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Opinion

Biodiversity Conservation and the Earth System: Mind the Gap

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One of the most striking human impacts on global biodiversity is the ongoing depletion of large vertebrates from terrestrial and aquatic ecosystems. Recent work suggests this loss of megafauna can affect processes at biome or Earth system scales with potentially serious impacts on ecosystem structure and function, ecosystem services, and biogeochemical cycles. We argue that our contemporary approach to biodiversity conservation focuses on spatial scales that are too small to adequately address these impacts. We advocate a new global approach to address this conservation gap, which must enable megafaunal populations to recover to functionally relevant densities. We conclude that re-establishing biome and Earth system functions needs to become an urgent global priority for conservation science and policy.

Highlights

The loss of large vertebrates (megafauna) from the world's ecosystems has been occurring throughout human history.

Emerging evidence suggests these losses can have dramatic impacts on ecological functions, including the near collapse of biogeochemical cycles at biome and Earth system scales.

Although the biodiversity conservation community increasingly recognises the need to restore ecological functions at landscape scales, it currently operates at scales that are too small to adequately address the functional consequences of megafaunal losses at biome and earth system scales.

Re-establishing biome and Earth system functions needs to become a global priority for the biodiversity conservation community, and we will need a new global initiative to deliver this.

Biodiversity Loss and Loss of Ecological Function

Prior to the Covid-19 pandemic, signatories to the **Convention on Biological Diversity** (CBD) (see Glossary) planned to meet in 2020 to agree a new global biodiversity framework. When it eventually takes place, this meeting will do so against a background of ongoing biodiversity loss [1,2], which would have been demonstrably more rapid had it not been for successful conservation action over recent decades [3–5]. Unsurprisingly, the loss of biodiversity has been accompanied by the loss of key functional groups, resulting in ecological communities that are highly modified in terms of their structure and function [6–8], and the existing diversity of global vertebrate ecological strategies is predicted to decline further over the coming century [9].

Large-bodied vertebrates (hereafter **megafauna**) are particularly susceptible to exploitation and there is a growing realisation that their loss can profoundly alter ecosystem dynamics, for example through changes in disturbance regimes and decoupling animal–plant mutualisms [10–12]. Our perspective on these changes is strongly influenced by contemporary observations, but the depletion of megafauna has been occurring throughout human history [13,14]. Recent work suggests that megafaunal losses can affect processes at **biome** or **Earth system** scales [15–17], with potentially serious impacts on **ecosystem structure and function**, and profound implications for biodiversity conservation. Here, we review the evidence linking the loss of megafauna with the loss of biome and Earth system function and argue that biodiversity conservation currently fails to address these issues because of the scales at which it operates. We highlight the need for a broader approach to conservation that explicitly recognises the scales at which biodiversity loss and its functional consequences occurs, and stress that the loss of biome and earth system function requires urgent attention by the conservation community.

Megafaunal Extinctions and the Loss of Biome and Earth System Function

Megafauna are widely understood to act as keystone species or ecosystem engineers through a range of functional pathways operating across a range of spatial scales (Figure 1). The presence and biomass of megafaunal assemblages (and often specific megafaunal taxa) has long been

