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Review

Large animal restoration and carbon storage across climate-relevant timescales

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SUMMARY

By virtue of their size and mobility, large animals can play important roles in Earth's carbon cycle. This has led to suggestions that restoring their populations can contribute to mitigating the climate crisis through removal and storage of atmospheric carbon. However, as animals can affect both release and sequestration of carbon, understanding when, where and how much they impact climate-relevant carbon is critical for evaluating their potential to become a trustworthy climate nature-based solution. Here, we review scientific evidence for the carbon impacts of elephants and great whales — two well-studied animal groups commonly cited for climate mitigation and suggested for carbon monetization. We identify six lessons to guide future research, policy and practice: first, large animal carbon impacts vary considerably by individual, species, ecosystem and biospheric conditions, making predictions of future impacts hard and wildlife-based carbon investments high-risk; second, meaningful carbon impacts will likely take longer to manifest than the Paris Agreement's mid-century net-zero target, but wildlife restoration should nonetheless begin now to realize immediate co-benefits and potentially support longer-term climate recovery; third, current conservation remains highest priority, as loss of animals may exacerbate climate breakdown; fourth, caution is needed when incorporating wildlife into climate policy to prevent false confidence in mitigation potential or perverse outcomes; fifth, potential wildlife carbon benefits should be communicated transparently and cautiously to manage expectations; sixth, robust monitoring and validation are essential to ensure carbon sequestration is real and durable. With these lessons in mind, conservation and restoration of large animals may realize their potential to aid long-term climate recovery as well as ecological resilience and adaptation under ongoing global change.

Introduction

As the climate crisis intensifies, restoring lost capacity of the biosphere to store carbon is essential for preventing global warming beyond 2°C[1]. This challenge coincides with the urgent need to reverse global biodiversity loss, generating support for nature-based solutions to climate change that address both crises simultaneously[2]. Until recently, natural climate solutions have predominantly focused on the management of photosynthetic organisms, soils and sediments, which function as Earth's main stores and sinks of carbon[3,4]. New research, however, has highlighted the important roles of large animals or megafauna (here defined as animals larger than 45 kg) in mediating carbon stores through their natural ecological functions[5–7], further incentivizing their inclusion in natural climate solutions[8–11]. Media coverage and carbon investment schemes have amplified these ideas, promoting the 'carbonization' of megafauna as climate solutions.

As interest in large animal restoration for climate mitigation grows and early implementation efforts begin[8,9,12,13], it is imperative that the mechanisms by which large animals might affect carbon sequestration are robustly assessed for their potential as trustworthy climate solutions and to guide effective carbon finance, policy and wildlife management decisions. Importantly, for such strategies to be considered meaningful, they must either be consistent with the Paris Agreement's mission of achieving net-zero by mid-century[1], or provide additional long-term benefits by helping restore disrupted carbon-cycle processes and supporting post-peak temperature recovery. Yet, comprehensive syntheses and comparison of taxa-specific impacts on carbon balance across time and space remain scarce, limiting our

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ability to evaluate when, where, and to what extent large animal conservation and restoration can be a reliable part of the greater portfolio of climate mitigation schemes.

In this review, we first provide a broad overview of the current integration of large animals into climate mitigation strategies with respect to the latest scientific evidence, media promotion, and early carbon finance and wildlife management efforts. We then synthesize and compare the specific carbon sequestration potential of elephants and great whales — the largest animals on land and in the ocean today — two groups frequently suggested for carbon monetization schemes, and among the most severely depleted animals. We highlight instances in which the conclusions for elephants and whales are likely to be relevant across other, less well-studied large animals. Our synthesis is intended to inform both scientists studying the role of large animals in carbon cycling and practitioners considering how to integrate such insights into climate policy and conservation strategies.

The current state of large animal restoration for climate mitigation

A scientific consensus on wildlife and climate

In June 2026, a Scientific Consensus on Wildlife and Climate was released at a session of the United Nations Framework Convention on Climate Change Subsidiary Bodies in Bonn. Signed by >350 post-PhD scientists from >40 countries, this consensus argues that animals play a key role in shaping ecosystem carbon balance and can in many cases help to mitigate and adapt to the current climate crisis. They should, thus, be explicitly included in climate policies and frameworks. This consensus is supported by numerous scientific studies showing that many animal species affect carbon through their roles in food webs and ecosystem functioning[6,9,13,14]. For example, a meta-study[13] found increased ecosystem carbon storage in 38 studies but also decreased storage in 26 others. Likewise, a modelling exercise estimates that protecting and restoring just nine animal groups could sequester 6.41 ± 4.84 billion tonnes (Gt) CO_2 per year; a value that, if realized, would meet >64% of the current global natural climate solution target[9].

With this growing recognition, the next challenge for scientists is to determine when and where large animal restoration might credibly contribute to climate mitigation (Figure 1). To date, estimates of large animal impacts on carbon balance have generally relied on upscaling limited field data and a new generation of models that explicitly incorporate animal carbon dynamics[6,15–19] and Earth's energy balance (e.g., through changes to albedo[20]). While these data and models have been instrumental in highlighting the important role of animals in carbon cycling, they integrate many complex parameters such as animal abundance, demography, space use, human influence, diet, ecological modifications and interactions with other species and biogeochemical processes[19]. Compounding uncertainties make quantifying and predicting animal roles in carbon cycles and long-term carbon sequestration extremely difficult[9,13]. Even robust and well-funded projects show high uncertainty and sensitivity to modelling assumptions[21]. This raises several fundamental questions: Can we robustly predict when, where, and how different animal groups will sequester or release carbon under different environmental, biological and anthropogenic circumstances over the coming century? How should animal roles in carbon cycling be valued and at what scale? Can this be done without compromising their intrinsic value or creating 'good' (carbon sequestering) and 'bad' (carbon releasing) populations or species? Is large animal restoration and rewilding a trustworthy solution for either short-term climate mitigation or longer-term post-peak temperature recovery?

Previous studies have touched on these questions (e.g., the lack of mechanistic understanding of many important processes[22] and the context-dependent roles of animals in carbon balance[23]), yet there remains a need for comprehensive, in-depth syntheses that robustly examine all known mechanisms of animal carbon impacts in different contexts. Integrating this evidence can reveal which mechanisms are most important, when they operate and where uncertainty remains. Such detailed syntheses are essential for moving from an understanding that animals are important for carbon cycling[13], to determining whether and how their restoration may be a viable climate mitigation strategy.

The role of media in promoting large animal restoration as a climate solution

Recently, media have promoted the '*carbonization*' of megafauna as climate solutions through headlines such as *Wildebeest and wolves: The secret weapons against climate change* (BBC) and *Animals Can Save Us—If We Let Them* (Time Magazine). Social media posts, podcasts and public talks, such as TED talks or Instagram posts by famous celebrities, also have received substantial attention. Such promotion is commonly linked to fundraising initiatives for chronically underfunded conservation efforts[8]. This growing media attention highlights the importance of accurately identifying the details of animal restoration as a climate mitigation strategy. While the nuances are often carefully described in scientific papers (e.g., regarding timescales and level of uncertainty[13,16,24]), they are rarely reported in the media[25]. In addition, simple analogies can mislead: for example, translating animal reintroduction into car emissions (e.g., 170 bison could help sequester CO_2 equivalent to the emissions from 43,000 cars) suggests that animal restoration can offset present-day actions[25] rather than sequestering historical carbon emissions and recovering ecological baselines[26,27]. Such communication may even hamper climate mitigation efforts if it leads to inaction or detraction from urgent climate action[28].

Early implementation of large animal restoration as a climate solution

Large animal restoration for climate is beginning to shape conservation policy, ecosystem management and carbon investment schemes[8,29]. For example, Tswalu Kalahari Reserve, a ~1,200 km^2 private wildlife reserve in South Africa, recently began operating carbon credits based on a modelling framework that attempts to optimize large herbivore densities and grazing impacts for increased soil organic carbon stocks[30]. Similarly, Meta, Netflix, British Airways and other multinational corporations have purchased >6 million carbon credits (total sales value >$90 million) from the Northern Kenyan Rangelands Carbon Project — the world's largest land-based wildlife management project that aims to sequester 50 million tonnes (Mt) of CO_2 over the next thirty years through changes in pastoral farming practices. In the marine realm, whales are being promoted as "Nature's solution to climate change" by the International

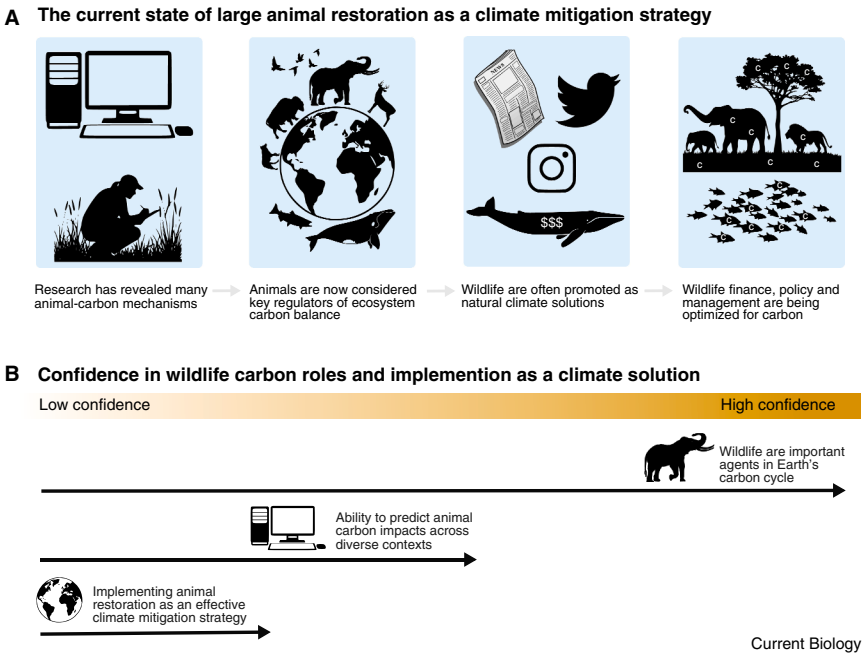


Figure 1. The current state of large animal restoration as a climate mitigation strategy. (A) Field and modelling studies of diverse animal groups on ecosystem carbon balance have helped demonstrate the potential climate benefits of large animal wildlife and expand natural climate solutions to include these animals. Media and carbon investment schemes have amplified these roles in recent years, leading to conservation finance and ecosystem management practices that are increasingly optimized for animal carbon functions. (B) Many scientists agree that animals play a role in shaping ecosystem carbon balance; however, understanding and predicting important nuances with respect to the magnitude, direction, durability and timescales of these impacts is extremely challenging across diverse environmental, biological and anthropogenic gradients. It is important that integration of animal carbon functions into policy and wildlife management does not outstrip underlying ecological knowledge. (Images: whales by KBelka/iStock; elephant and lion by Larisa/AdobeStock; birds by MoodMuseStudio; and fish by Tatiana Egorova.)

Monetary Fund, which has estimated the carbon value of great whales at over $1 trillion. Such carbon monetization schemes have been promoted by groups as diverse as the Te Ao Maori in their He Whakaputanga Moana (Whale Protection and Legal Personhood Declaration), released in February 2026, and the International Whaling Commission in its Conservation and Scientific committee reports. Similar integration of carbon roles have been included in efforts to finance bison restoration in North America[31]. Even de-extinction programs are promoting animal-mediated climate mitigation in their narrative to attract public support and funding. For example, Colossal's landmark woolly mammoth de-extinction program highlights carbon sequestration and high-latitude energy balance as the first of five goals for reviving this species[32].

Given recent efforts to finance and manage large wildlife populations for climate mitigation, it is imperative that the associated uncertainties and timelines are understood, communicated and appropriately incorporated into risk management. If expected carbon outcomes fail to materialize, occur too slowly or even convert ecosystems from sinks to short- or long-term sources, these projects risk blowback for themselves and the underlying science that supports them[28]. For example, the Northern Kenya Ranglelands Carbon Project has already faced widespread criticism for overestimating the negative carbon impacts of traditional grazing, restricting pastoral mobility (especially during periods of drought) and delaying climate action from multinational companies in the Global North[33]. These lessons parallel ongoing sagas surrounding tree planting for climate mitigation, including disrupted ecosystems, low permanence and greenwashing, reminding us of the complexities of biosphere-based climate mitigation strategies[34–36]. It is thus essential that implementation in policy or practice does not outstrip the underlying ecological knowledge informing such activities[28,37].

