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Ecological and evolutionary legacy of megafauna extinctions

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Ecological and evolutionary legacy of megafauna extinctions

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ABSTRACT

For hundreds of millions of years, large vertebrates (megafauna) have inhabited most of the ecosystems on our planet. During the late Quaternary, notably during the Late Pleistocene and the early Holocene, Earth experienced a rapid extinction of large, terrestrial vertebrates. While much attention has been paid to understanding the causes of this massive megafauna extinction, less attention has been given to understanding the impacts of loss of megafauna on other organisms with whom they interacted. In this review, we discuss how the loss of megafauna disrupted and reshaped ecological interactions, and explore the ecological consequences of the ongoing decline of large vertebrates. Numerous late Quaternary extinct species of predators, parasites, commensals and mutualistic partners were associated with megafauna and were probably lost due to their strict dependence upon them (co-extinctions). Moreover, many extant species have megafauna-adapted traits that provided evolutionary benefits under past megafauna-rich conditions, but are now of no or limited use (anachronisms). Morphological evolution and behavioural changes allowed some of these species partially to overcome the absence of megafauna. Although the extinction of megafauna led to a number of co-extinction events, several species that likely co-evolved with megafauna established new interactions with humans and their domestic animals. Species that were highly specialized in interactions with megafauna, such as large predators, specialized parasites, and large commensalists (e.g. scavengers, dung beetles), and could not adapt to new hosts or prey were more likely to die out. Partners that were less megafauna dependent persisted because of behavioural plasticity or by shifting their dependency to humans *via* domestication, facilitation or pathogen spill-over, or through interactions with domestic megafauna. We argue that the ongoing extinction of the extant megafauna in the Anthropocene will catalyse another wave of co-extinctions due to the enormous diversity of key ecological interactions and functional roles provided by the megafauna.

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Key words: anachronism, cerrado, botfly, seed dispersal, parasite–host interaction, dung beetles, plant defence, scavengers, megaherbivores, savanna.

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I. INTRODUCTION

Since the rise of the metazoans in the Phanerozoic, 567 million years ago, large animals have inhabited Earth. From giant 1-m-long marine arthropods to stunning 90000 kg terrestrial dinosaurs, or the 140000 kg extant blue whale (*Balaenoptera musculus*), large animals have played – and still play – an important role in the functioning of natural ecosystems. They provide disproportionate impacts as ecological engineers, predators, herbivores, competitors, and mutualists that affect the structure, function and diversity of terrestrial and aquatic ecosystems (Doughty *et al.*, 2016a; Estes *et al.*, 2016).

The rise and fall of groups of large metazoans has been attributed to changes in climate, ocean acidification, composition of gases in the atmosphere, volcanism, extra-terrestrial impact and other abiotic changes in the biosphere (Alvarez *et al.*, 1980; Raup & Sepkoski, 1986). However, in the Quaternary period, particularly in the Late Pleistocene and early Holocene, a selective, massive loss of large vertebrates has been strongly linked to the direct or indirect impact of modern humans (*Homo sapiens*), with the geography and chronology of these extinctions closely linked with human biogeographic history (Barnosky *et al.*, 2004; Sandom *et al.*, 2014; Araujo *et al.*, 2015b).

Until our ancestors evolved in Africa and spread across the globe, ecosystems were dominated by large vertebrates, including giant mammals (e.g. mammoths, gomphotheres, ground sloths), giant birds (e.g. elephant birds, moas), and giant reptiles (e.g. giant tortoises) (Barnosky, 2008). By the time humans had reached and populated every habitable continent and island, ending with the colonization of the most remote Polynesian islands (Nielsen *et al.*, 2017), at least 150 genera of mammals, >2000 species of birds and 15 genera of large tortoises had disappeared from Earth (Steadman, 2006; Faurby & Svenning, 2015; Rhodin *et al.*, 2015). In addition, at least three hominid species that survived until the Late Pleistocene (*Homo neanderthalensis*, *H. floresiensis* and *H. erectus*) were possibly driven to extinction by *H. sapiens* (Banks *et al.*, 2008; Klein, 2009) and are thus part of the megafauna extinctions of the late Quaternary (Hortola & Martinez-Navarro, 2013).

There has been fierce debate on the causes of megafauna extinctions, but only recently has attention shifted to the ecological roles played by these large animals and the consequences of their disappearance (Johnson, 2009; Malhi *et al.*, 2016; Smith *et al.*, 2016a) as well as the potential for ecological restoration of megafauna-deprived ecosystems (Svenning *et al.*, 2016). By extrapolating from studies of extant megafauna (e.g. elephants, rhinoceros, hippopotamus) it becomes evident that such large species

interacted with a myriad of organisms (e.g. food plants, parasites, predators, prey) (Owen-Smith, 1988), but there is no current review of the potential consequences of megafauna extinctions for these interactions. Herein, we compile examples of important ecological interactions of extinct late Quaternary terrestrial megafauna with other species, with a particular focus on parasitism, predation, herbivory, commensalism and mutualism. We complement our review by providing an overview of the extremely diversified web of ecological interactions involving both extant and extinct megafauna and their partners in their respective ecosystems (Fig. 1). Knowledge of ecological consequences of megafauna extinctions is particularly relevant because the massive and selective loss of large vertebrates continues across wide regions of our planet in the Anthropocene (Dirzo *et al.*, 2014; Ripple *et al.*, 2015, Johnson *et al.*, 2017).

II. DEFINING MEGAFUNA

The term megafauna has been used in many different ways. Notably, it has been widely, although arbitrarily, applied to species ≥ 45 kg in body mass, especially in palaeontological contexts (Martin, 1973) or more narrowly to herbivores of > 1000 kg (Owen-Smith, 1988). Megafauna can also be defined in a relative sense, i.e. as the largest species in a community or ecological guild prior to human defaunation, as many island ecosystems had functional megafauna often at least partially composed of species below 45 kg (Hansen & Galetti, 2009). Herein we include mammals, reptiles and birds ≥ 45 kg, as is usual in palaeontological studies (Roberts *et al.*, 2001; Barnosky, 2008; Turvey *et al.*, 2013).

The extinction of megafauna species is expected to result in the loss of other species that depend on them (co-extinction), particularly in highly intimate interactions such as specialist parasites, commensalists and mutualistic partners (Colwell, Dunn & Harris, 2012; Pires & Guimarães, 2013). However, co-extinctions could also occur due to more diffuse interactions *via* cascading effects within ecological assemblages (Pires *et al.*, 2015) and *via* the loss of the ecosystem engineering role of the megafauna (Haynes, 2012; Desbiez & Klyber, 2013). Although megafauna extinction may have led to many co-extinction events, some species associated with megafauna persisted by establishing new interactions with humans and their domestic species *via* host-switching (e.g. parasites) or domestication (e.g. plants). In other cases, pre-existing adaptations to megafauna appear inefficient in modern, non-megafauna scenarios. For example, some traits appear ‘suboptimal’ or unfit in present-day communities deprived of megafauna, illustrating situations of anachronisms. Here we review some archetypal and some unorthodox examples of each of these three possible outcomes to illustrate the diverse legacy of megafauna extinctions to current ecological systems.

III. CO-EXTINCTIONS

The extinction of a species in response to the extinction of a mutualistic, parasitic or commensal partner is poorly documented due to our ignorance about host specificity, limitations of historical collections, incomplete systematics of affiliate taxa and lack of experimental studies (Colwell *et al.*, 2012). The extinction of megafauna most likely triggers a series of co-extinction events, but because of the lack of fossils (of parasites, for instance), or other vestiges of species with close interactions and dependence we list below a series of potential co-extinction categories due to megafauna loss.

(1) Parasitism

Parasites are an exceptionally diverse and polyphyletic group of species, unified by a foraging strategy that appropriates host resources, leading to changes in host fitness, behaviour, physiology and/or morphology. The decline of populations of megafauna likely drove several parasite species to local or global extinction, by reducing the probability of successful transmission between host individuals (Strona, 2015). Parasites with complex life cycles (e.g. species that require multiple host species to co-occur at appropriate spatial and temporal scales) or density-dependent transmission (e.g. those that require a minimum threshold density of susceptible hosts) are expected to be especially prone to co-extinction.

