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An ecoregion-based approach to restoring the world's intact large mammal assemblages

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Assemblages of large mammal species play a disproportionate role in the structure and composition of natural habitats. Loss of these assemblages destabilizes natural systems, while their recovery can restore ecological integrity. Here we take an ecoregion-based approach to identify landscapes that retain their historically present large mammal assemblages, and map ecoregions where reintroduction of 1–3 species could restore intact assemblages. Intact mammal assemblages occur across more than one-third of the 730 terrestrial ecoregions where large mammals were historically present, and 22% of these ecoregions retain complete assemblages across > 20% of the ecoregion area. Twenty species, if reintroduced or allowed to recolonize through improved connectivity, can increase the area of the world containing intact large mammal assemblages by 54% (11 116 000 km^2). Each of these species have at least two large, intact habitat areas (> 10 000 km^2) in a given ecoregion. Timely integration of recovery efforts for large mammals strengthens area-based targets being considered under the Convention on Biological Diversity.

Keywords: ecoregions, faunal assemblages, large mammals, restoration, rewilding

Introduction

Intact ecosystems are recognized for their exceptional value in conserving biodiversity, stabilizing the climate, sustaining livelihoods of indigenous peoples and provisioning

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essential services for humanity (Watson et al. 2018). Recent conservation analyses elevate the importance of intact landscapes, estimated at about 23% of the Earth's terrestrial surface. Intact landscapes form a part of a larger matrix of between 41 and 46% of remaining habitat that can support biodiversity conservation (Venter et al. 2016, Beyer et al. 2020, Riggio et al. 2020). These studies presume that structural intactness of habitats – as inferred from remotely sensed data and anthropogenic disturbances – serve as proxies to estimate biotic intactness, a feature more challenging to assess globally (Plumptre et al. 2019). Notably, such structural analyses of habitat fail to detect defaunated ecosystems lacking large vertebrates and the important roles these species play in maintaining ecosystem function.

One measurable estimator of biotic intactness is the persistence of intact large mammal assemblages (Morrison et al. 2007). Large mammals serve as landscape engineers, shaping the structure and composition of natural habitats (Svenning 2020). Top predators also influence vegetation structure and composition, and populations of other species down to the level of soil invertebrates (Bakker et al. 2016, Morris and Letnic 2017, Andriuzzi and Wall 2018). Many species integral to maintaining stable natural systems have, however, experienced population extirpations or range collapse as a result of overhunting, habitat conversion and degradation (Ripple et al. 2014, 2015). Loss of top predators and large herbivores destabilizes or unravels natural ecosystems (Ripple et al. 2014, Guyton et al. 2020). The focus of this paper is to provide guidance to reverse this trend: to present an ecoregion-based approach to accelerate the recovery of large mammal faunas among more than 190 of the world's 730 ecoregions that historically contained large mammal species (Dinerstein et al. 2017).

Ecoregions – ecosystems of regional extent containing distinct assemblages of natural communities – provide a useful framework for examining ecosystem integrity (Plumptre et al. 2019). The importance of maintaining intact species assemblages at the ecoregion level is essential because ecoregions encompass biologically distinct asssemblages of species (González-Maya et al. 2017, Smith et al. 2018). Ecological functioning is often higher in ecoregions with intact large mammal assemblages compared to those without them, as large mammals play a key role in shaping and maintaining natural processes (Estes et al. 2011, Ripple et al. 2014); ecoregions that retain intact large mammalian faunas also sequester large amounts of carbon (Dinerstein et al. 2020). In addition, ecoregions have been widely used as the spatial unit for analysis in dozens of global and regional conservation planning and priority-setting processes (Olson et al. 2001, Dinerstein et al. 2017). Ecoregions also provide an appropriate scale of reference that can reflect variations in biome, habitat types, political boundaries and other natural and anthropogenic factors that influence the past and current distribution of large mammal species. Ecoregions have also served as the spatial unit in studies of the effects of climate on biotas (Yu et al. 2019). Using ecoregions as the biogeographical unit to examine large mammal assemblages therefore allows our findings to highlight specific regions of conservation interest, and to be integrated into biodiversity actions plans and programs for the protection and restoration of large mammal faunas.

We begin by reviewing where intact large terrestrial mammal assemblages – places containing all large mammals that were present 500 years ago – remain, organized by ecoregion. In addition to conserving these priority ecoregions, restoration and reintroductions can be done to increase the world's intact large mammal assemblages. We also examine where reintroductions programs are feasible and contribute to restoring intact assemblages. Specifically, we identify ecoregions that are missing 1–3 species from their intact large mammal faunas. To accelerate planning for recovery, we also propose a) a subset of 20 priority species whose reintroduction would lead to the greatest spatial expanse of restored faunas, and b) a list of 30 high-priority ecoregions providing suitable habitat and near-term opportunities to restore intact large mammal faunas.

From a practical perspective, our results can guide the formulation of updated National Biodiversity Strategies and Action Plans that can be prepared under the auspices of the Convention on Biological Diversity. They can also update spatially explicit maps created to achieve the Convention's post-2020 Global Biodiversity Framework, such as the Global Safety Net for biodiversity and climate (Dinerstein et al. 2020). Conserving and restoring intact large mammal faunas adds a critical missing dimension to ambitious area-based targets being considered under the Convention on Biological Diversity for 2030.

Methods

We used the IUCN Red List of threatened species, along with data on body mass, to generate a species list of 298 large extant terrestrial mammals (Smith et al. 2003, Jones et al. 2009, IUCN 2019, Myers et al. 2020, Supporting information). We defined 'large mammals' as those with maximum recorded body mass equal to or greater than 15 kg, a threshold that allows the inclusion of key predators, their prey and other large herbivores, and that is consistent with other studies (Ripple et al. 2014, Wolf and Ripple 2018, Ferreira et al. 2020, Salom-Pérez et al. 2021).

To identify intact and near-intact large mammal assemblages, we used data from the IUCN Red List (IUCN 2019) for current species ranges and data from Faurby and Svenning (2015) for natural ranges (Supporting information). Faurby and Svenning (2015) modeled mammal species ranges as the ranges would have been today in the absence of human influence. We chose regional presence at AD 1500 as the cutoff for natural ranges, following the rationale provided by Morrison et al. (2007) (see also the Supporting information for further information). Briefly, this marks a globally synchronous period after which there were the most profound anthropogenic changes to Earth's terrestrial area; it is the same demarcation used by the IUCN Red List as the cutoff for examining 'recent' extinctions. Moreover, all except six of the large mammal species ($\geq$ 15 kg) present in AD 1500 are still extant and have opportunities for in situ conservation. The six extinct species (EX) were removed from the analysis since there is no opportunity for their restoration; one species listed as extinct in the wild (EW; *Elapharus davidianus*) was retained.