Mechanisms by which large animals impact carbon balance

We focus on elephants and whales as two animal groups that have been promoted for their potential role in nature-based climate solutions[9,12,16,38]. Their charisma[39] and body size — and thus outsized ecological roles[40] — make them ideal models for how large animals can influence ecosystem carbon cycling across different environmental, biological and anthropogenic contexts (Figure 2). Lessons learned from these well-studied groups can provide a timely gauge on the general state of our mechanistic understanding and predictive capacity of animal carbon roles under diverse conditions and ultimately the potential for large animals to contribute meaningfully to climate mitigation efforts globally. We review the latest evidence regarding all suggested mechanisms of carbon capture and release by elephants and whales (see Supplemental information for details on the methodology of our systematic review) and contextualize animal roles in carbon cycling by comparing them to the annual CO_2e emissions (a standardized metric that expresses the combined climate warming impacts of different greenhouse gases in units of carbon dioxide) from the UK in 2022 (417 Mt CO_2e)[41] for national-level relevance and globally (57.4 Gt CO_2e)[42] for climate-mitigation impact.

African elephants

Elephants have received substantial attention because of their roles in modulating terrestrial carbon cycles as 'ecosystem engineers'[8,43]. Elephants influence ecosystems through a variety of unique ecological functions (e.g., tree toppling and long-distance seed dispersal) that cannot be replicated by higher numbers of smaller animals[40,44] (Table 1 and Figure 3A).

Estimating animal impacts on ecosystem carbon balance relies first on understanding their abundance. African elephant populations have declined by an estimated 98% since 1500 due to numerous anthropogenic pressures (e.g., poaching,





Figure 2. Elephants and whales are flagship megafauna species often promoted for their climate-mitigation roles.
The restoration of forest elephant (*Loxodonta cyclotis*) and humpback whale (*Megaptera novaeangliae*) populations has recently been promoted as a solution for climate change mitigation and the subject of carbon monetization efforts. Despite the clear importance of these species for mediating carbon cycling in ecosystems, there remains a high degree of uncertainty and context-dependency regarding the direction, magnitude, timescale and durability of their carbon impacts. (Photos: forest elephant by Roger de la Harpe under standard commercial licence from iStock, ID 2183869405; humpback whales by Lars Bejder, NMFS Permit #20311-01.)

habitat loss)[45]. Of the remaining ~415,000 African elephants[46], the majority are savanna elephants (*Loxodonta africana*). Savanna elephants can be accurately counted using aerial surveys[47,48], although such methods may be subject to errors[49]. Nevertheless, it was estimated that ~93% of savanna elephants (n = 352,271) were counted in 18 countries as part of the Great Elephant Census in 2014–2015[46]. In contrast, forest elephants (*Loxodonta cyclotis*) are elusive and occur in dense tropical forests leading to greater uncertainty in their abundance. Recent efforts in Gabon, the primary refuge for forest elephants, highlight the challenges associated with monitoring forest elephant populations. Using dung counts, a total of ~52,000 individuals have been estimated[50]. However, this method was highly sensitive to the rate of dung decay, which varies considerably under different environmental conditions[51]. A more recent parameterization[52] suggests there may be ~103,000 forest elephants, while alternative strategies (e.g., DNA-based assessments) provide wide 95% confidence intervals (58,872–131,349)[52].

Estimating the amount of carbon stored in an elephant's body is straightforward. An elephant is ~24% carbon by wet weight[8]. Assuming an average elephant individual mass of 1,725 kg[53], African elephants collectively store ~170,000 tonnes (t) of carbon in their bodies. Uncertainty in overall carbon storage arises from uncertainty in population abundance and demographics. Nevertheless, carbon stored in elephant bodies is negligible compared to their impacts on ecosystem processes and has minimal influence on atmospheric CO_2[54]. Even a doubling of elephant abundance would only sequester carbon equivalent to 0.04% of equivalent fossil fuel emissions in the UK during 2022, or 0.0000003% of global emissions in 2022.

Elephants release carbon directly into the atmosphere as CO_2 via respiration and as methane via enteric emissions (though methane generally breaks down into CO_2 after roughly a decade[55]). A large 4,750 kg savanna elephant is estimated to respire ~21 t CO_2 per year[24], a flux approximately two orders of magnitude higher than the stock of CO_2e captured in its elephant body. However, carbon consumed by elephants would otherwise be decomposed by microbes and other organisms[56], meaning their metabolism and respiration largely accelerate rather than add to carbon efflux. Elephants do, however, also produce methane via the bacteria in their guts. According to one estimate, a savanna elephant releases ~0.026 t methane, or ~0.728 t CO_2e, per year, after accounting for methane's higher heat trapping capacity[57], while another estimate[58] suggests approximately 0.12 t methane per year, or 3.36 t CO_2e for Asian elephants. Even applying the higher estimates[58] to 415,000 elephants across Africa would only equate to ~1.39 Mt CO_2e per year, or ~0.3% of the UK's fossil fuel emissions in 2022 and ~0.000002% of global emissions in 2022. These emissions are also negligible in the context of other elephant impacts on carbon balance (see below).

Elephants can instead impact aboveground carbon stored in vegetation in a variety of ways. These processes can be direct, such as herbivory and tree toppling, or indirect, such as seed dispersal, plant germination and altered fire regimes[43,59–65]. These impacts have been quantified with various degrees of certainty and demonstrate high levels of context-dependency based on abiotic and biotic factors (Table 1)[63,66,67]. For example, by dispersing seeds of carbon-dense tree species[68], reducing seed predation through protection in dung[68] and preferential browsing on soft-wood species, forest elephants have been modelled to modify forest structure to increase aboveground carbon stores in African rainforests by 6–9%[43]. Importantly, the accumulation of carbon through such processes is mediated by the slow pace of plant demographics, which can take decades to centuries to grow, especially for carbon-rich fruiting

Table 1. Studies estimating the present-day impact of African elephants (*Loxodonta africana*; *Loxodonta cyclotis*) and the great whales on carbon fluxes and storage.

Group	Mechanism		Carbon fate	Species	Location	Abundance/density	Abundance/ density uncertainty	Time	Carbon estimate	Carbon uncertainty/ range	Reference
African elephants	Carbon flux	Respiration	Emitted	Forest elephants	Tropical Africa	9.9×10^4	Not reported	Constant	1.12 Tg CO_2 per year	Not reported	9
		Enteric methane emissions	Emitted	Forest elephants	Tropical Africa	9.9×10^4	Not reported	Constant	0.34 Tg CO_2e per year	Not reported	9
	Carbon pool	Animal biomass	Stored	Forest elephants	Tropical Africa	9.9×10^4	Not reported	Constant	0.07 Tg C	Not reported	8
		Aboveground plant biomass	Sequestered	Forest elephants	Tropical Africa	0.5–1.0 ind/km^2	Not reported	Equilibrium	43 t AGB/ha	26–60 t AGB/ha	66
			Sequestered	Forest elephants	RoC; DRC	Not reported	Not reported	Not reported	7.5% AGC	5.8–9.2%	16
			Emitted	Savanna elephants	Namibia	Low (1.4 ind/km^2) High (4.1 ind/km^2)	±0.7 ind/km^2 ±0.6 ind/km^2	Not reported	6.4 t C/ha	~5 t C/ha	71
			Emitted	Savanna elephants	South Africa	0.5 bulls/km^2	Not reported	6 years	~4 t C/ha	~1 t C/ha	67
			Emitted	Savanna elephants	South Africa	Low (~0.4 ind/km^2) High (~0.7 ind/km^2)	Not reported	~50 years	1.3 t C/ha	~0.5 t C/ha	63
			Emitted	Savanna elephants	South Africa	Low to extreme	Not reported	18 years	0.7 t C/ha	~2 t C/ha	65
		Animal dung	Stored	Savanna elephants	Namibia	Low (1.4 ind/km^2) High (4.1 ind/km^2)	±0.7 ind/km^2 ±0.6 ind/km^2	Not reported	0.02 t C/ha 0.33 t C/ha	~0.04 t C/ha ~0.28 t C/ha	71
		Belowground carbon	Sequestered	Savanna elephants	Namibia	Low (1.4 ind/km^2) High (4.1 ind/km^2)	±0.7 ind/km^2 ±0.6 ind/km^2	Not reported	4.7 t C/ha	~4 t C/ha	71
			Sequestered	Savanna elephants	Kenya	0.7 ind/km^2	Not reported	20 years	~4 t C/ha	~10 t C/ha	80
Great whales	Carbon flux	Respiration	Emitted	Sperm whales	Southern Ocean	1.2×10^4	Not reported	Constant	0.16 Tg C per year	Not reported	104
		Whale falls	Sequestered	All baleen whales	Global	1.1×10^6	Not reported	Constant	0.062 Tg C per year	Not reported	7,95
		Whale pump	Fixed	Blue whale	Southern Ocean	5.2×10^3	Not reported	Constant	2.8 Tg C per year	1.2–4.5 Tg C per year	115
			Fixed	Blue, fin, humpback and Antarctic minke whales	Southern Ocean	Not reported	Not reported	Constant	22 Tg C per year	2.7–150 Tg C per year	7,119
			Exported	Sperm whales	Southern Ocean	1.2×10^4	Not reported	Constant	0.4 Tg C per year	Not reported	104
		Great whale conveyor belt	Fixed	Blue whales	Southern Hemisphere	1.2×10^3	Not reported	Constant	0.00051 Tg C per year	Not reported	92,114
	Carbon pool	Animal biomass	Stored	8 baleen whale taxa	Global	1.1×10^6	Not reported	Constant	2 Tg C per year	Not reported	7,95

Where estimates have been extracted from figures, approximate values are provided. Abbreviations: Republic of the Congo (RoC), Democratic Republic of the Congo (DRC), aboveground carbon (AGC), aboveground biomass (AGB), individuals (ind).

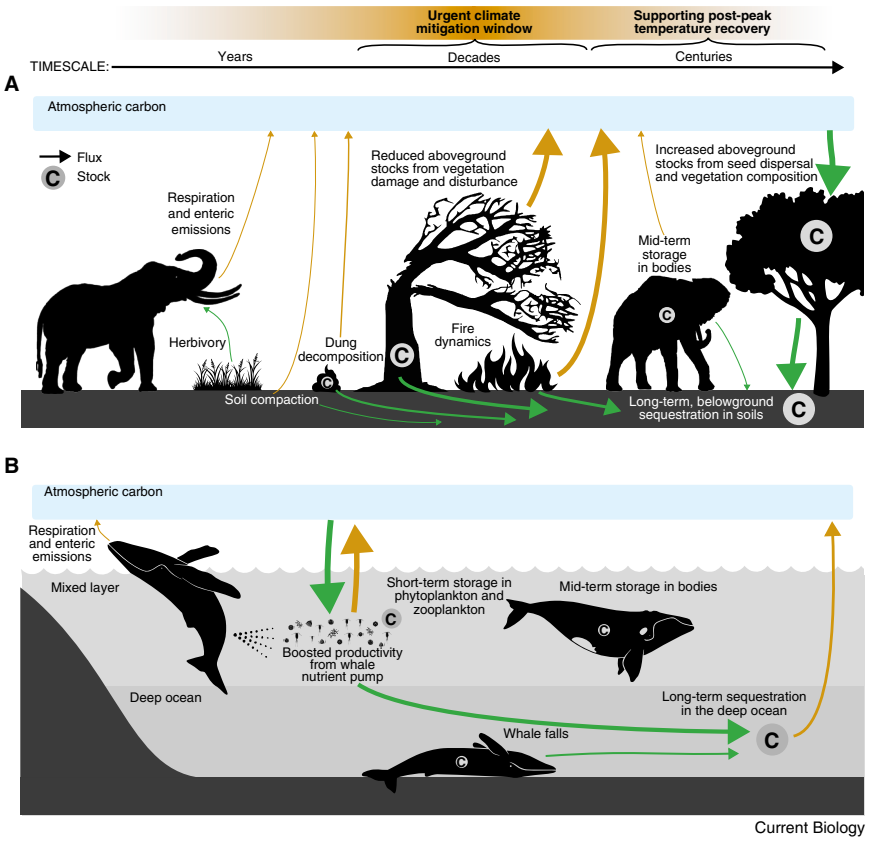


Figure 3. The magnitude, direction and timescales of large animal carbon mechanisms.