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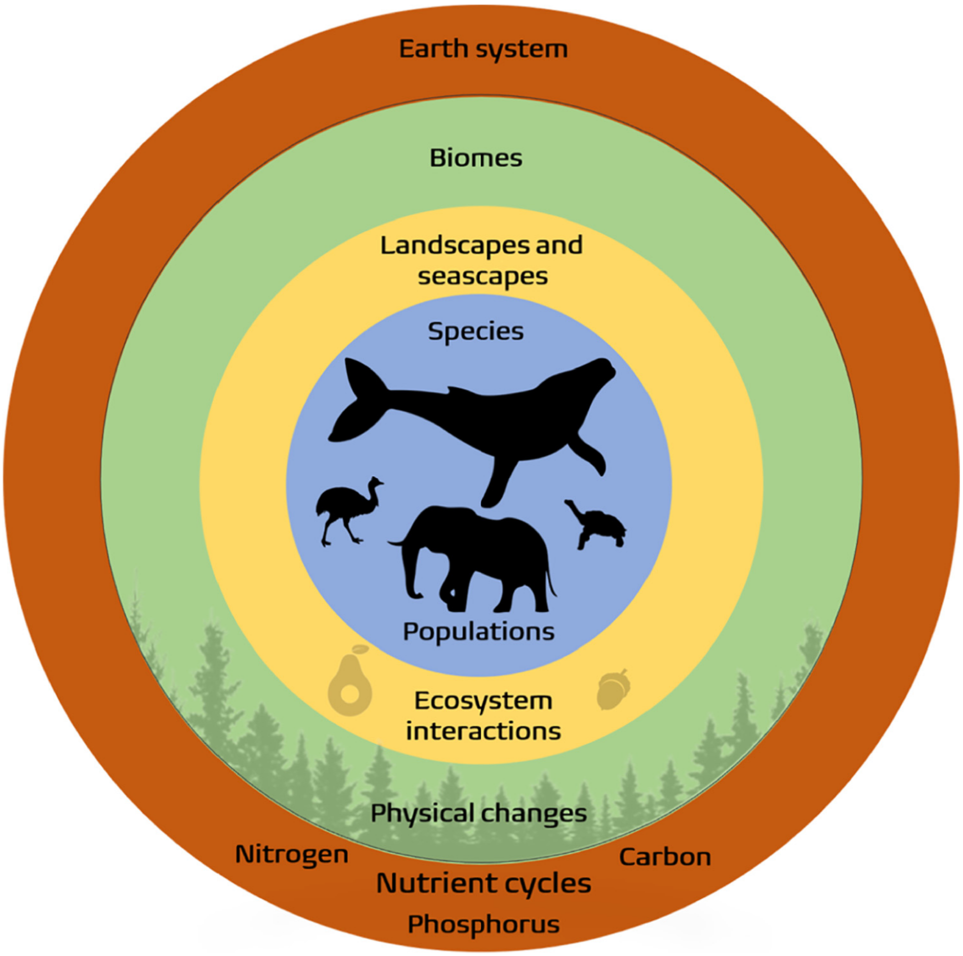


Figure 1. The Functional Roles Played by Large Vertebrates (Megafauna) across Spatial Scales. Important ecological processes driven by megafauna include the long-distance dispersal of seeds; browsing, grazing and physical disturbance of plant communities by herbivores; and predation by large carnivores. Large-scale movements by megafauna transport nutrients such as nitrogen and phosphorus across land and in the ocean when they urinate and defaecate, and when they die and decompose. These processes interact to drive biogeochemical cycles at biome (e.g., the Amazon) and Earth system scales. The loss of megafauna has had a significant impact on these processes, resulting in substantial reductions in nutrient flows at biome and earth system scales.

known to provide essential ecosystem functions through regulation of terrestrial vegetation structure and dynamics at both landscape and biome scales. Although individuals and small isolated populations can perpetuate localised interactions, functionality is driven by large populations and diverse assemblages, highlighting the vulnerability of megafauna-driven ecosystem regulation to population declines well before actual extinctions [18,19].

The role of large herbivores (including terrestrial and arboreal mammals, large birds, and giant tortoises) in promoting plant regeneration and regulating vegetation composition through dispersal of plant propagules, especially over long distances, is crucial in most terrestrial systems [20]. However, there has been substantial human-caused trophic downgrading of frugivore communities worldwide [21], and although coevolved plant species may persist beyond megafaunal extinction by exploiting alternative dispersal mechanisms, cascading effects of large