Intact and near-intact large mammal assemblages were identified by first converting current species range polygons into ~100 km^2 rasters to match the natural species range data. To ensure small ranges were not missed, any grid cells that overlapped the polygon were included. These raster layers of current and natural species ranges were then downscaled and refined to 10 km^2 using the Land Cover product published by the European Space Agency Climate Change Initiative (ESA CCI) (Bontemps et al. 2013). To perform this step, the ESA CCI landcover was first resampled to 10 km^2 and each landcover class was linked to habitat preferences from the IUCN Red List (IUCN 2019). For example, the ESA CCI landcover class 'tree cover, broadleaved, evergreen, closed to open (> 15%)' was linked to the IUCN habitat preference of 'Forest'. The individual 100 km^2 current and natural species range rasters were then downscaled by resampling them to 10 km^2 and removing grid cells that did not match the habitat preferences linked to the corresponding 10 km^2 landcover data. This process removes unsuitable habitat from each species' range, limiting errors of commission. Natural range maps were also downscaled using current landcover to ensure areas no longer suitable for a species were excluded as potential restoration areas. Thus, the spatial scale at which decisions were made about presence or absence of a particular large mammal species was at a fine-grained scale of 10 km^2. Only later in the analysis was the ecoregion boundary coverage overlayed on the relevant grid cells.

To identify areas where a species is no longer present but might have occurred in the absence of human influence, each species' current refined range was then subtracted from its refined natural range. These areas of loss for each species were then combined, yielding a raster of the number of species missing per grid cell. Using this raster, we identified places having all species present as intact large mammal assemblage areas. We identified near-intact large mammal assemblages as those with 1–3 missing species. We chose this range because our objective was to take a pragmatic approach to identify places for restoration to a complete assemblage. This decision serves as a reasonable starting place for operationally defining the term 'near-intact'. Our rationale was if restoration of the assemblage will require targeted, species-based reintroductions, major effort required will be needed for each species. Conversely, areas with more than three species missing are more likely to be degraded, isolated or have significant hunting pressures and make near-term restoration less feasible. We summarized grid cell output within ecoregion boundaries (Dinerstein et al. 2017, Supporting information).

We tallied the total area in which each of the 298 large mammal species is the only missing candidate of an intact large mammal assemblage in a grid cell. We counted the number of ecoregions and the number of large, continuous habitat blocks (> 10 000 km^2) in which these grid cells occur. This allowed us to rank the top 20 large mammal species whose reintroduction can restore intact assemblages to the largest potential areas missing only one species.

We identified a list of high-priority ecoregions for restoration by first selecting ecoregions that lacked intact large mammal assemblages, but were missing only 1–3 species over a large portion (> 80%) of the ecoregion. A second list of candidate ecoregions contained at least one intact large mammal assemblage, but had at least 20% of the area missing 1–3 species. From this list we selected ecoregions where intact mammal assemblages could feasibly be restored with 1–3 reintroductions in the next 5–10 years. To ensure the illustrative list of priority restoration ecoregions included places where restoration is practical in the near term, we used expert knowledge, ecoregion descriptions, range maps and both published and unpublished literature to select priority ecoregions in each of five biogeographical realms (Nearctic, Neotropic, Afrotropic, Palearctic and Indomalayan).

Results

The world's remaining intact large mammal assemblages

Extant large mammals would naturally be present in 730 of the World's 846 terrestrial ecoregions. Currently, most of these ecoregions (726 of 730, 99%) still support at least one extant large mammal species; large mammal species are completely extirpated from four ecoregions. Distributions of large mammal species varies by ecoregion and biogeographical realm as a result of biogeographical influences and human-caused extinctions occurring before AD 1500 (Fig. 1). There are clear asymmetries: species-rich sub-Saharan African ecoregions have diverse faunas versus South America and island ecoregions where, for historical and eco-evolutionary reasons, richness is low.

Forty-four percent of ecoregions (321 of 730) retain historically intact large mammal assemblages in more than 1% of the ecoregion's area. These occur on every continent except Antarctica (Fig. 2). Forty-one ecoregions (5.6% of 730) contain intact assemblages across more than 90% of their area and most of them are found in Tropical and Subtropical Moist Broadleaf Forests; Tropical and Subtropical Grasslands, Savannas and Shrublands; and Deserts and Xeric Shrublands biomes (Supporting information). One-hundred-five ecoregions (14.4% of 730) have intact species assemblages across more than 50% of their area (Fig. 3). These ecoregions are concentrated in Australasia and the Amazonian region of the Neotropics, but also span other biomes and regions (Fig. 3). For example, ecoregions across the Arctic Tundra, the seasonally inundated grasslands of the Pantanal, and the tropical forest ecoregions of the Philippines and Papua New Guinea all contain intact assemblages (Supporting information). Twenty-two percent of all ecoregions (159 of 730) retain complete mammal assemblages across more than 20% of the ecoregion area (Fig. 3, Supporting information). In total, about 15.5% (20 853 676 km^2) of Earth's terrestrial

