

Research

Introduced megafauna are rewilding the Anthropocene

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Large herbivorous mammals, already greatly reduced by the late-Pleistocene extinctions, continue to be threatened with decline. However, many herbivorous megafauna (body mass ≥ 100 kg) have populations outside their native ranges. We evaluate the distribution, diversity and threat status of introduced terrestrial megafauna worldwide and their contribution towards lost Pleistocene species richness. Of 76 megafauna species, 22 (~29%) have introduced populations; of these eleven (50%) are threatened or extinct in their native ranges. Introductions have increased megafauna species richness by between 10% (Africa) and 100% (Australia). Furthermore, between 15% (Asia) and 67% (Australia) of extinct species richness, from the late Pleistocene to today, have been numerically replaced by introduced megafauna. Much remains unknown about the ecology of introduced herbivores, but evidence suggests that these populations are rewilding modern ecosystems. We propose that attitudes towards introduced megafauna should allow for broader research and management goals.

Introduction

Terrestrial herbivorous megafauna are undergoing severe declines around the world. Of 74 extant large terrestrial herbivorous mammal species with body masses ≥ 100 kg, 44 (~60%) are threatened with extinction (Ripple et al. 2015). The decline of this functional group began 10 000–50 000 yr ago, most likely due to overhunting by humans during the late Pleistocene (Barnosky et al. 2004, Bartlett et al. 2015).

Large (≥ 100 kg) herbivorous megafauna (henceforth 'megafauna') perform distinct roles that contribute to the functioning of ecological systems. Megafauna consume fibrous vegetation, which can benefit smaller herbivores, reduce fire risk, accelerate rates of nutrient cycling by orders of magnitude, and shift plant community structure by facilitating coexistence between different plant functional types. Due to their large size, these organisms cause physical disturbance and disperse large seeds and nutrients great distances (Ripple et al. 2015). The considerable loss of this functionality at the end of the Pleistocene had dramatic effects on plant community structure, fire regimes, nutrient and mineral cycling across landscapes, and community assembly (Gill et al.

2009, Ripple and Van Valkenburgh 2010, Smith et al. 2015, Bakker et al. 2016a, Doughty et al. 2016a, b, c, Malhi et al. 2016). Modern declines have similar consequences for terrestrial ecosystems and community dynamics (Ripple et al. 2015) and have led to broad international calls for immediate action to conserve the world's remaining mammalian megafauna (Ripple et al. 2016, 2017).

Less well considered is the role of megafauna introductions on their conservation and on ecosystem function. Since the advent of the Anthropocene, particularly in the past 200 yr, megafauna have been moved to new regions and between continents. Introductions of megafauna worldwide may have inadvertently provided refuge for threatened megafauna, increased regional large herbivore species richness, and restored or added ecological functions. Acknowledgement of this possibility is being fostered by the burgeoning concept of 'rewilding,' which includes efforts to proactively introduce species in order to provide refuge and to restore lost ecological processes (Donlan et al. 2006, Svenning et al. 2016). However, much remains unknown about the contribution of already introduced populations to global conservation goals.

Given that introduced populations are often unwanted and considered components of anthropogenic harm, the existence of populations that are simultaneously introduced and threatened or extinct in their native ranges has been highlighted as a conservation paradox (Marchetti and Engstrom 2015). Indeed, the considerable redistribution of biota that characterizes the Anthropocene may be a countercurrent to the extinction crisis by providing refuge and new opportunities for threatened species (Wallach et al. 2015). However, comprehensive analyses of the interaction between the processes of extinction and redistribution have not been conducted.

To assess the potential conservation values of introduced megafauna we compiled current information on their threat statuses and population trends in their native ranges, their relative population sizes in and out of their native ranges, and their functional roles. To understand how introduced megafauna have potentially rewilded the world, we assessed the contribution of introduced megafauna to continental assemblages, and the contribution of introduced megafauna to Anthropocene richness relative to the Holocene and Pleistocene epochs.

Methods

We searched for introduced populations of herbivorous megafauna (mammals only) with body masses ≥ 100 kg based on Ripple et al. (2015) using Long (2003) and supplemented with online searches (Google Scholar and Google) using the terms 'feral', 'introduced', 'invasive', 'exotic' and 'non-native'. We used grey literature (e.g. government reports) and journalism sources (e.g. The New York Times) alongside peer-reviewed literature to identify megafauna populations outside their native ranges. Data collection concluded in July, 2017.

While some native megafauna populations live in fenced and managed conditions (e.g. Kruger National Park), only free-roaming wild introduced populations were included because it was not clear if fenced/managed introduced populations are ecologically viable in their new homes.

To understand to what extent introduced megafauna represent the taxonomic diversity of the world's remaining megafauna, we calculated the number of large herbivore families represented by introduced species, the number of genera of each family represented by introduced species, and the percentage of species with introduced populations within each taxonomic family.

