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ARTICLE

The fossil history of Grévy's zebra (*Equus grevyi*) in equatorial East Africa

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ABSTRACT

Aim Within the last several decades, Grévy's zebra (*Equus grevyi*) has undergone a massive reduction in geographical range and population size, largely as the result of human impacts. To place its recent decline in a deeper prehistoric context, and to understand the factors mediating its range and abundance over geological time frames, this study examines the fossil history of Grévy's zebra in equatorial East Africa.

Location Equatorial East Africa.

Methods Presence/absence data for ungulates recovered from fossil sites spanning the last c. 400,000 years in Kenya and Ethiopia were compiled from the literature and from previously unreported palaeontological sites. Associations between Grévy's zebra and other taxa were examined using principal coordinates analysis and non-random species pairs were identified using a Bayesian approach. Changes in rainfall were reconstructed using the average hypsodonty index of ungulate species from fossil assemblages.

Results Grévy's zebra was common during dry phases of the Pleistocene and was found to the south and west of its historical range, coinciding with an expansion of arid grasslands. At the onset of the Holocene, Grévy's zebra was extirpated from southern Kenya and almost completely disappeared from the fossil record. Grévy's zebra was associated with several specialized grazers that became extinct by the end of the Pleistocene. These extinctions and the decline of Grévy's zebra from the Pleistocene to the Holocene are explained by increased precipitation and the consequent loss of arid grasslands at the Pleistocene–Holocene transition. Grévy's zebra is never associated with domestic livestock, unlike the widespread plains zebra.

Main conclusions Grévy's zebra thrived in equatorial East Africa during periods of the Pleistocene when environmental conditions favoured an expansion of arid grasslands. Environmental change across the Pleistocene–Holocene transition contributed to decreases in the range size and abundance of Grévy's zebra, setting the stage for the anthropogenic decline observed in recent decades. The spread of pastoralists in the middle Holocene may have additionally contributed to its prehistoric decline. Contemporary climate change warrants further consideration in planning for the long-term survival of Grévy's zebra.

Keywords

East Africa, environmental change, extinctions, Grévy's zebra, Holocene, palaeoecology, palaeozoology, Pleistocene, species associations.

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INTRODUCTION

In the last few decades, Grévy's zebra (*Equus grevyi* Oustalet, 1882) has suffered a massive reduction in geographical range

and population size. Historically distributed across the Horn of Africa, its range is now discontinuous and restricted to central–northern Kenya and isolated pockets of Ethiopia (Fig. 1). This range reduction is associated with a population

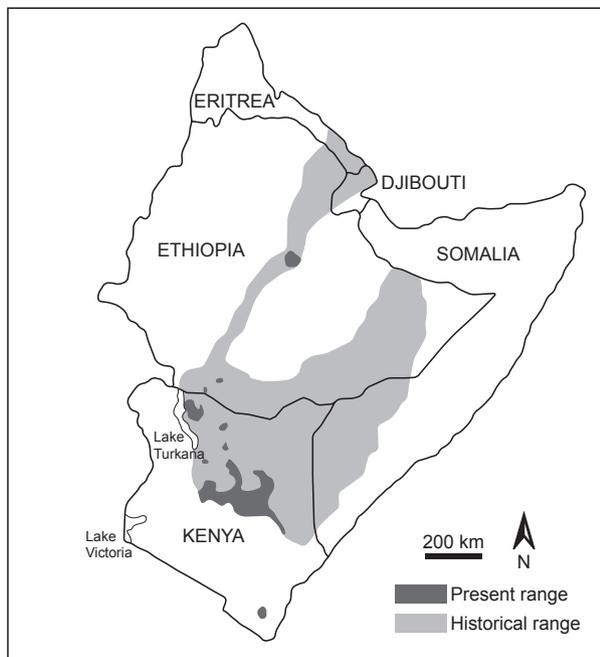


Figure 1 The historical and present range of Grévy's zebra, *Equus grevyi*, in equatorial East Africa (after Kingdon, 1982; Williams, 2002). The isolated population in southern Kenya represents a recent introduction to Tsavo East National Park.

decrease from 15,000 animals in the late 1970s to fewer than 2500 today, with the largest subpopulation including approximately 250 mature individuals (Williams, 2002; Moehlman *et al.*, 2008). As a result of this decline, *E. grevyi* has been listed as endangered by the IUCN since 1986 (Moehlman *et al.*, 2008).