(A) Elephants and (B) whales can promote both the capture (green arrows) and release (orange arrows) of carbon from ecosystems. The magnitude (indicated by size of symbols and arrows), direction, and timescale of large animal-mediated carbon stores and fluxes have been highlighted, although there remains much uncertainty and context-dependency in this knowledge. Notably, however, many of the key mechanisms through which these animal groups enhance carbon sequestration operate on timescales that are not relevant for urgent climate mitigation but may be important for long-term (50+ years) climate recovery. (Whale silhouettes by KBelka/iStock.)

trees[69]. This observation suggests that the loss of current forest elephant populations due to poaching may contribute to the release of currently stored carbon, although more empirical validation of the exact mechanisms by which this occurs is required. By contrast, the reintroduction of forest elephants into new habitats may result in short-term (10–100+ years) losses in aboveground carbon through increased herbivory and tree toppling, before longer-term sequestration benefits manifest[66,68,69]. Unlike forest elephants, savanna elephants generally reduce aboveground carbon stocks through herbivory, trampling and physical tree toppling[63,65,67,70–73]. For example, elephants on average knock down 5.4% (IQR: 3.0–8.3%) of trees in savanna ecosystems per year[73]. In Kruger National Park, the presence of elephants resulted in a decrease of 3.5–4.5 t of carbon per hectare over a six-year period[67]. However, these effects varied spatially, and aboveground carbon losses were only significant where bull density exceeded 0.5 bulls/km^2. In Namibia, aboveground carbon stocks were similarly reduced by around 6 t of carbon per hectare where elephant densities were highest[71].

Elephants can also indirectly influence aboveground carbon dynamics by altering fuel availability and fire regimes[73,74]. Repeat monitoring of tall trees that contribute substantially to aboveground carbon storage in Kruger National Park revealed that trees affected by savanna elephant damage became more vulnerable to mortality from fire damage[75]. However, at the same site, elephant-induced reductions in aboveground woody biomass exceeded losses from fire in high productivity areas and were equivalent in low-productivity areas[63]. In contrast to these effects by savanna elephants, forest elephants can alter fire regimes by repeatedly feeding on forest edges where fruit availability is highest, thereby creating natural fire breaks through the removal and trampling of vegetation fuel at the forest–savanna boundary. This has been shown to help stabilize the forest-savanna mosaic in Lope National Park, Gabon[76]. Because differences in fire regime can substantially alter whole ecosystem carbon storage (e.g., >30% in Kruger National Park[77]), and fire risk and frequency might increase with climate change[78], more research is needed to further understand how long-term carbon storage and fluxes are influenced by elephant–fire interactions across contexts. Thus, predictions of the impact of elephants on aboveground carbon stores must account for environmental variability (e.g., existing carbon stocks, plant demographics) and the context-dependency of elephant-mediated processes (Table 1)[70,79].

Belowground pools of carbon (i.e., soil carbon) may serve as more long-term, climate-resilient carbon stocks with increased persistence under global change[5]. However, only two studies[71,80] have examined elephant roles in mediating belowground carbon pools. Sandhage-Hofmann *et al.* demonstrated that, despite savanna elephants in Namibia decreasing aboveground carbon stocks by 6.4 ± 5.0 t carbon per hectare, belowground carbon stocks concurrently increased by 4.7 ± 4.0 t carbon per hectare. These findings align closely with estimates by Sitters *et al.* from Kenya, indicating ∼4 t per hectare higher soil carbon where savanna elephants were present compared to where they had been excluded for over 20 years (Table 1). Elephants directly accelerate the transfer of carbon from aboveground to belowground stores via herbivory, dung deposition and transfer of organic material to soils through tree toppling and branch breakage. Indeed, in Tsavo National Park, Kenya, savanna elephants were estimated to consume 22% of the available aboveground net primary production, and return 154 kg of dung/km^2/day to the soil pool[81]. During the wet season, coprophagous dung beetles rapidly remove and bury a proportion of the dung carbon in the soil, increasing below-ground

carbon stores[82]. No research has yet examined the impacts of forest elephants on belowground carbon, and this is not currently included in estimates of net-carbon impacts in tropical forests[8,9].

Elephants can also indirectly mediate soil carbon storage by stimulating plant root exudation, which provides carbon to microbial decomposer communities and can alter rates of organic matter turnover[83]. Additionally, elephants may influence the rate of microbial decomposition and release of carbon at the soil–atmosphere interface through modifications to soil structure, moisture and nutrient availability[80,84]. For example, soil compaction by trampling may reduce rates of soil carbon accumulation, but also reduce microbial decomposition of organic matter[71,85]. Release of nutrients (e.g., nitrogen, phosphorus, sodium) into soils via urine and dung may also enhance microbial and invertebrate decomposition of organic matter[86,87]. Altered fire regimes through herbivory effects may further influence the magnitude and temporality of carbon transfer from aboveground to belowground stores. For example, in Kruger National Park, South Africa, fire led to temporary increases in soil carbon stocks but long-term reductions[88]. Ultimately, however, all these pathways must be weighed against natural rates of plant root exudation and litter decomposition in the absence of elephants, which further complicates estimates of the net-carbon balance[56].

Despite the recognized importance of elephants on soil carbon, the underlying mechanisms remain poorly understood and indicate a high degree of context dependency across environments. For example, microbial respiration of CO_2 from elephant dung and other organic material increases in warmer and wetter environments[81,89]. Consequently, specific environmental and biotic conditions might influence whether the carbon flux from animal waste is a net carbon source or sink. For example, elephant dung in Chobe National Park, Botswana, decomposed faster during the wet season and in areas of higher arthropod abundance, while lower dung quality (e.g., higher carbon–nitrogen ratio) increased rates of CO_2 and CH_4 emissions[89,90]. Similarly, while litter decomposition by termites was reduced by the presence of large animals in a wet South African savanna, it was stimulated by their presence in dry savannas[91]. Resolving these knowledge gaps is critical for better estimating the net effects of elephants on ecosystem carbon balances.

Ultimately, elephants have little direct influence on atmospheric carbon through their own biomass, respiration or methane emissions. Instead, their major effects on carbon balance arise from how herbivory, tree damage, seed dispersal, dung deposition and altered fire regimes indirectly redistribute carbon. These effects vary strongly across species, densities, environments and biospheric conditions, highlighting the need to consider elephants as dynamic engineers in carbon cycling rather than simply as carbon sinks or sources.

Great whales

The great whales — i.e., the sperm whale (*Physeter macrocephalus*), and baleen whales[7] — are the largest animals to have ever existed on Earth. Through their extreme biomass, whales can exert a strong influence on primary and secondary productivity and thus carbon storage in the ocean[92,93]. As a result, restoring great whale populations has been promoted — most prominently by the International Monetary Fund[12,38] — as a potential strategy for increasing carbon sequestration in the ocean[7,94]. We summarize key processes and outcomes in a similar format as above for elephants to aide comparison (Table 1 and Figure 3B).

Because of industrial whaling, almost all populations of the great whales became significantly diminished[95,96]. For example, blue whales (*Balaenoptera musculus*) in the Southern Ocean were reduced to <1% of their historical abundance[97]. However, since 1986, when commercial whaling was banned in most countries, many populations have increased[96,98]. Confidence in estimates of historic and current whale population abundance varies between species and populations[99]. For example, the demographics of some populations, such as North Pacific humpback whales (*Megaptera novaeangliae*), are relatively well-known[100], whereas those of other species are less understood, especially for highly pelagic populations[101]. While advances in counting whales from satellite and aerial images may help refine population estimates in coming years[102], current uncertainty in abundance is one of the largest sources of error in quantifying the ecological functions of whales[103].

Nevertheless, estimating the amount of carbon stored in whale bodies is perhaps the most straightforward whale-carbon pathway[7]. For example, the largest and most abundant eight baleen whale species (Minke (*Balaenoptera acutorostrata*), Antarctic minke (*Balaenoptera bonaerensis*), sei (*Balaenoptera borealis*), Bryde's (*Balaenoptera brydei*), blue, fin (*Balaenoptera physalus*), bowhead (*Balaena mysticetus*), gray (*Eschrichtius robustus*), right (*Eubalaena* spp.), and humpback whales) are estimated to contain ~2.0 Mt of carbon across the global ocean[7]. Prior to industrial whaling, this value was around five-and-a-half times larger[7,95]. Yet, despite their size, great whale biomass, as mammalian biomass in general, is trivial in terms of global carbon pools[3,13]. Restoring these populations to their pre-industrial baselines would only sequester carbon in their bodies equal to 9.7% of fossil fuel emissions in the UK during 2022, or 0.00007% of global emissions in 2022.

Whales release carbon through respiration and digestive processes, but only few studies have included such estimates of carbon release[7]. Consequently, published carbon storage estimates often refer to gross impacts only. Yet, including these release processes is important. For example, a population of 12,000 sperm whales was crudely estimated to respire ~160,000 t carbon per year; a magnitude which reduces the net effect of whale-stimulated carbon sequestration (see below) by 40%[104]. An alternative, but more resource-intensive, method to estimate respiration emissions could be to use unmanned aerial systems imagery for obtaining information on body size, tidal lung volume, and respiration rate to calculate volume of carbon respired with each breath[105] and then scale this up to the population level. To our knowledge, no peer-reviewed study has examined CH_4 release from whales via gut emissions, although this could be important given the artiodactyl ancestry of cetaceans[106], which includes a four-chambered stomach with foregut fermentation[107,108].

Great whale carcasses, or 'whale falls', can provide large pulses of carbon to the deep ocean. Once carbon is exported to the deep sea (below 1,000 m), it is typically considered to be sequestered, remaining out of contact with the atmosphere for more than 100 years[109], though there is a great deal of

variation in the persistence of deep carbon across the oceans[110]. A high proportion of whale deaths are likely to occur during migration over the deep, pelagic ocean based on the evidence that even for coastal species with a robust monitoring network (e.g., North Atlantic right whale, *Eubalaena glacialis*), the estimated number of whale deaths is much higher than the number of carcasses observed[111]. Some carcasses, however, drift onto beaches or decompose in shallow ocean basins[112], returning carbon to the biosphere or the atmosphere. Based on population modelling and the estimate that 90% of rorqual (minke, Antarctic minke, blue, fin, sei, humpback; Balaenopteridae) and gray whale (*Eschrichtius robustus*) carcasses and 50% of right and bowhead whale (Balaenidae) carcasses are exported to the deep sea[95], whale fall is conservatively estimated to sequester ∼ 62,000 t of carbon per year in the present day and ∼360,000 t prior to industrial whaling[7]. Other modelling studies, however, have suggested that carbon export could be much larger; for example, just five baleen species in the southern ocean (fin, blue, humpback, minke and right whales) may have historically sequestered as much as ∼400,000 t carbon per year through whale fall, but only ∼60,000 t in 1972[18]. These estimated fluxes are, however, tiny in the context of global carbon cycling (e.g., 0.3% and 0.05% of UK 2022 fossil fuel emissions, or 0.000003% and 0.0000004% of global 2022 fossil fuel emissions, respectively) and subject to considerable uncertainty due to a weak understanding of whale fall abundance, whale fall locations and carbon persistence.