Glossary

Biogeochemical cycles: pathways through which chemical substances, for example, nitrogen or phosphorus, move through the biotic and abiotic components of ecological systems.
Biome: a distinct community of microorganisms, plants, and animals occupying an extensive geographical area, such as a tropical forest or desert.
Convention on Biological Diversity: a multilateral treaty for the conservation and sustainable use of biological diversity delivered through national strategies (www.cbd.int).
Convention on Migratory Species: an international agreement that aims to conserve migratory species within their migratory ranges (www.cms.int).
Earth system: physical, chemical, and biological processes interacting at a planetary scale and involving the atmosphere, land, oceans, and polar regions.
Ecological function: a process or set of processes that can change an ecological system over time, for example, seed dispersal, herbivory, or predation.
Ecosystem services: benefits that humans receive from ecosystems, for example, food, clean water, disease control, and cultural experiences.
Ecosystem structure and function: structure refers to the way an ecosystem is organised and includes its species composition, trophic structure or functional composition, and distribution of mass and energy between its components; function refers to the flow of mass and energy through an ecosystem.
Half-Earth Project: a call to protect half the global area of land and sea to reverse species extinctions and ensure long-term planetary health (www.half-earthproject.org).
International Convention for the Regulation of Whaling: an international agreement for the conservation of whale stocks and their sustainable exploitation.
Landscape: an area of land, its landforms, and their integration with human-made and natural elements, and typically covering a geographical area much smaller than a biome.
Megafauna: large-bodied animals. Specific mass thresholds used vary between studies, but the term often refers to animals >44.5 kg.

vertebrate loss include plant community reorganisation, reduction of megafauna-dependent plant abundance, distribution, and population structure, and local extinctions [10,12,22,23]. Recent evidence also shows megafauna influence the dispersal of microbes [24].

More direct regulation of habitat structure, ecosystem state, and associated species diversity and richness by herbivores is widely recognised, including suppression of plant growth and regeneration through grazing and browsing, and further physical modification of vegetation and geomorphology by trampling and other damage. **Megaherbivore** presence is often associated with increased landscape openness and heterogeneity, for example from closed-canopy forest to forest–grassland mosaic parkland landscapes [25,26], but can have numerous system-specific regulatory effects, such as a state shift between open-water wetlands and *Sphagnum* bogs in the Galápagos Islands driven by presence or absence of the giant tortoise (*Chelonoidis nigra*) [27]. Megaherbivores modify water tables and soil methane emissions and affect evapotranspiration and land surface albedo [28]. Megaherbivore extinction can also be associated with changed fire regimes, with the potential for increased fire frequency due to accumulation of uncropped plant material, and associated state shifts to more fire-resistant dominant vegetation communities [29,30]. Large carnivores also play an important role in regulating habitat structure through behaviourally mediated indirect interactions, by causing changes in prey distribution and associated **mesoherbivore**-vegetation interactions across landscapes (so-called landscapes of fear) [31–33], although the dynamics of such carnivore-induced trophic cascades are further modified by local presence of megaherbivores [34].

Megafaunal interactions such as propagule dispersal and nutrient transfer through faeces and urine play a further important role in regulating biogeochemical cycling. This is well recognised at landscape and biome scales. Loss of seed and fruit dispersers in tropical forests has a negative impact on ecosystem carbon storage through reduction of tree biomass. For example, extinction of forest elephants (*Loxodonta cyclotis*) would result in a 7% decrease in above-ground biomass in Central African rainforests, reducing efficiency of carbon sequestration [11]. Past megafaunal extinctions are predicted to have already reduced carbon storage capacity in globally important ecoregions such as the Amazon [12]. Megafaunal regulation of soil biogeochemical processes is particularly important in nutrient-poor cold or dry environments, and megafaunal disappearance in North Eurasia is posited to have locked nutrients into slowly decomposing plant matter within permafrost soils and decreased system productivity [35]. Megafauna play comparable functional roles in marine systems [36].

There is increasing recognition of the vital additional role played by megafauna in horizontal movement of carbon and nutrients both across **landscapes** and biomes and across system boundaries, thus scaling up the megafaunal keystone paradigm to wider continental and global contexts. Megafauna are now known to make a disproportionate contribution to lateral nutrient transfer, with large herbivores and carnivores both acting as important carbon and nutrient vectors by excreting organic matter derived from one system into another [37,38]. Megafauna-mediated translocation, either via feeding migrations or local-scale movements across system boundaries (between terrestrial, freshwater, and/or marine systems), can profoundly shape the ecology, productivity, and structure of recipient systems by increasing diffusion rates along concentration gradients and against hydrological flow directions [39]. This global megafauna-driven nutrient pump counters sedimentation, with large cetaceans recovering nutrients from the deep sea and acting as vertical and horizontal vectors [40], and a further chain of system-boundary transfers by other large vertebrates progressively moving nutrients upstream and into continental interiors [41]. Megafauna therefore regulate key Earth-system processes

