

# Chapter 3

## The Paleocological Impact of Grazing and Browsing: Consequences of the Late Quaternary Large Herbivore Extinctions



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### 3.1 Introduction

Extant species of large herbivorous mammals, considered here as taxa  $\geq 44$  kg, are the primary source of the world's remaining large mammal diversity. At the family-level, this includes Antilocapridae (pronghorn), Bovidae (antelopes), Camelidae (camels), Caviidae (cavys), Cervidae (deer), Elephantidae (elephants), Giraffidae (giraffes and okapi), Hippopotamidae (hippopotamuses), Rhinocerotidae (rhinoceroses), Suidae (pigs), Tapiridae (tapirs), and Tayassuidae (peccaries) (Wilson and Reeder 2005). By virtue of their diversity, abundance, and body size, these herbivores have massive impacts on their local environments and play important roles in maintaining ecosystem functionality and diversity (see Chapters in this Book). Such roles include, but are not limited to, altering fire regimes, facilitating nutrient cycling, promoting food web diversity, and modifying vegetation structure to the benefit of other species (Ripple et al. 2015; Malhi et al. 2016). For example, African savanna elephants (*Loxodonta africana*), the largest extant terrestrial herbivores, can disperse seeds up to 65 km from their source, while African forest elephants (*Loxodonta cyclotis*) are in many cases the sole disperser of the largest seeds (e.g., *Cola* spp.) of rainforest trees (Bunney et al. 2017). Grazing by white rhinoceros (*Ceratotherium simum*) maintains short-grass swards that are favored by smaller-

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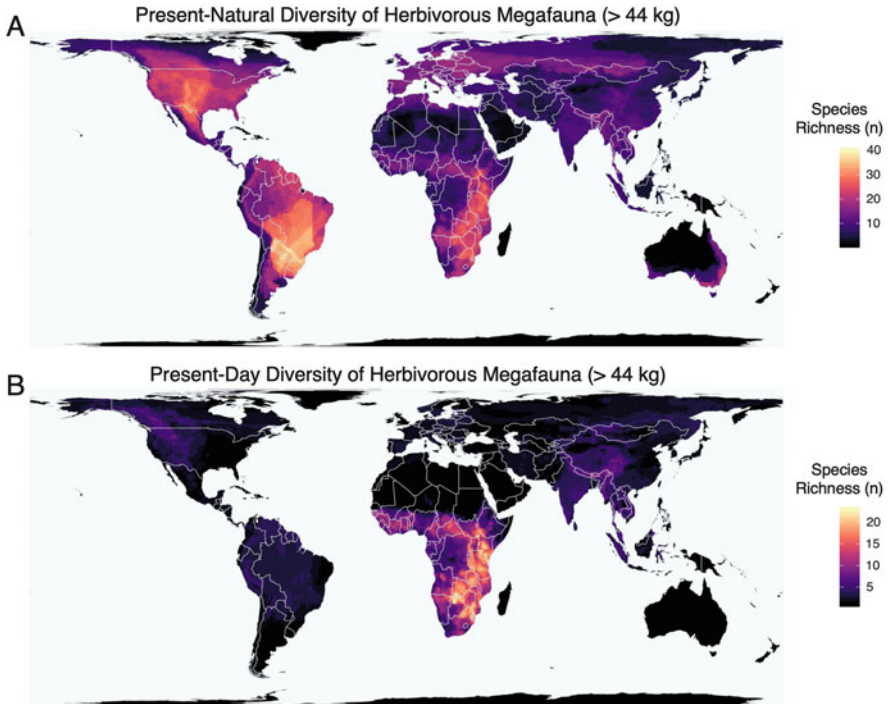
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bodied herbivores (e.g., blue wildebeest, *Connochaetes taurinus*) and reduces the strength and spread of wildfires (Waldram et al. 2008). Likewise, at a macroecological scale, the synergistic relationship between fire and herbivory regimes has been shown to delimit the major vegetation biomes across Africa (Hempson et al. 2015).

As implied by the examples above, the vast majority of our knowledge of large mammal functional ecology and its impacts comes from where they survive in greatest diversity today—sub-Saharan Africa and, to a lesser extent, southeast Asia (Olf et al. 2002; Ripple et al. 2015). However, as recently as ~50,000 years ago, large herbivore diversity paralleling present-day Africa could be found within virtually all of Earth’s major terrestrial regions (Fig. 3.1). This lost diversity includes familiar components of high-latitude Ice Age faunas—wooly mammoths (*Mammuthus primigenius*), woolly rhinos (*Coelodonta antiquitatis*), and long-horned bison (*Bison latifrons*)—as well as lesser-known taxa, such as the bizarre South American liptotern *Macrauchenia*, and the giant Australian marsupial



**Fig. 3.1** ‘Present-natural’ (a) versus present-day (b) maps of global species richness for large herbivores (species >44 kg). Note that the present-natural map does not reflect literal large herbivore distribution patterns during the late Quaternary, but instead estimates what the world might have looked like today if late Quaternary extinctions and extirpations never occurred [see Faurby and Svenning (2015) for more information]. Data from Faurby and Svenning (2015), Faurby et al. (2018), and the International Union for Conservation of Nature (IUCN) Red List

*Diprotodon* (Stuart 2015). Recent estimates suggest that, in total, two-thirds of the world's large mammal genera and over half of its species went extinct towards the end of the Pleistocene, the bulk of these being herbivores (Barnosky 2008). Based on our knowledge of present-day herbivore ecology, it follows that the abrupt loss of so many taxa within a relatively short span of time had significant, far-reaching impacts on terrestrial ecosystems. Moreover, given their recency, the ecological impacts of late Quaternary extinctions almost certainly linger to the present-day and are, therefore, critical to understanding the factors shaping current patterns of biodiversity and its future (Corlett 2013; Galetti et al. 2018).