To determine the potential conservation value of introduced megafauna as refuge populations, we compiled IUCN (2017) Red List threat statuses and trends in each species' historic native ranges and the proportion of each population that is currently outside of its native range (Supplementary material Appendix 2 Table A1). Wild post-domestic species were assigned the threat status of their pre-domestic ancestor. For example, introduced wild dromedary camels *Camelus dromedarius* originate from the domesticated form of an extinct camel species (possibly *C. thomasi*), and were therefore considered extinct in the wild in their native range.

To understand to what geographic extent introduced megafauna have rewilded the world, we calculated megafauna species richness by Taxonomic Databases Working Group level 3 countries (henceforth TDWG), which are biogeographic units defined by political (nation, state, province, or district) boundaries at a biologically relevant scale (Brummitt 2001). Inter- and intra-continental introductions were included in this comparison. The distributions of introduced megafauna were determined from literature and Google searches (Supplementary material Appendix 1 Data A1). Geographic ranges for native megafauna were downloaded from the IUCN (2017) Red List. The percentage of each TDWG country's megafauna assemblage that is introduced was calculated and compared between continents to understand how introductions have altered continental megafauna assemblages.

We assessed how Anthropocene megafauna richness compares to those of past geological epochs. For each continent, we compared megafauna species richness and conservation status between the late Pleistocene (50 000–10 000 BP), Holocene (< 10 000 BP), and Anthropocene (past ~200 yr) epochs. Only inter-continental introduced megafauna were included.

Pleistocene species were classified as 'extinct', 'extirpated' or 'survived' based on their fate through the late-Pleistocene extinction. Pleistocene megafauna presence was based on Sandom et al. (2014) and body masses (≥ 100 kg) were confirmed through literature searches. The Holocene included species from the end of the Pleistocene until the Anthropocene. Holocene species included 'survived' taxa, natural immigrants, and species that went extinct during the Holocene (e.g. aurochs *Bos primigenius* and dromedary

camel). Anthropocene species included ‘survived’, ‘survived, threatened’, ‘introduced’, and ‘introduced, threatened’ species, reflecting their current IUCN (2017) threat statuses (Supplementary material Appendix 3 Table A2).

To describe the range of functional traits of introduced megafauna, we reviewed their average body masses, habitat types, dietary types (grazer, browser, or intermediate), and other unique traits using the IUCN (2017) and published literature.

Results

Twenty-two (32%) of the 76 extant megafauna species have established wild populations outside their native ranges (Supplementary material Appendix 2 Table A1). Sixteen are inter-continental introductions, two are intra-regional but overcame oceanic barriers, and four are intra-continental. By including post-domesticates of extinct heritage, an additional two species (the dromedary camel and cattle *Bos taurus*) are added to the 74 remaining native megafauna. Six additional species were excluded from analysis: three species because they appear to be confined to game ranches, one because introduced populations are described as semi-wild, and two because of uncertain taxonomic relation to already included species.

Six (55%) of the eleven families containing megafauna species have established populations outside their native ranges. Introduced species represent between 29% (Equidae) and 56% (Cervidae) of the megafauna species within their families (Fig. 1). Likewise, introduced populations represent between 50% (Camelidae) and 100% (Equidae) of the megafauna genera within their families.

Of the 22 species with introduced populations, eleven (50%) are threatened or extinct in their native ranges (Fig. 2). This includes four (~18%) Vulnerable non-domesticated species, three (14%) post-domestics whose progenitors are Endangered, one (~5%) Endangered non-domesticated species, two (9%) post-domestic species whose wild progenitors are Extinct, and one (~5%) post-domestic whose progenitor is Critically Endangered. All six post-domestic species are extinct or threatened in their native ranges. Of the remaining eleven introduced megafauna, three (14%) are Near Threatened, and eight are ranked as Least Concern in their native ranges, of which 50% have stable population trends, 22% are increasing, and 11% are declining (Fig. 2). Of the 20 introduced species with surviving native populations, eleven (55%) are declining in their native ranges, five (25%) are stable, and four (20%) are increasing (Supplementary material Appendix 2 Table A1). In all, 64% of introduced megafauna are threatened or declining in their native ranges (Fig. 2).

On average, over 38% (ranging between <1 and 100%) of megafauna populations are outside of their native ranges. Whereas two species have relatively small (possibly ~100 individuals) populations outside their native ranges (hippopotamus *Hippopotamus amphibius*, and Asian elephant *Elephas maximus*), twelve populations are estimated in