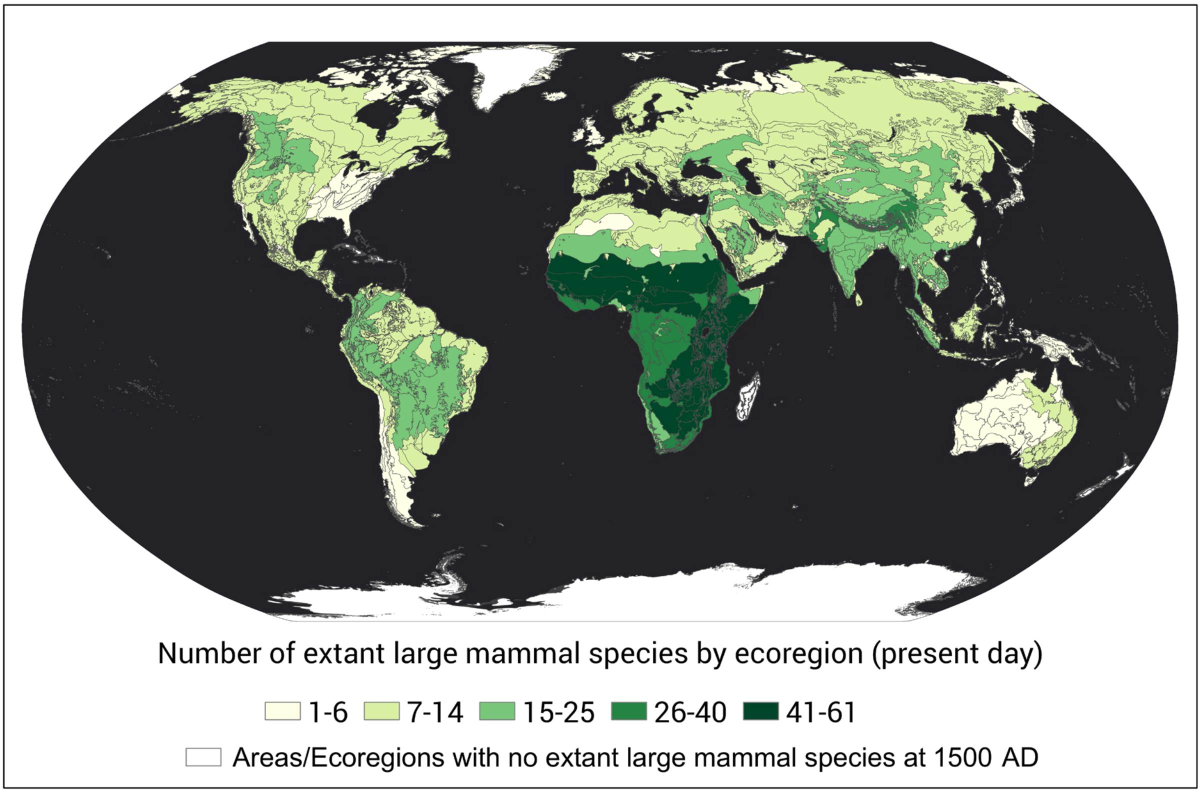

Figure 1. Species richness of extant large mammals by ecoregion (present day).

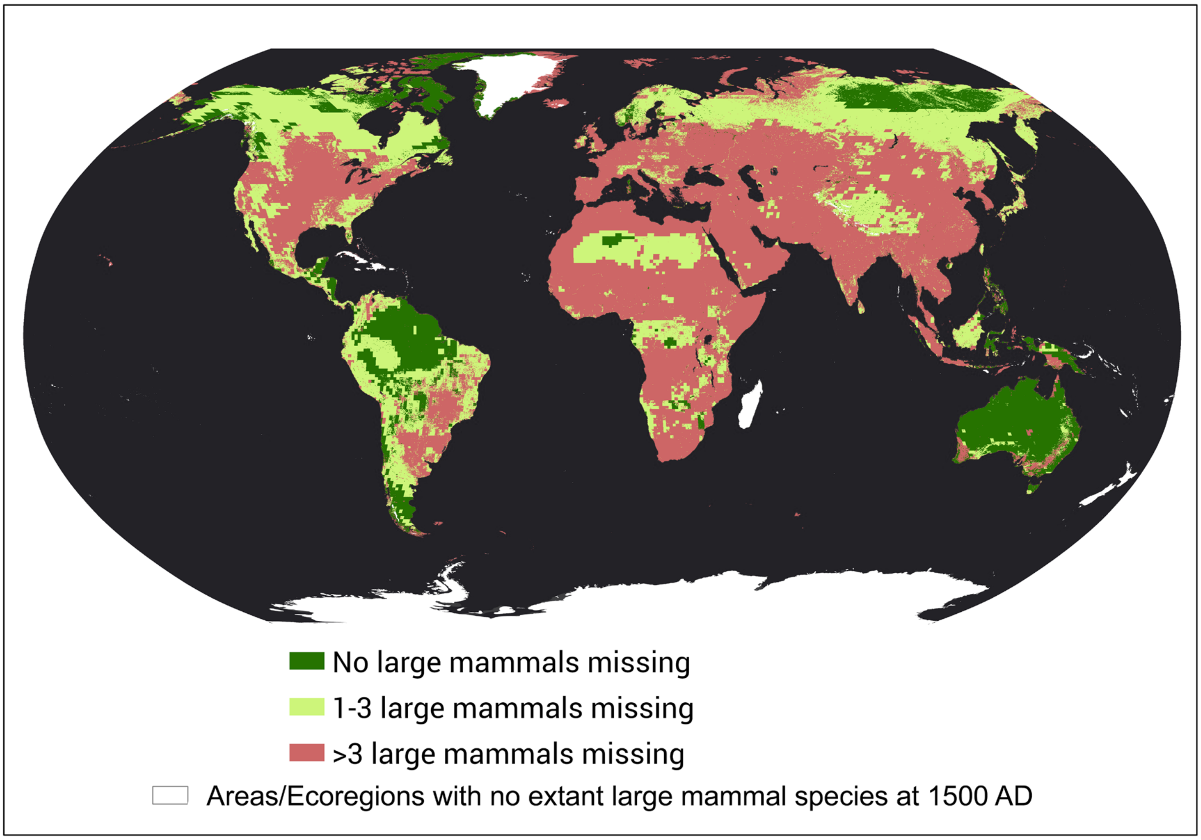

Figure 2. Areas with no (dark green), 1–3 (light green), or > 3 (red) large mammals missing, given 1500 AD distribution.