Here, we review global late Quaternary extinctions of large herbivores, emphasizing what is known about their consequences for the structure and functioning of ecosystems. In the literature on late Quaternary extinctions, most scholars follow Martin (1967) in describing mammalian species  $\geq 44$  kg as 'megafauna.' We use the terms 'large mammals' or 'large herbivores' instead to avoid potential confusion with the term 'megaherbivore,' which is often used for animals  $\geq 1000$  kg (after Owen-Smith 1988). Though we acknowledge the importance of many other extinctions that occurred during older time periods of the Cenozoic (e.g., the Eocene-Oligocene 'Grande Coupure'), we choose to focus this Chapter on the late Quaternary for three primary reasons. First, this interval is data-rich: late Quaternary extinctions are documented from well-constrained and highly fossiliferous assemblages across much of the world, providing a temporally detailed and geographically extensive sample (Saarinen Chap. 2). Second, there is a wealth of paleobiological and paleoecological data for extinct late Quaternary taxa, including body mass estimates (Smith et al. 2003, 2018) and dietary reconstructions from stable carbon isotopes (e.g., Koch et al. 1998; Coltrain et al. 2004) and other proxies (e.g., Rivals et al. 2007; Prideaux et al. 2009; González-Guarda et al. 2018). These data can then be compared to several late Quaternary paleoenvironmental records (e.g., charcoal, pollen), permitting analyses of the relationship between extinctions and ecosystem change through time. Third, because the late Quaternary extinctions preferentially affected the very largest mammal species (Lyons et al. 2004a; Smith et al. 2018), this event provides an important comparison for present-day biodiversity loss. It is now widely acknowledged that human activity since the Industrial Revolution (e.g., climate and land-use change) has fundamentally reshaped global biodiversity patterns (Barnosky et al. 2011; Ceballos et al. 2015). In many cases, this has caused extirpation and near-extinction among large-bodied mammals (e.g., Ripple et al. 2014, 2015), and it is likely that the extinction of many of these species, at least in the wild, will be a hallmark of anthropogenic activity in the twenty-first century (Barnosky et al. 2011; Ceballos et al. 2015). Thus, late Quaternary extinctions provide the best 'natural experiment' with which we can contextualize and compare present-day large mammal diversity loss and its downstream ecological consequences.

The structure of this Chapter is as follows: first, because our review is heavily reliant on paleoecological proxy data, we provide a brief overview of recent methods, focusing on advances using dung beetle and dung fungi proxies. This is followed by an introduction to the topic of late Quaternary extinctions and a brief overview of the major hypotheses for why they occurred. Regional summaries of

extinctions and their impacts are then presented for Australia, North America, and northern Eurasia, which form the bulk of studies to date. Finally, we conclude our Chapter by discussing the importance of late Quaternary extinctions for guiding conservation efforts aimed at preserving large mammal diversity today and mitigating losses of ecosystem functionality.

## 3.2 Paleocological Proxies

Traditional paleontological approaches for studying fossil mammals, namely those founded on the analysis of their hard-tissue skeletal remains, do not readily lend themselves to assessments of the paleoecological impacts of herbivory. This is because the vertebrate fossil record is discontinuous and patchy in both space and time, meaning that empirical fossil evidence for the appearance or disappearance of a species can often be off-the-mark by a considerable length of time. Likewise, most species are so infrequent in the vertebrate fossil record that it can be very difficult to assess temporal trends in their population histories (but see Boulanger and Lyman 2014; Broughton and Weitzel 2018). Together with chronological uncertainties typically in excess of 100 years (in the case of Late Pleistocene mammals), establishing causal linkages between the vertebrate fossil record and other indicators of paleoecological change has proven exceptionally difficult. However, analysis of other, non-vertebrate fossil proxies in recent years has allowed for the generation of exciting new insights into the environmental and ecological impacts of late Quaternary extinctions. We highlight two relatively new proxies related to large herbivore dung as examples.

### 3.2.1 *Dung Fungi*

The coprophilous fungi *Sporormiella* is often found in lake and bog sediments that also preserve ancient pollen (a record of vegetation history), charcoal (a record of fire history), and other paleoecological proxies, and is increasingly used as a measure of large herbivore biomass on Quaternary landscapes (e.g., Gill et al. 2009, 2012). Its use as a biomass proxy stems from the fact that the spores of *Sporormiella* must pass through the digestive system of mammalian herbivores in order to complete their life cycle: *Sporormiella* germinates on dung and releases spores that, under certain situations, become incorporated into sedimentary sequences (see review in Baker et al. 2013). Thus, in much the same way that palynologists infer vegetation change through the shifting abundance of different pollen taxa in a sedimentary sequence, it is reasoned that changes in the abundance of *Sporormiella* provide insight into the abundance of large herbivores on ancient landscapes. In an early and influential study, Davis (1987) observed that *Sporormiella* tends to be rare during much of the Holocene in the western United States, but are abundant prior to extinction of

Pleistocene mammals, and after the historic introduction of grazing livestock, leading to the inference that spores could be used to track herbivore biomass. Though well-recognized taphonomic problems can complicate this situation (e.g., Feranec et al. 2011; Johnson et al. 2015), a growing number of studies highlight the utility of *Sporormiella* as a reliable paleoecological proxy (e.g., Baker et al. 2013; Gill et al. 2013). For Quaternary scientists, this means that it is possible to combine *Sporormiella* abundance with other records and explore the relationship between large herbivore biomass, vegetation, and fire history through time (Gill et al. 2013).