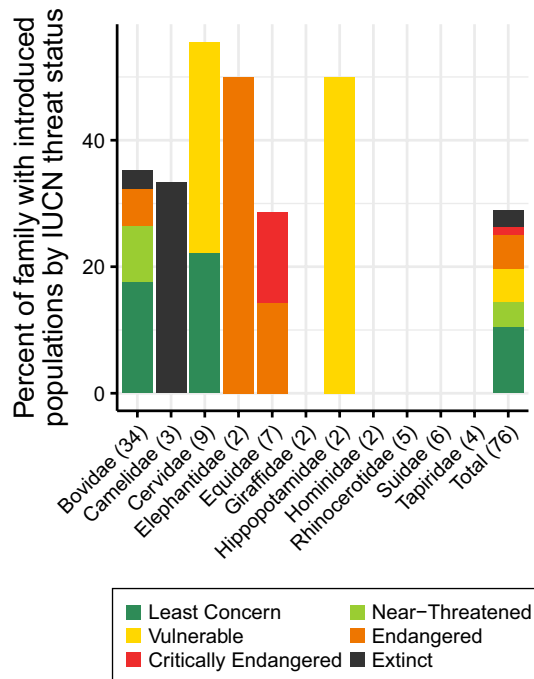


Figure 1. Threatened megafauna species are finding refuge outside their native ranges. Percentage of megafauna in each family with introduced populations, colored by IUCN threat categories in their native ranges. Number within parentheses indicates total number of megafauna within each family.

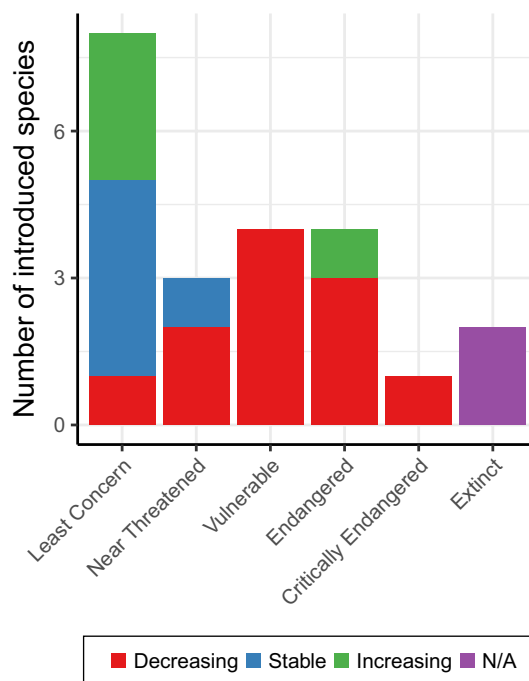


Figure 2. The number of introduced megafauna species by IUCN (2017) threat status and population trends in their native ranges. The majority (59%) of introduced megafauna are threatened or have declining populations in their native ranges.

the thousands and up to over 1 million individuals (Fig. 3, Supplementary material Appendix 2 Table A1).

By including introduced megafauna, the worldwide distribution of megafauna species richness increases significantly (Fig. 4). Introduced megafauna have substantially increased continental megafauna richness and TDWG-country-scale species richness within each continent: 62% of South American (mean \pm SD, 37% \pm 34%), 57% of North American (24% \pm 37%), 33% of European (36% \pm 33%), 11% of Asian (17% \pm 34%), and 11% of African (10% \pm 27%) megafauna are introduced. Introduced megafauna comprise at least 75% of the megafauna assemblages of 56 of the 369 (15%) TDWG countries.

Strikingly, the entire continental megafauna assemblage of Australia is composed of introduced species. Australia lost all megafauna species during the Pleistocene extinctions, yet has become home to eight introduced species in the Anthropocene, including the Endangered banteng *Bos javanicus*, the world's only population of wild dromedary camel, the Vulnerable sambar deer *Rusa unicolor*, and the water buffalo *Bubalus bubalis*, the descendant of the Endangered water buffalo *B. arnee*. Wild donkeys *Equus asinus*, whose progenitor, the African wild ass *E. africanus* is Critically Endangered, and Endangered horses *E. ferus caballus*, have also found refuge in Australia, as well as in North America, South America, and Europe.

Late Pleistocene losses of megafauna species (100% for Australia, 89% for South America, 89% for North America,

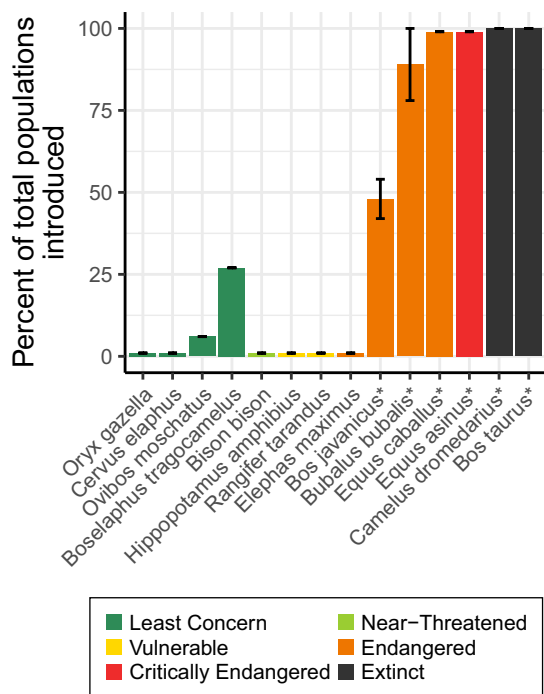


Figure 3. Percent of global populations of megafauna that are introduced. Color indicates IUCN (2017) status. Bars indicate high and low estimates if multiple estimates were found. Includes only species with known population sizes in native and non-native ranges. * indicates post-domestic species.