Grévy's zebras are the largest wild equid (350–450 kg) and they inhabit arid to semi-arid grasslands and shrublands where permanent water is available (Kingdon, 1982; Ginsberg, 1988; Bauer *et al.*, 1994; Williams, 1998; Rubenstein, 2010). Compared to the geographically widespread plains zebra (*E. quagga* – formerly *E. burchelli*, Groves & Bell, 2004; Leonard *et al.*, 2005), Grévy's zebras prefer habitats that are more xeric and are characterized by more sparsely distributed food and water supplies (Rubenstein, 2010). They are primarily bulk grazers, although capable of browsing when palatable grasses are scarce (Kingdon, 1982; Rowen & Ginsberg, 1992). Access to free-standing water is a requirement and plays a central role in mediating their movement across the landscape (Rubenstein, 2010). Adults can tolerate between 2 and 5 days without water, whereas lactating females can tolerate only 1 to 2 days away from water (Becker & Ginsberg, 1990; Williams, 2002).

The recent range reduction of Grévy's zebra is considered one of the most substantial declines of any African mammal (Moehlman *et al.*, 2008). Human impacts are largely to blame, with hunting contributing to initial losses in the 1970s and competition for resources and habitat loss and degradation responsible for its continued decline (Williams,

1998, 2002; Sundaresan *et al.*, 2007; Moehlman *et al.*, 2008; Cordingley *et al.*, 2009). In recent years, overgrazing by domestic livestock has altered the vegetation structure and has limited the availability of forage. Access to water has declined due to the monopolization of water holes by pastoralists and livestock, as well as excessive irrigation in highland areas, which has reduced the dry-season flow of perennial rivers. These resource limitations have forced Grévy's zebra to become increasingly mobile to find adequate water and forage, and this increased mobility is associated with elevated juvenile mortality and low recruitment (Williams, 2002). Although hunting has been curtailed, access to resources is likely to remain an ongoing challenge as most Grévy's zebras are found on community rangelands and commercial livestock ranches also inhabited by pastoralists (Williams, 2002). Protected areas make up less than 0.5% of the geographical range of Grévy's zebra (Williams, 2002; Moehlman *et al.*, 2008).

A growing body of fossil evidence documents the presence of Grévy's zebra well outside its historical range (Marean & Gifford-Gonzalez, 1991; Marean, 1992; Potts & Deino, 1995; Tryon *et al.*, 2010). This raises the possibility that populations of Grévy's zebra declined or have been declining long before the first historical observations of the species were made. It follows that in addition to human impacts over the last few decades, the decline of Grévy's zebra may be driven in part by mechanisms operating on temporal scales beyond the limits of human observation, as has been documented in the fossil histories of several other mammal species (Lyman, 1996; Grayson, 2005; Grayson & Delpech, 2005; Faith, 2012a,b).

It is becoming increasingly apparent that fossil evidence can provide valuable insight into the factors mediating the distribution and abundance of large mammals over geological time-scales (Lyman, 1996, 2006; Grayson, 2005; Grayson & Delpech, 2005; Faith, 2012a,b). To place the historical decline of Grévy's zebra in a deeper prehistoric context, and to understand better the factors responsible for its decline, we examine its fossil history in equatorial East Africa over the last *c.* 400,000 years. Our objectives are (1) to determine which ungulate species Grévy's zebra was associated with in the past, and (2) to understand how and why its range/abundance changed through time. We show that the recent anthropogenic decline is rooted in a long-term process of environmentally-driven faunal turnover in East Africa, with important implications for its survival in the face of contemporary global climate change.

MATERIALS AND METHODS

Fossil samples

The following analyses are based on presence/absence data for ungulates (domesticates included) reported from late Quaternary fossil sites spanning the last *c.* 400,000 years in Kenya and Ethiopia (see Appendices S1 & S2 in Supporting Information). We include only fossil taxa identified to genus

or species, with the exception of domestic sheep (*Ovis aries*) and goats (*Capra hircus*), which are combined into a single taxonomic category ('caprine') because the two species are rarely distinguished. The presence/absence matrix has been compiled from the published literature and also includes new fossil data derived from our fieldwork on the late Pleistocene deposits of Kenya's Lake Victoria Basin (Tryon *et al.*, 2010, 2012). Because the following analyses focus on species associations, the presence/absence matrix is restricted to assemblages with > 1 ungulate taxon, and to those species that occur in more than one assemblage. In total, the sample includes 40 taxa documented in 22 middle/late Pleistocene (from *c.* 400,000 to 12,000 years ago) and 57 Holocene (< 12,000 years ago) assemblages from 45 localities (Fig. 2, Appendices S1 & S2).