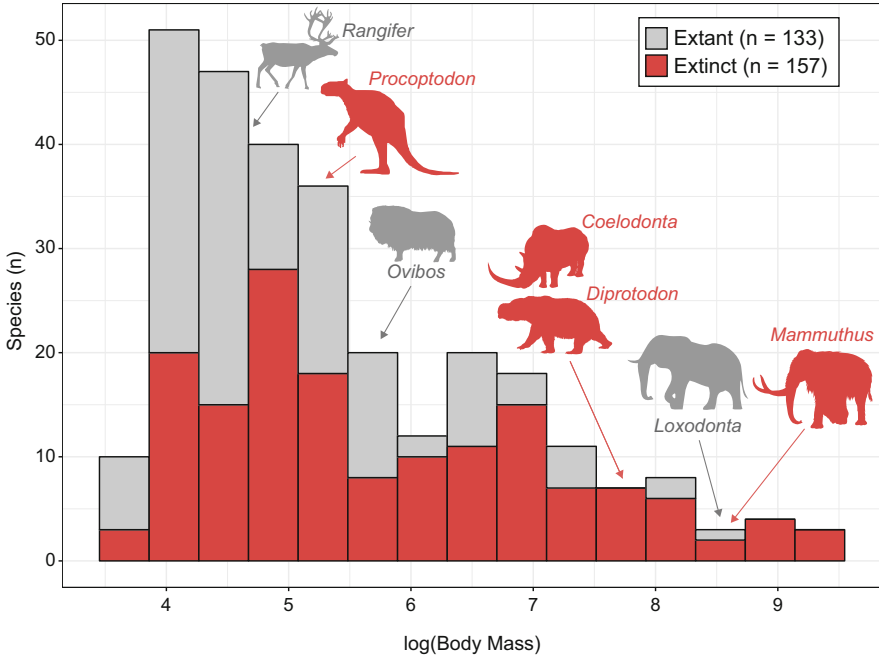
### 3.2.2 *Dung Beetles*

So-called ‘dung beetles’ include several lineages of the superfamily Scarabaeoidea (Order Coleoptera) that have evolved into specialized niches revolving around the consumption of vertebrate faeces, with the most dedicated coprophagous taxa falling into the subfamilies Scarabaeinae and Aphodiinae. Though dung beetles originated alongside the earliest truly massive herbivores—Mesozoic dinosaurs—nearly all lineages surviving the Cretaceous-Paleogene boundary (~66 million years ago) had switched to mammalian dung sources, and subsequently diversified and co-evolved with the radiation of mammals during the Cenozoic (Gunter et al. 2016).

The correlated diversification of dung beetles and their mammalian dung sources throughout the Cenozoic implies that the two have a tight ecological association. This is confirmed by studies of both the fossil record and modern ecosystems. For example, the flightless dung beetle (*Circellium bacchus*), a species endemic to southern Africa, preferentially consumes elephant faeces (Galetti et al. 2018). Though formerly widespread, this species is now restricted to a handful of areas retaining high elephant densities and is considered to be a species of conservation concern (Chown et al. 1995; Kryger et al. 2006; Galetti et al. 2018). Likewise, a study by Schweiger and Svenning (2018) showed that the mean body size of dung beetle assemblages was correlated with declines in large mammal diversity over the last ~50,000 years. Such studies imply that late Quaternary dung beetle assemblages provide a proxy for large mammal biomass and diversity on ancient landscapes.

## 3.3 Late Quaternary Extinctions and Their Ecological Consequences

Present-day large mammal communities are depauperate when compared to those of the Late Pleistocene. Between ~50,000 and 12,000 years ago, the majority of the world’s large mammals disappeared, either in a series of cascading extinctions over thousands of years, or within a comparatively shorter amount of time, depending on geography and other factors (Barnosky et al. 2004; Koch and Barnosky 2006; Stuart



**Fig. 3.2** Body mass histogram (log g) for large herbivore species that survived and did not survive the late Quaternary extinctions. Silhouettes represent a handful of species mentioned in the text as examples. From left to right: reindeer (*Rangifer tarandus*), giant kangaroo (*Procoptodon goliath*), muskox (*Ovibos moschatus*), woolly rhino (*Coelodonta antiquitatis*), diprotodon (*Diprotodon optatum*), African savanna elephant (*Loxodonta africana*), woolly mammoth (*Mammuthus primigenius*). Data from Faurby et al. (2018)

2015). Despite these regional differences, the most striking ecological characteristic of the late Quaternary extinctions as a whole was their selectivity for taxa of large body sizes (Fig. 3.2; Lyons et al. 2004a; Smith et al. 2018). Large body size is a trait correlated with low population densities and a slow life history profile (e.g., delayed reproduction, long inter-birth intervals) that, in turn, confers significantly greater extinction risk (Johnson 2002; Cardillo et al. 2005). However, several studies have demonstrated that the late Quaternary extinction is unique in comparison to body size selectivity in previous Cenozoic extinctions (e.g., Alroy 1999; Smith et al. 2018), a fact that has fostered ongoing debate over their underlying driver(s) (e.g., Koch and Barnosky 2006).

