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Collapse of the world's largest herbivores

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Large wild herbivores are crucial to ecosystems and human societies. We highlight the 74 largest terrestrial herbivore species on Earth (body mass ≥ 100 kg), the threats they face, their important and often overlooked ecosystem effects, and the conservation efforts needed to save them and their predators from extinction. Large herbivores are generally facing dramatic population declines and range contractions, such that $\sim 60\%$ are threatened with extinction. Nearly all threatened species are in developing countries, where major threats include hunting, land-use change, and resource depression by livestock. Loss of large herbivores can have cascading effects on other species including large carnivores, scavengers, mesoherbivores, small mammals, and ecological processes involving vegetation, hydrology, nutrient cycling, and fire regimes. The rate of large herbivore decline suggests that ever-larger swaths of the world will soon lack many of the vital ecological services these animals provide, resulting in enormous ecological and social costs.

INTRODUCTION

Terrestrial mammalian herbivores, a group of ~ 4000 species, live in every major ecosystem on Earth except Antarctica. Here, we consider the 74 wild herbivore species with mean adult body masses ≥ 100 kg. These largest species represent four orders (Proboscidea, Primates, Cetartiodactyla, and Perissodactyla) and 11 families (Elephantidae, Rhinocerotidae, Hippopotamidae, Giraffidae, Bovidae, Camelidae, Tapiridae, Equidae, Cervidae, Suidae, and Hominidae). Most of these species are entirely herbivorous, but some are generalists (for example, Suidae). Herein, we provide the first comprehensive review that includes the endangerment status and key threats to the world's largest herbivores (≥ 100 kg), the ecological consequences of their decline, and actions needed for their conservation. We review how the combined impacts of hunting, encroachment by humans and their livestock, and habitat loss could lead to the extinction of a suite of large herbivores relatively soon. By reviewing their ecological roles, we show how the loss of large herbivores can alter ecosystems, mostly to the detriment of other species, including humans, through the loss of ecological interactions and ecosystem services. We end by outlining future directions for research

and conservation action to help diminish the imminent possibility of losing the remaining large herbivores from many ecosystems throughout the world.

STATUS

According to the International Union for the Conservation of Nature (IUCN), 44 of the 74 largest terrestrial herbivores ($\sim 60\%$) are listed as threatened with extinction (including 12 critically endangered or extinct in the wild), and 43 ($\sim 58\%$) have decreasing populations [(1); table S1]. Their current population sizes exhibit large differences among species, spanning over four orders of magnitude, with some populations estimated to comprise fewer than 100 individuals [for example, Javan rhinoceros (*Rhinoceros sondaicus*)], whereas a few others [for example, Eurasian elk/moose (*Alces alces*)] comprise more than 1 million individuals (table S1).

Most large herbivore species are found in Africa ($n = 32$), Southeast Asia ($n = 19$), India ($n = 14$), China ($n = 14$), and the rest of Asia ($n = 19$) (Fig. 1A). Fewer species are found in Europe ($n = 7$), Latin America ($n = 5$), and North America ($n = 5$) (fig. S1). Overall, 71 species occur in developing countries, whereas only 10 occur in developed countries. The highest number of threatened large herbivores occurs in Southeast Asia ($n = 19$, east of India and south of China), followed by Africa ($n = 12$), India ($n = 9$), China ($n = 8$), Latin America ($n = 4$), and Europe ($n = 1$) (Fig. 1B and fig. S1). Notably, all of the threatened species of large herbivores are found in developing countries, with the exception of European bison (*Bison bonasus*), with developed countries having already lost most of their large mammals in the ongoing megafauna extinction (2).

Ecoregions [$n = 30$, based on (3)] with the most-threatened large herbivore species (≥ 5) are found in southern Asia, throughout much of extreme Southeast Asia, as well as Ethiopia and Somalia of eastern Africa (Fig. 1B and tables S2 to S4). The ecoregions with seven threatened large herbivore species are the Himalayan subtropical broadleaf forests, the Sunda Shelf mangroves, and the peninsular Malaysian rain forests (table S4). Hunting for meat is the predominant threat in all ecoregions

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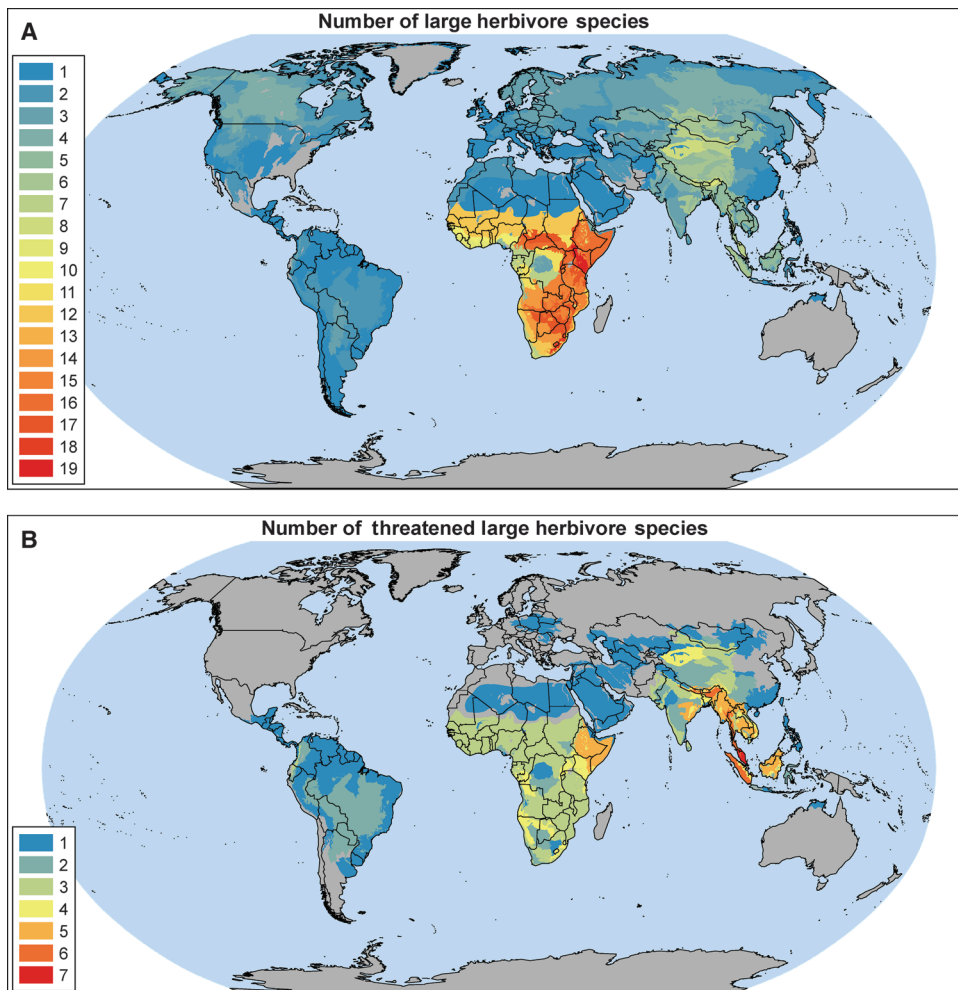


Fig. 1. Large herbivore total species richness (A) and threatened (B) at the ecoregion level. Ecoregion lists for each species were obtained using the IUCN Red List species range maps and (3) and are based on the ecoregions where each species is native and currently present.

containing at least five threatened large herbivore species (table S2). These ecoregions fall mostly within the tropical and subtropical moist broadleaf forests biome (20 of 30 ecoregions), but biomes containing combinations of grasslands, shrublands, savannas, mangroves, or other forest types represent the other 10 ecoregions with at least five threatened large herbivore species (table S3).