(a) Endoparasites

A burst of parasite co-extinctions likely followed the megafauna collapse. For example, palaeoparasitological research on parasites in coprolites found in New Zealand shows that several species of gastrointestinal trematodes declined along with the demise of moas, the large terrestrial birds that occupied the megafauna role in New Zealand (Wood *et al.*, 2013). From a simple linear relationship of contemporary estimates of host specificity per parasite and estimated number of helminth (worm) parasites per host (Poulin & Morand, 2000) we estimate that the loss of 177 mammalian megafauna species during the Pleistocene extinction event (Sandom *et al.*, 2014) may have led to co-extinction of at least 444 helminth species (142 species of Trematoda, 177 Cestoda, 11 Acanthocephala, 114 Nematoda). The accuracy of these estimates is obviously limited by knowledge gaps. While most parasites are host specialists, this specialization may not necessarily translate into higher co-extinction rates, because of the frequency of asymmetric interactions, where specialist parasites associate with generalist hosts that experience relatively lower extinction risk (Vazquez *et al.*, 2005; Strona, Galli & Fattorini, 2013). Moreover, host-switching – a paradoxically common event even for specialized parasites – may have occurred, and is associated with both phenotypic flexibility and phylogenetic conservatism in parasite traits related to host resource use (Araujo *et al.*, 2015a).

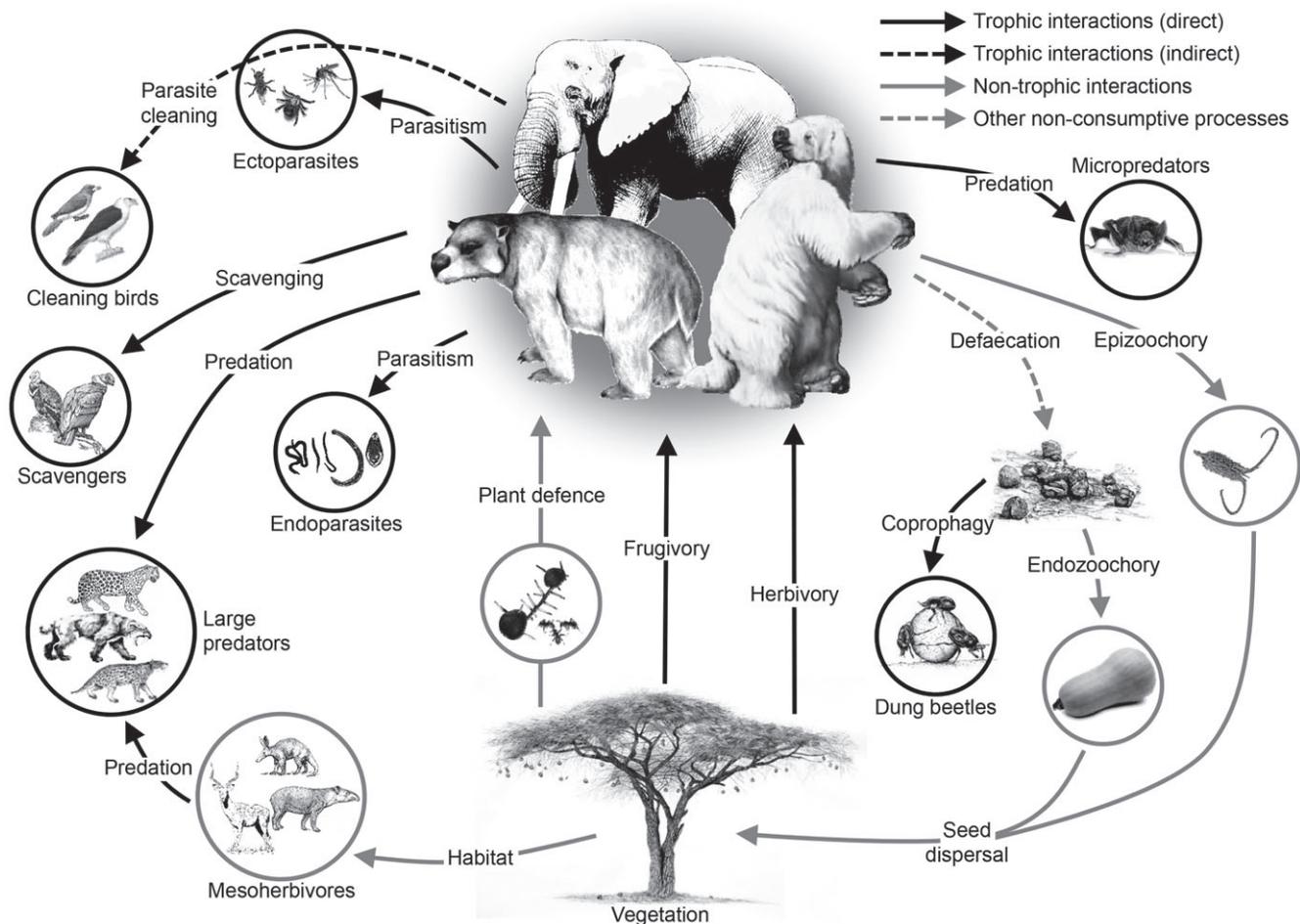


Fig. 1. Trophic and indirect interactions between a megafauna and its environment, here exemplified by the elephant (*Loxodonta africana*) from Africa, and two extinct megafauna: the giant sloth (*Megatherium americanum*) from South America and the giant marsupial *Diprotodon optatum* from Australia.

These considerations would reduce the estimated number of parasite extinctions triggered by megafauna extinction. However, such reductions could be offset by several other factors. Taxonomic knowledge of parasites is incomplete and the number of living species could be underestimated, leading to similar underestimation of co-extinction rates (Dobson *et al.*, 2008). Also, the sheer scale and speed of the megafauna collapse (measured in numbers of host individuals, species diversity, and loss of entire evolutionary clades; Alroy, 2001; Faurby & Svenning, 2015) may have impeded successful and long-lasting host-switching by their parasites. In addition, there is high risk of co-extinction even for those megafauna parasites whose populations are rebounding from previous precipitous declines. There are two reasons for this expectation. First, parasite co-extinctions are predicted to precede host extinctions when parasites require a minimum host density threshold for successful transmission (Anderson & May, 1978), and second, host density strongly predicts parasite abundance at the population level (Stringer & Linklater, 2015).

Early human dispersal most likely facilitated the process of host-switching by contributing to long-distance parasite dispersal, and by altering subsequent contact-rate dynamics between humans, wildlife and domestic animals. Humans also introduced their parasites to new continents (e.g. the transport of the nematodes *Acaris lumbricoides* and *Trichuris trichura* to Australia and the New World; Mitchell, 2013), or became incorporated as intermediate or final hosts in the places that they invaded (e.g. *Trypanosoma cruzi*; Araujo *et al.*, 2015c) and may have allowed some parasites to thrive even after the loss of their megafauna hosts.

(b) Ectoparasites

Ectoparasites such as ticks and lice are obligate blood-sucking arthropods that may have experienced co-extinction with the megafauna. Mihalca, Gherman & Cozma (2011) listed 63 endangered species of ticks associated with critically endangered, endangered and vulnerable mammals. However, documented co-extinction of ectoparasites is still

rare, with only two confirmed extinctions of lice species of the black-footed ferret (*Mustela nigripes*) (Harris, Livieri & Dunn, 2014). As is the case for most parasite co-extinctions, our understanding is constrained by limited data on host specificity, and minimal resampling of hosts for parasites (Colwell *et al.*, 2012). Because adult tick diversity increases with vertebrate host body size, the ongoing and frequently size-biased anthropogenic defaunation may result in several such co-extinction events (Esser *et al.*, 2016). For instance, the precarious conservation status of both African rhino species likely endangers three tick species: *Amblyomma rhinocerotis*, *A. personatum* and *Dermacentor rhinocrinus* (Baker & Keep, 1970; Knapp *et al.*, 1997; Walker, 1991).