Late Quaternary extinctions have long captured the attention of paleontologists and archaeologists alike, mainly because humans may have played a decisive role. Besides the unusual size selectivity of the extinctions, perhaps the most important reason why human impacts are invoked is that the timing of large mammal disappearances across continents roughly tracks the chronology of human dispersals out of Africa and across the globe during the Late Pleistocene (e.g., Martin 1984; Martin and Steadman 1999; Sandom et al. 2014). The alternative hypothesis to human

impacts is that the late Quaternary extinctions were the outcome of climate-driven environmental change, though many hypotheses rely on some combination of climatic or environmental drivers (e.g., Burney and Flannery 2005; Koch and Barnosky 2006). The influence of one driver over the other may have also varied by continent; for example, Barnosky et al. (2004) suggested that human impacts were mostly responsible for Australian and North American extinctions, whereas climate change was a more likely scenario for Eurasian extinctions. A consensus is emerging that it is probable that both human hunting and climate change acted in tandem, with glacial-interglacial transitions forcing the contraction and fragmentation of herbivore ranges, making populations more susceptible to the effects of human hunting (Barnosky et al. 2004; Koch and Barnosky 2006; Stuart 2015). Other hypotheses (e.g., comet impacts, hyperdisease) for the late Quaternary extinctions tend to be controversial and not widely accepted (Lyons et al. 2004b; Pinter et al. 2011; Holliday et al. 2014).

As discussed above, most research on late Quaternary extinctions has focused on the hypothesized extinction drivers (e.g., the relative roles of humans vs. climate change) and the magnitude of taxonomic losses across continents (Barnosky et al. 2004; Koch and Barnosky 2006). Recently, however, studies have turned their attention towards the downstream ecological impacts of late Quaternary extinctions for the structure and functioning of ecological communities both in the past and today (Malhi et al. 2016; Smith et al. 2016). Here, we synthesize the available paleobiological and ecological datasets bearing on large herbivore extinctions and corresponding ecosystem change from 50,000 years ago to the present-day in Australia, North America, and northern Eurasia, keeping in mind that the consequences of these extinctions can provide powerful insights into understanding the paleoecological impacts of browsing and grazing and the predicted consequences of further extinctions due to human impacts in the Anthropocene.

### **3.3.1 *Australia***

The chronology of late Quaternary extinctions in Australia has been heavily debated, with some studies favoring an early (>46 ka), prolonged, and climate-caused disappearance of the continent's large mammals (e.g., Wroe et al. 2013), whereas others argue that most extinctions occurred rapidly between 50 and 40 ka (e.g., Roberts et al. 2001; Rule et al. 2012) and relate to the appearance of humans on the continent (van der Kaars et al. 2017). It is generally accepted that by ~40 ka, most, if not all, extinctions had occurred (Roberts et al. 2001; Gillespie et al. 2006), with potential sites documenting late survival of extinct large mammals (e.g., the Cuddie Springs site) being highly controversial (Gillespie and Brook 2006). Regardless of its underlying drivers and exact chronology, the late Quaternary Australian extinction ranks among one of the most severe in the world. Although exact counts vary, it is generally estimated that this region lost ~88% of genera (Koch and

Barnosky 2006) and ~91% of species of large mammals, including all taxa >100 kg (Stuart 2015).

Extinct Australian herbivorous large mammals include a diversity of forms, all of which evolved from endemic marsupial lineages (Long et al. 2002). This includes several species with no modern analogs, either in Australia or globally. A prime example is the giant short-faced kangaroo (*Procoptodon goliath*), which is estimated to have weighed 230 kg, and stood up to two meters tall (Helgen et al. 2006). Multiproxy evidence from functional morphology, dental wear, and stable carbon isotopes suggests that this species was a specialized consumer of saltbushes (*Atriplex* spp.), a rare C<sub>4</sub> dicot (most C<sub>4</sub> plants are tropical grasses). If this dietary inference is correct, *P. goliath* would be the only known large mammal species to specialize on C<sub>4</sub> browse (Prideaux et al. 2009). Other enigmatic taxa of the Australian Quaternary include the largest marsupial ever to exist, *Diprotodon optatum*, which weighed nearly 2800 kg and had a shoulder height of 1.8 m (Wroe et al. 2004). In terms of diet, *D. optatum* has been reconstructed as either a browser (DeSantis et al. 2017), or a mixed-feeder preferring browse (Price et al. 2017), which invites ecological parallels in terms of both body size and diet with extant black rhinoceroses (*Diceros bicornis*) in Africa. A recent study by Price et al. (2017), used strontium isotope ratios (<sup>87</sup>Sr/<sup>86</sup>Sr) to show that *D. optatum* underwent roundtrip seasonal migrations of up to 200 km, rivaling those of some eastern Africa ungulates in the Serengeti today (Estes 2014).