Megaherbivore: large-bodied herbivorous animals >1000 kg in mass, for example, hippopotami and elephants.
Mesoherbivore: medium-sized herbivorous animals in the mass range 50–500 kg, for example, red deer.
Montreal Protocol: an international treaty designed to protect the ozone layer by phasing out substances responsible for ozone depletion.
Seascape: the equivalent of a landscape in the ocean.
Transboundary initiative: conservation initiatives that cross national borders, that is, that include two or more countries.

and global interconnectivity, and megafaunal extinctions have caused major perturbations to **biogeochemical cycles** at biome and earth system scales [15,41].

Conservation Scales

Over the past 30 years, biodiversity conservation has been focused primarily on area-based protection and restoration of threatened species and populations. These activities have been supported by global indicators such as the International Union for Conservation of Nature Red List and the Living Planet Index, which have enabled conservationists to prioritise the most threatened species, identify threatening processes, and monitor responses to conservation interventions [4,5,42,43]. This approach has tended to focus on threatened populations with geographically restricted ranges (e.g., relict populations that were formally part of much larger, connected ranges; island endemics). However, it has become increasingly clear that a focus on population-level or single-species conservation (and typically for populations already in serious decline) will not be sufficient to protect or restore key **ecological functions** at larger spatial scales (e.g., landscapes and biomes) [8,44], and that species' ecological roles need to be a more prominent part of the conservation agenda [45,46]. Furthermore, recognition of the links between biodiversity, **ecosystem services** and human well-being means that conservation is increasingly part of a transformative global agenda that is considering possible futures for nature and people [47].

Against this wider background, we now understand that megafauna can play a critical role in the restoration of landscapes with potentially wide-ranging benefits to biodiversity because of the key functions they perform [48–50]. This realisation is fundamental to the concept of rewilding, which aims to restore self-sustaining ecosystems that require minimal management interventions in the longer term. Within this framework, reintroductions of regionally extinct species and novel introductions of surrogate or analogue species are often used to replace lost ecological functions associated with historical removal of megafauna [51]. For example, large-bodied carnivores have been reintroduced at various sites in Europe and North America [e.g., grey wolves (*Canis lupus*) in Yellowstone National Park] to restore top-down regulation of ecosystems through trophic cascades. A wide range of large-bodied herbivores have been used as grazers, browsers, and agents of disturbance across different European rewilding projects to replace the roles of regionally extirpated species such as European horse (*Equus ferus ferus*), bison (*Bison bonasus*), and aurochs (*Bos primigenius*), and extant species of giant tortoise (e.g., *Aldabrechelys gigantea*) have been used to restore herbivory and seed dispersal functions to vegetation communities on tropical islands such as the Galápagos and Mauritius that have lost their endemic tortoise species. Even nonintentional replacement can restore at least some functionality of extinct taxa [52], and the introduction of non-native megafauna can have functional consequences [e.g., Pablo Escobar's hippos (*Hippopotamus amphibius*) in Colombia] [53].

These species-level and landscape-level approaches represent contrasting conservation scales (Figure 2). When viewed in this way, it becomes apparent that conservation has progressively expanded its scale of operation over the past 30 years from small (species and populations) to larger (e.g., landscapes) spatial scales. However, this perspective also reveals a worrying gap between the scales over which conservation currently operates, and the scales over which ecological functions are changing in response to the ongoing loss of megafauna. The loss of ecological functions at biome and Earth system scales is simply not adequately represented in contemporary approaches to conservation. For example, Yellowstone, into which grey wolves were reintroduced, covers an area of roughly 9000 km^2; in contrast, Amazonia covers an area of 7 000 000 km^2, and the area covered by the biogeochemical cycles supporting it represents a significantly larger area again. Consequently, our contemporary approach to biodiversity