Whales can, however, have outsized impacts on marine carbon cycles by modulating ocean primary productivity through the so-called 'whale pump'[113]. Many whales feed at depth and then return to the surface to respire, rest, and digest, often releasing buoyant, nutrient-rich fecal plumes in the euphotic zone and increasing nutrient availability for phytoplankton[113]. Moreover, through the "great whale conveyor belt"[114] whales also transport nutrients from high-latitude feeding grounds to low-latitude breeding grounds by releasing nutrient-rich byproducts (e.g., urine, sloughed skin, placentas). In this manner, whales recycle and distribute nitrogen, phosphorus, iron and other elements in the ocean, both vertically and horizontally[15,92,103,104,113–115]. In the Northern Hemisphere, whale pump research has focused on cycling of nitrogen, the main limiting nutrient for primary productivity in many coastal systems[15,103,113,116], whereas in the Southern Ocean[104,115,117–119] the focus has generally been on the availability of iron, which limits primary productivity in otherwise nutrient-rich waters[120].

Estimating the impact of whales on primary production and carbon sequestration requires assumptions about the bioavailability of nutrients in whale excreta, as well as phytoplankton nutrient limitation[121], both of which are still quite uncertain[101,103,122,123]. For example, there are many chemical and physical properties known to affect iron bioavailability to phytoplankton that have been overlooked in current studies[121,124] (e.g., assuming all iron released in whale feces is available for phytoplankton assimilation[104,115], which is instead constrained by multiple biogeochemical parameters[123,125]). Moreover, much of the nitrogen and iron released by relatively shallow-diving baleen whales in surface waters is likely to be recycled within the upper mixed layer and thus is unlikely to increase overall carbon uptake — assumptions that are at the heart of most monetization schemes[12]. In contrast, limiting nutrients released by sperm whales and other whales foraging beneath the thermocline are likely to be external nutrient inputs to surface waters, causing new primary production and potential carbon export and sequestration in the deep sea[7,104].

In general, the carbon held in whale-stimulated phytoplankton persists on timescales of several weeks or months, before consumption, decomposition and respiration by upper trophic levels (e.g., zooplankton) returns it back to the atmosphere[7]. For any carbon held in phytoplankton or upper trophic levels to meaningfully impact longer-term (>100 years) carbon cycles, it must be transported into the deep ocean[110]. It is usually assumed that 10% of net primary production is exported from the surface layer, of which only 10% of that is sequestered below 1,000 m, but export and sequestration efficiencies can vary regionally by over an order of magnitude[7,110,126,127]. Unfortunately, some studies in the Southern Hemisphere have made crude assumptions about export efficiency from the whale pump that most likely result in overestimates, such as an assumed export efficiency of almost 100%[104]. Accurately quantifying the differences in the fate of whale-stimulated carbon held in phytoplankton and upper trophic levels across regions holds the key for understanding the true impact of whale recovery as a climate mitigation strategy.

In short, carbon sequestered in whale bodies transports an important flux to the deep ocean, where it promotes biodiversity and sustains whale fall ecosystems[95,128], but this does not provide a meaningful climate mitigation function. Instead, through the whale pump, whales might have outsized impacts on ocean productivity and carbon sequestration. However, current claims that whales can promote 1% of global productivity in the ocean, resulting in the capture of 100 Mt of carbon[12], are unsupported by empirical evidence and likely vastly overestimated. More research is needed before we can robustly quantify the impacts of whales on carbon cycling in the oceans[7,94,129,130]. For example, despite using state-of-the-art empirical validation of baleen whale feeding ecology, tracking carbon fixation via the whale pump resulted in uncertainty that spans two orders of magnitude due to fundamental challenges in measuring whale fecal nutrient content, phytoplankton responses, and the portion of carbon exported to the deep ocean[131]. Any quantification of carbon sequestration associated with whale-induced nutrient fertilization should, therefore, be considered preliminary at this stage.

Direction, magnitude and context-dependency of large animal carbon effects

Elephants and whales have become flagship cases in discussions of megafauna-based climate solutions. As discussed above, these and many other large animals can play important roles in local carbon cycling and ecosystem functioning[5–7,132]. Yet, there is considerable uncertainty and context-dependency regarding the direction, magnitude, timescale and durability of their carbon impacts.

In general, most direct mechanisms of large animals on carbon cycling, including consumption, assimilation and respiration, can be reliably quantified using allometric and bioenergetic models that translate body stoichiometry and daily energetic

requirements into rates of carbon flux and storage[18,95]. However, while these estimates are relatively stable and predictable across populations and ecosystems, they are also trivial in magnitude with respect to changing atmospheric CO_2 concentrations. For example, carbon stored in the bodies of all African elephants is equivalent to just the carbon emissions of a small English town in a single year[41].

In contrast, the indirect influence of large animals on ecosystem productivity and storage of carbon in sediments, water, and plants can be orders of magnitude larger (Table 1)[132]. Yet, large animal impacts on ecosystem carbon sources or sinks vary substantially across populations and are considerably more difficult to quantify and predict, as they depend on complex interactions among multiple ecological variables and pools of carbon that vary across space and time. Scaling predictions of large animal indirect impacts on carbon cycling across broad areas adds another challenge. Animals do not use landscapes or the seas homogeneously, precluding simple extrapolations. For example, some areas may only be used by animals for short periods during seasonal migrations[114], while hotspot areas may accumulate substantial impacts, including carbon gains or disrupted ecological integrity[133]. Ecosystems often respond nonlinearly to animal impacts, alternating between multiple stable states. As a result, current broad-scale generalizations often fail to capture important variation among species, functional groups and ecosystems.

Resolving these interrelationships and uncertainties has appreciable implications for improving our understanding of when, where, and how large animals can influence ecosystem carbon storage across their present-day range and expected benefits during future restoration efforts. However, we note that even the upper estimates of elephant and whale impacts on carbon sequestration are small compared to current anthropogenic emissions[28,134], with optimistic population recoveries and carbon benefits for African forest elephants and baleen whales[24] equivalent to 0.024% of global fossil fuel emissions in 2022. While elephants and great whales are not expected to influence global carbon cycling alone, these groups make up ~8% and >75% of terrestrial and marine wild mammal biomass[135], respectively. Future, more accurate assessments of large animal contributions to carbon cycling at larger scales require more detailed knowledge of mechanisms and the ecological and abiotic contexts within which they play out.

Carbon persistence and novel biospheric conditions

For large animal restoration to be a durable climate solution, sequestered carbon must be reliably stored for long periods. However, the persistence of the carbon that large animals help sequester can vary considerably by ecosystem and mechanism. Notably, in both marine and terrestrial ecosystems, carbon sequestered by animals into more permanent stores are generally less well-understood. For example, the long-term fate of carbon influenced by whales depends on factors like ocean depth and geographic location; carbon is recycled much more quickly in shallow coastal waters — where many whale species feed and defecate — than in deeper regions where carbon can be sequestered for centuries or longer[129]. On land, the influence of large herbivores on soil carbon is often considered more durable than their effects on aboveground biomass[14], as soil carbon can remain stored for decades or centuries[5]. However, soil carbon processes in many areas (e.g., tropical rainforests)[136] and interactions with animals remain critically understudied[5,19].

Accelerating global change affects all ecosystems on Earth such that they face novel biospheric conditions in coming decades[137], making any long-term predictions highly uncertain[29]. Under novel biospheric conditions, the mechanisms by which large animals impact carbon cycles may also shift, potentially reducing or even reversing sequestration[36,138]. For example, altered elephant interactions with climate-changing fire and drought regimes may release previously stored carbon[63,78,139]. In addition, animal restoration projects also face uncertainty due to climate change and shifting local anthropogenic pressures, including poaching, habitat loss, land abandonment, human–wildlife conflict, vessel strikes, and fisheries entanglement[96,140–145]. Forest elephants and pelagic whale populations are particularly at risk due to their slower reproductive rates and greater difficulties in population monitoring for conservation[52,140,146]. By the end of this century, models predict declines and even extinctions due to climate-induced changes in food availability for several large whale species[96] as well as forest elephants[142]. If carbon sequestration requires continuous animal impact (e.g., grazing, nutrient recycling), any carbon gains realized during earlier periods of restoration efforts may become lost.

In the same way, the loss of current large animal populations (defaunation) may also jeopardize large carbon stores that have accumulated over time. For example, the loss of existing forest elephants is predicted to reduce aboveground carbon in protected areas by 6–9% over a 30 year period through reduced seed dispersal of carbon-rich fruiting trees[43]. Importantly, such defaunation may result in the release of carbon on decadal timescales, and thus contribute to exacerbating climate change[9,147] (Figure 3). This observation reflects an important asymmetry in ecosystem recovery: rebuilding large animal populations and the ecological processes they support typically requires decades to centuries, whereas the disruption of these processes begins immediately following rapid population declines and can occur quickly. A recent analysis across the Congo basin found that as much as 14.7–26.3 Gt of carbon may be released over the next 250 years as a result of large-scale defaunation, including forest elephants and other vertebrate species[147]. Thus, while there remains a high degree of uncertainty surrounding the magnitude and durability of animal roles in the carbon cycle, it is clearly prudent to avoid the potential for additional carbon release through defaunation.

Temporal and spatial scales of restoration

For large animal restoration to meaningfully contribute within the portfolio of climate mitigation strategies, it must either be aligned with the Paris Agreement's mission of achieving net-zero by mid-century[1] or provide additional long-term benefits by helping restore disrupted carbon-cycle processes and supporting temperature decline beyond net-zero. However, the most significant effects of large animals on carbon sequestration often require higher animal population densities and depend on ecosystem modifications that take decades or even centuries to accumulate (Figure 3).

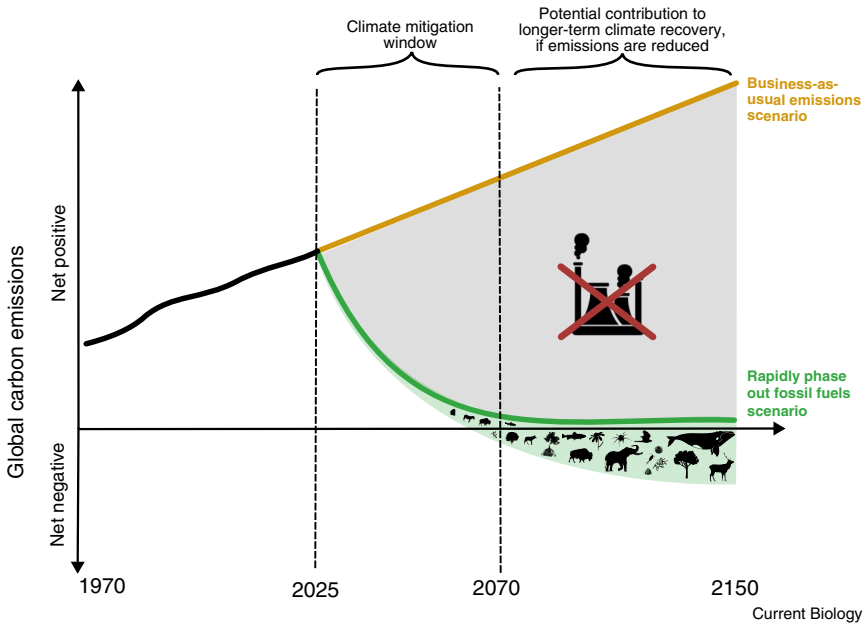


Figure 4. The potential contribution of resilient and recovering ecosystems towards achieving long-term climate recovery.

Historical anthropogenic carbon emissions before 2025 prelude either a "business-as-usual" emissions scenario (orange line) or a net emissions reduction trajectory required to prevent global warming from exceeding 2°C (green line). The green shaded area shows the potential contribution of nature-based solutions, including large animal restoration initiated now, with benefits accruing through to 2150. The carbon sequestration potential of large animal restoration is fundamentally constrained by slow reproductive cycles and the delayed mechanisms of carbon sequestration (e.g., those mediated by slow plant demographics). As a result, large animal restoration is not a reliable solution to mitigate urgent climate change, which must instead focus on rapidly transitioning from fossil fuels and other greenhouse gas emissions. Once anthropogenic emissions have been curbed, functionally intact, resilient ecosystems — including large animals — may play a meaningful role in global carbon budgets, including contributing to a post-peak temperature cooling of the Earth.