Although many localities examined here are outside the historical range of Grévy's zebra, its Pleistocene distribution encompasses southern Kenya and northern Tanzania. Kiseke II Rockshelter in northern Tanzania provides the southernmost record of Grévy's zebra, occurring approximately 500 km south of its present range (Marean & Gifford-Gonzalez, 1991). We exclude the Tanzanian fossil record from our analyses, however, because the complete Kiseke II faunal list remains unpublished and there are doubts about the taxonomic identifications of possible Grévy's zebra from other key localities in northern Tanzania, such as Mumba and Nasera rockshelters (Mehlman, 1989). We are confident that the Grévy's zebra records included in our analysis are accurate, having made or confirmed many of the identifications ourselves and relying on additional data reported by experts in African archaeozoology and palaeontology.

Data analysis

The following analyses focus largely on the association of Grévy's zebra with other ungulate taxa in the late Quaternary fossil record. To visualize these associations, we conducted a principal coordinates analysis (PCoA) on a similarity matrix obtained using the Dice–Sørensen coefficient for presence/absence data in the software package *PAST* version 2.15 (Hammer *et al.*, 2001). For a given pair of species, the Dice–Sørensen coefficient is calculated as $2j/(a+b)$, where j is the number of co-occurrences of species A and B, a is the number of occurrences of species A, and b is the number of occurrences of species B. Species that co-occur in the fossil record will cluster together in the PCoA, reflecting a similar fossil history due to a combination of shared habitat preferences and/or temporal ranges.

The identification of statistically meaningful species associations is a major research focus in biogeography and community ecology (Gotelli & Graves, 1996; Sfenthourakis *et al.*, 2005; Gotelli & Ulrich, 2010). A critical quantitative challenge is that for a presence/absence matrix of n species, there are $(n)(n-1)/2$ pairs of species, which can lead to a high frequency of Type I errors (false positives). For example, in our matrix of 40 taxa there are 780 species pairs. Using the $\alpha = 0.05$ benchmark, 39 of these pairs would be identified as 'significant' by virtue of chance alone (i.e. an average of approximately two associations per taxon).

To reduce false detection error rates, we employ the highly conservative empirical Bayes confidence limits criterion (Bayes CL criterion) developed by Gotelli & Ulrich (2010) using the *PAIRS* software package (Ulrich, 2008). This

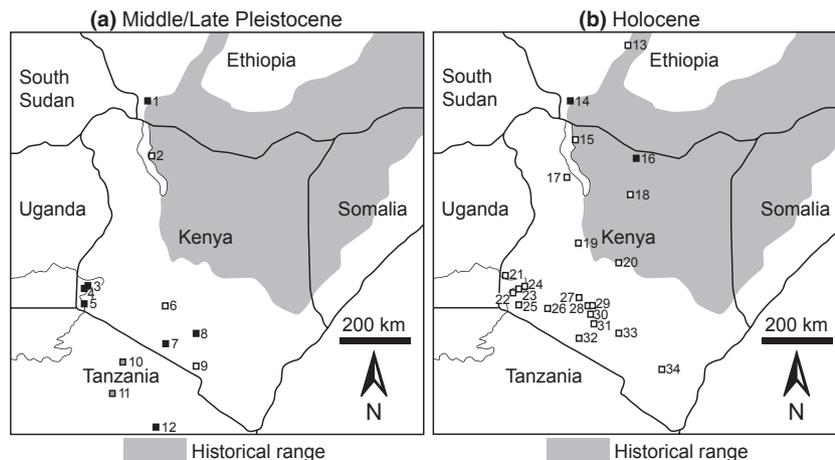


Figure 2 The fossil distribution of Grévy's zebra, *Equus grevyi*, in equatorial East Africa (black squares = present; open squares = absent; grey squares = possibly present). (a) Middle/late Pleistocene localities: 1 = Kibish Formation; 2 = East Turkana FwJj3; 3 = Rusinga Island – Nyamita, Nyamsingula, Wakondo; 4 = Mfangano Island; 5 = Karungu – Aringo, Kisaaka; 6 = Enkapune ya Muto; 7 = Lainyamok; 8 = Lukenya Hill – GvJm 19, GvJm 22, GvJm 46, GvJm 62; 9 = Amboseli; 10 = Nasera Rockshelter; 11 = Mumba Rockshelter; 12 = Kiseke II. (b) Holocene localities: 13 = Moche Borago; 14 = Kibish Formation; 15 = Dongodien; 16 = Ele Bor; 17 = Lothagam; 18 = Kulchurdo; 19 = Ngenyn; 20 = Shulumai Rockshelter; 21 = Pundo, Usenge 3; 22 = Luanda, White Rock Point; 23 = Kanam 2, Kanam East, Kanjera West 1, Kanjera West 2; 24 = Wadh Long'o; 25 = Gogo Falls; 26 = Ngamuriak; 27 = Prolonged Drift; 28 = Enkapune ya Muto, Marula Rockshelter, Maasai Gorge Rockshelter, Ndabibi; 29 = Crescent Island Main Site, Crescent Island Causeway, Naivasha Railway; 30 = Salasun; 31 = Akira; 32 = Narosura; 33 = Lukenya Hill – GvJm 19, GvJm 22; 34 = Kahinju, Kathuva. Historical range from Fig. 1. For full data, see Appendices S1 & S2.