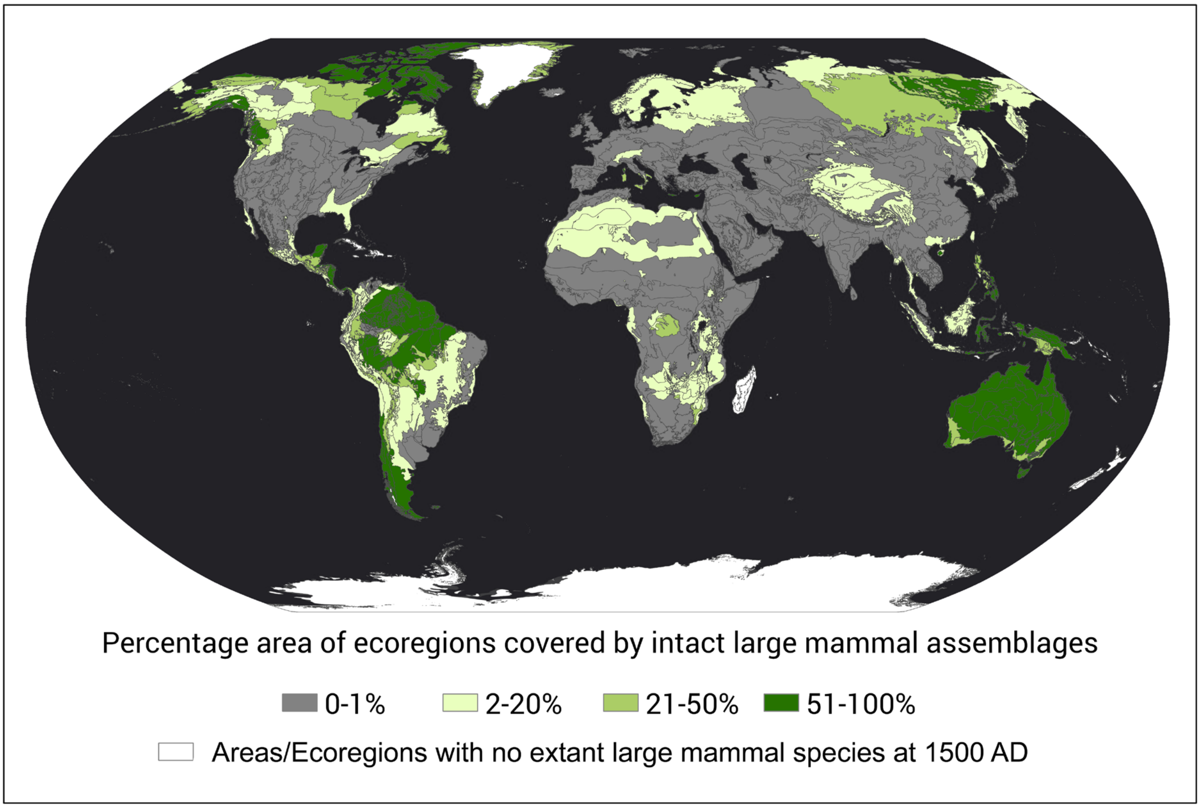

Figure 3. Percentage area of ecoregions of the world that retain intact assemblages of historically present large mammalian faunas. Shading depicts the amount of the ecoregion that is covered by these intact landscapes.

surface still contains intact large mammal assemblages (Fig. 2, Supporting information).

Priorities for restoring large mammal assemblages

We compared the geographic extent of the percentage area of ecoregions currently covered by intact large mammal assemblages (Fig. 3) with the percentage area of ecoregions covered by near-intact large mammal assemblages (Fig. 4). This comparison revealed that reintroducing a limited number of large mammal species to selected landscapes could exert the greatest effect throughout northern North America, much of South America, and northern Asia (Fig. 4). These zones of rewilding (sensu Svenning 2020) include 191 ecoregions with more than half of the area available as suitable habitat for full restoration from near-intact large mammal assemblages (i.e. no more than three species lost in every 100 km^2; Fig. 4, ecoregions in dark green shade; Supporting information).

A focus on restoration of a numerically small subset of species – 20 of the 298 large mammal species – could increase the area of the world containing intact large mammal assemblages by 54% (11 116 000 km^2; Table 1, Supporting information). These seven predators and 13 herbivores – whose reintroduction can restore intact large mammal assemblages to the largest potential areas missing only one species – occur across five continents and could return intact faunal assemblages to 97 ecoregions and expand ranges of nine globally threatened species (Table 1, Supporting information). In Europe, the reintroduction or recolonization of European bison *Bison bonasus*, Eurasian beaver *Castor fiber*, reindeer *Rangifer tarandus*, wolf *Canis lupus* and lynx *Lynx lynx* could expand the presence of historically intact large mammal assemblages to an additional 35 ecoregions. In Asia, restoration efforts focused on wild horse *Equus ferus* and wolf in the Himalayan ecoregions could increase the area with intact mammal assemblage in these 10 ecoregions by 89%. In Africa, reintroductions of hippopotamus *Hippotamus amphibius*, cheetah *Acinonyx jubatus*, common tsessebe *Damaliscus lunatus*, African wild dog *Lycaon pictus* and lion *Panthera leo* could expand intact assemblage coverage by 108% across 50 ecoregions. North America would support the full assemblages of large mammals restored across 17% of the continent (and a 117% increase in area with intact mammal assemblages) after the reintroduction or improved conservation management of brown bear *Ursus arctos*, American bison *Bison bison*, wolverine *Gulo gulo* and American black bear *Ursus americanus* into 22 ecoregions. Large blocks of habitat (> 10 000 km^2) remain within the historic range of each of the 20 species (Table 1).

We highlight 30 ecoregions that offer extensive suitable habitat and where restoration efforts focused on 1–3 species would recover or greatly expand the area of an ecoregion containing intact large mammal assemblages (Table 2, Supporting information). These efforts are in various stages of planning

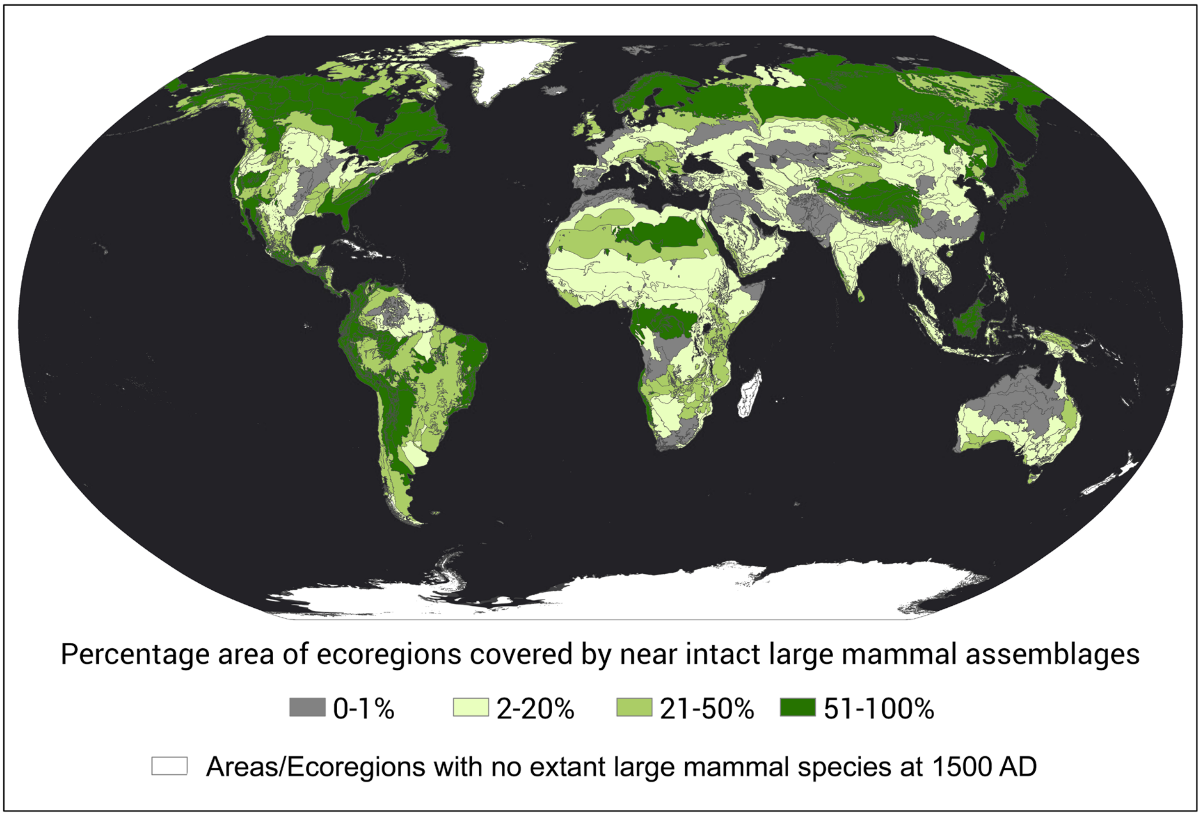

Figure 4. Percentage area of ecoregions of the world that retain near-intact (missing 1–3 species) assemblages of large mammalian faunas. Shading depicts the amount of the ecoregion that is covered by these near-intact landscapes.

for 11 predators and 19 herbivores to be reintroduced. All are feasible within the next 5–10 years. With adequate support, restorations would enable up to 61 countries to recover 22 IUCN threatened species in 10 biomes.