Another important group of parasites are the botflies. Botflies (Oestridae) are obligate producers of maggot infection in various mammals (including marsupials, elephants, rhinoceroses, horses, artiodactyls, rodents, lagomorphs and primates). Their larvae are found in subdermal boils (warbles), in the gastrointestinal tract, or in the naso-pharyngeal cavities of the hosts (Zumpt, 1965; Guimarães & Papavero, 1999). The current decline in non-domestic megafauna populations undoubtedly puts associated botflies under threat. For instance, the critically endangered Sumatran rhinoceros (*Dicerorhinus sumatrensis*) has a stomach botfly, *Gyrostigma sumatrensis*, which is known only from a batch of larvae passed in the faeces of a captive host at Hamburg Zoo more than a century ago (Brauer, 1884). African white rhinos (*Ceratotherium simum*) support populations of dung-breeding stomoxid flies like *Rhinomus cadutoiti*, and botflies like *Gyrostigma pavesii* that attach to the rhino's stomach wall (Zumpt, 1964). Similarly, each of the three species of extant elephants has several host-specific botflies. The woolly mammoth was also host to a now-extinct stomach botfly, *Cobboldia rissanovi*, known only from larval remains found in a frozen Siberian mammoth (Grunin, 1973).

A single species of botfly, *Tracheomyia macropi*, is native to the Australian continent. Its hosts are medium- and large-sized wallabies and kangaroos, where larvae develop in the anterior trachea (Portas & Spratt, 2008). It seems likely that the kangaroo botfly lineage arrived with a marsupial host dispersing from South America to Australia *via* Antarctica (Pape, 2006). The fact that all known extant nasopharyngeal botflies are currently found in the Old World – except for some species of the Holarctic genus *Cephenemyia* – could be an indication that naso-pharyngeal botflies may have occurred throughout the New World, and that their current absence might be a result of the late Quaternary megafauna extinctions. *Tracheomyia macropi* and the undescribed extinct New World naso-pharyngeal botflies would most likely have been associated with the megafauna, just as their extant relatives are. Apart from the kangaroo and wallaby hosts of *Tracheomyia macropi*, extant naso-pharyngeal botflies are known from a range of artiodactyls, elephants and equids. This may attest to an evolutionary potential that enabled naso-pharyngeal botflies to exploit several species of the now-extinct New World megafauna.

(2) Predation

(a) Micropredators

In contrast to parasites, micropredators are predators that consume small amounts of tissue (e.g. blood) from more than one prey without killing the prey (Lafferty & Kuris, 2002), for example, vampire bats. Only five bat species in three genera (*Desmodus*, *Diphyphylla* and *Diaemus*) are known to feed on blood (from ~1200 known bat species), and all of them occur in the Americas. Two of these species went globally extinct during the end of the Pleistocene or early Holocene, *Desmodus draculae* from South America and *D. stocki* from North America (Pardiñas & Tonni, 2000; Czaplewski, Peachey & Ammerman, 2003).

The three surviving species feed on birds (*Diphyphylla caudata*, *Diaemus youngi*) (Sazima & Uieda, 1980) or large mammals (*Desmodus rotundus*) (Galetti *et al.*, 2016), and two species are also known to feed on human blood (Ito, Bernard & Torres, 2016; Streicker & Allgeier, 2016). Because *Desmodus rotundus* is specialized in the blood of large-bodied mammals and is not able to spend more than 48 h without feeding (McNab, 1973), it is likely that the extinction of megafauna forced this species to feed on novel prey such as humans. Nowadays, the common vampire bat *D. rotundus* feeds on several introduced mammals (cattle, horse and pigs), but also on a few native ones such as capybaras, tapirs and deer (Galetti *et al.*, 2016). Today, humans and domestic pigs play a fundamental role in its diet, particularly in areas where the populations of large mammals are depleted (Bobrowiec, 2015).

Extinct giant vampire bats, *Desmodus draculae* and *D. stocki*, were ~25% larger than extant *D. rotundus*, and their remains have been found in caves used by megafauna (Morgan, 1988). It is unknown why giant vampire bats were unable to switch to smaller mammal prey or to feed on human blood, but changes in the abundance of megafauna, associated with the energetic requirements of these giant blood-feeding bats (McNab, 1973), may have led to their extinction.

(b) Large predators

Large carnivores were much more abundant in diverse Pleistocene communities and the body size distribution of hypercarnivores (i.e. species whose diet is >70% composed of vertebrates; Van Valkenburgh, 1989) was considerably skewed towards larger sizes (96–135 kg) when compared to modern communities (53–63 kg; Van Valkenburgh *et al.*, 2016). A likely cause of the extinction of large predators is the reduction in abundance and diversity of prey following the extinction of most large herbivores (Owen-Smith, 1989). For example, predators specialized in large prey, such as the sabertoothed cats (*Smilodon* spp.), were likely victims of the extinction of large herbivores (Meachen-Samuels & Van Valkenburgh, 2010). However, the circumstances of these extinctions are not straightforward. Whether large predators became extinct due to prey scarcity or fell victim to the

same factor that caused the extinction of large herbivores is uncertain.

A recent study on the chronology of extinctions in South America suggested that extinctions in the predator guild may have occurred before the extinction of many herbivores (Villavicencio *et al.*, 2016). Declines in the density of prey and competition with humans, either for prey resources or active culling of carnivores for protection (Villavicencio *et al.*, 2016) or status, could have precipitated the extinction of large Pleistocene carnivores. More likely, the extinction of hypercarnivores may have followed a more convoluted pathway. It is possible that as herbivore abundance declined due to climatic change or hunting by humans, carnivores would have broadened their diets *via* prey-switching, increasing dietary overlap and competition with other carnivores (Ripple & Van Valkenburgh, 2010). The reported increase in the frequency of tooth breakage, related to more-complete consumption of carcasses, supports the argument that competition among Pleistocene carnivores was intense (Van Valkenburgh, 2009). These examples illustrate that the effects of the decline of megafauna herbivores on their predators may not have been merely the result of direct trophic interactions. As abundance declines, interactions become progressively less frequent, before extinction happens. As interactions faded, indirect effects probably contributed to the demise of both prey and predators. These indirect effects may have contributed to the collapse of Pleistocene communities leading to the impoverished predator–prey food webs we see today (Pires *et al.*, 2015).

Co-extinctions of predators also occurred after the loss of megafauna continued in historical times. The extinction of Haast eagle (*Harpagornis moorei*) in New Zealand (Holdaway, 1989), and Madagascar crowned hawk-eagle (*Stephanoaetus mahery*) are attributed to the extinction of their prey (moas and lemurs, respectively) (Goodman & Jungers, 2014).

(3) Commensalism

(a) Dung beetles

Dung beetles (Scarabaeidae) have formed close associations with vertebrate dung ever since dinosaurs incorporated angiosperms into their diet in the mid-Cretaceous. Dung beetle species that survived the Cretaceous–Paleogene (K–Pg) mass extinction apparently adapted to use mammal faeces (Gunter *et al.*, 2016). While fossil evidence of a decline in beetle diversity is unclear because of the paucity of well-preserved Scarabaeinae fossil taxa (only 21 in total worldwide; Tarasov *et al.*, 2016), we can infer the consequences of megafauna extinction both from fossilized brood balls, and from evidence from recent megafauna extinctions.