approach makes use of Stone & Roberts' (1990) *C*-score, an index of species co-occurrence that is rescaled so that 0.0 indicates complete aggregation and 1.0 indicates complete segregation. The *C*-score is calculated for all 780 pairs of taxa, which are then grouped into 22 evenly spaced bins from 0.0 to 1.0. The use of 22 bins follows Gotelli & Ulrich (2010) and strikes a balance between statistical power and analytical precision. The presence/absence matrix is then randomized 1000 times using the 'fixed-fixed' algorithm, whereby species occurrences are randomized, but the sums of individual rows and columns are preserved. For each randomized matrix, the *C*-score is calculated for all species pairs, which are then grouped into the 22 bins. This generates a null distribution with 95% confidence limits for (1) the number of pairs expected in each bin, and (2) the expected *C*-score for all species pairs. Of all species pairs, the Bayes CL criterion considers only those in bins where the observed number of pairs exceeds the upper 95% confidence limits of the null distribution. Within this subset, statistically meaningful associations are identified for pairs where the observed *C*-score falls outside the 95% confidence limits of the null distribution. An observed *C*-score falling below the 95% confidence limits indicates that a pair is aggregated more often than expected by chance, whereas a value above indicates that a pair is segregated more often than expected by chance.

We analysed species associations for the Pleistocene and Holocene matrix in its entirety, rather than subdividing the matrix into finer temporal bins. The combined matrix maximizes climatic, environmental and taxonomic variability. This variability enhances our ability to detect species associations, which reflect a combination of shared temporal/geographical ranges and/or shared habitat preferences over the past 400,000 years. For comparative purposes, we examine species associations in both Grévy's zebra and plains zebra.

To explore palaeoenvironmental differences in the fossil samples, we calculate the average hypsodonty index (HI) of the ungulate species documented in a given assemblage. Following Janis (1988), the HI refers to mandibular M_3 crown height divided by width and reflects a combination of a species' diet and habitat preference, with high values observed in open habitat grazers and low values in closed habitat browsers. Eronen *et al.* (2010a,b) show that the average HI of herbivore species in modern and fossil communities is a strong predictor of precipitation, with average HI directly proportional to aridity. We conducted Mann–Whitney *U*-tests in PAST version 2.15 (Hammer *et al.*, 2001) to compare the average locality HI for extant species (data from Janis, 1988) in the Pleistocene and Holocene and in assemblages with or without Grévy's zebra. Extinct species are not included as we lack comparable HI values for some taxa.

RESULTS

There are 15 occurrences of Grévy's zebra in the fossil sample, 13 of which are Pleistocene in age and two of which

are Holocene in age (Appendix S1). The Pleistocene occurrences of Grévy's zebra range in age from *c.* 392,000–330,000 years ago at Lainyamok (Potts & Deino, 1995) to the terminal Pleistocene (12,000 years) at Lukenya Hill (Marean, 1992). The Holocene records date to between *c.* 5000 and 6500 years ago at Ele Bor in northern Kenya (Gifford-Gonzalez, 2003) and between *c.* 12,000 and 3500 years ago at Member IV of the Kibish Formation in Ethiopia (Assefa *et al.*, 2008) (Fig. 2). Both Holocene records fall within or along the boundary of the species' historical range. In contrast, the majority of Pleistocene occurrences of Grévy's zebra fall well outside of it (Fig. 2). A Fisher's exact test indicates that the proportion of Pleistocene assemblages with Grévy's zebra is significantly higher than that documented in all Holocene assemblages (Pleistocene = 13/22, Holocene = 2/57, $P < 0.001$), and in the 11 Holocene assemblages (Fig. 2, Appendix S2) within its historical range ($P = 0.034$).

PCoA axes 1 and 2 account for 15.2% and 13.5% of the variance, respectively (Fig. 3). The ordination places Grévy's zebra within a cluster consisting of white rhinoceros (*Ceratotherium simum*) and extinct Pleistocene grazers, including the giant long-horn buffalo (*Syncerus antiquus*), the giant wildebeest (*Megalotragus*), a small unnamed alcelaphine (cf. *Damaliscus* – referred to as small alcelaphine), and the medium-sized alcelaphine *Rusingoryx atopocranion*. The more densely populated cluster (axis 2 scores < 0.3) consists entirely of extant taxa.