Long interbirth intervals set fundamental constraints on large animal population growth[148]. For example, humpback whales may in principle increase by 5–9% annually under ideal conditions[149], but resource limitation, disease, predation and human–wildlife conflict often prevent populations from reaching these levels. Furthermore, the relationship between animal restoration and carbon outcomes is not always linear through time. For instance, the restoration of forest elephants into a landscape that has been missing elephants would likely reduce aboveground carbon storage in the short term (e.g., through grazing or trampling[66,150]), before long-term carbon sequestration processes (e.g., seeding carbon-rich fruiting trees) generate net carbon gains[69]. By contrast, the magnitude of carbon sequestration via the whale pump may be directly proportional to the population size, though variation among species and ecosystem are considerable[113,114]. Nevertheless, in general, we identify that the most significant processes by which large animals increase the accumulation of carbon in ecosystems — especially processes mediated by the slow demographics of population recovery for megafauna species, mature trees or soil formation[5,40] — fall outside the relevant timeline for urgent climate mitigation (Figure 3).

Beyond demographic constraints, the climate relevance of long-term large animal restoration also depends on achieving recovery over wide areas sufficient to influence regional or global carbon budgets. While restoration potential in the vast ocean is substantial, large animal population recovery on land inevitably clashes with human land-use, limiting the potential spatial scale of restoration outside of sparsely populated areas[148]. In southern Africa, for example, despite considerable efforts, savanna elephants have, on average, experienced an annual population growth of only 0.16% for the past quarter century[151]. Moreover, increased use of population regulation procedures (e.g., contraceptives, hunting) suggests space for further elephant population restoration may already be limited given the projected number and distribution of humans across Africa[152]. Thus, the space required for large animal restoration to generate substantial climate benefits is currently limited in many parts of the world.

Finally, it remains critical to clarify the potential of carbon storage anticipated from large animal population restoration. Removing fossil-fuel-derived carbon from the atmosphere requires sequestration that is reliable over long periods (thousands of years) to prevent re-release[26]. By contrast, ecological restoration aims to recover degraded ecosystems' natural carbon carrying capacity, effectively returning carbon stocks to historical baselines. While such restoration may enhance carbon storage relative to the degraded state, it does not necessarily achieve net removal of fossil carbon beyond natural ecosystem cycling. Realistic climate mitigation expectations require differentiating between restoring natural carbon baselines and achieving additional, long-term fossil carbon sequestration[26,27].

While large animal restoration may not be realistic for rapid climate change mitigation, such contributions could potentially, if started now, become significant over decadal-century timescales, provided emissions are substantially reduced; a central factor in all long-term nature-based climate mitigation strategies[2,4,134] (Figure 4). Restoring ecosystem processes driven by large animals enhances ecosystem recovery and resilience, helping to maintain and rebuild carbon stocks in the face of increasing climate variability. By promoting functions such as nutrient cycling, vegetation regeneration and soil formation, animals can help ecosystems regain their historical carbon-carrying capacity and biosphere–atmosphere feedbacks[24,132]. Such feedbacks are especially important in the post-peak emissions era, when active ecosystem recovery will be needed to gradually draw down excess atmospheric CO_2 and contribute to long-term planetary cooling[26,134,153]. In this context, large-animal conservation and restoration efforts as a way to restore functionally intact ecosystems represents a critical investment in the long-term climate stability of Earth and an important complement to immediate emissions reductions.

Financing and implementing large animal restoration as a climate solution

Both elephants and whales have been suggested as ideal candidates for inclusion in carbon markets as carbon offsets[8,12,38,154]. Such efforts follow a trend for the monetization of ecosystem services, which has long been debated[155]. On one hand, economics can play a role in halting and reversing biodiversity loss by enhancing the rigor of analyses and providing a quantitative tool for policy decision making[156,157]. On the other, such schemes can also induce perverse outcomes (e.g., ''bad'' carbon species), can be practically challenging to implement, and overlook the most important value systems, including inherent values of nature in itself[28,129,155,158]. Such values have been essential in effective legislation such as the Endangered Species Act and the Marine Mammal Protection Act and international agreements, such as the moratorium on commercial whaling under the International Whaling Commission. In each of these cases, monetization would likely result in the reduction of protection.

Ideas to monetize the role of elephants in the carbon cycle have solely focused on African forest elephants[8,12,38] and attribute 99% of their carbon-based value to the predicted impact of forest elephant populations on aboveground carbon gains in tree biomass. Under this modelling framework, a single forest elephant has been valued by economists at the International Monetary Fund at $1.75 million[12]. Similarly, whales have been promoted for carbon tradeoff schemes, with values across populations exceeding US $1 trillion, based on arbitrary assumptions about the carbon stored by the whale pump in widely publicized reports[12,38,154]. Ultimately, the evidence reviewed above indicates that these valuations are premature, unsupported by empirical evidence, and do not satisfy the level of scientific rigor required for implementation under leading carbon credit standards (e.g., Verra). There are three general considerations with proposed monetization efforts.

First, comprehensive assessments of the net effects of large animal populations on carbon across ecosystems are currently lacking. This absence has significant implications for understanding the true carbon impact. Individual mechanisms are often poorly constrained across contexts and simplified in ecological modelling frameworks. Field validation and rigorous assessment of baseline carbon stocks are essential to resolve these issues but represent a formidable challenge. New technologies offer opportunities (e.g., airborne and space-based lidar for evaluating elephant impacts on aboveground carbon in tropical forests[159]); however, such methods currently remain limited in their application. Missing, but potentially important, mechanisms further preclude comprehensive assessments of large animal impacts across all ecosystem pools (e.g., above and belowground). This may even have implications for whether large animal populations are considered a source or sink of carbon. For instance, research on savanna elephants has demonstrated that they consistently reduce aboveground carbon stores through tree-toppling and vegetation destruction, especially when they aggregate in large numbers or stay in one place for longer periods of time[63,67,71]. However, more recent appraisals found that losses aboveground can translate into increases in belowground soil carbon, resulting in a much smaller net carbon effect than would be inferred from aboveground impacts alone[71].

Second, net evaluations must ensure there is no carbon leakage through activities associated with large animal conservation or restoration programs[160]. For example, although the methods are unclear, whale economic valuations[12,38,154] include boosts to global fisheries as a result of whale activity; an industry that is responsible for 150–250 Mt of carbon emissions per year through benthic trawling, biomass extraction and fossil fuel consumption[161,162]. Additional release of carbon may also occur from activities associated with boosted ecotourism following large animal restoration, such as international air travel, local fuel consumption and accommodation. Globally, tourism accounted for 8.8% of global greenhouse gas emissions in 2019[163], and with hundreds of millions of people participating in nature-based tourism each year, the potential for additional carbon release is high[164]. Boosts to the whale-watching industry, for example, are included in whale valuations[12]. With >3,300 operators offering trips around the world[165], however, this would certainly be a source of carbon, not a sink.

Lastly, for large animals to contribute to carbon-market frameworks, the money generated by selling carbon credits must be linked to a conservation or restoration activity that would not have otherwise happened — the so-called 'additionality' requirement. A fundamental prerequisite is to be able to show that carbon storage actually increases from a baseline scenario without carbon credits. This is already a challenge for many projects relying on natural ecosystem dynamics due to the uncertain trajectory of existing ecosystem carbon pools in plants and soils. For example, 'passive' carbon uptake in plant biomass due to anthropogenic CO_2 fertilization must be accounted for in all nature-based carbon budgets[26]. Adding the link from the changes in carbon pools to animal conservation efforts would, at the very least, require accurate baselines and predictions of animal abundances. Even for the world's largest species, this challenge remains one of the primary sources of error in quantifying ecological functions[103,114].

Given these shortfalls and uncertainties, we suggest that efforts to place a carbon market or monetary value on elephants or whales based on their carbon cycling roles are premature. Moreover, such efforts could be detrimental to urgent climate change mitigation if they were to divert climate funding away from verified mitigation and emission reduction[28,153]. Conservation initiatives incorporating carbon objectives should therefore explicitly acknowledge uncertainties in magnitude, direction, durability and timescales of animal-mediated carbon impacts, while prioritizing rigorous monitoring and empirical validation. This will help ensure that carbon-based conservation strategies are grounded in sound ecological understanding, support effective climate mitigation and complement — rather than distract from — direct emissions reductions.

Six key lessons for leveraging large animal conservation and restoration as a long-term climate solution

Our understanding of elephant and whale conservation and restoration as a natural climate solution can help guide directions for other, less well-studied animal groups that have also been suggested to play important climate roles, such as Arctic herbivores, dugongs, wolves, bison, wildebeest or

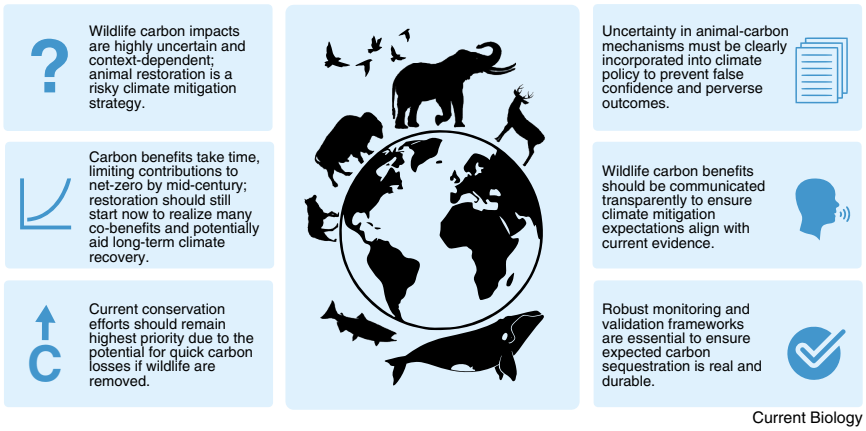


Figure 5. Six lessons for leveraging wildlife conservation and restoration as a long-term climate solution.
Based on the latest scientific understanding of elephant and great whale roles in Earth's carbon cycle and climate mitigation potential, we have identified six key lessons for effectively incorporating large animal conservation and restoration within the broader portfolio of climate mitigation strategies. These lessons are pertinent to other, less well-studied large animal groups that have also been suggested to play important climate mitigation roles and more general ecosystem management approaches that attempt to optimize animal-carbon mechanisms across diverse large animal communities.

tigers[166–169]. These also apply to more general wildlife and ecosystem management approaches that attempt to optimize across diverse large animal communities for increased carbon sequestration. Below we identify six key lessons for communicators, policymakers, managers and conservation practitioners (Figure 5).

Lesson 1: Predicting wildlife carbon impacts is hard, and animal restoration is a high-risk climate strategy

Large uncertainties in the magnitude, timescale, and durability of animal-carbon effects mean that wildlife restoration should currently be considered a high-risk climate mitigation pathway. Near-term investments should instead be justified primarily by robust side-benefits, including biodiversity conservation, ecosystem recovery and resilience to climate change, rather than only uncertain carbon returns.

Lesson 2: Restoration for long-term benefits should begin now

Wildlife population recovery, ecological responses and reaching meaningful scales will require many decades to develop. Initiating restoration now is nevertheless essential to realize potential long-term climate recovery benefits while delivering broader co-benefits in the near term (Figure 4).

Lesson 3: Conservation should remain the highest priority

Despite uncertainties surrounding animal-carbon roles, preventing further defaunation remains a prudent strategy to avoid additional carbon emissions. Large animal restoration and carbon accumulation can take centuries, but losses can occur rapidly. Therefore, protecting intact ecosystems and wildlife communities is critical, particularly in carbon-rich ecosystems, such as the Congo basin or Arctic permafrost[16,166].

Lesson 4: Animals must be carefully integrated into climate policy

It is essential that animals are explicitly recognized in climate policy frameworks, as carbon assessments without animals critically overlook their role as important and dynamic regulators of ecosystem carbon storage. However, caution is needed when incorporating animal effects into carbon assessments, mitigation targets, or climate finance mechanisms due to substantial variability in animal-carbon processes across species, systems, and timescales. Overestimating carbon impacts could misdirect climate investments, create false confidence in mitigation potential and lead to unintended management outcomes (e.g., "bad" carbon species or populations).