Fossilized dung beetle brood balls (ichnofamily Coprinisphaeridae; Genise, 2004) of Quaternary age have been recovered extensively across South America, Africa, Europe and Asia (Laza, 2006). Many of these fossil brood balls

have morphologies unlike those produced by extant dung beetles. For example, the exceptional large size of brood balls of *Coprinisphaera kitu* from the palaeosols of Andean Ecuador (Sanchez *et al.*, 2013) suggests that dung from mega-herbivores and large mesoherbivores, e.g. horses, ground sloths (Sanchez *et al.*, 2013) was used by correspondingly large dung beetles, including the extinct *Phanaeus violeatae* (Zunino, 2013). Modern larger-bodied dung beetles appear to depend on large dung pats deposited by contemporary megafauna (Nichols *et al.*, 2009), and the decline in larger-bodied mammals is a key driver of current dung beetle decline (Nichols *et al.*, 2009; Nichols & Gardner, 2011; Culot *et al.*, 2013). In addition, a significant proportion of the dung beetle fauna confirmed from the late Quaternary is known to be extinct, for example two of the six recorded dung beetle species from the La Brea tar pits of California (*Copris pristinus* and *Onthophaguos everestae*) (Miller, 1983).

The use of non-faecal food resources may have rescued some dung beetles from megafauna co-extinction because many dung beetles are generalist users of dung resources (Whipple & Hoback, 2012). Faecal material from large herbivores consists of a mix of undigested plant fibre and residues of bacteria that were involved in the digestion process, and dung beetles subsist on the bacterial bodies, rather than the fibre forming the bulk. Contemporary diet-switching between faecal types, or between faeces and other foods (e.g. acorns, fruit pulp) as a function of resource availability, appears common (Hanski *et al.*, 2008; Verdu *et al.*, 2011). This significant dietary plasticity likely arose as a response to the inherently patchy spatiotemporal availability of faecal resources (Verdu *et al.*, 2011). However, dietary plasticity appears to have had limited effect on dampening co-extinctions. For example, the Malagasy dung beetle lineage Helictopleurini (Scarabaeidae: Coprinae) co-radiated with lemurs some 25–30 Mya (Wirta, Orsini & Hanski, 2008). After the extinction of the largest lemur species, many of the large dung beetles went extinct, although some Helictopleurini species were able to switch to dung of cattle (Hanski *et al.*, 2008). Endemic dung beetles are also rare to the point of extinction on the island of Mauritius, sometimes found in only one location (Motala *et al.*, 2007), while their remains are plentiful in Holocene subfossil deposits filled with the bones of island megafauna tortoises and the dodo (Rijsdijk *et al.*, 2015). In addition, the large-bodied elephant-specialist *Helicocopris* species remain abundant in regions across continental Africa that have historically retained higher elephant densities, such as Kruger National Park. Conversely, these species are rare in reserves where elephants were hunted to local extinction before park boundaries were delimited (Cambefort, 1982). Similarly, *Circellium bacchus*, a large, flightless dung generalist with a preference for elephant dung was formerly widespread throughout southern Africa but is now restricted to a few isolated localities of high elephant density (Chown *et al.*, 1995; Kryger *et al.*, 2006).

(b) Scavengers

Very large herbivores may appear invulnerable to predation as prime-aged adults, but eventually become debilitated and are killed or die of malnutrition, disease or old age, making their carcasses available to a range of carnivores (Owen-Smith, 1988). Larger carcasses support a wide spectrum of consumer species because they last longer and are more conspicuous (Moleón *et al.*, 2015). Thus, it is not surprising that scavenging was a widespread feeding behaviour in theropod dinosaurs (Kane *et al.*, 2016), and that a high diversity of scavenging species was reached during the mammalian domination of Earth, especially in the Plio-Pleistocene epochs. For instance, in the Pleistocene, American vultures were represented by at least 11 genera, only 5 of which are part of the extant avifauna (Rich, Wilbur & Jackson, 1983; Alvarenga & Olson, 2004; Alvarenga *et al.*, 2008; Tyrberg, 2008). Also, bone-cracking hyaenids such as the giant hyena (*Pachycrocuta brevirostris*), which were well adapted to dismembering herbivore carcasses and fracturing large bones (Palmqvist *et al.*, 2011), were common during the Plio-Pleistocene in Eurasia (Turner & Antón, 1996).

Impoverishment of the vulture fauna during the Late Pleistocene has frequently been attributed to the decline in diversity of large terrestrial mammals (Fox-Dobbs *et al.*, 2006; Zhang *et al.*, 2012). Vultures were among the species most severely affected by the wave of avian extinctions that followed megafauna loss, especially in the Nearctic and Neotropical regions (Tyrberg, 2008). Vulture extinctions were non-random, being skewed to larger species (Rich *et al.*, 1983; Fig. 2). Other species did not undergo extinction, but suffered considerable range contractions, like the griffon (*Gyps fulvus*) and cinereous vulture (*Aegypius monachus*) in Europe, which became limited to certain areas in southern Europe (Holm & Svenning, 2014), as well as the Andean condor (*Vultur gryphus*) and king vulture (*Sarcoramphus papa*) in South America (Cenizo, Agnolin & Pomi, 2015). The same happened with the California condor (*Gymnogyps californianus*), which once occurred throughout North America, but retreated to the west coast where it could exploit carcasses of stranded marine megafauna (Chamberlain *et al.*, 2005; Fox-Dobbs *et al.*, 2006).

Facultative scavengers such as many raptors and some corvids (Mateo-Tomás *et al.*, 2015) also became extinct at the same time (Tyrberg, 2008). This includes the last species of teratorns – giant flying birds that likely were more predaceous carnivores than scavengers (Campbell & Tonni, 1981). Among mammals, the regional disappearance of the Ice Age spotted hyena (*Crocuta crocuta spelaea*) from Eurasia (Louys, Curnoe & Tong, 2007), which was widespread in Europe and Asia from the Middle Pleistocene until the end of the Late Pleistocene (Sheng *et al.*, 2014), was arguably the result of megaherbivore loss (Varela *et al.*, 2010) along with other factors such as direct competition with humans (García & Arsuaga, 1999).

Invertebrate scavengers would also have been affected by the decline in megafauna diversity, although this is difficult to document. The flies known as bone skippers (Piophilidae:

Thyreophorinae) are all necrophagous and associated with large vertebrate carrion, and the larvae have a preference for feeding on the marrow of the long bones (Freidberg, 1981). The three western Palaearctic species were long considered to be extinct until re-discovered in small and scattered populations (Pape, Bickel & Meier, 2009; Martín-Vega, Baz & Michelsen, 2010), where their survival appears to be associated with domestic goats, sheep and equids.

(c) Megafauna–bird interactions

At the end of the Pleistocene and the beginning of the Holocene, many species of birds died out. Some of the bird extinctions were probably related to human predation, such as the extinction of some flightless species, e.g. the sea duck *Chendytes lawi* (Jones *et al.*, 2008) and moas (Holdaway & Jacomb, 2000). However, most bird extinctions at the Pleistocene/Holocene transition were apparently the outcome of co-extinction cascades triggered by the extinction of the megafauna (Steadman & Martin, 2003). In fact, several Late Pleistocene extinct bird species whose surviving relatives are closely associated with megafauna (e.g. cowbirds and caracaras) became extinct (Oswald & Steadman, 2011, 2015; Suárez & Olson, 2014). The impact of megafauna on scavengers was discussed in Section III.2*b*. Here, we argue that the extinction of scavenging birds discussed above represents one extreme outcome of the impact of the megafauna on multiple bird populations. The diversified interactions between birds and extant large mammals and livestock (Sazima *et al.*, 2012) strongly suggests that multiple megafauna–bird interactions could have been affected to a variable degree, with potential effects on bird populations. Megafauna–bird interactions vary from sporadic use of megafauna faeces as foraging sites (e.g. *Molothrus bonariensis*) or nest material (e.g. *Cariama cristata*), to following large mammals to feed on invertebrates disturbed by the megafauna (e.g. the flycatcher *Machetornis rixosa*; Sick, 1997).

One of the most conspicuous interactions between megafauna and birds is the removal of parasites of megafauna by birds, hereafter termed parasite cleaning. The archetype of such parasite cleaning is between oxpeckers (Buphagidae) and large ungulates in Africa. Oxpeckers have extremely specialized lifestyles, relying completely on large mammals for feeding (Koenig, 1997). They forage exclusively on large herbivore bodies, removing ticks from their hosts. Among the two extant species, the yellow-billed oxpecker (*Buphagus africanus*) has specialized on large, mostly hairless animals like elephants, rhinos and buffalos. This species became locally extinct in many parts of South Africa following decimation of large mammals (Stutterheim & Brooke, 1981). Subsequent reintroduction of these oxpeckers into Kruger National Park seems to have been successful. Both oxpecker species are mostly missing from cattle ranching areas, suffering from poisoning by chemical dips used to control tick infestations. In some areas oxpeckers exacerbate wounds in their animal hosts, behaving as parasites (Weeks, 2000).