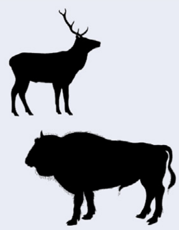
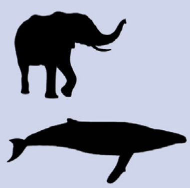
Conservation scales		Conservation actions	Role of megafauna	
Populations and species	10s – 100skm^2	Threatened species recovery programmes		Very system specific e.g., use of analogue species such as tortoises to restore functional relationships
Landscapes and seascapes	100s – 1000s km^2	Restoration of functional communities and associated ecosystem services		Restoration of ecological processes that are critical for ecosystem function e.g., grazing, browsing, disturbance, predation
Biomes and the Earth system	1 000 000s km^2	Limited focus on restoring important functional relationships		Key functional roles in large-scale biogeochemical cycles

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Figure 2. Conservation Scales. Contemporary biodiversity conservation is focused on populations and species, and on landscapes and **seascapes**. Associated actions typically cover areas of a few thousand square kilometres at most. At biome or Earth system scales, limited attention is being given to re-establishing the key functional roles and relationships provided by megafauna. This conservation gap is particularly serious given recent evidence showing substantial reductions in nutrient flows at these spatial scales.

conservation focuses on spatial scales that are too small to adequately address changes in ecological function at biome or earth system scales. Given the magnitude of changes in biogeochemical cycles at these scales since the late Quaternary, the conservation community therefore urgently needs to address the gap between the scales over which conservation currently operates, and the scales over which ecological functions are changing.

Bridging the Conservation Gap

The depletion of megafauna has occurred over millennia, and the loss of associated ecological functions occurs across a range of spatial scales, including biome and earth system scales (Figure 1). Furthermore, although the scales over which contemporary conservation operates have arguably expanded over recent decades, these responses remain too localised to address the scale of the problem (Figure 2). We need urgent action at biome and Earth system scales: in other words, a genuinely integrated, global response.

Environmental science and policy have had a significant impact at global scales. For example, the **Montreal Protocol**, an international treaty that came into force in 1987, was established to protect the ozone layer by phasing out the production and use of numerous substances responsible for ozone depletion. Over 190 countries participate in the treaty, and it has resulted in the phase-out of 99% of nearly 100 ozone-depleting chemicals. Without this treaty, the ozone layer is predicted to have collapsed by the mid-21st century [54], with hugely serious implications for human health. Although important work to further mitigate the impact of ozone-depleting chemicals is still necessary, recent research shows that the ozone layer is recovering [55]. Some megafaunal conservation efforts have also operated at global scales. The International Whaling Commission (IWC) was set up under the **International Convention for the Regulation of Whaling** in 1946. Although some of its activities remain contentious, a moratorium on hunting was introduced in the 1980s, and whale sanctuaries were established in the Indian Ocean (1979) and Southern Ocean (1994), covering an area of over 50 million km^2. A further sanctuary in the South Atlantic is currently under discussion. Several whale populations are showing signs of recent recovery [56–58], and although many remain below their historical baselines, the IWC represents one of the few initiatives aimed at the conservation of megafauna at appropriately large spatial scales.

Despite examples of global initiatives that have delivered demonstrable environmental benefits, there is little overall evidence that biodiversity conservation is currently operating at the scales required to address functional consequences at biome and Earth system scales. The majority of global conservation conventions, such as the CBD and **Convention on Migratory Species** (CMS), are implemented at national scales through a shared responsibility approach, which almost inevitably means that progress is piecemeal, and coordination and integration across systems and scales is poor. A number of **transboundary initiatives** have developed globally in recent years [59,60], which include the conservation of megafaunal species. These initiatives often reflect the long-held view that large-scale interventions are needed to restore ecologically functional communities [46]. Furthermore, there have been recent calls by conservationists for a **Half-Earth Project** to conserve half of the Earth's biodiversity. It seems unlikely, however, that these projects will adequately address the depletion of megafauna and restore the biome or earth system functions they drive without including measures specifically designed to do so. Indeed, where the conservation community has had some recent successes in conserving megafaunal populations, this can result in increased conflict between wildlife and local people unless adverse impacts can be appropriately managed [61,62]. In addition, human infrastructure such as fences, roads, and other urbanisation of landscapes often significantly restricts animal movement [63,64], constraining the scales over which key ecological functions can operate and hence limiting restoration potential even if megafaunal populations are locally able to recover.