53% for Europe, 41% for Asia, and 27% for Africa) and Holocene losses (14% for Europe, 5% for Asia, and 3% for Africa) were substantial. Following the Pleistocene, North American species richness increased from 4 to 6 due to immigration of wapiti *Cervus canadensis* and moose *Alces alces* from Eurasia concurrent with the arrival of the first humans to the continent (Hundertmark et al. 2002, Meiri et al. 2014). Reductions in species richness on all continents since the Pleistocene have been counteracted by gains from introduced megafauna in the Anthropocene, so that there are currently more megafauna species per continent than at the end of the Holocene. Introduced megafauna have numerically replaced extinct species richness in Australia by 67%, in South America by 21%, in North America by 26%, in Europe by 33%, in Asia by 15%, and in Africa by 31% (Fig. 5, Table 1).

Megafauna are likely to have significant functional roles in their introduced ranges. Their average body masses ranges from 109 to 3270 kg (median = 256 kg, mean = 526 kg, SD = 697 kg) (Table 2), which is representative of the native megafauna body mass distribution ranging from 100 to 3825 kg (median = 238 kg, mean = 496 kg, SD = 666 kg). Introduced megafauna are primarily grazers (45% of species) or intermediate grazers and browsers (41% of species), and three species (14%) are primarily browsers (Table 1). Introduced megafauna are adapted for habitats ranging from Arctic tundra (muskox *Ovibos moschatus*) to tropical forest (sambar deer) and deserts (dromedary camels) (Table 1). Although there is little known about the specific ecological functionalities of several introduced megafauna, many introduced species are known for unique traits, such as the ability to drink brackish water and consume halophytic plants (dromedary camel) or to survive without surface water (gemsbok *Oryx gazella*) (Table 2).

Discussion

Introduced megafauna represent a significant proportion of the remaining taxonomic diversity of their functional group and are themselves significantly threatened in their historic native ranges. This raises the question of how to assign conservation value in an era of extinction and redistribution. Conservation biology is a field driven by a plurality of values, which offer various visions at different scales and times (Sandbrook et al. 2011). Many current schools of thought prioritize the conservation of species considered to be native at the local and regional scale. However, given the ongoing global extinction process, more research and dialogue is needed to understand when these values may undermine other conservation goals and values.

While many introduced populations were formerly domesticated, they may still effectively represent their wild relatives. Introduced populations of Endangered banteng in northern Australia have maintained high genetic fidelity to their pre-domestic ancestors (Bradshaw et al. 2005).