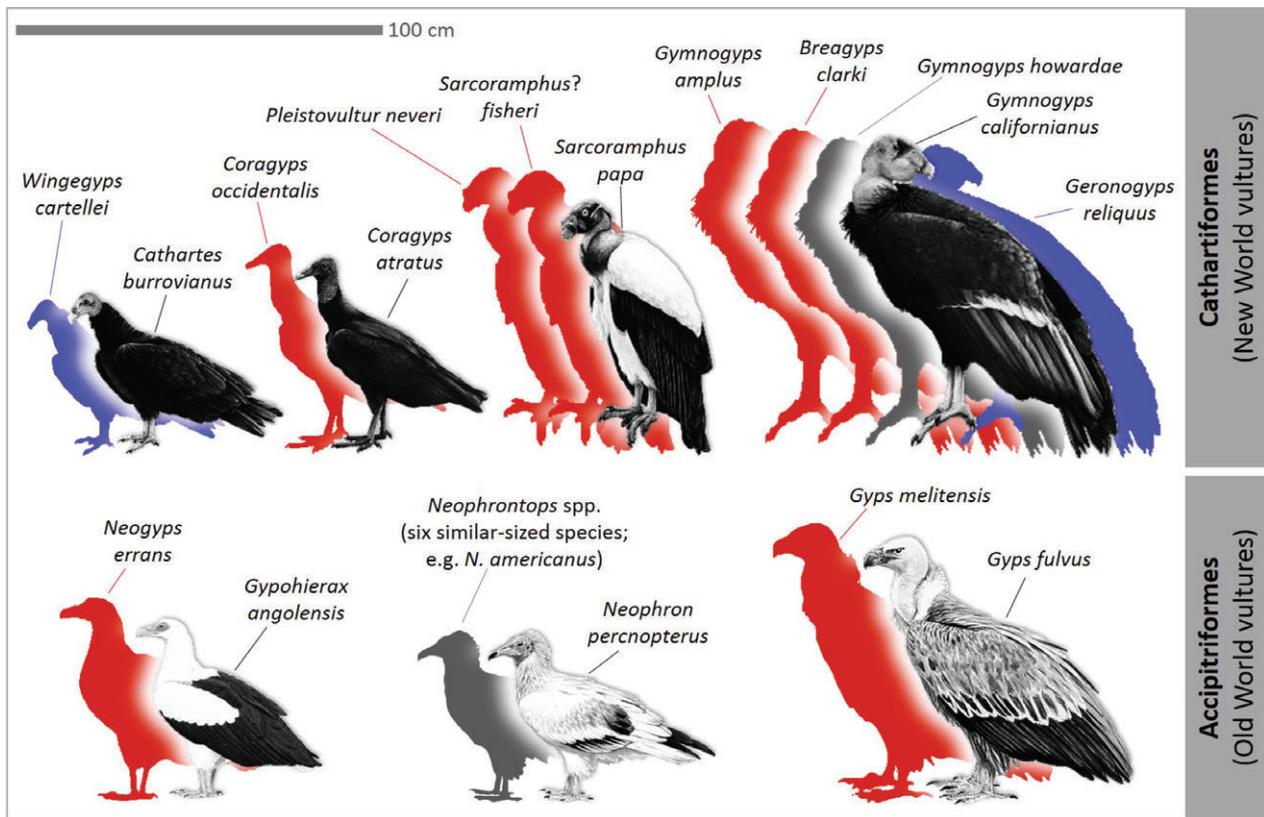


Fig. 2. The extinction of Late Pleistocene vultures was generally skewed towards large species. The figure compares the approximate size of a non-exhaustive array of extinct species (coloured silhouettes) with their closest living relatives or the anatomically most similar vulture species in the case of extinct genera. The extant species included encompass the complete range of current vulture sizes, from the heaviest species (*Gymnogyps californianus*) to the smallest (e.g. *Cathartes burrovianus* and *Neophron percnopterus*). Red = larger than, blue = smaller than the extant relative. Note that the reduction in vulture size since the Late Pleistocene was not only due to a selective loss of species, but also to a gradual reduction in body size of some extant species.

No extant bird species in the Americas relies completely on parasite cleaning of megafauna for feeding, with extant interactions frequently involving generalized taxa (Sazima *et al.*, 2012). Parasite cleaning in South America involves species from multiple families, including Cathartidae (*Coragyps atratus*), Cuculidae (*Crotophaga ani*), Furnariidae (*Furnarius rufus*), Icteridae (*Molothrus bonariensis*), Jacanidae (*Jacana jacana*), and the Tyrannidae (*Machetornis rixosa*). Parasite-cleaning interactions between birds and megafauna are best illustrated by the foraging behaviour of some caracaras (Falconidae) in South America. For instance, the yellow-headed caracara (*Milvago chimachima*) has the largest list of large mammal hosts among all cleaning birds, interacting with both livestock (cattle, horse, donkey) and wild animals such as capybara (*Hydrochoerus hydrochaeris*), marsh deer (*Blastocerus dichotomus*), and tapir (*Tapirus terrestris*) (Sazima *et al.*, 2012). The black caracara (*Daptrius ater*) removes ticks from tapirs, capybaras, and deer (Peres, 1996). The chimango caracara (*Milvago chimango*) and the crested caracara (*Caracara plancus*) also show cleaning behaviour, although less frequently and with a smaller list of mammalian hosts (capybaras, cattle, and horses) than *M. chimachima* (Sazima *et al.*, 2012).

The evolutionary origin of the cleaning behaviour of caracaras remains unclear. It may be an outcome of the adaptability of caracaras to different food resources. Alternatively, the facts that (i) in Falconidae, cleaning behaviour is restricted to caracaras, (ii) caracaras diverged from other falconids in the Miocene, 10 million years ago (Mya), in South America, (iii) in this period there was a rich megafauna in South America that could support external parasites such as ticks and flies, and (iv) the cleaning interactions between caracaras and some large, native herbivores often involve specific behavioural responses of both organisms, suggest that co-evolutionary dynamics between megafauna and caracaras shaped the cleaning interactions. Regardless of whether these interactions were a consequence of co-evolved behavioural traits, it is very likely that these same bird species also removed parasites of a diversity of megafauna species in the Pleistocene.

IV. ADAPTATIVE SHIFTING

Megafaunal extinctions can trigger phenotypic changes in species that interacted with them. Some of these changes are

morphological and are the likely outcome of rapid evolution due to strong selection. Examples include body size change in some apex predators and scavengers. By contrast, other changes in interacting partners are likely to be the outcome of behavioural responses, including the identity of partners visited by parasite-cleaning birds.

(1) Parasitism

The Neotropical human botfly, *Dermatobia hominis*, is common and widespread in the warmer parts of the Neotropics and is known from a suite of hosts, including humans, cattle, and dogs (Guimarães & Papavero, 1999), but there are few documented hosts from the native wildlife (Stephens *et al.*, 2017). Insect egg carriers chosen by *Dermatobia hominis* are diurnal species of mosquitoes and zoophilous flies with an affinity for large mammals; with the extant megafauna apparently immune to infection, it seems inescapable that the original host was found among the now extinct megafauna. Thus, *Dermatobia hominis* may have survived the extinction of its primary megafauna hosts by dietary plasticity, switching to immunologically naïve newcomers such as humans and their domestic dogs. Other potential cases of parasite spill-over from extinct megafauna to humans are the New World screw worm (*Cochliomyia hominivorax*) and Chigoe flea (*Tunga penetrans*) for which the wildlife host is poorly documented (Stephens *et al.*, 2017).