Sediment cores from paleolakes yielding pollen, charcoal, and *Sporormiella* have greatly improved our knowledge of the ecological impacts of late Quaternary extinctions. Rule et al. (2012) analyzed the relationship between inferred herbivore biomass and ecosystem change using a 130,000-year paleoenvironmental record based on two sediment cores from Lynch's Crater paleolake (northeast Australia). Collectively, the Lynch's Crater records show three major, stepwise vegetation shifts over the last 130 ka. The first two occurred at ~125 ka and ~75 ka and correspond to the termination of the Last Interglacial (Marine Isotope Stage 5e) and the onset of Marine Isotope Stage 4, respectively, both of which witnessed cooling and aridification of Australia. These climate changes led to the replacement of rainforest angiosperms by rainforest gymnosperms and sclerophyll taxa. At ~41 ka, the third major vegetation change has no climatic explanation but instead follows, within a few hundred years, the loss of large-bodied herbivores as inferred from the abrupt drop in *Sporormiella* abundance to near-zero. At the same time, charcoal increased in abundance, and sclerophyll taxa and grasses quickly came to dominate local plant communities. Rule et al. (2012) proposed that the sudden disappearance of large herbivores and relaxed herbivory ~41 ka created larger fuel loads which, in turn, lead to larger and more intense fires, favoring the replacement of rainforest vegetation by fire-tolerant sclerophyllous plant communities and grasses. Though the *Sporormiella* proxy tells us nothing about which species were involved, and there is little direct large mammal fossil evidence nearby, such changes are fully consistent with contemporary observations highlighting the influence of herbivory on fire regimes (e.g., Waldram et al. 2008).



A similar study by Johnson et al. (2016) on a 135,000-year sediment core from Caledonia Fen suggests that herbivore extinctions may have had varying impacts on ecosystems depending on geography and primary productivity. Caledonia Fen is a high-elevation site in southeast Australia that was covered by low grasslands and shrub steppe for much of the Pleistocene, especially during glacial phases with reduced temperature, precipitation, and atmospheric CO<sub>2</sub> levels (Kershaw et al. 2007). Like Lynch's Crater, this site suggests an abrupt loss of large-bodied herbivores midway through the Late Pleistocene ~52–45 ka based on *Sporormiella* abundance. Unlike Lynch's Crater, however, the loss of herbivorous large mammals at Caledonia Fen occurred independent of any significant shift in fire regimes or vegetation structure. Johnson et al. (2016) propose that climatic constraints on plant growth and primary productivity likely limited the ability of vegetation to respond to relaxed herbivory pressures. For shrubby and grassy landscapes, like those of glacial-phase Caledonia Fen, such responses might have been an increase in woody plant cover and an overall increase in vegetation density if fires remained infrequent, as indicated by charcoal abundance. The record from Caledonia Fen thus highlights the role of climate and primary productivity in modulating the magnitude of large herbivore loss on ecosystems.

Outside data from paleolake cores, evidence of large herbivore extinction impacts in Australia are detectable in the morphology of extant plants, as discussed in Weber's (2013) recent review of the co-evolution of plants with extinct herbivores. For example, many of Australia's acacias are heavily equipped with large, sharp thorns. In Africa, such defenses prevent or lessen consumption of acacias by giraffes (*Giraffa camelopardalis*) and other large-bodied browsers (Tomlinson et al. 2016), but no such animal exists in Australia today—the largest browsers are wallabies, no more than a meter tall (Menkhorst and Knight 2011). When looking to the late Quaternary record, however, it is clear that the thorny spines of Australia's acacias likely evolved to deter consumption by several extinct large-bodied browsers, such as the massive *Diprotodon optatum* mentioned above. A similar case of anachronistic plant morphologies involves fruits of the rainforest vine *Omphalea*, which can be up to 12.5 cm wide and are, therefore, too large to be dispersed by any living mammalian herbivore. They are not consumed by the large rainforest bird, the southern cassowary (*Casuarius casuarius*), which is Australia's largest fruit-dispersing species today, potentially suggesting their disperser was likely a mammalian casualty of the late Quaternary extinctions, but this remains to be shown.

### 3.3.2 North America

Like the extinctions in Australia, those in North America were dramatic in terms of both magnitude and the breadth of taxonomic and ecological diversity that disappeared. In total, at least 37 genera went extinct (tally from Grayson and Meltzer 2015), as did a handful of species with surviving North American congeners (*Oreamnos harringtoni*, *Dasypus bellus*, *Panthera atrox*, *Canis dirus*). Though

many of North America's extinct large mammals are familiar, such as mammoths (*Mammuthus*) and mastodons (*Mammut*), a substantial number are decidedly not. The giant ground sloth *Eremotherium*, for example, overlapped in body mass with African elephants (~3500 kg), whereas the glyptodont *Glyptotherium*, broadly resembling a heavily armored armadillo, was about the size of small car (~1100 kg). Altogether, North America lost at least 73% of its large mammal genera (tally updated from Koch and Barnosky 2006 to include *Cuvieronius* and *Mixotoxodon*), including all of those weighing >1000 kg (*Camelops*, *Mammuthus*, *Mammut*, *Cuvieronius*, *Glyptotherium*, *Eremotherium*, *Glossotherium*, *Mixotoxodon*).

Of the 37 extinct genera, 17 are securely dated to the terminal Pleistocene, between 12,000 and 10,000 radiocarbon years ago (= ~14,000 and 11,500 calendar years ago). The others tend to be rare in the fossil record and are poorly dated, which means that a well-known sampling phenomenon (the Signor-Lipps effect) could very well explain their apparent absence from the terminal Pleistocene. Indeed, quantitative analysis of the existing radiocarbon chronology are consistent with a more or less synchronous loss of all genera at this time (Faith and Surovell 2009). The timing of the extinctions shortly follows (at least over geological timescales) the arrival of the earliest *Homo sapiens* in North America, a temporal correspondence that played a key role Paul Martin's (1967, 1984, 2005) formulation of the overkill hypothesis, which proposes that human hunting was directly responsible for extinctions in North America. Similar parallels between the timing of extinctions and human arrival elsewhere led him to extend this hypothesis to account for the demise of the planet's large mammals across the globe. Though, as noted above, the overkill hypothesis is hotly contested, particularly among archaeologists (e.g., Grayson and Meltzer 2015; Meltzer 2015; Nagaoka et al. 2018).