Discussion

Ranges of many large mammals have receded in the last 50 years. Even where complete species rosters remain, overall population numbers for many species represent a fraction of historic densities. The results presented here, however, offer scope for reversing range collapse and erosion of intact faunas through proactive, science-based restoration programs. These opportunities exist in all biomes and could be used to chart a pathway towards recovery of robust large mammal communities across much of the terrestrial realm.

Remaining intact assemblages

Most of the Earth's terrestrial surface still has some extant large mammals, but only 15% contain intact large mammal assemblages. These remaining places include many of the best examples of well-protected and high functioning ecosystems remaining on Earth, and contribute substantially to conservation of many threatened large mammals. Large mammal species are particularly sensitive to human activities through habitat alteration and direction exploitation. Thus, areas where intact faunal assemblages still remain showcase conservation success stories. These include places where assemblages have been protected by Indigenous communities' land tenure practices (e.g. in the Amazon, parts of east Africa), where intensive restoration or conservation efforts have been successful (e.g. part of the western United States, Europe and even in heavily populated regions of Asia), and where extensive tracts of intact habitat has allowed for persistence despite intensive development activities (e.g. in the boreal and Arctic regions).

Over the last five centuries, the more severe loss of large mammal species occurred across much of Africa and East and West Asia (Supporting information). Large tracts of habitat that hosted large mammal species in India, eastern Europe, the central United States and Brazil are no longer available (Supporting information). In Africa, areas that are among the highest in large mammal richness – with many places having more than 40 large mammal species – suffered some of the most significant decreases in large mammal representation both by number and proportion, where multiple species were extirpated at the same time (Supporting information). Today, few ecoregions in the region retain > 1% of their area with an intact assemblage (Fig. 3).

The distribution of protected area networks provides one aspect to interpret the presence of intact large mammal assemblages. The Brazilian Amazon, southern Africa, Australia and

Table 1. Top 20 species of large mammals whose reintroduction can restore intact large mammal assemblages to the largest potential areas missing only one species. See the Supporting information for the expanded version of this table with the list of individual ecoregions shown.

Species common name (IUCN Red List status)	IUCN scientific name	Area that can be restored to intact assemblage after their reintroduction (km²)	Number of ecoregions in which reintroduction of the species in at least one grid cell restores an intact mammal assemblage	Number of large habitat blocks (> 10 000 km²) available and number of ecoregions in which they occur (in parentheses)
Brown bear (LC)	*Ursus arctos*	1 505 187	79	16 (12)
Dhole (EN)	*Cuon alpinus*	1 350 688	36	11 (8)
American bison (NT)	*Bison bison*	1 306 979	32	14 (12)
Wild horse (EN)	*Equus ferus*	836 241	57	12 (7)
Pacarana (LC)	*Dinomys branickii*	824 600	12	9 (9)
Jaguar (NT)	*Panthera onca*	736 970	58	8 (8)
Pampas deer (NT)	*Ozotoceros bezoarticus*	684 500	21	14 (7)
European bison (NT)	*Bison bonasus*	482 477	6	2 (2)
Cougar (LC)	*Puma concolor*	468 010	34	10 (8)
Tiger (EN)	*Panthera tigris*	449 835	14	5 (4)
Eurasian beaver (LC)	*Castor fiber*	353 843	68	3 (2)
Marsh deer (VU)	*Blastocerus dichotomus*	343 200	15	7 (4)
White-lipped peccary (VU)	*Tayassu pecari*	284 368	54	9 (8)
Wolverine (LC)	*Gulo gulo*	266 103	8	4 (2)
Dama gazelle (CR)	*Nanger dama*	240 400	4	4 (4)
Reindeer (VU)	*Rangifer tarandus*	231 120	22	5 (4)
American black bear (LC)	*Ursus americanus*	224 164	18	6 (5)
Hippopotamus (VU)	*Hippopotamus amphibius*	206 608	36	4 (3)
South Andean deer (EN)	*Hippocamelus bisulcus*	166 149	6	4 (2)
Elk/moose (LC)	*Alces alces*	154 482	21	3 (3)

the Himalayas are examples of where intact large mammal assemblages are hosted within connected networks of established protected areas (Dinerstein et al. 2020; <www.globalsafetynet.app/viewer>). Conversely, areas where large mammal assemblages are missing also lack systems of protected areas, particularly in north Africa and southeastern China.

A pattern of co-location of intact and near-intact areas may be revealing a pattern of loss: intact areas are surrounded by areas having lost a few species, which are in turn circumscribed by areas with more severely defaunated assemblages. This pattern is particularly evident across Asia, Africa and North and South America (Fig. 2). Concentric layers showing this pattern in the Congo Basin rainforest, Sahara desert, Cascades forests, Brazilian Amazon and Siberian taiga might be demonstrating the gradual range contractions of large mammal populations as a result of increasing anthropogenic disturbance. The presence of intact 'strongholds' for mammals should be a priority for focused conservation effort. The surrounding near-intact areas are excellent candidates for restoration programs that can rely on natural dispersal.

We acknowledge that identification of intact areas is based on a historical baseline of where species were present that has implications for what constitutes 'intact'. The selection of AD 1500 follows Morrison et al. (2007), and is a widely used, conservative timeframe for assessing conservation and restoration potential using extant species. Nevertheless, the patterns of recently extinct large mammal species have relevance for restoration of faunal assemblages on our landscapes. Human-induced mammal extinctions before AD 1500 resulted in altered ecosystems throughout the world, but particularly in North America, South America, Eurasia and Australia (MacPhee and Flemming 1999, Cardillo and Bromham 2001, Faurby and Svenning 2015).

Restoration priorities

We identified 20 large mammal species that, if reintroduced or allowed to recolonize through enhanced connectivity, can trigger restoration of intact large mammal assemblages over millions of square kilometers (Table 1). Each of the candidates in this vanguard can be reintroduced to at least one or more large blocks of intact habitat per ecoregion. Starting with assessments of these intact areas would be a logical first step in national and regional efforts focused on restoration. For instance, there are more than 30 blocks of habitats over 1000 km² in size across the Nearctic and Neotropics where *Puma concolor* can be reintroduced to restore intact large mammal assemblages. Many of these ecoregions cross international boundaries so transboundary collaboration is essential (such as the Andean puna across Argentina, Peru, Bolivia and Chile). Nine of the 20 species with greatest restoration potential by area are globally threatened and thus a

Table 2. Ecoregions where reintroduction of 1–3 target species will restore intact large mammal assemblages within the context of a 1500 AD baseline.