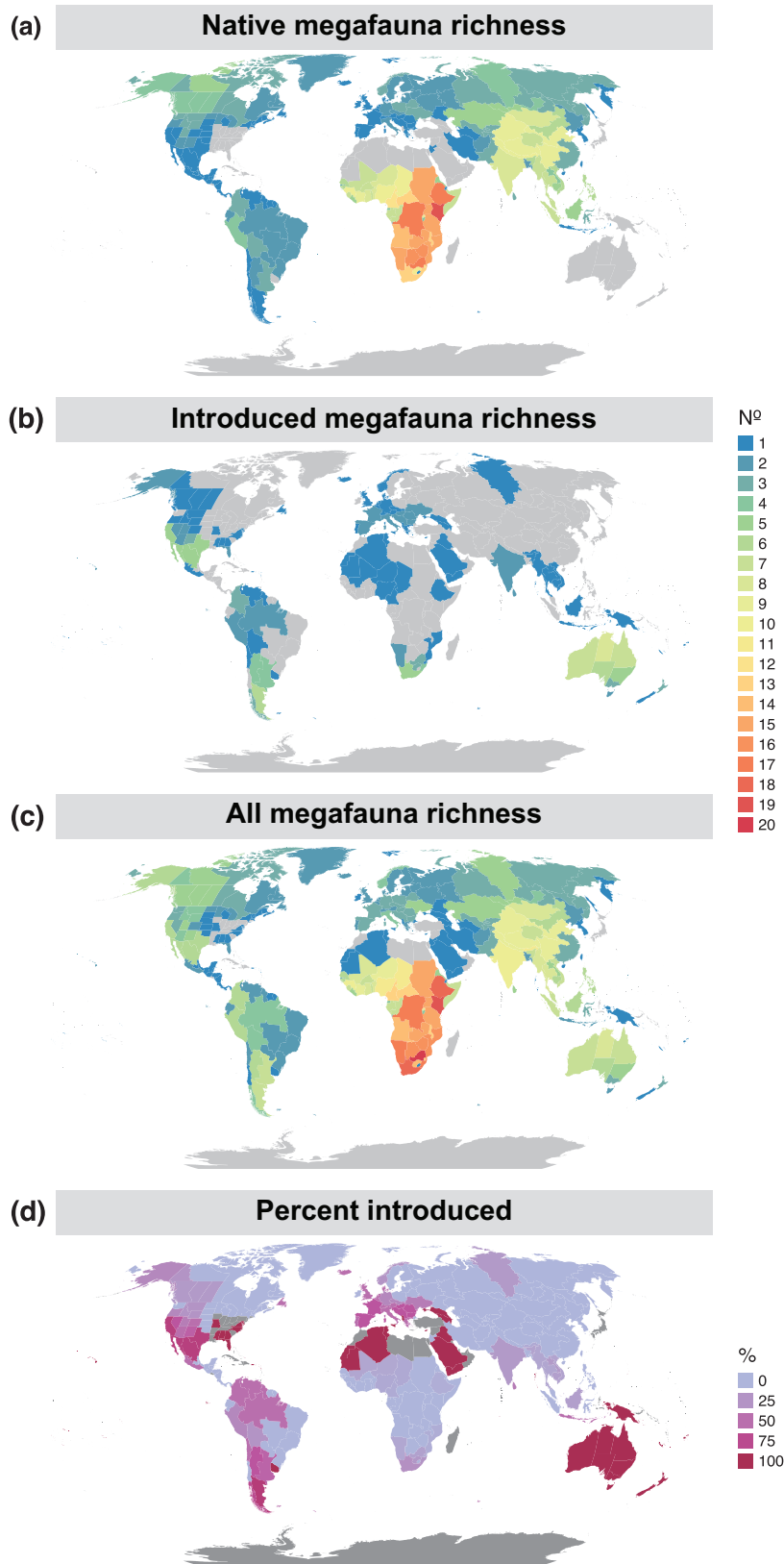


Figure 4. Contribution of introduced megafauna to TDWG-country species richness. (a) Native megafauna species richness (b) introduced megafauna species richness, (c) all megafauna species richness, and (d) percent contribution of introduced species to TDWG-country megafauna assemblages. Inter- and intra-continental introductions were included. Native richness was derived from IUCN (2017) species distribution data. Introduced species distributions are available in Supplementary material Appendix 1 Data A1.

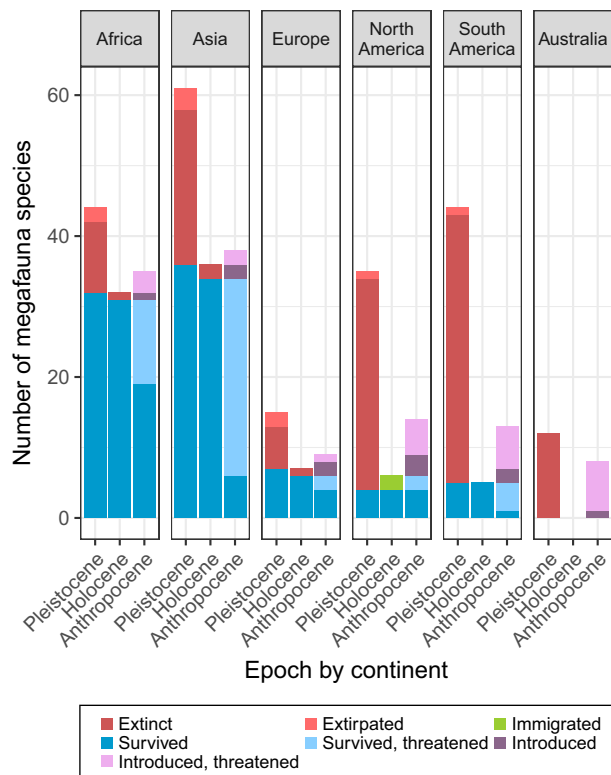


Figure 5. Megafauna species richness per epoch by continent. ‘Extinct’ indicates species that went extinct in the wild on all continents; ‘extirpated’ are species that survived elsewhere; ‘immigrated’ are species that immigrated without human intervention; ‘introduced’ indicates species introduced by humans; ‘introduced, threatened’ are introduced species threatened in their native ranges; ‘survived’ are species that were still present into the following epoch; ‘survived, threatened’ are threatened native species (Supplementary material Appendix 3 Table A2).

Likewise, domesticated horses retain a substantial component of the genetic diversity of extinct Holarctic horse lineages (Lippold et al. 2011). Given that the closest wild relatives of all six post-domestic megafauna are Endangered or extinct, it appears that domestication has provided a crucial bridge for certain species from the pre-pastoral wild landscapes of the early Holocene to the post-industrial wild landscapes of the Anthropocene.

Evolutionary and ecological change has also been witnessed in post-domestic populations. Wild goats *Capra aegragus* on Aldabra Atoll regularly drink saltwater when freshwater is absent (Burke 1990). Wild sheep *Ovis aries* show higher resistance to local parasites than sympatric domestic sheep. Wild Ossabaw island pigs *Sus scrofa* have unique lipid structures (Van Vuren and Hedrick 1989). Wild cattle in Mexico do not linger in riparian areas like their sympatric domestic cousins due to altered predation threats (Hernandez et al. 1999). Native Torresian crows *Corvus orru* appear to have developed a mutualistic grooming behavior on introduced banteng in Australia (Bradshaw and White 2006).