Regardless of the cause(s) of North America's large mammal extinctions, given what is known about the ecological roles of large-bodied herbivores (Owen-Smith 1988; Ripple et al. 2015; Malhi et al. 2016), we should expect that the disappearance of so many large-bodied species would have had tremendous downstream effects (Johnson 2009; Gill 2014). A growing body of evidence suggests that this is indeed the case (Robinson et al. 2005; Gill et al. 2009, 2012). Perhaps the most compelling evidence comes from late Quaternary pollen, charcoal, and *Sporormiella* records from two sites in the Midwestern United States, Appleman Lake in Indiana (Gill et al. 2009) and Silver Lake in Ohio (Gill et al. 2012). Both records show that spores of *Sporormiella* decline in abundance shortly after ~14,000 years ago, roughly coincident with human arrival in the Americas (e.g., Halligan et al. 2016). This decline precedes the youngest-dated fossils of extinct species in the region (e.g., Faith and Surovell 2009; Woodman and Athfield 2009), so it is interpreted as representing population collapse and local functional extinction.

At both Appleman Lake and Silver Lake, the collapse of large herbivore populations is followed by vegetation change and altered fire regimes. Broad-leaved deciduous trees, namely *Fraxinus* (ash) and *Ostrya* (hophornbeam), rapidly increase in abundance. Such species are known to be suppressed by browsing pressure from extant large-bodied herbivores, leading to the inference that their increase is related

to herbivory release stemming from the functional loss of large herbivores. The temporal resolution at Silver Lake is sufficiently high to show that this phenomenon occurred within 20 years of the *Sporormiella*-inferred herbivore decline. As was also demonstrated at Lynch's Crater in Australia (Rule et al. 2012), the decline of large herbivores is also linked to charcoal peaks that imply enhanced fire regimes relative to preceding intervals, likely due to the accumulation of fuel loads in the absence of large mammal herbivory. Paleocological archives from southeastern New York State show a similar pattern of enhanced fire regimes following the decline of *Sporormiella* at the end of the Pleistocene ~14,000 to 11,500 years ago (Robinson et al. 2005).

A common consequence of large mammal extinctions is the loss of seed dispersers for plant species that bear large fruits (Janzen and Martin 1982; Galetti et al. 2018; Pires et al. 2018). In many cases, this has led to range contractions and near-extinctions of mammal-dispersed plant taxa, as was likely the case for *Omphalea* in Australia. In North America, Kistler et al. (2015) showed using multiple lines of evidence that squashes, pumpkins, and gourds of the genus *Cucurbita* were heavily impacted by late Quaternary extinctions. For example, though many species are rare or extinct in the wild today, *Cucurbita* is common and widespread in Late Pleistocene archaeological and paleontological assemblages, revealing a greater diversity and broader distribution in the past. These assemblages include fossilized *Cucurbita* seeds in the dung of American mastodons (*Mammuth americanum*), suggesting that the fruits of this genus co-evolved with and were mostly reliant upon megaherbivores (species >1000 kg) for their dispersal (Newsom and Muhlbachler 2006). Thus, their survival from the early Holocene to today has solely relied on several independent cases of domestication by early agriculturalists following the late Quaternary extinctions (Kistler et al. 2015).

Finally, we can consider how the ecological impacts of late Quaternary extinctions of plant-consuming species might extend beyond the herbivore guild. Though data from modern ecosystems indicate that megaherbivores have relatively low predation risk (Sinclair et al. 2003), this might not have been the case in the past. Late Pleistocene ecosystems in North America contained a diversity of extinct carnivores, such as saber-toothed felids (e.g., *Smilodon* and *Homotherium*) and large relatives of extant lions (e.g., *Panthera atrox*) and gray wolves (e.g., *Canis dirus*). There is some evidence suggesting that these extinct carnivores might have favored, and were capable of, hunting megaherbivore prey in the past. For example, Marean and Ehrhardt (1995) used zooarchaeological data to show that a Late Pleistocene den of *Homotherium serum* from Texas (Friesenhahn Cave) was dominated by juvenile remains of Columbian mammoth (*Mammuthus columbi*), implying that large saber-toothed felids may have specialized on megaherbivore prey. Likewise, Van Valkenburgh et al. (2016) used comparative analyses of predator-prey relationships to argue that Late Pleistocene carnivores could effectively hunt subadult proboscideans, including individuals >1000 kg. Collectively, these studies suggest that the extinction of large herbivores had cascading effects into the carnivore guild and may be, at least in part, responsible for the extinction of many

carnivore taxa during the late Quaternary (see Faith et al. 2018 for an example of megaherbivores in African ecosystems).