All 10 large herbivore species within the families Elephantidae, Hippopotamidae, Hominidae, and Tapiridae are currently threatened (Fig. 2). The large herbivores of the families Suidae, Rhinocerotidae, Equidae, and Camelidae are also highly endangered, with 15 of 20 member species threatened (Fig. 2). Only eight terrestrial megafauna species (≥ 1000 kg) exist today as opposed to more than five times that number (~ 42) that were present in the late Pleistocene (4–6). The eight remaining species are split between Africa (African elephant, *Loxodonta africana*, hippopotamus, *Hippopotamus amphibius*, and the white and black rhinoceros, *Ceratotherium simum* and *Diceros bicornis*, respectively) and Southeast Asia (Asian elephant, *Elephas maximus*, and the Indian, Javan, and Sumatran rhinoceros, *Rhinoceros unicornis*, *R. sondaicus*, and *Dicerorhinus sumatrensis*, respectively). Of these, seven are threatened,

including four critically endangered, and the white rhinoceros is nearly threatened with the current poaching crisis likely to alter its status downward in the near future. Ironically, this endangerment follows one of the greatest success stories in the history of modern conservation: the recovery of the southern white rhino (*C. simum simum*) from a single population of fewer than 100 individuals in the early 1900s to about 20,000 today [(7), table S1]. Even with the current crisis of rhinoceros poaching, this illustrates that, with sufficient protection, recovery is possible for relatively slow-breeding species that are highly prized by poachers.

Many of the largest herbivore species have ranges that are collapsing (8, 9). Estimates of range contractions have been made for 25 of the 74 species, and on average, these species currently occupy only 19% of their historical ranges (table S1). This is exemplified by the elephant, hippopotamus, and black rhinoceros, all of which now occupy just tiny fractions of their historical ranges in Africa (Fig. 3). Furthermore, many of these declining species are poorly known scientifically, and badly in need of basic ecological research. Scientific research effort, as measured by the number of published articles on each species, has been much greater for nonthreatened ($\bar{x} = 296$, $SE_{\bar{x}} = 129$) than threatened species ($\bar{x} = 100$, $SE_{\bar{x}} = 33$), and greater overall for species in developed countries ($\bar{x} = 790$, $SE_{\bar{x}} = 376$) than developing countries ($\bar{x} = 172$, $SE_{\bar{x}} = 33$). Indeed, those that have been most studied are primarily game species in wealthy countries, includ-

ing red deer (*Cervus elephus*), reindeer (*Rangifer tarandus*), and moose/Eurasian elk (*A. alces*) (fig. S2). In contrast, 18 of the large herbivore species from developing regions have been featured in fewer than 10 published articles each (fig. S2), which, in part, reflects negative or indifferent attitudes toward some species, or low levels of scientific funding, making it difficult to garner government and public support for scientific studies and conservation of these taxa (10). For example, although highly threatened, the six large-bodied species in the Suidae family are collectively represented by only 26 published articles ($\bar{x} = 4$ per species, range = 0 to 14) (table S5 and fig. S2).

Between 1996 and 2008, the conservation status of seven herbivore species ≥ 100 kg deteriorated, whereas only two species improved (table S1). By contrast, small herbivores are doing relatively well with just 16% of species below 5 kg in body mass classified as threatened (fig. S3). In contrast to the developing world, effective game laws and extirpation of large predators in developed countries of northern latitudes have frequently resulted in an overabundance of large herbivores. In the absence of wolves (*Canis lupus*) and other large carnivores, overabundant cervids can negatively impact biodiversity, stream morphology, carbon sequestration,

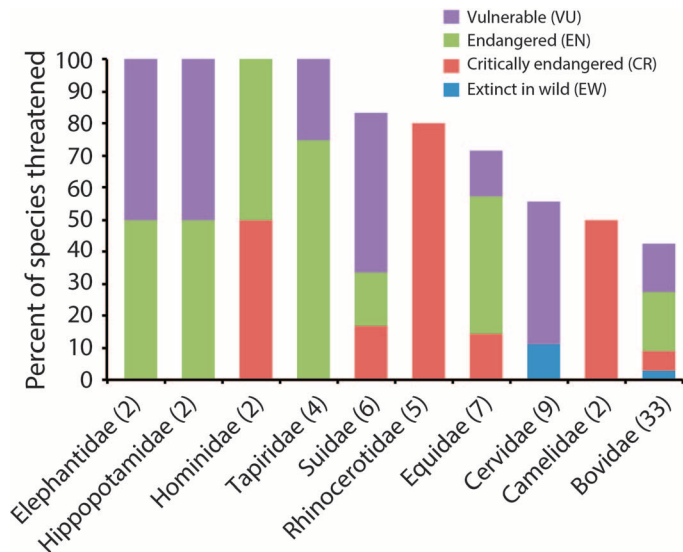


Fig. 2. Proportion of large herbivore species listed as threatened by IUCN. The total number of herbivore species in each family is shown after each family name. Individual threatened species by family include Elephantidae: African elephant (VU), Asian elephant (EN); Hippopotamidae: hippopotamus (VU), pygmy hippopotamus (EN); Hominidae: eastern gorilla (EN), western gorilla (EN); Tapiridae: Malayan tapir (VU), Baird's tapir (EN), lowland tapir (VU), mountain tapir (EN); Suidae: Philippine warty pig (VU), Oliver's warty pig (EN), Visayan warty pig (CR), Palawan bearded pig (VU), bearded pig (VU); Rhinocerotidae: Indian rhinoceros (CR), Javan rhinoceros (CR), Sumatran rhinoceros (CR), black rhinoceros (CR); Equidae: Grevy's zebra (EN), mountain zebra (VU), African wild ass (CR), Przewalski's horse (EN), Asiatic wild ass (CR); Cervidae: sambar (VU), barasingha (VU), Père David's deer (EW), white-lipped deer (VU); Camelidae: bactrian camel (CR); Bovidae: Indian water buffalo (EN), gaur (VU), kouprey (CR), European bison (VU), wild yak (VU), banteng (EN), takin (VU), lowland anoa (EN), tamaraw (CR), mountain nyala (EN), scimitar-horned oryx (EW), mountain anoa (EN), Sumatran serow (VU), walia ibex (EN). Scientific names in table S1.

and ecosystem function (11). Confining large herbivores within fixed boundaries can also lead to overabundance as with bison (*Bison bison*) in North America (12) and elephants in Africa (13).