Biome	Ecoregion	Target species for restoration	Status of recovery effort, if known
Nearctic Realm (7 of 115 ecoregions)			
Temperate Conifer Forests	North Cascades Conifer Forests (358)	*Ursus arctos*	Planning phase complete
Temperate Conifer Forests	South Central Rockies Forests (367)	*Ursus arctos*, *Bison bison*, *Gulo gulo*	Planning phase complete
Temperate Grasslands, Savannas and Shrublands	Northern Shortgrass Prairie (396)	*Bison bison*, *Canis lupus*	Active at some sites for bison
Boreal Forests/Taiga	Eastern Canadian Shield Taiga (374)	*Rangifer tarandus*	
Temperate Broadleaf and Mixed Forests	Appalachian Mixed Mesophytic Forests (329), Appalachian-Blue Ridge Forests (331)	*Puma concolor*	
Deserts and Xeric Shrublands	Chihuahuan desert (428)	*Canis lupus*, *Bison bison*	Mexican wolf reintroductions being tested; bison reintroductions planned
Neotropic Realm (5 of 179 ecoregions)			
Tropical and Subtropical Grasslands, Savannas, and Shrublands	Dry Chaco (569)	*Catagonus wagneri*, *Priodontes maximus*	Active
Montane Grasslands and Shrublands	Central Andean Dry Puna (587)	*Tremarctos ornatus*	Natural recolonization possible
Tropical and Subtropical Moist Broadleaf Forests	Xingu-Tocantins-Araguaia Moist Forests (518)	*Pteronura brasiliensis*, *Priodontes maximus*	Natural recolonization possible
Tropical and Subtropical Grasslands, Savannas, and Shrublands	Talamancan Montane Forests (506)	*Tapirus bairdii*, *Tayassu pecari*	Planning phase
Tropical and Subtropical Grasslands, Savannas, and Shrublands	Sinú Valley Dry Forests (564)	*Ateles hybridus*	Active
Palearctic Realm (8 of 205 ecoregions)			
Temperate Conifer Forests	Alps Conifer and Mixed Forests (689)	*Ursus arctos*	Historic assessment (1990s); some translocations have occurred
Temperate Conifer Forests	Caledon Conifer Forests (691)	*Lynx lynx*, *Castor fiber*	Under consideration (lynx); active (beaver)
Temperate Conifer forests	Carpathian Montane Forests (692)	*Bison bonasus*	Active
Temperate Broadleaf and Mixed Forests	Appenine Deciduous Montane Forests (644)	*Lynx lynx*	
Temperate Broadleaf and Mixed Forests	Baltic Mixed Forests (647)	*Alces alces*, *Bison bonasus*, *Lynx lynx*	Planning under way (bison, moose); bison introduced to fenced area.
Temperate Broadleaf and Mixed Forests	Cantabrian Mixed Forests (648)	*Lynx lynx*	National legislation promotes reintroduction of *Lynx lynx*
Temperate Broadleaf and Mixed Forests	Pyrenees Conifer and Mixed Forests (676)	*Lynx lynx*, *Canis lupus*	National legislation promotes reintroduction of *Lynx lynx*; natural recolonization by wolf possible
Temperate Broadleaf and Mixed Forests	Central European Mixed Forests (654)	*Alces alces*	Natural recolonization in eastern parts; small-scale reintroduction in Denmark
Afrotropic Realm (5 of 116 ecoregions)			
Tropical and Subtropical Grasslands, Savannas, and Shrublands	Dry Miombo Woodlands (42)	*Loxodonta africana*, *Syncerus caffer*, *Panthera leo*, *Diceros bicornis**	

Continued

Table 2. Continued.

Biome	Ecoregion	Target species for restoration	Status of recovery effort, if known
Tropical and Subtropical Grasslands, Savannas, and Shrublands	Northern *Acacia-Commiphor*a Bushlands and Thickets (51)	*Giraffa camelopardalis*, *Diceros bicornis*	
Tropical and Subtropical Moist Broadleaf Forests	Central Congolian Lowland Forests (3)	*Loxodonta africana*	
Flooded Grasslands and Savannas	Sudd Flooded Grasslands (74)	*Kobus megaceros*, *Hippopotamus amphibius*	
Deserts and Xeric Shrublands	South Sahara Desert (842)	*Addax nasomaculatus*, *Nanger dama*	Active
Indomalayan Realm (6 of 106 ecoregions)			
Tropical and Subtropical Moist Broadleaf Forests	Mindoro Rain Forests (248)	*Bubalus mindorensis*	Active
Tropical and Subtropical Moist Broadleaf Forests	Upper Gangetic Plains Moist Deciduous Forests (287)	*Cuon alpinus*	Approved; action plan in preparation
Tropical and subtropical moist broadleaf forests	Upper Gangetic Plains Moist Deciduous Forests (287)	*Rhinoceros unicornis*, *Bubalus arnee*	Assessment undertaken, reintroduction planned for 2022 for rhinoceros
Tropical and subtropical dry broadleaf forests	Khathiar-Gir Dry Deciduous Forest (295)	*Acinonyx jubatus*	Planned for 2022–2025
Deserts and Xeric Shrublands	Aravalli West Thorn Scrub Forests (314), Thar Desert (318)	*Acinonyx jubatus*	Planned for 2022–2025

*Four species are listed here as there are landscapes within the ecoregion where at least one of these occur, so there are still opportunities to restore with 1–3 reintroductions or recolonizations.

conservation priority in their own right (Table 1). Nearly all are species of concern at national or regional levels.

We identified 30 near-term opportunities where reintroduction efforts could lead to restoration of complete large mammal assemblages in each biogeographic realm. We used a simplistic approach to identify these areas that was based on our identification of locations missing just 1–3 species, and then assessments of feasibility of efforts and likelihood of a successful outcome in 5–10 years. Interestingly, 16 of the 30 ecoregions identified require only a single species restoration to complete the faunal assemblage. In a decade where restoration might be driven by carbon storage and ecosystem function, there are widespread opportunities in all corners of the world to restore biodiversity and complete faunal assemblages.

