's late Quaternary fossil record are classified based on their dental morphology and through assessment of the diets of their extant relatives (e.g, Faith, 2014; Klein, 1980). However, many mammalian herbivores likely had greater dietary flexibility in the past than is observed today (e.g., Codron et al., 2024; Faith, 2011a; Kaiser and Franz-Odendaal, 2004; Stynder, 2009), and the extension of modern dietary assignments into the Pleistocene may not be representative of fossil herbivore diet. For instance, dental mesowear analysis of Pleistocene (~1 Ma to 600 ka) herbivores from Elandsfontein indicates that many presumed grazers (e.g., alcelaphin antelopes) consumed more dicots than suggested by their craniodental morphology or by their extant relatives (Stynder, 2009). Likewise, we have previously noted that isotopic analyses of fossil herbivores from several Pleistocene localities in the interior of South Africa—where most grasses follow the C_4 photosynthetic pathway—frequently indicate an important C_3 dietary component in grazer lineages (e.g., equids and alcelaphins) (e.g., Codron et al., 2008, 2023, 2024; Ecker et al., 2018b; Lee-Thorp and Beaumont, 1995). Though this may be indicative of C_3 grass consumption (Ecker et al., 2018a; Lee-Thorp and Beaumont, 1995), it is also possible that Pleistocene 'grazers' in southern Africa consumed more dicots than their present-day counterparts. A plausible mechanism is lower atmospheric CO_2 concentrations during glacial Pleistocene, which can enhance plant nitrogen content and reduce secondary compound concentrations (Owensby et al., 1996), perhaps increasing the palatability of dicots. If many of the Pleistocene species presumed to be grazers were instead mixed feeders, then this may also account for the apparent decoupling between faunal and pollen records in our analysis—i.e., the prevalence of 'grazers' in the Late Pleistocene is not indicative of more grass or greater year-round availability of grass, but rather by an expanded dietary niche that includes grasses and dicots. Future paleodietary investigations (e.g., mesowear and dental microwear) are needed to more fully explore this hypothesis.

5. Conclusion

Our analysis of the faunal and pollen records from the Pleistocene-Holocene Transition in southern Africa demonstrates a decoupling between trends in grazer diversity and grassy vegetation across this interval. These findings contradict the long-standing hypotheses that the extinction and extirpation of grazers in these records are a function of contracting or disappearing grasslands. The persistence of grass in the pollen records suggests a more complicated relationship between grazers and grasslands and possibly implicates seasonality as a driver of faunal change and extinction. We hypothesize that strengthening of winter rainfall systems during glacial Pleistocene played a key role by enhancing year-round availability of grasses in the interior and by elevating moisture availability and productivity in the Cape Floristic Region. Alternatively, it is also possible that late Quaternary faunal turnover in southern Africa reflects a contraction of the expanded dietary niches of presumed 'grazers' to the grazing niche observed today. Further investigation of trends in paleo-seasonality and paleodiets in southern Africa during the late Quaternary will be necessary to better characterize ecosystem change and what forces drove these extinctions.

CRediT authorship contribution statement

Alexandra L. Norwood: Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Formal analysis, Conceptualization. **John Rowan:** Writing – review & editing, Formal analysis, Conceptualization. **J. Tyler Faith:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by NSF grants 2403566 (to A.L.N.), 1826666 and BCS-2149759 (to J.T.F.). We thank Brian Chase for his helpful comments on this work at SASQUA and the two anonymous reviewers for their feedback, which improved the clarity of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.qsa.2024.100259.

Data availability

All data are available in the supplementary material.

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