THREATS

The main threats to large herbivores are hunting, competition with livestock, and land-use change such as habitat loss, human encroachment, cultivation, and deforestation (Fig. 4 and fig. S4). Extensive overhunting for meat across much of the developing world is likely the most important factor in the decline of the largest terrestrial herbivores (14–17). Slow reproduction makes large herbivores particularly vulnerable to overhunting. The largest- and slowest-to-reproduce species typically vanish first, and as they disappear, hunters turn to smaller and more fecund species (14), a cascading process that has likely been repeated for thousands of years (6, 18, 19). In synergy with changes in land use, hunting for meat has increased in recent years due to human population growth, greater access to wildlands due to road building, use of modern firearms and wire snares, access to markets, and the rising demand for wild meat (14, 20). Wild meat harvests have been especially

high in tropical forests, leading to vertebrate extirpations on large spatial scales, a process originally dubbed the “empty forest” syndrome (21). Annual consumption of wildlife meat was estimated to be 23,500 tons in Sarawak, Malaysia (22), and 89,000 tons in the Brazilian Amazon (23). Wild meat hunting also represents an increasing threat in African savannas, resulting in widespread declines in herbivore populations (17). Because wildlife populations outside of protected areas wane, hunters are shifting their attention more to populations in protected areas (17). Demand for wild meat is intensifying, supply is declining, and protected area management budgets for protecting wildlife from overhunting are often inadequate, particularly in developing nations. This creates a “perfect storm,” whereby overhunting often imparts catastrophic population declines (17). Between 1970 and 2005, large mammal populations in Africa's protected areas decreased by about 59% (16). In part due to overhunting, current ungulate biomass was recently calculated to be only 21% of estimated potential ungulate biomass in Zambia's national parks (24).

Hunting large herbivores for body parts is also driving down populations of some species, especially the iconic ones. Organized crime is facilitating a dramatic decline of elephants and rhinoceros in parts of Africa and southern Asia, reversing decades of conservation accomplishments. Poaching and illegal trade in elephant products are currently the top threats to elephants (25). Ivory poaching has surged in recent years, largely due to a rise in demand for and price of ivory in China (26). The number of forest elephants (*L. africana cyclotis*) in central Africa declined by 62% between 2002 and 2011 (25). Currently, 75% of elephant populations are declining and at risk of extirpation, and the range of elephants has drastically declined (26). More than 100,000 African elephants were poached during the 3-year period from 2010 to 2012 (26). This level of illegal kills represents 20% of the current estimated population size of 500,000 African elephants, and even populations of savanna (or bush) elephants (*L. africana africana*) are now declining (26). Poaching of rhinoceros for their horns has also soared in recent years because of its use in traditional Chinese medicine. The number of rhinoceros poached in South Africa grew by two orders of magnitude from 13 in 2007 to 668 in 2012 (27) and 1004 in 2013 (28). The situation is so desperate that an emergency intervention is planned in which large numbers of white rhinoceros will be translocated out of South Africa's Kruger National Park and placed in potentially more secure areas (29). Furthermore, at least in part due to poaching, Africa's western black rhinoceros (*D. bicornis longipes*) was declared extinct in 2011 (1). This slaughter is driven by the high retail price of rhinoceros horn, which exceeds, per unit weight, that of gold, diamonds, or cocaine (27). If accelerated poaching by organized crime syndicates continues, Africa's rhinoceroses may become extinct in the wild within 20 years (27). Numerous species of other large herbivores are also hunted for their body parts, including hippopotamus for their ivory teeth, bovids for horns and skulls, equids for hides, tapirs for feet and hides, cervids for antlers, giraffids for hides, and gorillas for heads, hands, and feet (1). Large herbivores are more vulnerable than smaller herbivores to overharvesting through a combination of the generally higher value of larger bodies or their parts, and the slow life history of the larger herbivores. Together, these increase the likelihood of large herbivores being harvested and reduce their ability to recover from such harvests.

Livestock continues to encroach on land needed for wild grazers and browsers, particularly in developing countries where livestock production tripled between 1980 and 2002 (30). There are an estimated 3.6

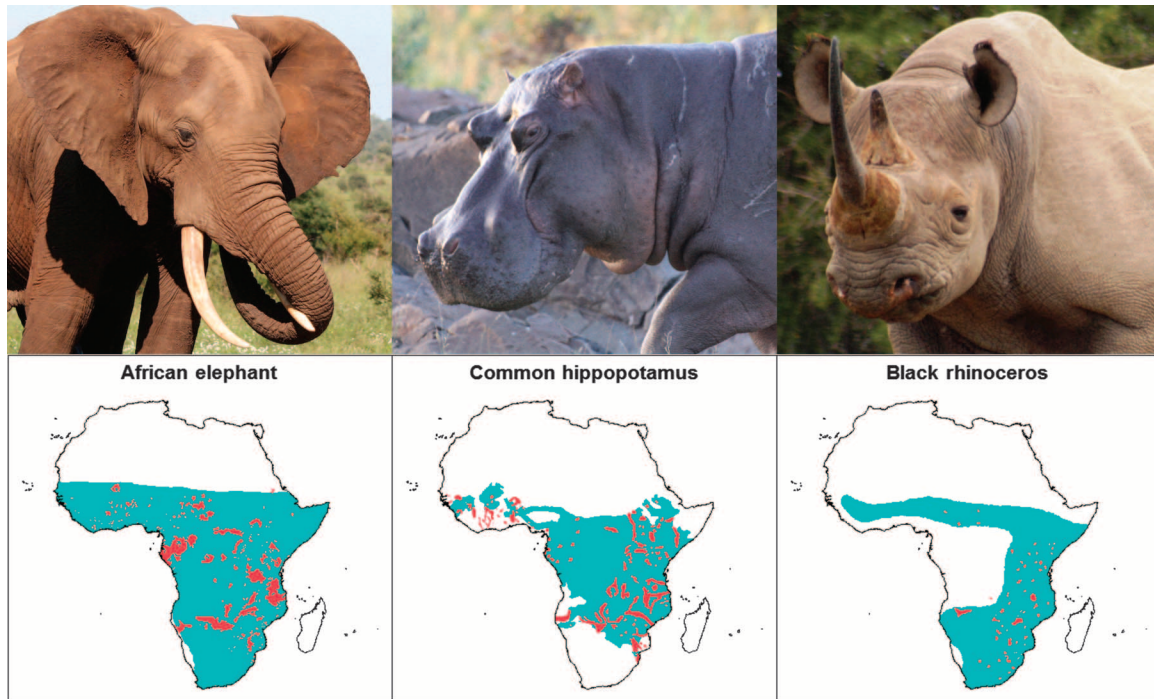


Fig. 3. Range contractions over time for three iconic African herbivores. African elephant (ca. 1600 versus 2008), common hippopotamus (ca. 1959 versus 2008), and black rhinoceros (ca. 1700 versus 1987). The historical ranges are in blue, whereas the most recent ranges are represented by darker-colored polygons. For security purposes, the most recent black rhinoceros range polygons (1987) have been moved by random directions