(2) Predation

The waning of predator–prey interactions following the extinctions of large herbivores also had consequences for surviving predators. A recent study on the prey preferences of the jaguar (*Panthera onca*) shows that the body-size distribution of prey is biased towards smaller-bodied species compared to other large felids (Hayward *et al.*, 2016). However, fossil jaguars from both North and South America suggest that the species was larger in the Pleistocene (Kurtén, 1973), and larger herbivores would have been more frequent in its diet (Hayward *et al.*, 2016). Isotope and fossil data support that the Patagonian jaguar (*Panthera onca mesembrina*) preyed upon large, now-extinct herbivores, such as camelids, equids and ground sloths (Prevosti & Martin, 2013; Martin, 2016). The wide range of prey used by the jaguar reflects an opportunistic behaviour that may have allowed it to persist by shifting to smaller prey (Hayward *et al.*, 2016). This shift in diet and body size over time suggests that as interactions with large prey waned, selection may have favoured smaller phenotypes. A similar phenomenon may have happened in the coyote (*Canis latrans*) in North America, which attained larger body sizes in the Pleistocene (Meachen & Samuels, 2012). The abundance of large prey may have provided enough hunting and scavenging opportunities (Van Valkenburgh *et al.*, 2016) for three large canids (*C. latrans*, *C. dirus* and *C. lupus*) to co-exist. As prey availability declined and interactions became less frequent, competition between wolves and coyotes probably intensified and character displacement may have reduced the body size of current populations.

The average body size of both the grey wolf (*C. lupus*) and the coyote is related to prey availability (Schmitz & Lavigne, 1987), and coyotes seem to attain larger body size where wolves have been extirpated, releasing them from potential competition (although interbreeding with wolves also seems to be an important factor defining coyote size; Kays, Curtis & Kirchman, 2010).

(3) Commensalism

The extinction of megafauna during the Late Pleistocene and early Holocene also triggered functional, morphological and behavioural responses in scavenger species. A reduction in body size has been documented within several vulture species, with fossil forms being larger than modern specimens (Hertel, 1994). Parallel to this overall reduction in size was the disappearance of more extreme skull morphologies (Hertel, 1994). Thus, the extinction of large mammals led also to smaller-sized and more specialized vulture assemblages.

Among facultative avian scavengers, there is evidence that birds of prey such as the golden eagle (*Aquila chrysaetos*) and the bald eagle (*Haliaeetus leucocephalus*) used carcasses of megafauna when they were abundant (Martin & Steadman, 1999). Consequently, megafauna extinctions may have led to an increase in the ecological specialization of these species, reducing niche widths. It is not clear, however, whether the extinction of megafauna led to phenotypic changes in cleaning birds and other commensal species that interacted with them.

V. ANACHRONISMS

Anachronisms are morphological or behavioural traits that are not ecologically effective today, but reflect past ecological interactions (Janzen & Martin, 1982; Barlow, 2002). Recurrent examples are overbuilt fleshy fruits with inefficient present-day seed dispersal mechanisms (Janzen & Martin, 1982), and the presence of spines, prickles and thorns (Janzen, 1986) in plants that protect themselves against large herbivores that no longer exist (Greenwood & Atkinson, 1977; Bond & Silander, 2007).

(1) Mutualism

(a) Seed dispersal

The best-studied case of megafauna-related anachronism is morphological traits of fleshy fruits associated with the dispersal of seeds by large mammals (Janzen & Martin, 1982; Barlow, 2002; Guimarães, Galetti & Jordano, 2008). Because there is a strong correlation of fruit and seed size with disperser size (Wheelwright, 1985; Chen & Moles, 2015; Federman *et al.*, 2016), the occurrence of overbuilt fruits in megafauna-deprived continents such as the Americas and Australia suggests that large vertebrates were an important selective agent for the evolution and distribution of such large fruits.

Megafauna can disperse large amounts of seeds by ingesting fruits with large seeds, by ingesting small seeds associated with grasses, or by transporting adhesive fruits or seeds in their fur (Sorensen, 1986). Large frugivores can provide an ecologically unique seed-dispersal service because they travel extensive distances daily (Carbone *et al.*, 2005) and tend to retain the seeds in their gut for longer periods (Guttal *et al.*, 2011), which in turn, may result in increased seed-dispersal distances compared to smaller species (Nathan *et al.*, 2008).

Although there is no strong evidence of any plant species becoming extinct due to the loss of megafauna, it has been suggested that several plant species adapted to megafaunal dispersal persisted only due to domestication by humans (Kistler *et al.*, 2015), or by using other means of secondary seed dispersal (Guimarães *et al.*, 2008; Jansen *et al.*, 2012). However, for many plant species the extinction of large-bodied seed dispersers resulted in a significant reduction in dispersal services, decreasing seed germination and establishment (Cochrane, 2003), increasing spatial aggregation (Bueno *et al.*, 2013; Caughlin *et al.*, 2015), disrupting long-distance dispersal (Pérez-Méndez *et al.*, 2016; Pires *et al.*, 2017), reducing gene flow between plant populations (Collevatti, Grattapaglia & Hay, 2003), shifting phenotypic selection mode and strength on seed size (Galetti *et al.*, 2013) and ultimately affecting important ecosystem services, such as carbon storage (Bello *et al.*, 2015; Doughty *et al.*, 2016b; Peres *et al.*, 2016). In west-central Africa, several forest trees that are dependent on elephant seed dispersal are facing population collapse due to ivory poaching (Beaune *et al.*, 2013).

Megafauna fruits were defined by Janzen & Martin (1982) as being: (i) large indehiscent fruits, rich in sugar, oil or nitrogen, (ii) looking, feeling and tasting like those eaten by large mammals in Africa, and (iii) having seeds protected by thick, tough or hard endocarp (or if seeds are soft, they are very small). Several plants have been suggested to fit the 'megafauna dispersal syndrome' in Costa Rica (Janzen & Martin, 1982), North America (Zaya & Howe, 2009; Waitman, Vander Wall & Esque, 2012; Boone *et al.*, 2015), South America (Guimarães *et al.*, 2008; Zaya & Howe, 2009; Cornejo & Mori, 2012; Muñoz-Concha, Fariás & Méndez, 2015), Australia (Hall & Walter, 2013), South-East Asia (Campos-Arceiz & Blake, 2011), Africa (Blake *et al.*, 2009) and on oceanic islands (McConkey & Drake, 2002; Hansen, Kaiser & Muller, 2008). However, as the traits of megafauna fruits described by Janzen & Martin (1982) were not quantitatively defined, much controversy and critique about the validity of a megafauna fruit syndrome arose (Howe, 1985) until Guimarães *et al.* (2008) suggested an operational (morphological) classification for megafauna fruits. This classification is based on the two main typologies of fruits consumed by extant rhinoceros and elephants: (i) large fleshy fruits (4–10 cm in diameter) with up to five seeds, and (ii) extremely large fleshy fruits (>10 cm diameter) with numerous seeds.

We compiled information on fruit traits (fruit and seed size) from the literature to provide an overview of the distribution

of megafauna fruits. We screened papers, books, and thesis (Cooper, 1994; Van Wyk & Van Wyk, 1997; Lorenzi, 1998; Grant & Thomas, 1998; Engel, 2000; Grant, Thomas & Van Gogh, 2001; Thomas, Grant & Van Gogh, 2004) and fitted each plant species into the operational classification of megafauna fruit (Guimarães *et al.*, 2008).