The association between Grévy's zebra and other ungulates is reported in Table 1, which compares the observed *C*-score to the average *C*-score (with 95% confidence limits) generated in the null distribution. Also provided are the body mass and dietary habits of ungulate species (from Janis, 1988; Reed, 1998; Smith *et al.*, 2003; Skinner & Chimimba, 2005). The Bayes CL criterion identifies non-random associations of Grévy's zebra with *Oryx*, the small extinct alcelaphine, the giant long-horn buffalo, and the giant wildebeest. A less conservative statistical test would also identify a significant association with *Connochaetes taurinus*, for which the observed *C*-score is below the 95% confidence limits of the null model (Table 1). However, this is not significant according to the Bayes CL criterion and potentially represents a Type I error. From an ecological perspective, the species associated with Grévy's zebra are biased towards grazers (Table 1), with grazers accounting for all 4 species associated with Grévy's zebra compared to 15 of the 35 remaining species (Fisher's exact test: $P = 0.047$). There are no detectable differences in body mass between those species associated with Grévy's zebra and those that are not (Mann–Whitney *U*-test: $P = 0.342$). Significant segregations are observed between Grévy's zebra and domestic livestock (cows and sheep/goats), which never co-occur in the fossil record (Table 1, Appendix S2). No other associations are statistically significant. In contrast to Grévy's zebra, the Bayes CL criterion identifies no significant species pairs involving plains zebra (Appendix S3).

Table 1 The association of ungulate taxa with Grévy's zebra, *Equus grevyi*, in equatorial East Africa (overlaps, non-overlaps, C-score) compared to the mean C-score and its confidence limits (CL) obtained for 1000 randomized matrices; significant associations (following the Bayes CL criterion) are in bold. G = grazer, B = browser, MF = mixed feeder, O = omnivore, F = fruit/leaves.

Taxon	Diet	Body mass (kg)	Overlaps	Non-overlaps	C-score	Randomized C-score	
						Mean	95% CL
Small alcelaphine	G	69 ^a	12	3	0.04	0.58	0.28–0.87
Oryx	G	170	11	3	0.06	0.59	0.34–0.87
Syncerus antiquus	G	1000	6	1	0.09	0.66	0.31–1.00
<i>Connochaetes taurinus</i>	G	216	12	22	0.13	0.38	0.18–0.65
<i>Phacochoerus</i>	G	100	12	31	0.14	0.29	0.14–0.52
Megalotragus	G	350 ^b	4	1	0.15	0.69	0.32–1.00
<i>Equus quagga</i>	G	235	11	23	0.18	0.38	0.18–0.65
<i>Alcelaphus buselaphus</i>	G	136	11	25	0.19	0.36	0.19–0.57
<i>Gazella thomsonii</i>	MF	20	11	26	0.19	0.35	0.14–0.58
<i>Rusingoryx atopocranium</i>	G	150 ^b	3	1	0.20	0.71	0.20–1.00
<i>Ceratotherium simum</i>	G	3000	3	1	0.20	0.71	0.20–1.00
<i>Ourebia ourebi</i>	G	18	8	12	0.28	0.52	0.28–0.78
<i>Redunca</i>	G	37	9	23	0.29	0.40	0.18–0.64
<i>Cephalophus</i>	FL	61	2	1	0.29	0.71	0.29–1.00
<i>Oreotragus oreotragus</i>	B	13.5	4	3	0.31	0.63	0.31–1.00
<i>Syncerus caffer</i>	G	620	7	27	0.42	0.38	0.18–0.65
<i>Litocranius walleri</i>	B	43	2	2	0.43	0.70	0.20–1.00
<i>Sylvicapra grimmia</i>	B	13	6	17	0.44	0.49	0.24–0.79
<i>Gazella granti</i>	MF	62	6	17	0.44	0.49	0.24–0.79
<i>Tragelaphus strepsiceros</i>	B	215	1	1	0.47	0.72	0.00–1.00
<i>Loxodonta africana</i>	MF	6000	3	6	0.53	0.65	0.30–1.00
<i>Raphicerus campestris</i>	B	13.5	4	11	0.54	0.58	0.28–0.87
<i>Taurotragus oryx</i>	MF	511	4	12	0.55	0.57	0.30–0.88
<i>Giraffa camelopardalis</i>	B	1075	4	15	0.58	0.53	0.27–0.78
<i>Hippopotamus amphibius</i>	G	3200	4	17	0.59	0.51	0.29–0.78
<i>Madoqua</i>	B	4.5	4	18	0.60	0.50	0.23–0.79
<i>Hippotragus</i>	G	250	2	5	0.62	0.67	0.31–1.00
<i>Damaliscus</i>	G	150	1	2	0.62	0.70	0.29–1.00
<i>Potamochoerus</i>	O	103	3	16	0.67	0.53	0.27–0.78
<i>Tragelaphus scriptus</i>	B	58	3	21	0.70	0.49	0.25–0.79
<i>Kobus ellipsiprymnus</i>	G	205	2	11	0.73	0.60	0.32–0.86
<i>Aepyceros melampus</i>	MF	53	2	12	0.74	0.59	0.34–0.87
<i>Hylochoerus meinertzhageni</i>	B	235	0	5	1.00	0.69	0.32–1.00
<i>Kobus kob</i>	G	58	0	4	1.00	0.71	0.20–1.00
<i>Diceros bicornis</i>	B	1800	0	2	1.00	0.72	0.00–1.00
<i>Tragelaphus spekii</i>	MF	74	0	2	1.00	0.75	0.00–1.00
<i>Tragelaphus buxtoni</i>	B	183	0	2	1.00	0.73	0.00–1.00
Bos taurus (cows)	G	600	0	30	1.00	0.42	0.13–0.58
Caprine (sheep/goats)	MF	50	0	39	1.00	0.33	0.22–0.64