Key considerations and caveats

Our results show large areas of the terrestrial realm hold suitable habitat and restoration opportunity. There are also qualifiers. First, national and regional evaluations of feasibility of rewilding should consider both causes and consequences of extirpations. For example, where hunting pressures remain, these must be mitigated before initiating rewilding programs (Carver et al. 2021). Reintroduction efforts must promote human–wildlife coexistence, particularly for conflict-prone species such as grizzly bears and wolves (Proctor et al. 2018). For top predators, such as tigers or jaguars, ensuring an adequate prey base prior to reintroduction is vital (Wolf and Ripple 2016). Many herbivores will require habitat improvement, which can be coupled with rewilding efforts to achieve multiple restoration benefits. Additionally, protecting macrorefugia and restoring climate corridors is also essential for large mammal restoration (Mendoza and Araújo 2019, Carroll and Noss 2020). We recognize that our approach using fewer numbers of species (1–3) as a proxy for feasibility is simplistic: ecological role, home range size and habitat quality will need to be considered as reintroductions are planned. We also recognize that in some cases restoring one species where many are absent might provide more of an ecological benefit than restoration of an intact faunal assemblage.

Practically speaking, land ownership patterns can be a major impediment to restoration of large mammal populations. This is particularly true for species with large home range sizes. The framework presented here will need additional analysis best carried out at regional scales to assess feasibility, and priority actions that are critical to establishing a successful restoration program. Regional models and efforts like those underway in ‘Cascadia’ of Washington State (US) and British Columbia (Canada) are enabling wildlife managers to assess recovery potential across an international border and between land management jurisdictions. Here, land management can be informed by a newly released, regional-scale toolkit that provides constantly up-to-date habitat and connectivity models for recovering large mammals including lynx, wolverine and grizzly bear (<www.cascadia.terradapt.

org>). Regional managers are able to assess strategies that will be necessary based on land ownership patterns, and how habitat is likely to shift for these species given climate change.

These tools are being built to be readily exportable to other regions of the world. Even in regions without cutting edge data and tools, and where diverse types of land management patterns exist, there are excellent models of conserving full assemblages or 'restoration-in-practice'. In the Indo-Malayan realm, the Terai-Arc Landscape is a transboundary network of 14 protected areas across Nepal and India connected via corridors created by community-managed forests and buffer zones (Wikramanayake et al. 2010). In the Afrotropical realm, tribal and pastoralist communities in East Africa have coexisted with wildlife for centuries; many of the richest wildlife areas today are within Maasai and Samburu lands (Burgess et al. 2004). In the Neotropics, the Brazilian Cerrado – a habitat mosaic of grasslands, savannas, woodlands and patches of dense forest – is an example of federal law mandating conservation on private lands allowing for persistence of complete faunas in agricultural landscapes bordering strict protected areas (Vynne et al. 2011, Ferreira et al. 2020). Also in South America, there have been extraordinary rewilding success stories both of individual species across large, former areas of their range and with multi-species efforts such as the Iberá Rewilding Program in Argentina (Zamboni et al. 2017).

Integrating biodiversity in the agenda for the 'Decade of Restoration'

The UN Decade on Ecosystem Restoration (decadeonrestoration.org) provides a global policy framework to integrate a rewilding component into habitat recovery. This refinement requires that the resurgence of large mammal populations becomes an explicit target. There are companion efforts falling under the jurisdiction of the Convention on Biological Diversity to set science-based goals and targets for the next decade. Being discussed are area-based targets, such as protecting 30% of the terrestrial realm by 2030, or the more ambitious 50% by 2030 (Dinerstein et al. 2020; cbd.int/sp/targets). Priority ecoregions for restoring intact faunas (Table 2, Supporting information) strengthen area-based targets under consideration. Without this ecological feature, area-based percentages can be misleading and miss key constituent species. For example, for a species such as the black rhino which numbered > 1 000 000 individuals around 1900, the main constraint for recovery across the historic range is not the shortage of suitable habitat in sub-Saharan Africa, but rather the shortage of black rhinos due to poaching.

Compounding the problem of monitoring the recovery of large mammal species is that their presence or the trajectories of their populations are blurred within various indexes currently in use. For example, the biodiversity intactness index – an estimated percentage of the original number of species that remain and their abundance in any given area – assigns the same value to the critically endangered Sumatran and Javan rhinoceros as to a common rhinoceros beetle (family Scarabidae; Newbold et al. 2016). In many other global data sets and rankings using species richness as an indicator, the presence of the five rare rhinoceros species in a pixel or polygon contributes the same value to the total for mammalian species richness as does a ubiquitous murine rodent. In the Living Planet Index, trends in rhinoceros populations are weighted equally as trends in other mammal species for which there is longitudinal data. Relying only on these coarse metrics, we lack a way to gauge if vital components of the Earth's biota are increasing or in freefall.

The disproportionate contribution of intact large mammal faunas to the structure and function of ecosystems and their endangered status call for their own set of metrics and indicators (Svenning 2020). We propose establishing a wildlife recovery index, a set of metrics and indicators that could track the restoration of endangered large mammal populations and provide a simple, clear metric to assess global conservation efforts. New technologies and freely available data can identify potential landscapes for restoration (Brancalion et al. 2019). These spatial data could underpin a proposed wildlife recovery index. Without being too prescriptive, these data sets could be tailored to specific landscapes, but we can imagine a focus on the key elements of landscape ecology. The wildlife recovery index could start by incorporating an assessment of the grids of intactness, the extant and historic ranges, presented in this paper and in other sources. The size and areal extent and trajectory of core breeding populations would be an essential feature, as would the declaration of wildlife corridors and microrefguia along dispersal routes. The designations of new parks and reserves would be another clear metric as would be new legislation promoting rewilding. The recent referendum in the state of Colorado to allow for reintroduction of wolf packs and similar measures in eastern and western Europe offer new opportunities and are examples of recovery that should be tracked.

We envisage a wildlife recovery index that can be structured under general headings with key variables for each:

- protection: (e.g. creation or expansion of reserves in core breeding areas and restoration of corridors);
- management interventions: (e.g. range expansions through reintroduction efforts, anti-poaching programs, human–wildlife coexistence programs in place);
- enabling policies: (e.g. new legislation promoting rewilding).

The variables included under the three headings of the wildlife recovery index can be readily disaggregated to monitor progress at the local level, or by province, state or ecoregion. For reporting at international conventions, the data could be aggregated by country to assess progress. The wildlife recovery index should promote recognized rewilding principles (Carver et al. 2021). The design could be flexible enough to allow IUCN Species Specialist Groups to monitor progress of the species within their remit. Compiled in this way, the wildlife recovery index could validate other formulations in the public domain with a more positive casting.

The global pandemic has likely affected timetables for restoration programs. This is largely manifested by cuts in funding and reallocation of human resources to basic park protection (Smith et al. 2021). In contrast, reduced human activities in some landscapes might have promoted natural recolonization or dispersal through once hostile areas to formerly safe parts of species' ranges (Corlett et al. 2020). Even in the midst of the pandemic, however, science-backed programs led by citizen scientists or private organizations, such as Rewilding Argentina and Tompkins Conservation Fund, have been mobilizing to promote rewilding to complement government-led reintroductions (rewild.org/news/jaguars-a-keystone-species-are-reintroduced-to-the-ibera-wetlands). The opportunity exists to position rewilding as a central pillar of 'building back better,' across many of the world's terrestrial ecoregions. This neglected but essential component of biodiversity conservation – the restoration of large mammal faunas – should become a global imperative in the decade ahead.