and distances. The black rhinoceros range has continued to shrink since 1987 across most of Africa, but has expanded locally in Zambia, South Africa, and Namibia through recent reintroductions, and the most current range polygons are not shown because of the recent poaching pressure on the rhinoceros. Photo Credits: Elephant and hippopotamus (K. Everatt), rhinoceros (G. Kerley).

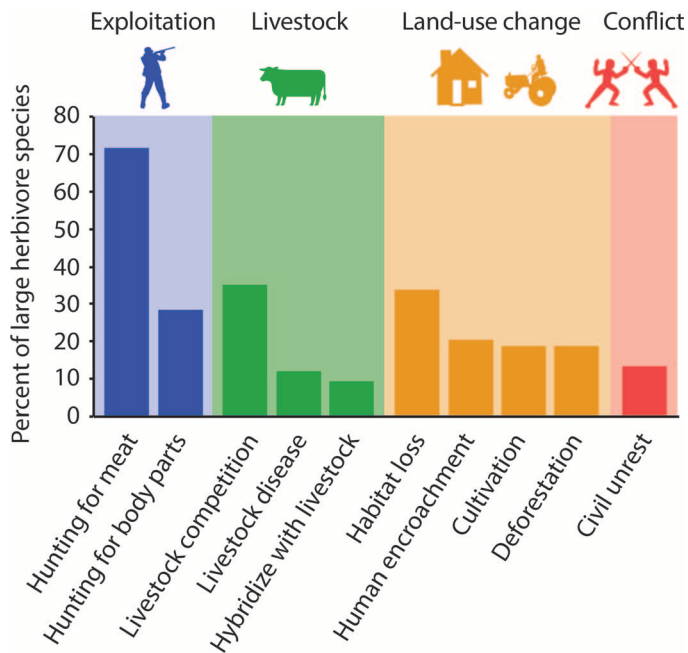


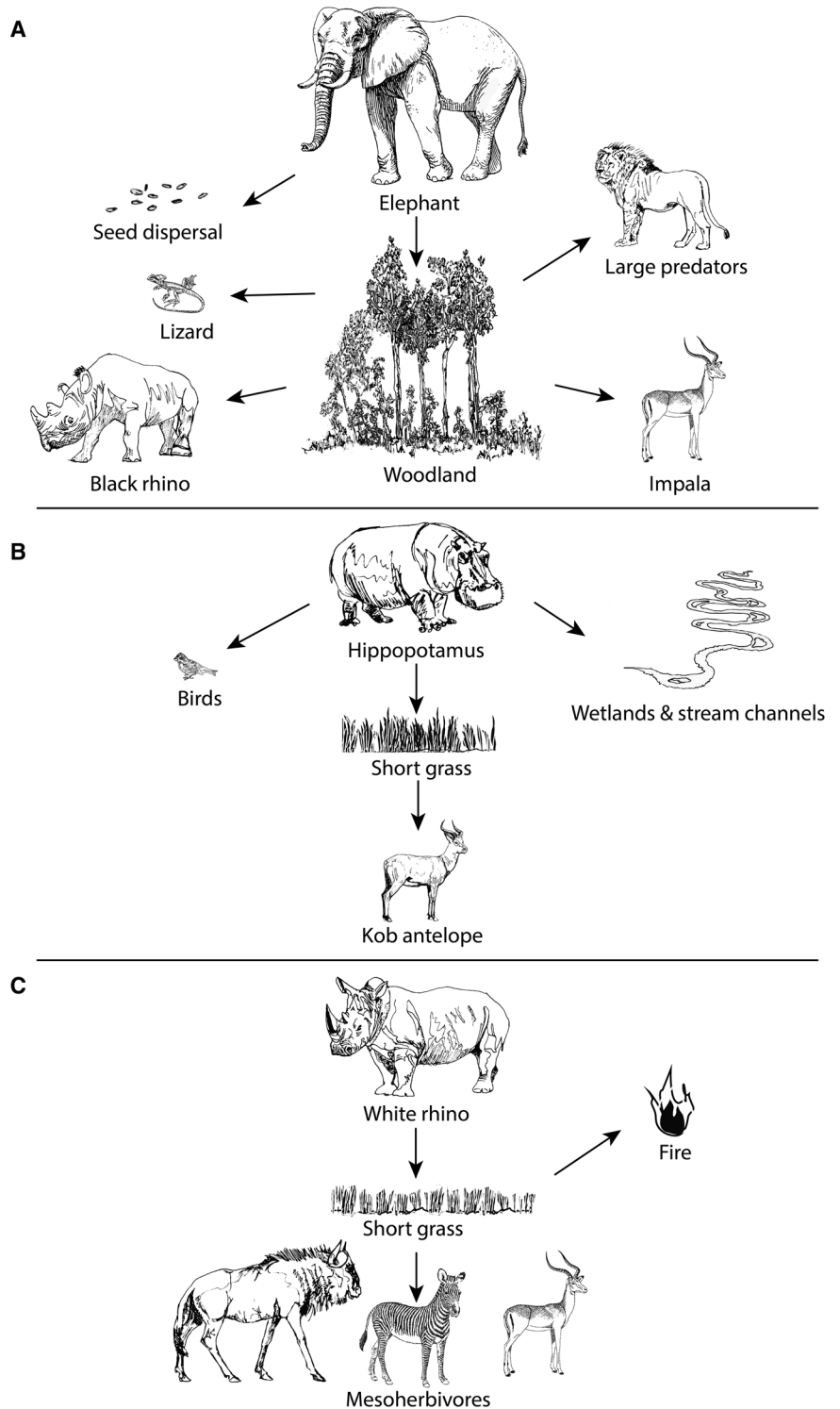
Fig. 4. Proximate threats faced by large herbivores globally. Threats faced by each species were categorized using information in the IUCN Red List species fact sheets. The total adds up to more than 100% because each large herbivore species may have more than one existing threat.