^aattributed the same body mass as *Damaliscus pygargus*.^bestimated.

Rubenstein (2010) shows that where the two species are found together, increased frequencies of the mesic-adapted plains zebra are associated with diminished forage intake in Grévy's zebra. It follows that increased rainfall contributed to the decline of Grévy's zebra through a combination of habitat loss and competition with moist-grass grazers.

The PCoA shows that the fossil distribution of Grévy's zebra parallels that of extinct Pleistocene ungulates, including *S. antiquus*, *Megalotragus*, *Rusingoryx* and the small alcelaphine (Fig. 3). As indicated by their morphological adaptations and palaeoenvironmental associations, these taxa were grazers that preferred open and seasonally arid

grasslands (Vrba, 1987; Marean & Gifford-Gonzalez, 1991; Marean, 1992; Klein, 1994; Tryon *et al.*, 2010, 2012; Faith *et al.*, 2011), which seem to have been widespread in East Africa during much of the middle/late Pleistocene (Marean & Gifford-Gonzalez, 1991; Marean, 1992; Potts & Deino, 1995; Tryon *et al.*, 2010, 2012). These extinct ungulates can be distinguished from their extant relatives by extreme hypsodonty or massive body size, with *Megalotragus* and *S. antiquus* among the largest of their respective lineages (Alcelaphini and Bovini). Grévy's zebra is the largest living species of *Equus*, and its combination of large body size, dietary habit, and habitat preference parallels the ecological

profile of the extinct taxa. The similarly massive and arid-adapted Cape zebra (*Equus capensis*) disappeared from southern Africa during the late Pleistocene to early Holocene (Thackeray, 1979; Klein, 1980, 1984; Thackeray *et al.*, 1981; Faith, 2012a). *Equus capensis* has been considered by some to be closely related to Grévy's zebra (Churcher, 1993, 2006; but see Orlando *et al.*, 2009), further underscoring the similarities between Grévy's zebra and extinct ungulates.

Although an improved extinction chronology is necessary for some of the East African taxa, it is believed that environmental change at the onset of the Holocene is responsible for the extinctions (Marean & Gifford-Gonzalez, 1991; Marean, 1992; Faith *et al.*, 2011). In particular, the extinctions are attributed to the same factors responsible for the extirpation of Grévy's zebra from southern Kenya, namely increased rainfall and the loss of arid grasslands together with increased competition with mesic-adapted grazers. This implies that the decline of Grévy's zebra across the Pleistocene–Holocene transition is part of a broader pattern of faunal turnover in equatorial East Africa. Grévy's zebra can be viewed as a surviving relict of a now extinct grazing community with no modern analogue (see also Faith *et al.*, 2011).