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Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p8cz8w9rs> (Vynne et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

References

Andriuzzi, W. S. and Wall, D. H. 2018. Soil biological responses to, and feedbacks on, trophic rewilding. – Phil. Trans. R. Soc. B 373: 20170448.

Bakker, E. S. et al. 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. – Proc. Natl Acad. Sci. USA 113: 847–855.

Beyer, H. L. et al. 2020. Substantial losses in ecoregion intactness highlight urgency of globally coordinated action. – Conserv. Lett. 13: 1–9.

Bontemps, S. et al. 2013. Consistent global land cover maps for climate modeling communities: current achievements of the ESA's land cover CCI. – ESA Living Planet Symp. 2013: 9–13.

Brancalion, P. H. S. et al. 2019. Global restoration opportunities in tropical rainforest landscapes. – Sci. Adv. 5: eaav3223.

Burgess, N. et al. 2004. Terrestrial ecoregions of Africa and Madagascar: a conservation assessment. – Island Press.

Cardillo, M. and Bromham, L. 2001. Body size and risk of extinction in Australian mammals. – Conserv. Biol. 15: 1435–1440.

Carroll, C. and Noss, R. F. 2020. Rewilding in the face of climate change. – Conserv. Biol. 35: 155–167.

Carver, S. et al. 2021. Guiding principles for rewilding. – Conserv. Biol. 35: 1882–1893.

CBD (Convention on Biological Diversity) 2019. Twenty-third meeting of the subsidiary body on scientific, technical and technological advice, 25–29 November 2019, Montreal, Canada, <www.cbd.int/meetings/SBSTTA-23>.

Corlett, R. T. et al. 2020. Impacts of the coronavirus pandemic on biodiversity conservation. – Biol. Conserv. 246: 108571.

Dinerstein, E. et al. 2017. An ecoregion-based approach to protecting half the terrestrial realm. – Bioscience 67: 534–545.

Dinerstein, E. et al. 2020. A 'global safety net' to reverse biodiversity loss and stabilize Earth's climate. – Sci. Adv. 6: 1–14.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.

Faurby, S. and Svenning, J. C. 2015. Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. – Divers. Distrib. 21: 1155–1166.

Ferreira, G. B. et al. 2020. Strict protected areas are essential for the conservation of larger and threatened mammals in a priority region of the Brazilian Cerrado. – Biol. Conserv. 251: 108762.

González-Maya, J. F. et al. 2017. Distribution of mammal functional diversity in the neotropical realm: influence of land-use and extinction risk. – PLoS One 12: e0175931.

Guyton, J. A. et al. 2020. Trophic rewilding revives biotic resistance to shrub invasion. – Nat. Ecol. Evol. 4: 712–724.

IUCN 2019. The IUCN Red List of threatened species. Ver. 2019-1. – <www.iucnredlist.org>, accessed 15 June 2019.

Jones, K. E. et al. 2009. PanTHERIA: a species-level database of life history, ecology and geography of extant and recently extinct mammals. – Ecology 90: 2648.

MacPhee, R. D. E. and Flemming, C. 1999. Requiem Æternam: the last five hundred years of mammalian species extinctions. – In: Macphee, R. D. E. (ed.), Extinctions in near time. Advances in vertebrate paleobiology, vol 2. Springer, pp. 333–371.

Mendoza, M. and Araújo, M. B. 2019. Climate shapes mammal community trophic structures and humans simplify them. – Nat. Commun. 10: 5197.

Morris, T. and Letnic, M. 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. – Proc. R. Soc. B 284: 20170111.

Morrison, J. et al. 2007. Persistence of large mammal faunas as indicators of global human impacts. – J. Mammal. 88: 1363–1380.

Myers, P. et al. 2020. The animal diversity web (online). – <https://animaldiversity.org>.

Newbold, T. et al. 2016. Dataset: global map of the biodiversity intactness index. – In: Newbold, T. et al. (eds), Has land use pushed territorial biodiversity beyond the planetary boundary? A global assessment. – Science 353: 288–289.

Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. – BioScience 51: 933–938.

Plumptre, A. et al. 2019. Are we capturing faunal intactness? A comparison of intact forest landscapes and the 'last of the wild in each ecoregion'. – Front. For. Global Change 2: art. 24.

Proctor, M. F. et al. 2018. Conservation of threatened Canada-USA trans-border grizzly bears linked to comprehensive conflict reduction. – Hum. Wildl. Interact. 12: 348–372.

Riggio, J. et al. 2020. Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. – Global Change Biol. 26: 4344–4356.

Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.

Ripple, W. J. et al. 2015. Collapse of the world's largest herbivores. – Sci. Adv. 1: e1400103.

Salom-Pérez, R. et al. 2021. Forest cover mediates large and medium-sized mammal occurrence in a critical link of the Mesoamerican Biological Corridor. – PLoS One 16: e0249072.

Smith, F. A. et al. 2003. Body mass of late quaternary mammals. – Ecology 84: 3403.

Smith, J. R. et al. 2018. A global test of ecoregions. – Nat. Ecol. Evol. 2: 1889–1896.

Smith, M. K. S. et al. 2021. Sustainability of protected areas: vulnerabilities and opportunities as revealed by COVID-19 in a national park management agency. – Biol. Conserv. 255: 108985.

Svenning, J.-C. 2020. Rewilding should be central to global restoration efforts. – One Earth 3: 657–660.

Venter, O. et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. – Nat. Commun. 7: 12558.

Vynne, C. et al. 2011. Resource selection and its implications for wide-ranging mammals of the Brazilian Cerrado. – PLoS One 6: e28939.

Vynne, C. et al. 2021. Data from: An ecoregion-based approach to restoring the world's intact large mammal assemblages. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.p8cz8w9rs>.

Watson, J. E. M. et al. 2018. The exceptional value of intact forest ecosystems. – Nat. Ecol. Evol. 2: 4.

Wikramanayake, E. et al. 2010. The Terai Arc Landscape: a tiger conservation success story in a human-dominated landscape. – In: Tigers of the world. William Andrew Publishing.

Wolf, C. and Ripple, W. J. 2016. Prey depletion as a threat to the world's large carnivores. – R. Soc. Open Sci. 3: 8.

Wolf, C. and Ripple, W. J. 2018. Rewilding the world's large carnivores. – R. Soc. Open Sci. 5: 3.

Yu, D. et al. 2019. Projecting impacts of climate change on global terrestrial ecoregions. – Ecol. Indic. 103: 114–123.

Zamboni, T. et al. 2017. A review of a multispecies reintroduction to restore a large ecosystem: the Iberá Rewilding Program (Argentina). – Perspect. Ecol. Conserv. 15: 248–256.