billion ruminant livestock on Earth today, and about 25 million have been added to the planet every year (~2 million/month) for the last 50 years (31). This upsurge in livestock has resulted in more competition for grazing, a reduction in forage and water available to wild herbivores, a greater risk of disease transmission from domestic to wild species (32), and increased methane emissions (31). In central Asia, the expansion of goat grazing for cashmere wool production for international export has reduced habitats available to large herbivores with consequent impacts on their predators including snow leopards (*Panthera uncia*) (33). Livestock competition is also a significant threat to large herbivores elsewhere in Asia, with multiple species jeopardized by this threat in India ($n = 7$), China ($n = 7$), and Mongolia ($n = 4$) (fig. S4). Hybridization with domestic livestock varieties is also a serious problem for some wild species such as the Indian water buffalo (*Bubalus arnee*), Bactrian camel (*Camelus ferus*), wild yak (*Bos mutus*), Przewalski's horse (*Equus ferus*), and several wild pig species (*Sus* spp.) in Southeast Asia (1). Ironically, in many pastoral settings in Africa, domestic livestock are abundant but not regularly consumed for subsistence, and are instead kept as a means of storing wealth, as a status symbol, or for consumption on special occasions (14). Livestock is a private good, and so, people invest significant energy to protect it, whereas wild herbivores are typically a public good, often resulting in weak incentives for their conservation and in many cases open access to the resource, both of which commonly result in overuse.

Habitat loss is a significant threat to large herbivores in parts of Latin America, Africa, and Southeast Asia (Fig. 4). The causes of this threat have important drivers originating in developed countries due

Fig. 5. Conceptual diagrams showing the effects of elephants, hippopotamus, and rhinoceros on ecosystems.

(A) African elephants (*L. africana*) convert woodland to shrubland (53), which indirectly improves the browse availability for impala (*A. melampus*) (53) and black rhinoceros (*D. bicornis minor*) (54). By damaging trees, African elephants facilitate increased structural habitat complexity benefiting lizard communities (100). Predation by large predators (for example, lions) on small ungulates is facilitated when African elephants open impenetrable thickets (48). African elephants are also great dispersers of seeds over long distances (13). **(B)** Hippopotamus (*H. amphibius*) maintain pathways in swamps, leading to new channel systems (101). Areas grazed by hippopotamus are often more nutritious, which benefits kob (*K. kob*) (55). Mutualism and semiparasitism between hippopotamus and birds have also been shown, via the latter eating insects on hippopotamus (73). **(C)** White rhinoceros (*C. simum*) maintain short grass patches in mesic areas, which increases browse for other grazers (impalas, wildebeests, *C. taurinus*, and zebra, *Equus burchelli*) and changes fire regimes (71).



to demand for agricultural and other products. Southeast Asia has the highest rate of deforestation among tropical regions, and if trends continue, Southeast Asia could lose 75% of its original forests and nearly half of its biodiversity by the end of this century (34). Habitat loss is typically asymmetrical with respect to quality, with remaining habitat generally being less productive. A similar trend is found in the tendency to create protected areas in steep, rocky, or dry terrain (35), trapping species of conservation concern in suboptimal habitats (36). Additionally, the greater area requirements of larger species make them unable to persist in smaller fragments of habitat, which may still support smaller herbivores. Their larger area requirement also makes larger species that persist in fragments increasingly susceptible to conservation challenges that affect small populations. This suggests a greater likelihood of extinction among the larger rather than smaller herbivores.

Other threats to large herbivores include human encroachment (including road building), cultivation of crops, and civil unrest, all of which contribute to population decline (Fig. 4). In the future, synergies among the factors discussed here will exacerbate the dangers to large herbivores, as is the case when increased hunting results from people being given access to fragmented, isolated forest remnants within previously extensive and less accessible areas (19). Beyond declines in abundance, the most threatened large herbivores are further imperiled by a loss of genetic diversity. The European bison, for instance, passed through a severe genetic bottleneck in the early 20th century and now suffers from balanoposthitis, a necrotic inflammation of the prepuce that inhibits breeding (37).

CONSEQUENCES OF LARGE HERBIVORE DECLINE

Large herbivores shape the structure and function of landscapes and environments in which they occur (Fig. 5). They directly and indirectly affect other animal species throughout the food web, including their predators and smaller herbivores, and modify abiotic processes involving nutrient cycles, soil properties, fire regimes, and primary production. The roles of large herbivores thus cannot be taken over or compensated for by smaller herbivores. These effects of large herbivores on ecosystems are further discussed below.

Large herbivores as ecosystem engineers

Large herbivores, through their size and high biomass, exert many direct effects on vegetation via trampling and consumption of plants (38). Hence, they maintain patch heterogeneity in systems that would otherwise support continuous woody vegetation. Even in wetter climates, which favor trees over grasses, elephants can maintain open patches (39). Bison also maintain and expand grasslands, and their wallows increase habitat diversity for a variety of both plants and animals (40). Indeed, the larger herbivores consume and, hence, influence the fate of a larger variety of plant species than coexisting mesoherbivores (13). The Pleistocene megafauna extinction can be viewed as a global-scale natural experiment that highlights the continental scale of the ecological impacts that result from the loss of large herbivores. Evidence from Australia suggests that mixed rainforest was converted to sclerophyll vegetation in the aftermath of megafaunal loss (41), whereas in North America, novel plant communities formed that have no modern analogs (42), and in Europe, a heterogeneous mosaic of vegetation structures was replaced with more closed woodland communities (43) as a result of the particularly severe megafaunal declines in these regions (2).

Predators and scavengers

Large herbivores are the primary source of food for predators and scavengers that have high energetic demands, making them an integral component of the food web (11). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) prefer prey above ~90-kg body mass, and all of the world's largest terrestrial carnivores prey on large herbivores (11, 44). Indeed, even the megaherbivores (≥ 1000 kg) such as elephants are not immune to predation (45), because their juveniles are within the size range preferred by some large carnivores (46). Notably, large herbivores may even facilitate the hunting success of predators when their foraging activities open up dense vegetation, making small herbivores more vulnerable (47, 48). Large herbivore carcasses yield more nutrients to a wider suite of scavengers than those of smaller species because the latter are usually consumed completely, whereas large carnivores tend to consume relatively less of large carcasses, thereby leaving more for other species (49). In Yellowstone National Park, gray wolves have been shown to buffer the negative impacts of shorter winters through the food subsidies they provide for a suite of scavengers [for example, coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), ravens (*Corvus corax*), and eagles (*Haliaeetus* spp.)] (50). Given the pivotal and positive role of top predators in many ecosystems, it is unfortunate that depletion of their prey is a serious threat in developing countries (11, 33, 51), particularly for obligate meat eaters such as jaguars (*Panthera onca*), tigers (*Panthera tigris*), lions, leopards (*Panthera pardus*), and snow leopards (*P. uncia*). For example, overhunting of large herbivores in West Africa has reduced the prey base, which, at least in part, has caused regional lion populations to become critically endangered (52).