Lesson 5: Potential carbon benefits of wildlife should be communicated transparently

To align climate mitigation expectations with current evidence, it is critical that animal carbon roles are communicated transparently with respect to magnitude, direction, timescales, durability and associated uncertainties. This includes clearly distinguishing between carbon recovered through ecosystem restoration following historical degradation and carbon emissions from ongoing fossil fuel use, which wildlife restoration cannot directly offset.

Lesson 6: Monitoring and validating animal restoration programs is essential

Even for well-studied species, such as elephants and whales, confident estimates of net carbon outcomes are challenging. The most valuable research will come from integrated (e.g., above- and belowground carbon pools) long-term monitoring programs implemented alongside animal restoration efforts, allowing carbon stocks, fluxes and ecosystem responses to be measured as populations recover. Such assessments should also include other climate-relevant pathways, such as changes in local energy budgets.

In summary, wildlife conservation and restoration are essential for many reasons, including their roles in carbon cycling that remain challenging to accurately predict and generalize. By continuing to investigate, critically evaluate and transparently communicate these roles, we can build responsible pathways for addressing the interconnected biodiversity and climate crises.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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REFERENCES

1. (2021). IPCC, 2021: Summary for policymakers. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, V.P. Masson-Delmotte, P. Zhai, S.L. Pirani, C. Connors, S. Péan, N. Berger, Y. Caud, L. Chen, M.I. Goldfarb, and P.M. Scheel Monteiro, eds. (Cambridge University Press), pp. 3–32. https://doi.org/10.1017/9781009157896.001.

2. Girardin, C.A.J., Jenkins, S., Seddon, N., Allen, M., Lewis, S.L., Wheeler, C.E., Griscom, B.W., and Malhi, Y. (2021). Nature-based solutions can help cool the planet — if we act now. Nature *593*, 191–194. https://doi.org/10.1038/d41586-021-01241-2.

3. Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. Proc. Natl. Acad. Sci. USA *115*, 6506–6511. https://doi.org/10.1073/pnas.1711842115.

4. Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., *et al*. (2017). Natural climate solutions. Proc. Natl. Acad. Sci. USA *114*, 11645–11650. https://doi.org/10.1073/pnas.1710465114.

5. Kristensen, J.A., Svenning, J.-C., Georgiou, K., and Malhi, Y. (2022). Can large herbivores enhance ecosystem carbon persistence? Trends Ecol. Evol. *37*, 117–128. https://doi.org/10.1016/j.tree.2021.09.006.

6. Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M., Davies, A.B., and Goetz, S.J. (2018). Animals and the zoogeochemistry of the carbon cycle. Science *362*, eaar3213. https://doi.org/10.1126/science.aar3213.

7. Pearson, H.C., Savoca, M.S., Costa, D.P., Lomas, M.W., Molina, R., Pershing, A.J., Smith, C.R., Villaseñor-Derbez, J.C., Wing, S.R., and Roman, J. (2023). Whales in the carbon cycle: can recovery remove carbon dioxide? Trends Ecol. Evol. *38*, 238–249. https://doi.org/10.1016/j.tree.2022.10.012.

8. Berzaghi, F., Chami, R., Cosimano, T., and Fullenkamp, C. (2022). Financing conservation by valuing carbon services produced by wild animals. Proc. Natl. Acad. Sci. USA *119*, e2120426119. https://doi.org/10.1073/pnas.2120426119.

9. Schmitz, O.J., Sylvén, M., Atwood, T.B., Bakker, E.S., Berzaghi, F., Brodie, J.F., Cromsigt, J.P., Davies, A.B., Leroux, S.J., and Schepers, F.J. (2023). Trophic rewilding can expand natural climate solutions. Nat. Clim. Change *13*, 324–333.

10. Bello, C., Dent, D.H., and Crowther, T.W. (2024). Animals in restoration to achieve climate biodiversity targets. Trends Ecol. Evol. *39*, 979–982. https://doi.org/10.1016/j.tree.2024.08.011.

11. Cromsigt, J.P.G.M., te Beest, M., Kerley, G.I.H., Landman, M., le Roux, E., and Smith, F.A. (2018). Trophic rewilding as a climate change mitigation strategy? Philos. Trans. R. Soc. B Biol. Sci. *373*, 20170440. https://doi.org/10.1098/rstb.2017.0440.

12. Chami, R., Fullenkamp, C., Berzaghi, F., Espanol-Jiménez, S., Marcondes, M., and Palazzo, J. (2020). On valuing nature-based solutions to climate change: a framework with application to elephants and whales. Preprint at SSRN, https://dx.doi.org/10.2139/ssrn.3686168.

13. Malhi, Y., Lander, T., le Roux, E., Stevens, N., Macias-Fauria, M., Wedding, L., Girardin, C., Kristensen, J.Å., Sandom, C.J., and Evans, T.D. (2022). The role of large wild animals in climate change mitigation and adaptation. Curr. Biol. *32*, R181–R196.

14. Wu, Y., Yang, W., Jian, Z., Ye, J., Yao, B., Hu, Q., and Xu, J. (2026). Herbivorous vertebrates decrease CO_2 sequestration across global terrestrial ecosystems. Global Biogeochem. Cy. *40*, e2025GB008878. https://doi.org/10.1029/2025GB008878.

15. Freitas, C., Skogen, M.D., Sigurðsson, G.M., Biuw, M., Haug, T., Lindblom, L., and Gundersen, K. (2025). Impact of baleen whales on ocean primary production across space and time. Proc. Natl. Acad. Sci. USA *122*, e2505563122. https://doi.org/10.1073/pnas.2505563122.

16. Berzaghi, F., Bretagnolle, F., Durand-Bessart, C., and Blake, S. (2023). Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. Proc. Natl. Acad. Sci. USA *120*, e2201832120. https://doi.org/10.1073/pnas.2201832120.

17. Rizzuto, M., Leroux, S.J., and Schmitz, O.J. (2024). Rewiring the carbon cycle: A theoretical framework for animal-driven ecosystem carbon sequestration. J. Geophys. Res. Biogeosciences *129*, e2024JG008026. https://doi.org/10.1029/2024JG008026.

18. Durfort, A., Mariani, G., Tulloch, V., Savoca, M.S., Troussellier, M., and Mouillot, D. (2022). Recovery of carbon benefits by overharvested baleen whale populations is threatened by climate change. Proc. R. Soc. B Biol. Sci. *289*, 20220375. https://doi.org/10.1098/rspb.2022.0375.

19. Cheng, Y., O'Keeffe, J.A., Abraham, A.J., Christiansen, J.R., Philipsen, F.N., Larsen, K.S., Berzaghi, F., Mueller, C.W., Vesterdal, L., Kristensen, J.A., *et al*. (2026). Integrating large mammalian herbivores into Dynamic Global Vegetation Models: Status and next steps. Funct. Ecol., https://doi.org/10.1111/1365-2435.70409.

20. McGregor, S., Cromsigt, J.P.G.M., te Beest, M., Chen, J., Roy, D.P., Hawkins, H.-J., and Kerley, G.I.H. (2024). Grassland albedo as a nature-based climate prospect: the role of growth form and grazing. Environ. Res. Lett. *19*, 124004. https://doi.org/10.1088/1748-9326/ad8765.

21. Rana, P., Fleischman, F., and Sharma, A. (2026). Why carbon offsets may fail in complex systems: A causal inference perspective. Environ. Sci. Policy *176*, 104325. https://doi.org/10.1016/j.envsci.2026.104325.

22. Meyer, G.A., and Leroux, S.J. (2023). Towards a mechanistic understanding of animal–ecosystem interactions. J. Anim. Ecol. *92*, 2244–2247. https://doi.org/10.1111/1365-2656.14023.

23. Burak, M.K., Ferraro, K.M., Orrick, K.D., Sommer, N.R., Ellis-Soto, D., and Schmitz, O.J. (2024). Context matters when rewilding for climate change. People Nat. *6*, 507–518. https://doi.org/10.1002/pan3.10609.

24. Schmitz, O.J., Sylvén, M., Atwood, T.B., Bakker, E.S., Berzaghi, F., Brodie, J.F., Cromsigt, J.P.G.M., Davies, A.B., Leroux, S.J., Schepers, F.J., *et al*. (2023). Trophic rewilding can expand natural climate solutions. Nat. Clim. Change *13*, 324–333. https://doi.org/10.1038/s41558-023-01631-6.

25. Pearce, W., Brown, B., Nerlich, B., and Koteyko, N. (2015). Communicating climate change: conduits, content, and consensus. WIREs Clim. Change *6*, 613–626. https://doi.org/10.1002/wcc.366.

26. Allen, M.R., Frame, D.J., Friedlingstein, P., Gillett, N.P., Grassi, G., Gregory, J.M., Hare, W., House, J., Huntingford, C., Jenkins, S., *et al*. (2025). Geological Net Zero and the need for disaggregated accounting for carbon sinks. Nature *638*, 343–350. https://doi.org/10.1038/s41586-024-08326-8.

27. Mackey, B., Prentice, I.C., Steffen, W., House, J.I., Lindenmayer, D., Keith, H., and Berry, S. (2013). Untangling the confusion around land carbon science and climate change mitigation policy. Nat. Clim. Change *3*, 552–557. https://doi.org/10.1038/nclimate1804.

28. Duvall, E.S., le Roux, E., Pearson, H.C., Roman, J., Malhi, Y., and Abraham, A.J. (2024). Resisting the carbonization of animals as climate solutions. Nat. Clim. Change *14*, 892–895. https://doi.org/10.1038/s41558-024-02106-y.

29. Stark, G., Weissgerber, M., Fernández, N., Quintero-Uribe, L.C., Giergiczny, M., Poulsen, N.R., Villar, N., Mols, B., Bakker, E.S., Smith, A.M., *et al*. (2026). Toward climate-smart rewilding: An integrated framework for biodiversity, climate change, and society. One Earth *9*, 101704. https://doi.org/10.1016/j.oneear.2026.101704.

30. Child, M., Child, A., Fouche, T., and Venter, Z. (2024). Tswalu Kalahari Carbon Project (Rewild Capital), https://www.crediblecarbon.com/wp-content/uploads/2024/06/PR01a-Tswalu-Credible-Carbon-PIN_02022023-FINAL.pdf.

31. Thoumi, G., Kroll, M., and Thaggard, C. (2025). Bison bond: A financial opportunity whose time has come (Responsible Alpha), https://responsiblealpha.com/wp-content/uploads/2025/12/BISON-BOND.pdf.

32. Poquérusse, J., Brown, C.L., Gaillard, C., Doughty, C., Dalén, L., Gallagher, A.J., Wooller, M., Zimov, N., Church, G.M., Lamm, B., *et al*. (2024). Assessing contemporary Arctic habitat availability for a woolly mammoth proxy. Sci. Rep. *14*, 9804. https://doi.org/10.1038/s41598-024-60442-7.

33. Counsell, S. (2024). Blood carbon: How a carbon offset scheme makes millions from indigenous land in Northern Kenya. Indig. Policy J. *34*, 280.

34. Kristensen, J.Å., Barbero-Palacios, L., Barrio, I.C., Jacobsen, I.B.D., Kerby, J.T., López-Blanco, E., Malhi, Y., Le Moullec, M., Mueller, C.W., Post, E., *et al*. (2024). Tree planting is no climate solution at northern high latitudes. Nat. Geosci. *17*, 1087–1092. https://doi.org/10.1038/s41561-024-01573-4.

35. Parr, C.L., te Beest, M., and Stevens, N. (2024). Conflation of reforestation with restoration is widespread. Science *383*, 698–701. https://doi.org/10.1126/science.adj0899.

36. Abraham, A.J., Duvall, E.S., Moracho, E., Ruiz-López, M.J., Gilbert, L., Ellis-Soto, D., Prys-Jones, T., and Marjakangas, E.-L. (2026). Double-edged dispersal: animal-mediated transport in the Anthropocene. Trends Ecol. Evol. *41*, 703–714. https://doi.org/10.1016/j.tree.2026.04.014.