### 3.3.3 Northern Eurasia

Unlike the relatively abrupt late Quaternary extinction of North America, Quaternary extinctions in Eurasia occurred in a series of waves. Stuart (2015) considered four major extinction waves to have occurred: one during the early Last Glacial (~117–40 ka), one near the onset of the Last Glacial Maximum (~30–27 ka), one spanning the Pleistocene-Holocene boundary (~15–4 ka), and another one beginning in the latest Holocene and continuing today (~4 ka to the present-day). Among large mammals, Eurasia is estimated to have lost ~35% of its genera and ~37% of its species, revealing a much more limited extinction than that of Australia and North America (Koch and Barnosky 2006; Stuart 2015). It is often proposed that limited Eurasian extinctions relate to the fact that human ancestors have been present in the region since at least ~500,000 years ago in the form of Paleolithic tool-bearing species like *Homo heidelbergensis* and Neanderthals, perhaps in some way buffering these prey species from the more recent appearance of *Homo sapiens* (e.g., Sandom et al. 2014).

Eurasian extinctions are instead often explained in relation to interglacial-glacial climate change and corresponding vegetation shifts (Prins 1998; Barnosky et al. 2004; Koch and Barnosky 2006). During interglacial periods, such as warm and wet Marine Isotope Stage 5e (~124,000–119,000 years ago), temperate and Mediterranean forests were widespread across western Europe and correspond to broad distributions of the extinct straight-tusked elephant (*Palaeoloxodon antiquus*) and narrow-nosed rhino (*Stephanorhinus hemitoechus*) (Stuart 2015). Marine Isotope Stage 5e climates in Eurasia were so amicable that today what we consider a distinctly tropical species, *Hippopotamus amphibius*, could be found in Great Britain and was somewhat larger than its extant African relatives (Stuart 1982). The population decline and eventual extinction of these common interglacial species shows clear climatic patterning, such as cyclical north-south range shifts through time. In terms of vegetation, their extinctions seem to be related to the widespread replacement of Mediterranean deciduous forest and woodland by open and herb-dominated steppe tundra—so called ‘mammoth steppe’—during glacial periods (Allen et al. 2010; Stuart 2015).

The mammoth steppe, stretching from western Europe, northern Asia, and Beringia to the Yukon (Alaska), was the world’s largest vegetation biome for much of the late Quaternary and hosted the period’s most iconic fauna. This includes its namesake, the woolly mammoth (*Mammuthus primigenius*), extinct steppe bison (*Bison priscus*), and woolly rhino (*Coelodonta antiquitatis*), as well as a handful of extant species (e.g., muskox *Ovibos moschatus*, saiga *Saiga tatarica*, reindeer *Rangifer tarandus*, and onager *Equus hemionus*). Many of the largest species were specialized grazers, and it is believed that grazing pressure by megaherbivores,

especially mammoth and rhino, may have helped to maintain open steppe environments during glacial phases (e.g., Guthrie 2001; Zimov 2005).

Yeakel et al. (2013) used stable isotope ratios and bipartite network analysis to show that population fluctuations of herbivore species before, during, and after the Last Glacial Maximum (~26,000–19,000 years ago) cascaded upwards into the large carnivore guild. For example, large felids in Europe (cave lion *Panthera spelea*, and saber-tooth felid *Homotherium serum*) show shifts towards reindeer-dominated diets after the Last Glacial Maximum in response to declining availability of other prey items. Yeakel et al. (2013) suggest that this post-glacial dietary specialization may explain the eventual disappearance of large felids from Eurasia, assuming that niche specialization makes species more prone to extinction. This also explains why generalist carnivores (*Canis* and *Ursus*) survived the late Quaternary and are still found in the region today. Prey-loss as an extinction driver of cave lions was also discussed by Stuart and Lister (2011) in their review of this taxon.

Other studies show how the collapse of the mammoth steppe fauna could also cascade downwards, all the way to invertebrate and vegetation communities. An interesting study by Sandom et al. (2015) used fossilized beetle remains from Great Britain to test the contested ‘wood-pasture hypothesis’, which proposes that a high diversity and density of large-bodied herbivores during interglacial phases of the late Quaternary was associated with heterogeneous vegetation. They found that beetle assemblages from the Last Interglacial (~132,000–110,000 years ago) document a mixture of semi-open vegetation consisting mainly of grassy woodlands, and that beetles reliant on herbivore dung sources comprise over 50% of assemblages, speaking to a diverse and abundant large herbivore community. On the other hand, beetle assemblages from the early Holocene (~10,000–5000 years ago) contained taxa mainly indicative of closed forest conditions, with dung-consuming beetles comprising only 29% of fossil assemblages. These results suggest that large mammals were sufficiently abundant during past interglacial periods to prevent the formation of large stands of closed forest. The prevalence of forests during the early Holocene is likely related to the fact that this period post-dates the extinctions in Eurasia, thus having a significantly lowered diversity and abundance of large herbivores to exert varied browsing and grazing pressures, including limiting tree recruitment (Sandom et al. 2015).