Synergy between herbivores

Megaherbivores, primarily via their effects on vegetation structure, can facilitate the existence and survival of a suite of mesoherbivores. For example, in northern Botswana, browsing by African elephants helps convert woodland to shrubland, increasing the dry season browse for impalas (*Aepyceros melampus*) (53). In Addo Elephant National Park, South Africa, African elephants create pathways in impenetrable thickets, facilitating black rhino browsing (54). In some seasons, areas grazed by hippopotamus in Benue National Park, Cameroon, are more nutritious with regard to structure and nutrients, which is advantageous for kob (*Kobus kob*) (55). In contrast, high densities of large herbivores inside reserves or in the absence of their predators can be detrimental where overgrazing decreases foraging opportunities for coexisting browsers (56), particularly during periods of low rainfall (57). However, by generally promoting the replacement of tall mature woodlands or grasslands by rapidly growing shrubs or short grasses, large herbivores are more likely to have positive than negative impacts on mesoherbivores (38).

Seed dispersal

Extinct megaherbivores once played a critical role in the colonization of woody plants (58). Even today, large herbivores are irreplaceable as seed dispersers because, relative to smaller frugivores, they are able to consume larger seeds and deliver many more seeds per defecation event over longer distances. Elephants may consume more seeds from a greater number of species than any other taxon of large vertebrate (13, 59, 60). In Congo alone, forest elephants (*L. africana cyclotis*) disperse ca. 345 large seeds per day from 96 species, consistently more than 1 km from the parent trees (61). Indian rhinoceros (*R. unicornis*) move large tree seeds from forest canopies to grasslands, generally with successful germination and recruitment (62). Even smaller species, such as tapirs (*Tapirus* spp.) and gorillas (*Gorilla gorilla*) are effective seed dispersers, which helps to maintain the distribution and abundance of plant species (63, 64). For instance, in African lowland rainforests, primate-dispersed tree species were less abundant at sites with depleted primate populations due to intense hunting by humans compared with sites with low hunting pressure (65). Thus, the loss of large seed dispersers may lead to a wave of recruitment failures among animal-dispersed species (66) with potential consequences for important ecological services (67).

Nutrient cycling

Large herbivore communities consume disproportionately more plant biomass per unit area than small herbivores (68). They affect nutrient cycles via direct and indirect mechanisms that have consequences for ecosystem functioning. For example, large herbivores directly influence nutrient cycling via the consumption of plants, which indirectly causes the reallocation of carbon and nutrients within the plant, while also shifting plant species composition toward species with different rates of litter decomposition (69). Herbivores can greatly accelerate the nutrient cycle in ecosystems through consumption and subsequent defecation, returning nutrients to the soil at rates that are orders of magnitude faster than processes of leaf loss and decay. Moreover, as leaves and twigs are consumed, large herbivores excrete urine and feces and create patches of concentrated nutrients that can last for several years (69). On longer time scales, as the location of concentrated patches shifts over time, large herbivores may play a disproportionate role in diffusing nutrients across landscapes (68). Carcasses also add a variety of nutrients to the soil such as calcium, with effects that can persist several years after the death of the animal (68, 70).

Fire

By altering the quantity and distribution of fuel supplies, large herbivores can shape the frequency, intensity, and spatial distribution of fires across a landscape. There are even unique interactions among large herbivore populations that can influence fire regimes. For example, facilitative interactions between white rhinoceros and mesoherbivores result in reduced fuel loads and fuel continuity, and consequently fewer large, intense fires (71). Other factors can influence the frequency and intensity of fires, particularly in locations where the total area burned is strongly related to ungulate population size. For example, Serengeti wildebeest (*Connochaetes taurinus*) populations irrupted after the rinderpest virus was eradicated in the 1960s, and the subsequent increase in grazing pressure led to a widespread reduction in the extent of fires and delayed recovery of tree populations (72). The removal of plant biomass by browsing also reduces fire fuel loads and decreases fire susceptibility. Thus, there is scant evidence of fire in much of Australia until the megafauna disappeared after humans arrived (5).

Small animals

Despite huge differences in body size, large herbivores interact with a suite of small animals including birds, insects, rodents, lizards, and others (Fig. 5). For example, several fish species feed on flesh wounds of hippopotamus (73), and the dung of Asian elephants may be used by amphibians as daytime refuge, particularly in the dry season when leaf litter is scarce (74). Bison wallows support amphibians and birds by creating ephemeral pools, and bison grazing may facilitate habitat for prairie dogs (*Cynomys* spp.) and pocket gophers (geomyids) (40). Oxpeckers (*Buphagus* spp.) depend on the large herbivores for their diet of ectoparasites, and blood-sucking insects such as tsetse flies (*Glossina* spp.) largely depend on herbivores for food. The presence of large herbivores can also reduce the negative effects of rodent outbreaks. For example, in Kenya, the pouched mouse (*Saccostomus mearnsi*) markedly increased in density after the exclusion of large herbivores, due to an increase in the availability and quality of food (75). Thus, a reduction in large herbivore populations could have unintended consequences if rodent abundance increases, particularly if there are (i) negative effects on plant communities, (ii) increased risks of rodent-borne diseases, or (iii) increases in predators that specialize on rodents (76, 77).

Humans

The loss of large herbivores has direct effects on humans, especially for food security in developing regions. It is estimated that 1 billion people rely on wild meat for subsistence (15). Under a business-as-usual scenario, food security will continue to falter given that wild meat in African forests is expected to decline by more than 80% during the next 50 years (78). Moreover, charismatic large herbivores are important flagship fauna (Fig. 6) that draw many tourists to protected areas, especially when they are sympatric with large carnivores (79). Although the consistency of ecotourism can be interrupted by unpredictable events such as disease epidemics and civil unrest, a decline of large flagship species translates directly into reduced tourism (animal watching, photo and hunting safaris) and thereby a decline in trade balances and employment, particularly in rural parts of the developing world where most megaherbivores persist and poverty is common.

FUTURE DIRECTIONS

Saving the remaining threatened large herbivores will require concerted action. The world’s wealthier populations will need to provide the

resources essential for ensuring the preservation of our global natural heritage of large herbivores. A sense of justice and development is essential to ensure that local populations can benefit fairly from large herbivore protection and thereby have a vested interest in it. The presence of a diversity of large charismatic species can yield financial benefits that flow to local communities (80). For example, with the African photo safari industry, the prospect of simply observing large carnivores, elephants, or rhinoceros can drive tourism revenue. The ultimate forces behind declining large mammal populations are a rising human population and increasing per capita resource consumption (Fig. 7). As is the case for the conservation of most taxa, programs



Fig. 6. Photos of selected threatened large herbivore species. Endangerment status and photo credits include the following: lowland tapir (*Tapirus terrestris*), vulnerable, T. Newsome; mountain nyala (*T. buxtoni*), endangered, H. Hrabar; European bison (*B. bonasus*), vulnerable, G. Kerley; eastern gorilla (*Gorilla beringei*), endangered, P. Stoel; mountain zebra (*Equus zebra*), vulnerable, H. Hrabar.