37. Monk, J.D., Barker, K.J., Maher, S.M.L., Serota, M.W., Shawler, A.L., Verta, G., Xu, W., Middleton, A.D., and Gherardi, L.A. (2026). Comparisons of wild and domestic ungulate zoogeochemical impacts rarely evaluate mechanisms underlying functional dissimilarity. J. Anim. Ecol., https://doi.org/10.1111/1365-2656.70317.

38. Chami, R., Cosimano, T., Fullenkamp, C., and Oztosun, S. (2019). Nature's solution to climate change. Finance Dev. *56*, 34–38.

39. Berti, E., Monsarrat, S., Munk, M., Jarvie, S., and Svenning, J.-C. (2020). Body size is a good proxy for vertebrate charisma. Biol. Conserv. *251*, 108790. https://doi.org/10.1016/j.biocon.2020.108790.

40. Enquist, B.J., Abraham, A.J., Harfoot, M.B.J., Malhi, Y., and Doughty, C.E. (2020). The megabiota are disproportionately important for biosphere functioning. Nat. Commun. *11*, 699. https://doi.org/10.1038/s41467-020-14369-y.

41. Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I.T., Olsen, A., Peters, G.P., *et al*. (2022). Global Carbon Budget 2022. Earth Syst. Sci. Data *14*, 4811–4900. https://doi.org/10.5194/essd-14-4811-2022.

42. UNEP (2022). Emissions Gap Report 2022: The Closing Window (Climate Crisis Calls for Rapid Transformation of Societies (UN)), https://unepccc.org/emissions-gap-report-2022/.

43. Berzaghi, F., Bretagnolle, F., Durand-Bessart, C., and Blake, S. (2023). Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. Proc. Natl. Acad. Sci. USA *120*, e2201832120. https://doi.org/10.1073/pnas.2201832120.

44. Pringle, R.M., Abraham, J.O., Anderson, T.M., Coverdale, T.C., Davies, A.B., Dutton, C.L., Gaylard, A., Goheen, J.R., Holdo, R.M., Hutchinson, M.C., *et al*. (2023). Impacts of large herbivores on terrestrial ecosystems. Curr. Biol. *33*, R584–R610. https://doi.org/10.1016/j.cub.2023.04.024.

45. Ritchie, H. (2024). The state of the world's elephant populations (Our World Data), https://archive.ourworldindata.org/20260727-131016/elephant-populations.html.

46. Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., *et al*. (2016). Continent-wide survey reveals massive decline in African savannah elephants. PeerJ *4*, e2354. https://doi.org/10.7717/peerj.2354.

47. Huang, R.M., Maré, C., Guldemond, R.A.R., Pimm, S.L., and Van Aarde, R.J. (2024). Protecting and connecting landscapes stabilizes populations of the Endangered savannah elephant. Sci. Adv. *10*, eadk2896. https://doi.org/10.1126/sciadv.adk2896.

48. Jachmann, H. (1991). Evaluation of four survey methods for estimating elephant densities. Afr. J. Ecol. *29*, 188–195. https://doi.org/10.1111/j.1365-2028.1991.tb01001.x.

49. Ferreira, S., Crowhurst, E., Greaver, C., and Simms, C. (2024). Sample-based estimates of elephants in Kruger National Park, South Africa. Afr. J. Wildl. Res. *54*, https://doi.org/10.3957/056.054.0122.

50. Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba'a, R., Abitsi, G., Ambahe, R.D., Amsini, F., *et al*. (2013). Devastating decline of forest elephants in Central Africa. PLoS One *8*, e59469. https://doi.org/10.1371/journal.pone.0059469.

51. Barnes, R.F.W., and Barnes, K.L. (1992). Estimating decay rates of elephant dung piles in forest. Afr. J. Ecol. *30*, 316–321. https://doi.org/10.1111/j.1365-2028.1992.tb00508.x.

52. Laguardia, A., Bourgeois, S., Strindberg, S., Gobush, K.S., Abitsi, G., Bikang Bi Ateme, H.G., Ebouta, F., Fay, J.M., Gopalaswamy, A.M., Maisels, F., *et al*. (2021). Nationwide abundance and distribution of African forest elephants across Gabon using non-invasive SNP genotyping. Glob. Ecol. Conserv. *32*, e01894. https://doi.org/10.1016/j.gecco.2021.e01894.

53. Laws, R.M. (1966). Age criteria for the African elephant. Afr. J. Ecol. *4*, 1–37. https://doi.org/10.1111/j.1365-2028.1966.tb00878.x.

54. Berzaghi, F., Cosimano, T., Fullenkamp, C., Scanlon, J., Fon, T.E., Robson, M.T., Forbang, J.L., and Chami, R. (2022). Value wild animals' carbon services to fill the biodiversity financing gap. Nat. Clim. Change *12*, 598–601. https://doi.org/10.1038/s41558-022-01407-4.

55. Lelieveld, J., Crutzen, P.J., and Dentener, F.J. (1998). Changing concentration, lifetime and climate forcing of atmospheric methane. Tellus B *50*, 128–150. https://doi.org/10.1034/j.1600-0889.1998.t01-1-00002.x.

56. Pausas, J.G., and Bond, W.J. (2020). On the three major recycling pathways in terrestrial ecosystems. Trends Ecol. Evol. *35*, 767–775. https://doi.org/10.1016/j.tree.2020.04.004.

57. Crutzen, P.J., Aselmann, I., and Seiler, W. (1986). Methane production by domestic animals, wild ruminants, other herbivorous fauna, and humans. Tellus B Chem. Phys. Meteorol. *38*, 271–284. https://doi.org/10.3402/tellusb.v38i3-4.15135.

58. Benedict, F.G., and Lee, R.C. (1938). Further observations on the physiology of the elephant. J. Mammal. *19*, 175–194. https://doi.org/10.2307/1374612.

59. Beaune, D., Fruth, B., Bollache, L., Hohmann, G., and Bretagnolle, F. (2013). Doom of the elephant-dependent trees in a Congo tropical forest. For. Ecol. Manag. *295*, 109–117. https://doi.org/10.1016/j.foreco.2012.12.041.

60. Campos-Arceiz, A., and Blake, S. (2011). Megagardeners of the forest — the role of elephants in seed dispersal. Acta Oecologica *37*, 542–553. https://doi.org/10.1016/j.actao.2011.01.014.

61. Gordon, C.E., Greve, M., Henley, M., Bedetti, A., Allin, P., and Svenning, J.-C. (2023). Elephant rewilding affects landscape openness and fauna habitat across a 92-year period. Ecol. Appl. *33*, e2810. https://doi.org/10.1002/eap.2810.

62. Keany, J.M., Burns, P., Abraham, A.J., Jantz, P., Makaga, L., Saatchi, S., Maisels, F., Abernethy, K., and Doughty, C.E. (2024). Using multiscale lidar to determine variation in canopy structure from African forest elephant trails. Remote Sens. Ecol. Conserv. *10*, 655–667. https://doi.org/10.1002/rse2.395.

63. Pellegrini, A.F.A., Pringle, R.M., Govender, N., and Hedin, L.O. (2017). Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. J. Ecol. *105*, 111–121. https://doi.org/10.1111/1365-2745.12668.

64. Poulsen, J.R., Beirne, C., Rundel, C., Baldino, M., Kim, S., Knorr, J., Minich, T., Jin, L., Núñez, C.L., Xiao, S., *et al*. (2021). Long distance seed dispersal by forest elephants. Front. Ecol. Evol. *9*, 789264. https://doi.org/10.3389/fevo.2021.789264.

65. Schröcker, C.C. (2022). Elephants and aboveground carbon stocks in a South African protected savanna. Second cycle, A2E (Umeå: SLU, Department of Wildlife, Fish and Environmental Studies), http://urn.kb.se/resolve?urn=urn:nbn:se:slu:epsilon-s-18510.

66. Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., and Doughty, C.E. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. Nat. Geosci. *12*, 725–729. https://doi.org/10.1038/s41561-019-0395-6.

67. Davies, A.B., and Asner, G.P. (2019). Elephants limit aboveground carbon gains in African savannas. Glob. Change Biol. *25*, 1368–1382. https://doi.org/10.1111/gcb.14585.

68. Deblauwe, V., Luskin, M.S., Assola, S.D., Hardy, O.J., Jansen, S., Loubières, C., Mempong, G.G., Ntsihe, J.M., Oum Ndjock, G., Onguene Kwecheu, E.R., *et al*. (2025). Declines of ebony and ivory are inextricably linked in an African rainforest. Sci. Adv. *11*, eady4392. https://doi.org/10.1126/sciadv.ady4392.

69. Sullivan, M.K., Jasperse-Sjolander, L., Lewis, M., Masseloux, J., Poulsen, J., and Meier, A.C. (2026). Context-dependent forest elephant seed dispersal: implications for pathways of elephant-driven patterns of biodiversity and carbon storage. Oikos *2026*, e11507. https://doi.org/10.1002/oik.11507.

70. Guldemond, R., and Van Aarde, R. (2008). A meta-analysis of the impact of African elephants on savanna vegetation. J. Wildl. Manag. *72*, 892–899. https://doi.org/10.2193/2007-072.

71. Sandhage-Hofmann, A., Linstädter, A., Kindermann, L., Angombe, S., and Amelung, W. (2021). Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass. Glob. Chang. Biol. *27*, 4601–4614. https://doi.org/10.1111/gcb.15779.

72. Coverdale, T.C., Boucher, P.B., Singh, J., Palmer, T.M., Goheen, J.R., Pringle, R.M., and Davies, A.B. (2024). Herbivore regulation of savanna vegetation: Structural complexity, diversity, and the complexity–diversity relationship. Ecol. Monogr. *94*, e1624. https://doi.org/10.1002/ecm.1624.

73. Archibald, S., Courtenay, A.P., Mtsetfwa, F., da Silva, D.F.P.F., Bunney, K., Guldemond, R., Mograbi, P., Ransom, C., Ryan, C.M., and Owen-Smith, N. (2026). The "Too-Few Elephant Problem": Quantitative analysis of historical elephant tree-toppling rates across Africa. Ecosystems *29*, 79. https://doi.org/10.1007/s10021-026-01089-5.

74. Rouet-Leduc, J., Pe'er, G., Moreira, F., Bonn, A., Helmer, W., Shahsavan Zadeh, S.A.A., Zizka, A., and van der Plas, F. (2021). Effects of large herbivores on fire regimes and wildfire mitigation. J. Appl. Ecol. *58*, 2690–2702. https://doi.org/10.1111/1365-2664.13972.

75. Shannon, G., Thaker, M., Vanak, A.T., Page, B.R., Grant, R., and Slotow, R. (2011). Relative impacts of elephant and fire on large trees in a savanna ecosystem. Ecosystems *14*, 1372–1381. https://doi.org/10.1007/s10021-011-9485-z.

76. Cardoso, A.W., Malhi, Y., Oliveras, I., Lehmann, D., Ndong, J.E., Dimoto, E., Bush, E., Jeffery, K., Labriere, N., Lewis, S.L., *et al*. (2020). The role of forest elephants in shaping tropical forest–savanna coexistence. Ecosystems *23*, 602–616. https://doi.org/10.1007/s10021-019-00424-3.

77. Zhou, Y., Singh, J., Butnor, J.R., Coetsee, C., Boucher, P.B., Case, M.F., Hockridge, E.G., Davies, A.B., and Staver, A.C. (2022). Limited increases in savanna carbon stocks over decades of fire suppression. Nature *603*, 445–449. https://doi.org/10.1038/s41586-022-04438-1.

78. Singo, M.V., Chikoore, H., Engelbrecht, F.A., Ndarana, T., Muofhe, T.P., Mbokodo, I.L., Murungweni, F.M., and Bopape, M.-J.M. (2023). Projections of future fire risk under climate change over the South African savanna. Stoch. Environ. Res. Risk Assess. *37*, 2677–2691. https://doi.org/10.1007/s00477-023-02412-5.