Based on this extensive literature survey we identified 80 families including 295 genera and 643 species of trees fitting the megafauna dispersal mode. These species mainly inhabit forests (85%) and to a lesser degree savannas (14%). Megafauna fruit plants are globally distributed with representatives in South America (50 families, 130 genera, 255 species), Australasia (23 families, 39 genera, 77 species), South-East Asia (10 families, 11 genera, 26 species), Oceania (five families, four genera, 11 species), Africa (46 families, 117 genera, 202 species) and Madagascar (three families, three genera, four species). Megafauna fruit representatives of 16 plant families occur only in South America, five families are exclusive to Australasia, 15 families occur only in Africa, three families in South East Asia and one family is restricted to Madagascar (Fig. 3). It is likely that many megafauna fruit plants in the Americas and Australia have lacked efficient dispersal agents since megafauna extinction, with likely negative effects on the effectiveness of their seed dispersal (regeneration and distribution) (Barlow, 2002; Guimarães *et al.*, 2008; Weber, 2013). Currently, cassowaries in Australia and tapirs, large primates and rheas in South America are the largest endozoochorous seed dispersers of these fruits, with kangaroo rats, agoutis and other scatter-hoarding rodents being secondary short-distance seed dispersers (Forget & Vander Wall, 2001). Megafauna dispersers like elephants and rhinoceros are still present in Africa and Asia but increasingly limited to small conservation areas and functionally extinct in many sites due to strongly reduced population sizes (Ripple *et al.*, 2015). Ongoing pressure on the remaining megafauna in these parts of the world will pose increasing challenges to plants that are dependent on these dispersers.

Another type of megafauna fruit is those with adaptations allowing them to adhere to mammal fur or bird plumage. Seed dispersal by adhesion probably evolved in the late Eocene (Poinar & Columbus, 1992) and has been considered an adaptation to dispersal by mammals, although some large birds may also be dispersers. At least two families independently evolved large epizoochoric (dispersal by adhesion on fur or feathers) fruits (Pedaliaceae in Africa and Martyniaceae in the Americas; Fig. 4B) (Gormley, Bedigian & Olmstead, 2015). The genera *Proboscidea* in the Americas, and *Harpagophytum* in Africa (Martyniaceae), herbaceous plants of deserts and grasslands, have large epizoochoric fruits that were probably dispersed by Pleistocene megafauna. In South America, *Martynia* also produce hard epizoochoric fruits that require large mammals to disperse their seeds (A. Coccuci, personal communication).

Large flightless birds were probably important epizoochoric seed dispersers on islands without (or with a sparse) mammal megafauna, e.g. New Zealand (Thorsen, Seddon & Dickinson, 2011) and Madagascar (Midgley & Illing, 2009).

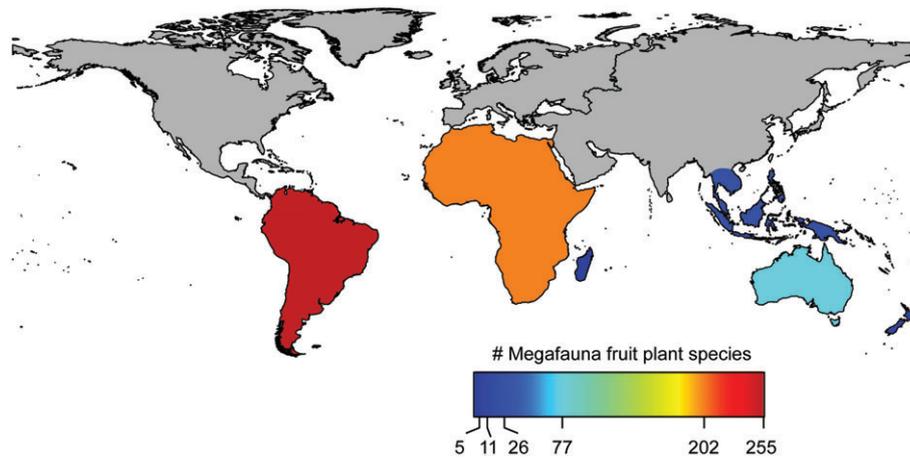


Fig. 3. Global distribution of megafauna fruits based on their size. Values are probably underestimates in tropical South East Asia because of a lack of data.

For instance, the endemic Malagasy genus *Uncarina* (Pedaliaceae) has trample burrs that are considered an adaptation related to dispersal by elephant birds (Midgley & Illing, 2009).

(2) Antagonism

(a) Plant defences

Herbivores, including large mammals, often reduce plant growth, reproduction and survival (Lindroth, 1989; Marquis, 1992). Plants have evolved three strategies to lessen these negative fitness impacts: escape (producing vulnerable tissue when herbivores are absent or inactive, passing quickly through vulnerable states, growing in habitats where herbivores are not present, and crypsis); resistance (morphological and chemical traits that deter herbivores either directly or indirectly); and tolerance (the capacity to maintain fitness following herbivore damage) (Duffy & Hay, 1990; Boege & Marquis, 2006). There are many examples of plant defences that can be considered anachronisms. The distinct architectural traits of some plant species in Madagascar and New Zealand, where no large herbivores currently occur but where large ratites were once abundant, are the most likely candidates (Atkinson & Greenwood, 1989; Bond & Silander, 2007). Thorns in the leaves and bark in many trees in America's savannas are another likely example of anachronism.

Numerous traits allow plants to escape their herbivores in time or space, that is, they decrease the likelihood that herbivores will interact with the plant altogether, or lessen the chance of an interaction when the plant is most vulnerable. Vesey-FitzGerald (1973) and Archibald & Bond (2003) proposed that for African trees megaherbivores might select for rapid growth through a vulnerable juvenile stage. Height in New Zealand plants may have been positively selected for by extinct moas (Atkinson & Greenwood, 1989). Plants may be selected to grow in habitats that are physically inaccessible to vertebrate herbivores (cliff faces in case of

megaherbivores: Janzen, 1986) or too physically stressful for herbivores or where exposure to their predators is too high (Hay, 1981). Current African megaherbivores are more abundant in low-rainfall regions of Africa (500–1000 mm rainfall per year) than above or below this range (Hempson *et al.*, 2015). Whether there were habitats too physically stressful (0–500 mm rainfall or >1000 mm rainfall) for extinct megaherbivores is not clear. Elephants forage in the deserts of Namibia (Viljoen, 1989) and in closed canopy forests (Short, 1981), but perhaps very low and very high rainfall areas were unsuitable for other megaherbivores. Finally, ontogenetic changes in leaf characteristics with increasing plant size are consistent with moa-selected leaf crypsis in *Elaeocarpus hookerianus* (Fadzly & Burns, 2010). Leaves on *E. hookerianus* juveniles, which would have been accessible to moas, are brown, variable in shape in size, and blend with leaves of the litter layer, while leaves of full-grown plants are green and occur at a height that would have been out of reach of the moa (Bond, Lee & Craine, 2004).

Two sets of traits, plant armature and plant architecture, are the most likely candidates to be anachronistic resistance traits. Spines and thorns can provide resistance against vertebrate herbivores but are ineffective against invertebrates (e.g. Cooper & Owen-Smith, 1986; Pollard, 1992) (Fig. 4A, C–E). Experimental exclusion of large vertebrate herbivores demonstrates that plants have a plastic response to their presence. For example, irritant hairs decrease in *Urtica* following herbivore exclusion (Pollard, 1992). Spine size and density are higher on leaves of three palm species in areas of Brazilian Pantanal browsed by cattle for 30 years than in areas from which cattle had been excluded (Göldel *et al.*, 2016). Spine length decreases in African acacias that have been protected from vertebrate herbivores (Young *et al.*, 2013). In addition, the frequency of plants with spines is higher in deserts, where the loss of succulent tissue would seem to be at a premium, and lower on vertebrate-free islands (Burns, 2014). The wide swathes of cactus in Mexico ('nopaleras') and the Sonoran desert



Fig. 4. Examples of anachronisms: (A) spiny Sonoran desert vegetation (photograph J-C. Svenning), (B) epizoochoric fruit of *Ibicella lutea* (Martyniaceae) (photograph A. Cocucci), (C) spiny trunk of *Ceiba speciosa* (photograph M. Galetti), (D, E) fleshy fruit of *Caryocarp brasiliensis* showing the oily yellow pulp (D) (photograph M. Mercadante) and longitudinal dissection showing the spines around the seed (E) (photograph N. Rios), (F) divaricate plants of New Zealand.

might be the result of lack of megaherbivores (Janzen, 1986; Fig. 4A). Experiments that manipulate vertebrate herbivore access to New World desert vegetation would help clarify the role that megaherbivores might have had on present vegetation patterns and plant traits.