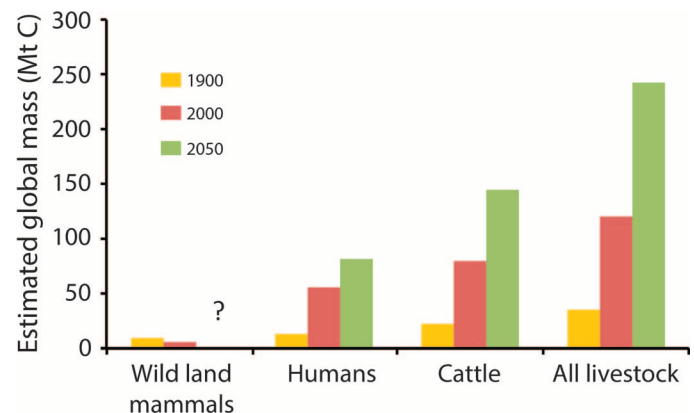


Fig. 7. Global change in the collective mass for wild mammals, humans, cattle, and all livestock for the years 1900–2050. Values for 1900 and 2000 are from (102). Human, cattle, and livestock biomass forecasts are based on projected annual growth in human population, beef production, and meat production, respectively (88, 102).

that help to lower human birth rates in rapidly growing regions such as those that enhance educational and development opportunities, particularly for young women, are a high priority. However, the reality is that strategies for conserving herbivores in the context of high human population densities are likely to be increasingly important. Increasing levels of human carnivory are at the crux of the problem. Lowering human consumption of domestic ruminants could help conserve herbivore populations by reducing demand for rangeland forage, water, and feed crops. Reducing consumption of wild herbivores can also be effective, and enforced wildlife management such as via wildlife ranching has proven to be very successful at maintaining sustainably high harvests of wild meat while providing subsistence food resources to local people. The implementation of wildlife management strategies such as male-only harvests, age-specific harvests, and quotas has the potential to improve both conservation and food security if improved governance can allow for implementation of these strategies. In the near future, urgent action is needed to prevent the extinction of species with extremely low populations, especially those with limited captive populations (for example, Bactrian camel, rhinos, and suids). Decisive steps will be required to address key threats facing threatened large herbivores including, among others, the following.

Focusing research efforts

Basic data and information on the status and ecology of a significant number of large herbivore species are still lacking. From a conservation perspective, we call for a major shift in the large herbivore research effort from the few nonthreatened species in developed countries (for example, red deer, reindeer, and moose/Eurasian elk) to the many threatened species in developing countries (43 species; fig. S2). We urgently recommend more research on the most threatened large herbivores in Southeast Asia, Africa, and Latin America. Species in need of immediate attention include the critically endangered tamaraw (*Bubalus mindorensis*), Visayan warty pig (*Sus cebifrons*), and walia ibex (*Capra walie*), as well as the endangered Oliver's warty pig (*Sus oliveri*), mountain anoa (*Tragelaphus buxtoni*), lowland anoa (*Bubalus depressicornis*), and mountain tapir (*Tapirus pinchaque*), all having fewer than 10 published articles per species (fig. S2). In particular, more research is needed to understand the various ways that rising human and livestock densities (Fig. 7), changing climate, habitat loss, and hunting, as well as different combinations of these factors, affect these large herbivores. We urge large carnivore researchers and conservation agencies to invest more money and attention on the large herbivores that comprise large carnivore prey, because depletion of prey is a significant global threat to large carnivores (11). In an attempt to shift the research effort from well-studied species in developed countries to highly threatened species in developing countries, we recommend the establishment of a fund to finance graduate students to conduct empirical ecological and socioeconomic research that would benefit endangered large herbivores. Examples of potential thesis topics could include (i) replicated studies of the basic ecology of large, rare herbivores that are the least studied, (ii) seed dispersal and woody flora recruitment in areas with and without large herbivores, (iii) effects of diversity of large herbivore species on financial benefits flowing to communities from tourism, (iv) success of stall-feeding livestock programs for potentially reducing competition between livestock and wild herbivores, and (v) potential for increases in traditionally grown protein-rich plant foods rather than domestic or wild meat as a primary protein source for humans.

Addressing poaching

Solving the current crisis associated with poaching for meat and body parts is an essential step, although one that is extremely challenging. Trade bans alone can sometimes succeed but can also fail because they limit supply, causing prices to rise, thereby driving more poaching for the black market (27). Multifaceted bold new policies are urgently needed that (i) increase the effectiveness of law enforcement both through antipoaching and strengthened penal systems related to poaching, (ii) incentivize local communities to conserve wildlife (for example, increasing tourism income), (iii) reduce demand for illegally sourced wildlife products through market mechanisms of controlled trade of products or farming animals (17, 81), and (iv) aid a cultural shift away from luxury wildlife products in industrializing countries such as China and Vietnam. Social marketing and environmental education programs can also be highly effective in reducing demand for wildlife. For example, shark fin sales plummeted after social media pleas by basketball celebrity Yao Ming. Likewise, other prominent Chinese celebrities have also started speaking out to reduce demand for ivory and rhinoceros horn in Southeast Asia.

Managing protected areas

Globally, only ~10% of conservation funding for protected areas is spent in developing countries (82). Underfunding of protected area networks, particularly in the tropics, results in failure to control key threats to herbivores. In the absence of funds for law enforcement, poaching for meat or body parts proceeds unhindered, and many protected areas are being encroached by human settlement, livestock, and logging. Large herbivores, including those that are migratory, need large areas to support viable populations. Given the global tendency for protected areas to be small (<10,000 ha), many protected areas are unable to effectively contribute to the persistence of large herbivores (83). Therefore, expanding protected areas and increasing connectivity between them are important. In some contexts, fencing can assist by demarcating boundaries and reducing human encroachment, while at the same time reducing edge effects and making law enforcement easier (84). Technological approaches such as the use of drones may help to patrol parks with limited resources, but for effectiveness, this technology will need to be low cost, easy to use, durable, and efficient. Without the cooperation of people who live near wildlife, conservation efforts are likely to fail. To ensure just outcomes, it is essential that local people be involved in and benefit from the management of protected areas. Local community participation in the management of protected areas is highly correlated with protected area policy compliance (85). For instance, to protect wildlife, Nepal has successfully adopted a policy of sharing of revenues from protected areas with local people who live adjacent to the reserves (86).

Focusing conservation efforts

In southern Asia and other developing areas, oil palm plantations, pulp and paper, and other commodity crops are rapidly replacing wet tropical forests where large herbivore populations are at risk. In this situation, it makes sense to shift agricultural expansion to abundant degraded low-carbon density lands while sparing the high carbon stock lands for climate change mitigation and animal conservation (87). Infrastructure and mining development are additional important factors in habitat loss. Initiatives are needed to encourage mining companies to underwrite conservation efforts. Moreover, mining sites could be used as de facto wildlife refuges by bringing security to places

that lack it, in turn providing a safe haven for large mammals away from poachers. Moreover, the move of poor rural populations to cities and towns leaves a great opportunity for restoration of large mammals in the hinterlands.