Like all herbivores, introduced megafauna can exert strong grazing or browsing pressure to the detriment of other species, most notably where apex predators are extirpated or continue to be persecuted (Wallach et al. 2010). Unfortunately, much of the research to document these effects has ignored the ecological context of predator control, which is to ignore an important explanatory variable for the density-dependent effects of all herbivores. Indeed, wild horses in the United States may be limited by mountain lions (Turner and Morrison 2001) and dingoes appear to suppress populations of wild donkeys in Australia (Wallach et al. 2010). The potential to influence the ecologies of introduced megafauna by protecting or restoring large predators is an important topic for further research.

In the Pleistocene, the ecological influences of herbivorous megafauna on disturbance regimes, seed dispersal, nutrient cycling, and community structure were ubiquitous. Introduced megafauna have potentially augmented this lost functional and taxonomic diversity across most continents, particularly in those regions most depleted: Australia, North America, and South America (Fig. 4). Asia and Africa have retained many Pleistocene megafauna and have fewer introduced species. Several of these introductions restore taxonomic analogues to extinct Pleistocene species. For example, introduced donkeys are morphologically similar to congeneric extinct North American and South American stilt-legged horses, and the modern wild horse is the same species as the horse of the Holarctic Pleistocene (Weinstock et al. 2005).

The late Pleistocene extinctions in Australia included all megafauna and many browsing herbivores, the loss of which

Table 1. Changes in megafauna species richness from the Pleistocene to the Anthropocene. In column 2, percent survived is the percent of megafauna to survive the late Pleistocene extinctions; in column 3, percent lost/gained is the percent change in Holocene species richness due to extinction/immigration during the Holocene; in column 4, percent replaced is the percent of all extinct megafauna richness (Pleistocene and Holocene) to be numerically replaced by introductions in the Anthropocene. * indicates natural immigration from Eurasia to North America during the early Holocene.

Continent	Pleistocene species richness	Holocene species richness (percent survived)	Holocene extinctions/immigration (percent lost/gained)	Anthropocene richness (percent replaced)
Africa	44	32 (73%)	-1 (-3%)	35 (31%)
Asia	61	36 (59%)	-2 (-6%)	38 (14%)
Australia	12	0 (0%)	N/A	8 (67%)
Europe	15	7 (47%)	-1 (-14%)	9 (33%)
North America	35	4 (11%)	+2 (+33%)*	14 (26%)
South America	44	5 (11%)	0 (0%)	12 (18%)

Table 2. Functional traits of introduced megafauna. ABM is average body mass (Jones et al. 2009); foraging type is 'B' is browser, 'G' is grazer, and G/B are intermediate; habitats are derived from IUCN Redlist species accounts IUCN (2017) Red List.

Species	Common name	ABM	Type	Habitat	Known or potential unique ecological functions
<i>Alces alces</i>	Moose	541	B	Woodlands, tundra, montane forests	Browse at heights up to 2 m, affecting stand height and canopy composition (Pastor et al. 1988).
<i>Bison bison</i>	Bison	625	G	Grasslands, open forests	Create wallows that become ephemeral pools, serve as fire breaks, and increase landscape scale plant diversity (Knapp et al. 1999).
<i>Bos javanicus</i>	Banteng	636	G/B	Open dry forests	Open trails in dense shrubland, capable of jumping 2.5 m high, potentially sustaining seed/nutrient dispersal in fenced landscapes (Leslie 2008).
<i>Bos taurus</i>	Cattle	613	C	Numerous	
<i>Boselaphus tragocamelus</i>	Nilgai	182	G/B	Open grasslands	Used for conservation grazing to maintain open water habitat for birds and fish (BBC News 2004).
<i>Bubalus bubalis</i>	Water buffalo	919	G/B	Moist grasslands, marshes	Salt-tolerant (Root-Bernstein and Svenning 2016); large home ranges (Spencer et al. 2012), may redistribute sodium (Doughty et al. 2016a).
<i>Camelus dromedarius</i>	Dromedary camel	488	B	Desert scrub	Ecological engineer in native range by dispersing large seeds and removing trees (Donlan et al. 2006). Digs wells used by other species.
<i>Cervus elaphus</i>	Red deer	241	G/B	Generalist	
<i>Connochaetes gnou</i>	Black wildebeest	157	G	Short-grass grasslands	Feeds on coarse, abrasive grasses (Naundrup and Svenning 2015).
<i>Elephas maximus</i>	Asian elephant	3270	G/B	Tropics	Maintain grazing meadows, fertilize riparian systems (Bakker et al. 2016b), unstudied in introduced range.
<i>Equus asinus</i>	Donkey	180	G/B	Deserts	Riparian grazer, likely influences riparian vegetation and river geomorphology (Naiman and Rogers 1997, IUCN 2017). Dig wells used by other species (Hamilton et al. 1977). Few other herbivores adapted to extreme arctic environment (Schmidt et al. 2015).
<i>Equus caballus</i>	Horse	400	C	Grasslands, open forests	
<i>Hippopotamus amphibius</i>	Hippopotamus	1536	G	Aquatic daytime refuge; grasslands	Grazing can alter arctic albedo, causing temperature reductions that may counteract climate change (te Beest et al. 2016). Uniquely capable of digesting lichens (Palo 1993).
<i>Hippotragus niger</i>	Sable antelope	236	G/B	Woodland edges	
<i>Kobus ellipsiprymnus</i>	Waterbuck	204	C	Savanna woodlands	Riparian grazer, likely influences riparian vegetation and river geomorphology (Naiman and Rogers 1997, IUCN 2017).
<i>Oryx gazella</i>	Gemsbok	188	G	Desert scrub, desert grassland	Few other herbivores adapted to extreme arctic environment (Schmidt et al. 2015).
<i>Ovibos moschatus</i>	Muskox	313	C	Arctic tundra	
<i>Ovis ammon</i>	Argali	114	C	Steep, rocky environments	Grazing can alter arctic albedo, causing temperature reductions that may counteract climate change (te Beest et al. 2016). Uniquely capable of digesting lichens (Palo 1993).
<i>Rangifer tarandus</i>	Reindeer	109	G/B	Mountains, arctic tundra	
<i>Rucervus duvaucelii</i>	Barasingha	171	C	Forests, riparian grasslands	Riparian grazer, likely influences riparian vegetation and river geomorphology (Naiman and Rogers 1997, IUCN 2017).
<i>Rusa unicorn</i>	Sambar	178	G/B	Generalist	