In addition to the association of Grévy's zebra with extinct grazers, the PCoA (Fig. 3) shows that Grévy's zebra has a similar fossil history to the white rhinoceros (*Ceratotherium simum*). The white rhinoceros is the largest extant grazer, with a preference for grasslands or open woodlands. Among megaherbivores (> 1000 kg), its pure grazing diet is shared only with extant *Hippopotamus* and a greater number of extinct species (e.g. *S. antiquus*) (Owen-Smith, 1988). The white rhinoceros is unknown from Kenya in historical times, although populations have been introduced. Fossil remains from the pastoralist site Prolonged Drift in Kenya (Fig. 2) indicate that its extirpation occurred within the last c. 2000 years (Gifford *et al.*, 1980). Although we can only speculate at present, possible explanations for its extirpation include human impacts, perhaps related to competition with pastoralists and livestock, or continued environmentally driven habitat loss of the sort that caused extinctions at the onset of the Holocene. In short, the emerging pattern is that the fossil history of Grévy's zebra is similar to grazing specialists that went extinct at or near the end of the Pleistocene or, in the case of the white rhinoceros, were extirpated more recently.

The analysis of species associations (Table 1) broadly confirms the PCoA, showing Grévy's zebra to co-occur more often than expected by chance alone with three of the extinct species (*S. antiquus*, *Megalotragus* and the small alcelaphine). These associations reflect a combination of similar fossil history, characterized by abundance in the Pleistocene and rarity (or absence) in the Holocene, together with a shared preference for arid grasslands. Grévy's zebra is also associated with arid-adapted *Oryx* (most likely *O. beisa*), which sheds further insight into understanding the primary drivers of its

recent decline. The current range of *O. beisa* broadly corresponds to the historical range of Grévy's zebra, although *O. beisa* extends into southern Kenya and northern Tanzania (Kingdon, 1982). Like Grévy's zebra, *Oryx* occurs more often in the Pleistocene (10/22) than in the Holocene (4/57) (Fisher's exact test, $P < 0.001$) and exhibits a broader range during the late Pleistocene (Tryon *et al.*, 2010). Despite their overlapping geographical distribution and parallel declines from the Pleistocene to the Holocene, the conservation status of *O. beisa* is considerably more optimistic, with an estimated 67,000 surviving today (IUCN SSC Antelope Specialist Group, 2008). The relative success of *Oryx* can be explained by differences in ecology and physiology. Although both species are grazers with the ability to browse when grasses are rare (Kingdon, 1982; Rowen & Ginsberg, 1992), *Oryx* is less dependent on water, exhibiting physiological adaptations to reduced water intake and able to dig for water-storing roots, bulbs and tubers when free-standing water is not available (Kingdon, 1982). Whereas forage limitations should affect both species similarly, water limitations should affect Grévy's zebra to a much greater extent. This ecological contrast implies that competition for free-standing water may be more important than lack of forage in driving the recent decline of Grévy's zebra.

Grévy's zebra never co-occurs with domestic species in the fossil record, a pattern shown to be statistically significant by our analysis (Table 1). This segregation can be explained largely by the fact that domestic species are purely Holocene in age whereas most Grévy's zebra date to the Pleistocene. It is intriguing, however, that three sites within or adjacent to the historical range of Grévy's zebra (Kulchurdo, Ngenyn and Shulumai Rockshelter, Fig. 1) include abundant remains of domestic species but no Grévy's zebra (Appendix S2). In the Holocene sequence at Ele Bor (Fig. 1) Grévy's zebra disappears just prior to the appearance of sheep/goats (Gifford-Gonzalez, 2003). This raises the possibility that the spread of pastoralism played a role in the prehistoric decline of Grévy's zebra, probably through increased competition for food and water, as documented today (Williams, 1998, 2002; Sundaesan *et al.*, 2007; Moehlman *et al.*, 2008). A substantially expanded Holocene sample is needed to test this hypothesis in further detail.

The lack of significant species associations involving the plains zebra is informative with respect to Grévy's zebra. The plains zebra is commonly recovered in the fossil record (34 occurrences) and is found together with extinct arid-adapted bovids (13 localities) during the Pleistocene and with domestic livestock (16 localities) in the Holocene (Appendix S2). Its presence in assemblages sampling a range of climatic and environmental conditions explains the lack of significant species associations. This attests to its greater ecological flexibility compared to Grévy's zebra, consistent with its massive geographical range, which extends from southern Africa to Ethiopia (Skinner & Chimimba, 2005). This contrast further implies that access to a narrow range of habitat types (arid grasslands) is crucial to Grévy's zebra.