Africa has more large herbivores than any other world region and lower endangerment rates (12 of 32 are threatened) than any other region in the developing world (fig. S1). However, over the next half century, sub-Saharan Africa will have the world's highest projected growth rates of human population and livestock production (88) (fig. S5), which are potential drivers of hunting for meat, habitat loss, and livestock competition. With land use and human demographic patterns in sub-Saharan Africa becoming more similar to those in Southeast Asia, where all 19 large herbivore species are threatened with extinction, it is critical to develop a geographic approach to conservation that focuses on areas with high species diversity, and this should address both human issues (as indicated above) and conservation management. Additionally, conservation actions are dependent on available money. We advocate for a global government-funded scheme for rare large herbivores beyond elephants and rhinoceros, as well as the establishment of a nongovernmental organization that focuses exclusively on rare large herbivores, like what the Arcus Foundation does for apes or what Panthera does for large cats.

Addressing climate change

There are potential combined strategies (joined-up policies) that would mitigate climate change and at the same time benefit large herbivores. Examples include (i) curbing ruminant livestock numbers while increasing high-protein plant-based foods or nonruminant meat so as to lower greenhouse gas (for example, methane and carbon) emissions while also reducing competition with large herbivores (31), and (ii) enhancing carbon storage by preventing tropical forests from being logged while also protecting habitat for large herbivores. In addition, tropical large herbivores disperse large seeds that are typically from slow-growing and densely growing tree species important for carbon storage. By 2050, climate change has the potential to leave many of Earth's species destined for extinction (89). Additional research is urgently needed to better predict changes in large herbivore population sizes and ranges with climate change while accounting for the current threats they face.

FINAL THOUGHTS

The wave of species extinctions that obliterated 80% of the Pleistocene megaherbivores (≥ 1000 kg) on planet Earth appears to be continuing today in Africa and Southeast Asia. The very recent extinctions of Africa's western black rhinoceros and Vietnam's Javan rhinoceros are sober reminders of this long-term trend (1, 90). Then as now, the Pleistocene extinctions were triggered in part by human hunters (2, 91). Solving the current poaching crisis, a sinister development of organized crime, will help but will likely be insufficient to stem, much less reverse, impending declines and future extinctions among the few remaining megafauna. Megafauna remain beset by long-standing and generally escalating threats due to land-use change and ongoing poaching by locals. The situation for the 66 species of large herbivores having body masses of 100 to 1000 kg is not as dire as for those ≥ 1000 kg, but still ominous because 55% of these herbivores are currently threatened (fig. S3). Within this body mass range, hominid, tapirid, suid, and equid species are the most highly threatened families (Fig. 2). Some

species may be slipping away even before they are discovered and described by science. Recently, two rare large herbivores were discovered: a fifth species of tapir, the kabomani tapir (*Tapirus kabomani*), in the Amazon (92) and a bovid, the saola (*Pseudoryx nghetinhensis*), in Southeast Asia (93). To jump-start protection for the saola, conservationists recently removed 27,000 snares from the forests of Vietnam and Laos (94).

The problem of large herbivore declines may not be solved by the current Convention on Biological Diversity target of protecting 17% of terrestrial land by 2020 (95). Given the substantial area requirements of large herbivores, 17% of land in isolated fragments is unlikely to provide sufficient protection to slow or reverse declines, particularly given that inadequate policing/funding can effectively reduce the size of protected areas (96). This is further exacerbated by the global tendency for protected areas to be in low-quality habitats (35), effectively reducing the densities, and hence numbers, that can be conserved in these areas (36).

The range contractions (fig. S6) and population declines of large herbivore species have ecological and evolutionary implications. Range contractions inevitably result from the loss of local populations, many of which are genetically distinct, thus representing a major and under-appreciated pulse of biological extinction (97). Even if they survive in protected areas, many of these largest species might already be below the minimum numbers to be effective in generating ecological cascades (Fig. 5) or allowing evolutionary processes such as speciation (98). Furthermore, 11 of the 44 threatened species are on the Evolutionarily Distinct and Globally Endangered (EDGE) list due to their unique characteristics while being on the verge of extinction. These are the mountain, Asian, and Baird's tapirs (*Tapirus* spp.), black, Javan, and Sumatran rhinoceros, Bactrian camel, Asian elephant (*E. maximus*), pigmy hippopotamus (*Choeropsis liberiensis*), African wild ass (*Equus africanus*), and western gorilla (99). Thousands of years ago, equids were among the most abundant large grazing animals of the grasslands and steppes of Africa, Asia, and the Americas, whereas today, after many of their populations have been decimated, five of the remaining seven species are threatened and at risk of extinction (1). These are the African wild ass, Asiatic wild ass (*Equus hemionus*), Przewalski's horse, Grevy's zebra (*Equus grevyi*), and mountain zebra (*E. zebra*).

Growing human populations, unsustainable hunting, high densities of livestock, and habitat loss have devastating consequences for large, long-lived, slow-breeding, and, therefore, vulnerable herbivore species, their ecosystems, and the services they provide. Large herbivores, and their associated ecological functions and services, have already largely been lost from much of the developed world. The scale and rate of large herbivore decline suggest that without radical intervention, large herbivores (and many smaller ones) will continue to disappear from numerous regions with enormous ecological, social, and economic costs. We have progressed well beyond the empty forest to early views of the "empty landscape" in desert, grassland, savanna, and forest ecosystems across much of planet Earth. Now is the time to act boldly, because without radical changes in these trends, the extinctions that eliminated most of the world's largest herbivores 10,000 to 50,000 years ago will only have been postponed for these last few remaining giants.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/4/e1400103/DC1>

Fig. S1. Regional patterns of endangerment of large herbivores.

Fig. S2. Number of published scientific articles by species.

Fig. S3. Comparison of Pleistocene extinctions by body mass with current threatened species by body mass.

Fig. S4. Global distribution of the four main threats faced by large herbivores.

Fig. S5. Human population trends and projections by region (top) and ruminant livestock trends by region (bottom).

Fig. S6. Current range maps (sorted by family) for the 72 large herbivores not classified as extinct in the wild (EW).

Table S1. Data on the 74 large terrestrial herbivores above 100 kg.

Table S2. The number of large herbivores (threatened, total, and facing each of the four main threats) found in each ecoregion.

Table S3. The number of large herbivores (threatened and total) found in each ecoregion.

Table S4. The threatened large herbivores found in each of the ecoregions with at least five threatened large herbivores.

Table S5. Summary of research effort for the period 1965 to June 2014.

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