Plant architectural traits (rhizomatous growth, intercalary meristems in grasses, prostrate growth, and divaricate branching) have been suggested to be resistance traits against vertebrate herbivores. Prostrate growth and divaricate branching (branching at different angles to produce impenetrable canopies; Fig. 4F) in New Zealand (Greenwood & Atkinson, 1977), and divaricate growth in Madagascar (Bond & Silander, 2007) are hypothesized to have been selected by now-extinct ratite birds. Using phylogenetically controlled contrasts, Bond & Silander (2007) showed that plants from 25 families and 36 genera of Madagascar were more likely to exhibit a divaricating growth form than close relatives in southern Africa. The Madagascar species have

a divaricating growth form similar to that found in New Zealand suggesting convergence.

Plants have evolved traits that feed (extrafloral nectaries and food bodies) and sometimes house ants. Often, these plant traits result in indirect defence, that is, the ants deter herbivore attack resulting in lower tissue loss (Trager *et al.*, 2010). Extrafloral nectaries were first proposed to have evolved as defences against herbivorous mammals (Brown, 1960). Both young giraffes (Madden & Young, 1992) and elephants (Goheen & Palmer, 2010) are deterred from feeding by the presence of ants in *Acacia depreanobium* in Kenya. Furthermore, exclusion of megaherbivores in Africa results in reduced investment by swollen thorn acacias, both in hollow thorns that house ants and in extrafloral nectar that feeds ants (Palmer *et al.*, 2008). Although these studies are suggestive of a role of extinct megaherbivores on the evolution and maintenance of ant–plant symbioses, it remains unclear whether the current distribution of indirect

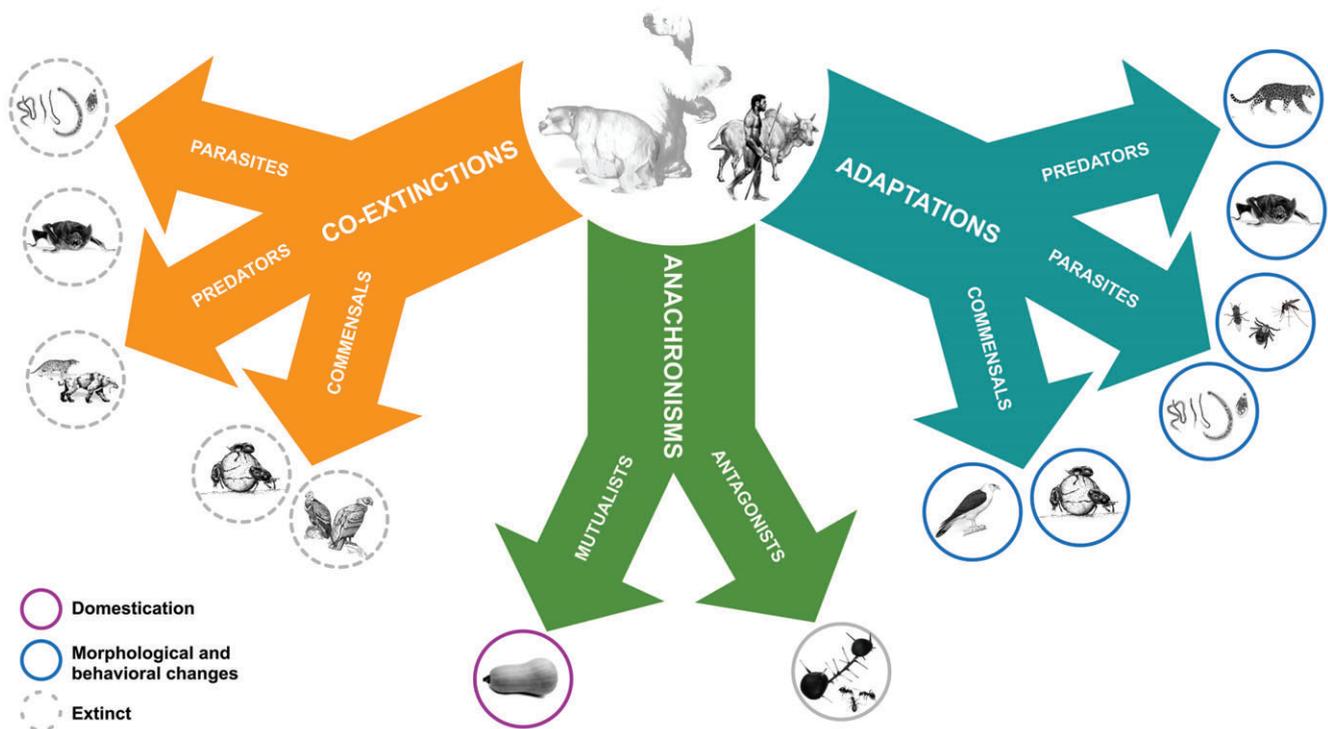


Fig. 5. Examples of effects of megafauna extinction on ecological interactions. Co-extinctions (orange): giant vampire bat *Desmodus draculae*, parasites, predators (e.g. *Smilodon* spp.), dung beetles, large scavengers. Anachronisms (green): domestication of fruits (e.g. squash) and thorns. Adaptations (blue): botfly and ticks, vampire bats (*Desmodus rotundus*), jaguar (*Panthera onca*), commensalism (smaller scavengers, bird cleaners). Circle line types and colours indicate potential co-extinction interactions (dashed), evolutionary changes in morphology and behaviour after megafauna extinction (blue), and persistence through human intervention (domestication, cultivation and propagation).

ant defences is a product of past interactions with vertebrate herbivores, the abundance of extant vertebrate herbivores, or attack by past and current herbivorous insects.

Large herbivores also played a major role in debarking trees and trampling seedlings and may have been important in the selection of tolerance, both within and among species (Gadd, 2002; Ihwagi *et al.*, 2010). In the Serengeti National Park, tolerance to extant megaherbivores is important for tree survival: the ability of a tree species to re-sprout following chronic elephant herbivory is significantly correlated with survival (Morrison, Holdo & Anderson, 2016), and growth form, particularly in grasses, can contribute to both resistance and tolerance. Prostrate growth decreases the ability of grazers to consume tissue, while rhizomatous growth protects meristems below ground, allowing regrowth following above-ground grazing. McNaughton (1984) and Hempton *et al.* (2015) documented differences in growth form within and between grass species associated with predictable patterns in grazing in Africa. In the western USA, caespitose bunch grasses dominate west of the Rocky Mountains where bison and antelope have been absent since the beginning of the Holocene, while rhizomatous grasses dominate east of the Rockies where such vertebrate herbivores were common (Mack & Thompson, 1982). Introduction of cattle and sheep west of the Rockies converted the grasslands to vegetation

dominated by winter annual dicots, supporting the hypothesis that large vertebrates determined the relative distribution of the two growth forms, if not their evolution (Mack & Thompson, 1982).

VI. CONCLUSIONS

(1) The extinction of the megafauna likely affected myriad ecological interactions, primarily of three forms: co-extinctions, shifts in interactions or in the interactor, and anachronisms (Fig. 5).

(2) We have compiled some of the possible interactions that may have been lost or changed due to megafauna extinction. Our ability to detect past co-extinctions is very limited because many species do not leave fossils (parasites), or because many interactions were unique to certain species with no analogues.

(3) The effects of recent (Holocene) extinctions on mutualist interactions show that when megaherbivores are lost, the fitness and evolution of their ecological partners is directly affected (Traveset, Gonzalez-Varo & Valido, 2012; Galetti & Dirzo, 2013; Beaune *et al.*, 2013; Beaune, 2015) with potential consequences for ecosystems and the biosphere (Bello *et al.*, 2015; Smith *et al.*, 2016a).

(4) We argue that looking at the multiple ecological consequences of extinctions, such as co-extinctions, shifts and anachronisms, is a necessary step towards being able to predict how ongoing defaunation or potential megafaunal restoration will change ecological systems.

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