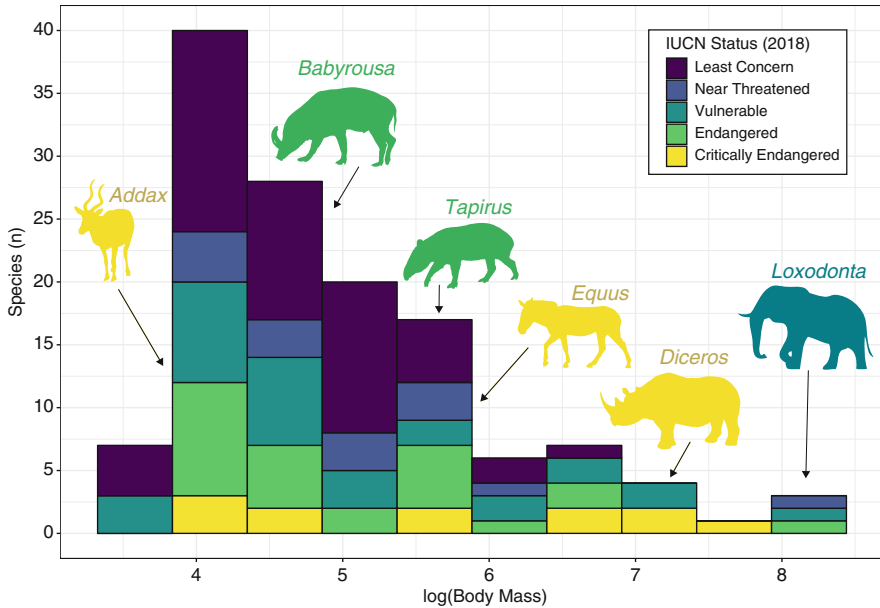
A study by Schweiger and Svenning (2018) used a similar record of Eurasian dung beetle assemblages to ask whether downsizing of large herbivore communities during the late Quaternary reverberated into invertebrate communities. They showed that over the last ~50,000 years, the mean body size of fossil dung beetle assemblages gradually declined before abruptly crashing after the Pleistocene-Holocene boundary, which corresponds to the termination of prehistoric mammal extinctions.

### 3.4 Synthesis, Conclusions, and the Future

Our review suggests that the disappearance of the majority of Earth's large-bodied herbivores during the late Quaternary fundamentally altered the structure and functioning of ecosystems. Though the underlying drivers and exact chronology of extinctions varied between Australia, North America, and northern Eurasia, many of the ecological outcomes of extinctions are shared between them, which speaks to some degree of universality of the impacts of browsing and grazing mammals. First, the disappearance of large herbivores fundamentally alters fire regimes and vegetation communities, keeping in mind that there were important feedbacks between the two (e.g., Gill et al. 2012), as was seen in the late Quaternary of both Australia and North America. Second, high herbivore diversity and abundance can maintain heterogeneous vegetation across landscapes, whereas the decline and subsequent disappearance of large mammals may have led to homogenization of plant communities. Third, herbivore losses have cascading effects on both higher and lower trophic levels. Losses of herbivorous large mammals are clearly linked to the collapse of large carnivore guilds in North America and Eurasia, but also to invertebrate communities that have mutualistic relationships with them (e.g., dung beetles). Such effects are likely to cascade through food webs as large carnivores provide important scavenging resources for smaller carnivorous species, whereas dung beetles play important roles in nutrient cycling and secondary seed dispersal. Fourth, as was seen in both Australia and North America, the disappearance of large herbivores severely hinders the ability of many large fruit-bearing plant species to disperse, leading to lower recruitment and in some cases near-extinction in the wild. Though not discussed here, this anachronism is well-known in South America where extinct proboscideans once roamed, and many large fruits lack dispersers today (Janzen and Martin 1982; Pires et al. 2018).

The examples from global late Quaternary extinctions reviewed here underscore the important role of large herbivores in maintaining ecosystem diversity, functionality, and stability. Such late Quaternary 'natural experiments' assume even greater relevance today considering that many extant large herbivores are declining and at risk of extinction. When plotting the body mass of present-day herbivorous large mammals by their International Union for Conservation of Nature (IUCN) Red List status (Fig. 3.3), we see that many of the very largest species are of major conservation concern (i.e., listed by the IUCN as Vulnerable, Endangered, or Critically Endangered). Across the globe, these species are being decimated by human populations via bushmeat hunting, deforestation, and the establishment of agricultural lands and associated with habitat change and competition with domestic livestock (Ripple et al. 2015). Indeed, it is now generally accepted that the decline and disappearance of the world's remaining large mammals will likely be a hallmark of Earth's human-induced sixth mass extinction over the next century (Barnosky et al. 2011; Ceballos et al. 2015).

Though mitigating current and future extinctions are of high conservation significance in terms of both taxonomic and phylogenetic diversity (e.g., Davis et al. 2018), of greater importance is preserving the ecological roles and interactions of



**Fig. 3.3** Body mass histogram (log g) for extant large herbivores, colour-coded by their conservation status according to the International Union for Conservation of Nature (IUCN) Red List. Silhouettes represent a handful of threatened species. From left to right: addax (*Addax nasomaculatus*), babyrousa (*Babyrousa togeanensis*), Baird’s tapir (*Tapirus bairdii*), wild ass (*Equus africanus*), black rhino (*Diceros bicornis*), and African savanna elephant (*Loxodonta africana*). Data from Faurby et al. (2018)

these species (Estes et al. 2011). A newly emerging subdiscipline of conservation biology and restoration ecology known as ‘rewilding’ seeks to restore the lost ecological functions of taxa that have been extirpated or driven to extinction by human activity. Though there is vigorous debate about what baseline we should use to rewild landscapes (e.g., Pleistocene vs. pre-Industrial Revolution baselines), the potential benefits of large herbivore reintroductions are clear (Svenning et al. 2016). This has sometimes been done through the reintroduction of formerly native species (e.g., *Bison bonasus* in European forests), and conservationists are now increasingly open to the idea of using introduced (non-native) species for restoring vacated ecological roles and restoring lost ecosystem functionality (Wallach et al. 2018). It is well understood that we do not yet know enough about the potential ecological function of such introduced large mammals, and that future research in modern systems is essential (Lundgren et al. 2018). We agree, and note that a better understanding of ancient systems can also help in our efforts to sustain biodiversity into the future.

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