Parallels with South African grazers

The decline of Grévy's zebra at the onset of the Holocene and in recent decades parallels the history of several recently extinct or conservation-dependent ungulates from South Africa. Following European colonization of South Africa, the blue antelope (*Hippotragus leucophaeus*) and the quagga (*E. quagga quagga*) became extinct. Two other grazers, the bontebok (*Damaliscus pygargus pygargus*) and Cape mountain zebra (*E. zebra zebra*), only narrowly averted extinction (Skinner & Chimimba, 2005; Skead *et al.*, 2011). Fossil evidence shows that these taxa were abundant during the late Pleistocene (Klein, 1980, 1983; Faith, 2011a, 2012a) and the blue antelope had a much broader distribution than observed historically (Klein, 1974; Kerley *et al.*, 2009). Like Grévy's zebra, they were associated with extinct Pleistocene grazers, including *S. antiquus* and *Megalotragus*, among others. At the beginning of the Holocene, the Pleistocene grazers became extinct and the surviving grazers declined in abundance as browsers and mixed feeders rose to prominence (Klein, 1980, 1983, 1984; Faith, 2011a, 2012a). The decline of grazers is attributed primarily to the loss of grassland availability and productivity at the onset of the Holocene (Klein, 1980, 1984; Thackeray, 1980; Brink, 1999; Faith, 2011a,b, 2012a), although the possibility of anthropogenic contributions to the extinctions (i.e. hunting pressure) has been suggested by some (Klein, 1980, 1984; Thackeray, 1980).

Although long-term environmental change was insufficient to cause the extinction of the blue antelope, quagga, bontebok and Cape mountain zebra, it contributed to a reduction in range and population size that is likely to have increased their extinction risk in the face of subsequent anthropogenic disturbances (e.g. Kerley *et al.*, 2009; Faith, 2012a). Nearly 12,000 years later, landscape transformation and hunting pressure associated with European colonization of South Africa rapidly brought about the extinction of the blue antelope and the quagga (Skinner & Chimimba, 2005; Kerley *et al.*, 2009; Skead *et al.*, 2011). The bontebok and Cape mountain zebra were only spared the same fate thanks to decisive conservation efforts (van Rensburg, 1975; Skinner & Chimimba, 2005), which included the establishment of the Mountain Zebra National Park and the Bontebok National Park.

The recent and fossil history of these South African grazers closely parallels that of Grévy's zebra. Together, they suggest that many of the recent human-mediated declines of large African grazers have a deeper history of range contractions and population reductions driven by environmental processes. These prehistoric environmental shifts may very well have set the stage for the conservation challenges observed today.

Future outlook: response to global climate change

As documented by our examination of the fossil evidence, the range and abundance of Grévy's zebra is sensitive to environmental change, with implications for its long-term

survival in the face of contemporary climate change. At present, there are conflicting projections concerning the effects of global climate change in East Africa. Climate models predict that global warming will cause an increase in annual precipitation over East Africa (Christensen *et al.*, 2007). This projection is supported by palaeoenvironmental data showing an association between warm and wet versus cool and dry climates in the past (Bonnefille *et al.*, 1990; Wolff *et al.*, 2011). However, a number of studies suggest that warming Indian Ocean sea surface temperatures could result in decreased annual precipitation (Funk *et al.*, 2008; Williams and Funk, 2011), consistent with the decline in precipitation observed over the last several decades.

Should the global climate models prove correct, an increase in rainfall over the next several decades could be disastrous to Grévy's zebra. This is precisely the sort of change that contributed to its decline 12,000 years ago, through the loss of arid grassland habitats and increased competition with moist-grass grazers. On the other hand, decreased precipitation would have the opposite effects on the habitat of Grévy's zebra, perhaps paralleling the more arid conditions observed in the Pleistocene (Bonnefille *et al.*, 1990; Bonnefille & Chalié, 2000; Kiage & Liu, 2006; Wolff *et al.*, 2011). However, decreased precipitation would almost certainly increase competition between Grévy's zebra and pastoralists and livestock for water. This reinforces the recognized need to strengthen local community conservation programmes, as protected areas make up only a small portion of Grévy's zebras range and much of the remaining land is shared with people (Williams, 2002; KWS, 2008; Low *et al.*, 2009).

CONCLUSIONS

Grévy's zebra thrived in equatorial East Africa during arid phases of the middle/late Pleistocene, when reduced precipitation promoted an expansion of arid grassland environments. Environmental change across the Pleistocene–Holocene transition contributed to a shift in its range and abundance, setting the stage for the massive anthropogenic decline observed over the last several decades. Thus, we suggest that the declining population and distribution of Grévy's zebra today is the combined result of environmental change in the past coupled with intensifying human impacts in the present. The future of Grévy's zebra in the face of contemporary climate change is uncertain, but our study highlights the need to consider climate change, and to better understand and mitigate its effects, when planning for its long-term survival.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Kenyan and Ethiopian ungulate samples (< 400,000 years) and occurrences of Grévy's zebra.

Appendix S2 Presence/absence matrix for ungulates from Pleistocene and Holocene assemblages.

Appendix S3 The association of ungulate taxa with plains zebra.

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BIOSKETCH

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