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Late Pleistocene and Holocene mammal extinctions on continental Africa

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ABSTRACT

Understanding the cause of late Quaternary mammal extinctions is the subject of intense debate spanning the fields of archeology and paleontology. In the global context, the losses on continental Africa have received little attention and are poorly understood. This study aims to inspire new discussion of African extinctions through a review of the extinct species and the chronology and possible causes of those extinctions. There are at least 24 large mammal (>5 kg) species known to have disappeared from continental Africa during the late Pleistocene or Holocene, indicating a much greater taxonomic breadth than previously recognized. Among the better sampled taxa, these losses are restricted to the terminal Pleistocene and early Holocene, between 13,000 and 6000 yrs ago. The African extinctions preferentially affected species that are grazers or prefer grasslands. Where good terrestrial paleoenvironmental records are present, extinctions are associated with changes in the availability, productivity, or structure of grassland habitats, suggesting that environmental changes played a decisive role in the losses. In the broader evolutionary context, these extinctions represent recent examples of selective taxonomic winnowing characterized by the loss of grassland specialists and the establishment of large mammal communities composed of more ecologically flexible taxa over the last million years. There is little reason to believe that humans played an important role in African extinctions.

Contents

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1. Introduction

The last ~100,000 yrs witnessed massive extinctions of large mammals across the continents. Understanding what caused these extinctions is one of the most contentious problems in Quaternary science, with debate focusing primarily on the extent to which anthropogenic or climatic drivers are to blame (MacPhee, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006; Wroe et al., 2013). Compared to the losses in North America, Australia, and Eurasia, the late Quaternary extinctions (LQE) on continental Africa have received little attention and are considered to be poorly understood (Martin and Steadman, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006).

Klein (1984b) provided the most comprehensive review of African LQE to date, with particular attention to the South African record. However, within the context of the global megafaunal extinction debate, it is Maglio and Cooke's (1978) volume on the evolution of African mammals that provides the ultimate primary reference for most accounts of African species thought to have disappeared during the late Pleistocene and Holocene (e.g., Martin, 1984; Smith et al., 2003; Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006). The species lists generated from this volume have yet to be updated or vetted by contemporary standards, despite substantial gains in African paleontology over the last several decades (Werdelin and Sanders, 2010). The result is that species now known to have disappeared during the middle Pleistocene routinely appear on lists of taxa thought to have disappeared within the last ~100,000 yrs (e.g., the bovid *Parmularius* and the equid *Hipparion*) (e.g., Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006), whereas more recent additions do not appear at all (e.g., Bagtache et al., 1984; Pickford and Thomas, 1984; Brink, 1999; Faith et al., 2011, 2012).

A comprehensive account of the mammals involved is needed if Quaternary scientists are to begin to understand the causes of African LQE. The goal of this paper is to provide such a synthesis for the late Pleistocene (126,000 to 12,000 yrs ago) and Holocene (<12,000 yrs ago) of continental Africa, in addition to an assessment of the extinction chronology and possible explanations.

2. Africa and the extinctions debate

2.1. Africa in the global context

Despite being poorly understood, the African LQE play an important role in the global extinction debate. The African losses are often characterized as less severe than extinctions elsewhere (Martin, 1984; Barnosky et al., 2004; Koch and Barnosky, 2006). Martin (1984: 380) remarks that the African mammals "escaped being greatly altered by late Pleistocene extinctions" while Koch and Barnosky (2006: 221) consider Africa "a fortunate anomaly." This is true in the sense that Africa supports an exceptionally diverse large mammal community today (Kingdon, 1982). For example, there are 38 genera of extant African megafauna (>44 kg), compared to fewer than 20 on other continents (Eurasia: 17; North America: 13; South America: 10; Australia: 2) (Koch and Barnosky, 2006).

The apparently anomalous survival of Africa's large mammals is thought by some to reflect long-term co-evolution of human predators and their prey (Martin, 1984; Lyons et al., 2004). The earliest representatives of our genus (*Homo habilis*) appeared in Africa ~2.3 million yrs ago (Kimbel et al., 1997; Antón, 2012), with fossil and genetic evidence pointing to an African origin of *Homo sapiens* between 200,000 and 100,000 yrs ago (White et al., 2003; McDougall et al., 2005; Gonder et al., 2007; Campbell and Tishkoff, 2010; Brown et al., 2012). African hominins incorporated animal tissues into their diet perhaps as early as 3.4 million yrs ago (McPherron et al., 2010; but see Domínguez-Rodrigo et al., 2010) and there is ample evidence for the exploitation of terrestrial prey by ~2.6 to 1.5 million yrs ago (Bunn, 1981; Potts and Shipman, 1981; Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2005; Pobiner et al., 2008; Domínguez-Rodrigo et al., 2009; Ferraro et al., 2013). Although there is debate about when early hominins became proficient hunters (Marean and Assefa, 1999; Klein, 2001; Domínguez-Rodrigo, 2002; Faith, 2008; Ferraro et al., 2013), the long-term development of hunting behavior is argued to have translated to the evolution of defense mechanisms in African prey, rendering them relatively immune to the impacts of prehistoric hunters (Martin, 1984).

The co-evolution argument is central to Martin's (1967, 1984, 2005) overkill hypothesis, which proposes that human hunters caused