appears to have led to increased fire frequency and altered plant community structure (Miller et al. 2005, Rule et al. 2012). Introduced megafauna, especially browsers such as dromedary camels, may reverse these ecological state shifts. However, determining how introductions of taxonomically dissimilar species restore or add new functionalities within insular ecosystems (there are no surviving taxonomic analogues to Australia's Pleistocene marsupial megafauna) requires further research into the relative importance of co-evolutionary history versus ecological context in determining species coexistence and ecosystem function (Wallach et al. 2015).

Introduced megafauna vary in body mass considerably, which influences their ability to open thickets and digest coarse fibrous vegetation and thus their relation to plant communities and other herbivores. Introduced megafauna also possess unique functional adaptations that may be of ecological significance in their new ranges. For example, introduced camels are capable of ingesting brackish water and consuming halophytic plants (Root-Bernstein and Svenning 2016), which in conjunction with their large home ranges (Spencer et al. 2012) may contribute to the megafaunal redistribution of terrestrial salts (Doughty et al. 2016a). Likewise, the ability of gemsbok *Oryx gazella* to

survive without surface water (Hamilton et al. 1977) likely allows it to occupy novel niches in the North American deserts in which it now lives.

There is substantial and growing evidence that introduced species can perform significant and desirable ecological roles (Schlaepfer et al. 2011). Bighorn sheep forage more efficiently, with less time invested in vigilance behaviors in mixed herds with introduced wild horses (Coates and Schemnitz 1994). Giant tortoises introduced onto oceanic islands as substitutes for extinct species are dispersing large-seeded endemic plants and shaping plant communities through grazing (Hansen et al. 2010). Intentional introductions of horses and cattle in the Oostvaardersplassen nature reserve in the Netherlands have created Pleistocene-like savanna conditions in a temperate deciduous forest environment (Vera 2009). In North America and Australia, the drying and constriction of desert springs and the extinction of several endemic fish populations was linked to the removal of wild introduced megafauna whose grazing appeared to maintain open-water habitat (Kodric-Brown and Brown 2007).

Likewise, our own ongoing research is yielding similarly surprising observations. For example, in the Sonoran Desert of North America, wild donkeys ('burros', *E. asinus*) dig