These major constraints mean that addressing the loss of megafauna and its functional consequences requires a new global initiative. At its heart, we need large, transboundary functional units capable of delivering key ecological functions at Earth system scales, and within which megafauna and their associated functional pathways can be maintained or restored. It is likely that surviving large intact terrestrial biomes, such as the Amazonian, Central African and Russian forests, the Sahel and the Eurasian Steppe, should represent key components of such an initiative, as would large protected marine areas such as the existing marine mammal sanctuaries designated by the IWC. Coupling between terrestrial and marine regions is also important to incorporate into any global initiative that aims to effectively address megafauna-driven functionality, given that the biogeochemical cycles we wish to restore are themselves driven by both aquatic and terrestrial processes [15]. Restoring a functional Earth system in this way will not be achieved by simply protecting megafaunal species, but their populations must be enabled to recover to functionally relevant densities and have ecological impacts at functionally relevant scales. This represents a fundamental shift in the scale at which global conservation operates.

Such an endeavour will require unprecedented international agreement and cooperation, and an expansion and reframing of the current global conservation paradigm. Identifying, protecting and restoring transboundary functional units will require an interdisciplinary approach to science and policy that has thus far been largely an academic exercise rather than a practical reality.

Implementation will be challenging, not least because it will require individual countries and their inhabitants to act as custodians of Earth system functions from which we will all benefit. We recognise that previous global initiatives targeted at the atmosphere (Montreal Protocol) and oceans (IWC) are less complex in terms of national sovereignty than a global initiative that includes terrestrial and aquatic systems plus linkages between them. Success will inevitably depend, therefore, on benefit sharing, equality, and social justice, which in turn will require us to reform the dominant political and economic ideologies that have shaped global society for over 50 years. While daunting, we already recognise the need to address these issues if we are to create a shared future for nature and people [47,65]. We are simply arguing that restoring a functional earth system needs to be a key global priority for biodiversity conservation within this wider debate.

Concluding Remarks

The loss of megafauna due to human activities has been taking place for millennia, but it is only recently that we have begun to understand the implications of this loss for the structure and function of ecological systems at biome and Earth system scales. Although the biodiversity conservation community increasingly recognises the need to restore and conserve whole systems, its priorities and interventions remain focused on scales that are too small to address biome or earth system functions. We argue that a new global initiative is required to address the past and ongoing loss of megafauna and its functional implications.

We acknowledge the significant challenges involved with designing and delivering such an initiative (see Outstanding Questions). The consequences of a failure to act are, however, beyond serious. The collapse of the ozone layer would have had health implications for millions of people globally. We face impacts of similar scale and magnitude due to the depletion of megafauna. There are also key dependencies with other global environmental initiatives. For example, the Paris Climate Agreement requires the Earth system to play its part in the global carbon cycle. The restoration of megafauna and their functional roles will need to be a key part of any nature-based climate solutions. As we write this paper, the world is managing a global coronavirus pandemic; a poignant reminder that nature shows little respect for human constructs like national borders. As a global biodiversity conservation community this is a lesson we need to learn, and quickly. The conservation and restoration of megafauna needs to be an urgent, global conservation priority, not only for their inherent biodiversity value, but to maintain a healthy planet that supports both nature and people.

Outstanding Questions

What are the functional roles of megafauna in historic and contemporary systems at biome and Earth system scales?

How has the depletion of megafauna impacted the function of ecological systems at biome and Earth system scales, and what are the implications of these changes for the long-term structural and functional integrity of these systems?

What are the human impacts of the depletion of megafauna and degradation in their functional roles at biome and Earth system scales?

Where will the restoration of megafauna have the greatest impact on Earth system processes?

How can we restore megafauna populations and their key ecological functions at biome and Earth systems scales, and what are the social and ecological barriers to restoration?

How do we need to reform our social, economic and political systems to incentivise nations to cooperate to restore and protect functional ecological systems at biome and Earth system scales, and to ensure costs and benefits are shared equitably?

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