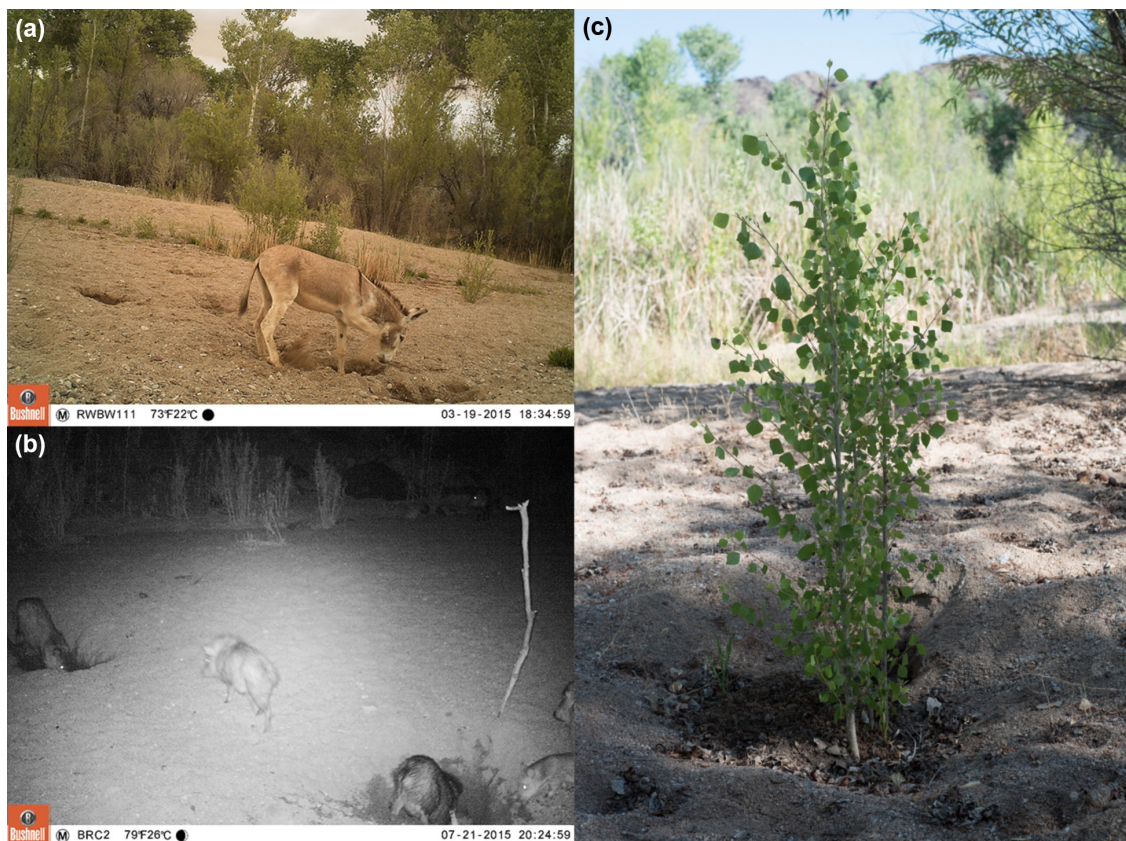


Figure 6. Wild donkeys *Equus asinus* increase surface water availability in the Sonoran Desert. (a) Wild donkey digging well to water table ('burro well'), (b) troop of javelina *Pecari tajacu* bathing and drinking in burro wells, and (c) several-year-old Fremont's cottonwood *Populus fremontii* growing in an abandoned burro well on a high channel bar.

groundwater wells of more than a meter in depth (Supplementary material Appendix 4 Movie A1). These wells are common wherever groundwater approaches the surface, have been recorded in use by more than thirty mammal and bird species, and in certain conditions become nurseries for riparian trees (Fig. 6). It is possible that by creating new water sources across the landscape, maintaining access to receding water-tables during droughts, and providing conditions ideal for the germination of riparian trees, wild donkeys play a facilitative role, one that may improve the resilience of these arid ecosystems to climate change. Furthermore, given the ubiquity of taxa whose contemporaries dig wells, such as Proboscideans (Ramey et al. 2013) and other equids (Feh et al. 2002) in the North American Pleistocene, it is likely that introduced donkeys have restored a functionality lost from these landscapes.

Unfortunately, little more is known about the ecological functions of megafauna outside their native ranges because the majority of studies are conducted on the premise that introduced species are harmful and should be suppressed or eradicated. Future research on the ecological functions of introduced megafauna, under varying ecological contexts (e.g. predator control, landscape connectivity), will be essential to understand the novel megafaunal communities of the Anthropocene.

Reassessing conservation attitudes towards introduced megafauna may find synergy with other conservation goals. Introduced megafauna are likely vulnerable to similar threats as native megafauna as they require large tracts of land and may be vulnerable to exploitation. Valuing introduced megafauna as umbrella or flagship species in efforts to expand protected areas or establish movement corridors would contribute to important conservation goals. Broadening the range of wildlife valued and protected by conservation practitioners could also help form alliances with public advocates of introduced megafauna, who are often alienated by projects that treat these species as pests. Conflicts between these groups and conservation professionals erode trust and undermine conservation efficacy (Crowley et al. 2017), yet these groups are natural allies in their concern for the welfare and persistence of non-human life (Bruskotter et al. 2017). It is likely that incorporating broader value systems towards these organisms would offer a range of practical benefits towards conservation objectives and could strengthen the diversity and inclusiveness of the conservation community.

The introduced megafauna of the world have restored species richness across many continents to levels approaching the Pleistocene, contribute fascinating and potentially important ecological functions, and are an important refuge for their functional group. We propose that further research and dialogue on how introduced megafauna interact with and without potential predators in the novel ecosystems of the Anthropocene will be essential in reconciling the concerns of local managers with global conservation efforts and will bring new attention to the emerging eco-evolutionary trajectories of these populations.

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Supplementary material (Appendix ECOG-03430 at <www.ecography.org/appendix/ecog-03430>). Appendix 1–4.