79. Guldemond, R.A.R., Purdon, A., and van Aarde, R.J. (2017). A systematic review of elephant impact across Africa. PLoS One *12*, e0178935. https://doi.org/10.1371/journal.pone.0178935.

80. Sitters, J., Kimuyu, D.M., Young, T.P., Claeys, P., and Venterink, H. (2020). Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. Nat. Sustain. *3*, 360–366. https://doi.org/10.1038/s41893-020-0490-0.

81. Anderson, J.M., and Coe, M.J. (1974). Decomposition of elephant dung in an arid, tropical environment. Oecologia *14*, 111–125. https://doi.org/10.1007/BF00344902.

82. Menéndez, R., Webb, P., and Orwin, K.H. (2016). Complementarity of dung beetle species with different functional behaviours influence dung–soil carbon cycling. Soil Biol. Biochem. *92*, 142–148. https://doi.org/10.1016/j.soilbio.2015.10.004.

83. Khatri, P., Sharma, B., Ong, L., and Campos-Arceiz, A. (2026). Simulated elephant foraging alters tree root exudation rates: Species-specific responses and implications for belowground carbon dynamics in tropical forests. Plants People Planet *8*, 1733–1745. https://doi.org/10.1002/ppp3.70152.

84. Haynes, G. (2012). Elephants (and extinct relatives) as earth-movers and ecosystem engineers. Geomorphology *157–158*, 99–107. https://doi.org/10.1016/j.geomorph.2011.04.045.

85. Kotzé, E., Sandhage-Hofmann, A., Meinel, J.-A., du Preez, C.C., and Amelung, W. (2013). Rangeland management impacts on the properties of clayey soils along grazing gradients in the semi-arid grassland biome of South Africa. J. Arid Environ. *97*, 220–229. https://doi.org/10.1016/j.jaridenv.2013.07.004.

86. Clay, N.A., Donoso, D.A., and Kaspari, M. (2015). Urine as an important source of sodium increases decomposition in an inland but not coastal tropical forest. Oecologia *177*, 571–579. https://doi.org/10.1007/s00442-014-3183-4.

87. Kaspari, M., Clay, N.A., Donoso, D.A., and Yanoviak, S.P. (2014). Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. Ecology *95*, 795–800. https://doi.org/10.1890/13-1274.1.

88. Strydom, T., Smit, I., and Van Tol, J.J. (2024). Short and long-term fire effects on soil C and N in an African savanna. Geoderma Reg. *37*, e00802. https://doi.org/10.1016/j.geodrs.2024.e00802.

89. Zhu, Y., Merbold, L., Leitner, S., Pelster, D.E., Okoma, S.A., Ngetich, F., Onyango, A.A., Pellikka, P., and Butterbach-Bahl, K. (2020). The effects of climate on decomposition of cattle, sheep and goat manure in Kenyan tropical pastures. Plant Soil *451*, 325–343. https://doi.org/10.1007/s11104-020-04528-x.

90. Masunga, G.S., Andresen, Ø., Taylor, J.E., and Dhillion, S.S. (2006). Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. Mycol. Res. *110*, 1214–1226. https://doi.org/10.1016/j.mycres.2006.07.004.

91. Buitenwerf, R., Stevens, N., Gosling, C.M., Anderson, T.M., and Olff, H. (2011). Interactions between large herbivores and litter removal by termites across a rainfall gradient in a South African savanna. J. Trop. Ecol. *27*, 375–382. https://doi.org/10.1017/S0266467411000125.

92. Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J., Nicol, S., Pershing, A., and Smetacek, V. (2014). Whales as marine ecosystem engineers. Front. Ecol. Environ. *12*, 377–385. https://doi.org/10.1890/130220.

93. Freitas, C., Gundersen, K., Lindblom, L., Biuw, M., and Haug, T. (2023). Nutrient concentrations in minke whale faeces and the potential impact on dissolved nutrient pools off Svalbard, Norway. Prog. Oceanogr. *210*, 102927. https://doi.org/10.1016/j.pocean.2022.102927.

94. Meynecke, J.-O., Samanta, S., de Bie, J., Seyboth, E., Prakash Dey, S., Fearon, G., Vichi, M., Findlay, K., Roychoudhury, A., and Mackey, B. (2023). Do whales really increase the oceanic removal of atmospheric carbon? Front. Mar. Sci. *10*, 1117409.

95. Pershing, A.J., Christensen, L.B., Record, N.R., Sherwood, G.D., and Stetson, P.B. (2010). The impact of whaling on the ocean carbon cycle: Why bigger was better. PLoS One *5*, e12444. https://doi.org/10.1371/journal.pone.0012444.

96. Tulloch, V.J.D., Plagányi, É.E., Brown, C., Richardson, A.J., and Matear, R. (2019). Future recovery of baleen whales is imperiled by climate change. Glob. Chang. Biol. *25*, 1263–1281. https://doi.org/10.1111/gcb.14573.

97. Branch, T.A., Stafford, K.M., Palacios, D.M., Allison, C., Bannister, J.L., Burton, C.L.K., Cabrera, E., Carlson, C.A., Vernazzani, B.G., Gill, P.C., *et al*. (2007). Past and present distribution, densities and movements of blue whales Balaenoptera musculus in the Southern Hemisphere and northern Indian Ocean. Mammal Rev. *37*, 116–175.

98. Roman, J., Dunphy-Daly, M.M., Johnston, D.W., and Read, A.J. (2015). Lifting baselines to address the consequences of conservation success. Trends Ecol. Evol. *30*, 299–302. https://doi.org/10.1016/j.tree.2015.04.003.

99. Smith, C., Roman, J., and Nation, J. (2019). A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. J. Mar. Res. *77*, 283–302. https://doi.org/10.1357/002224019828474250.

100. Cheeseman, T., Southerland, K., Acebes, J.M., Audley, K., Barlow, J., Bejder, L., Birdsall, C., Bradford, A.L., Byington, J.K., and Calambokidis, J. (2023). A collaborative and near-comprehensive North Pacific humpback whale photo-ID dataset. Sci. Rep. *13*, 10237.

101. Attard, C.R., Beheregaray, L.B., and Möller, L.M. (2016). Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. Sci. Rep. *6*, 22291.

102. Guirado, E., Tabik, S., Rivas, M.L., Alcaraz-Segura, D., and Herrera, F. (2019). Whale counting in satellite and aerial images with deep learning. Sci. Rep. *9*, 14259. https://doi.org/10.1038/s41598-019-50795-9.

103. Gilbert, L., Jeanniard-du-Dot, T., Authier, M., Chouvelon, T., and Spitz, J. (2023). Composition of cetacean communities worldwide shapes their contribution to ocean nutrient cycling. Nat. Commun. *14*, 5823.

104. Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J.G., and Smetacek, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proc. R. Soc. B Biol. Sci. *277*, 3527–3531. https://doi.org/10.1098/rspb.2010.0863.

105. Sumich, J.L., Albertson, R., Torres, L.G., Bird, C.N., Bierlich, K.C., and Harris, C. (2023). Using audio and UAS-based video for estimating tidal lung volumes of resting and active adult gray whales (Eschrichtius robustus). Mar. Mammal Sci. *40*, e13081.

106. Thewissen, J.G., Cooper, L.N., Clementz, M.T., Bajpai, S., and Tiwari, B.N. (2007). Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature *450*, 1190–1194.

107. Domning, D.P. (2018). Sirenian evolution. In Encyclopedia of Marine Mammals, B. Würsig, J.G.M. Thewissen, and K.M. Kovacs, eds. (Academic Press), pp. 856–859.

108. Sanders, J.G., Beichman, A.C., Roman, J., Scott, J.J., Emerson, D., McCarthy, J.J., and Girguis, P.R. (2015). Baleen whales host a unique gut microbiome with similarities to both carnivores and herbivores. Nat. Commun. *6*, 8285. https://doi.org/10.1038/ncomms9285.

109. Passow, U., and Carlson, C.A. (2012). The biological pump in a high CO_2 world. Mar. Ecol. Prog. Ser. *470*, 249–271.

110. Siegel, D.A., DeVries, T., Doney, S.C., and Bell, T. (2021). Assessing the sequestration time scales of some ocean-based carbon dioxide reduction strategies. Environ. Res. Lett. *16*, 104003.

111. Smith, C.R., and Baco, A.R. (2003). Ecology of whale falls at the deep-sea floor. Oceanogr. Mar. Biol. *41*, 311–354.

112. Moore, M.J., Mitchell, G.H., Rowles, T.K., and Early, G. (2020). Dead cetacean? Beach, bloat, float, sink. Front. Mar. Sci. *7*, 333.

113. Roman, J., and McCarthy, J.J. (2010). The whale pump: marine mammals enhance primary productivity in a coastal basin. PLoS One *5*, e13255.

114. Roman, J., Abraham, A.J., Kiszka, J.J., Costa, D.P., Doughty, C.E., Friedlaender, A., Hückstädt, L.A., Marcondes, M., Wetsel, E., and Pershing, A.J. (2025). Migrating baleen whales transport high-latitude nutrients to tropical and subtropical ecosystems. Nat. Commun. *16*, 2125. https://doi.org/10.1038/s41467-025-56123-2.

115. Lavery, T.J., Roudnew, B., Seymour, J., Mitchell, J.G., Smetacek, V., and Nicol, S. (2014). Whales sustain fisheries: Blue whales stimulate primary production in the Southern Ocean. Mar. Mammal Sci. *30*, 888–904. https://doi.org/10.1111/mms.12108.

116. Freitas, C., Gundersen, K., Lindblom, L., Biuw, M., and Haug, T. (2023). Nutrient concentrations in minke whale faeces and the potential impact on dissolved nutrient pools off Svalbard, Norway. Prog. Oceanogr. *210*, 102927.

117. Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K.M., and Van Der Merwe, P. (2010). Southern Ocean iron fertilization by baleen whales and Antarctic krill. Fish Fish. *11*, 203–209. https://doi.org/10.1111/j.1467-2979.2010.00356.x.

118. Smith, L.V., McMinn, A., Martin, A., Nicol, S., Bowie, A.R., Lannuzel, D., and van der Merwe, P. (2013). Preliminary investigation into the stimulation of phytoplankton photophysiology and growth by whale faeces. J. Exp. Mar. Biol. Ecol. *446*, 1–9.

119. Savoca, M.S., Czapanskiy, M.F., Kahane-Rapport, S.R., Gough, W.T., Fahlbusch, J.A., Bierlich, K.C., Segre, P.S., Di Clemente, J., Penry, G.S., and Wiley, D.N. (2021). Baleen whale prey consumption based on high-resolution foraging measurements. Nature *599*, 85–90.

120. Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F., *et al*. (2007). Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. Nature *446*, 1070–1074. https://doi.org/10.1038/nature05700.

121. Browning, T.J., and Moore, C.M. (2023). Global analysis of ocean phytoplankton nutrient limitation reveals high prevalence of co-limitation. Nat. Commun. *14*, 5014. https://doi.org/10.1038/s41467-023-40774-0.

122. Ratnarajah, L., Lannuzel, D., Townsend, A.T., Meiners, K.M., Nicol, S., Friedlaender, A.S., and Bowie, A.R. (2017). Physical speciation and solubility of iron from baleen whale faecal material. Mar. Chem. *194*, 79–88. https://doi.org/10.1016/j.marchem.2017.05.004.

123. Monreal, P.J., Savoca, M.S., Babcock-Adams, L., Moore, L.E., Ruacho, A., Hull, D., Pallin, L.J., Nichols, R.C., Calambokidis, J., Resing, J.A., *et al*. (2025). Organic ligands in whale excrement support iron availability and reduce copper toxicity to the surface ocean. Commun. Earth Environ. *6*, 20. https://doi.org/10.1038/s43247-024-01965-9.

124. Collins, S., Whittaker, H., and Thomas, M.K. (2022). The need for unrealistic experiments in global change biology. Curr. Opin. Microbiol. *68*, 102151. https://doi.org/10.1016/j.mib.2022.102151.

125. Hassler, C.S., Schoemann, V., Nichols, C.M., Butler, E.C.V., and Boyd, P.W. (2011). Saccharides enhance iron bioavailability to Southern Ocean phytoplankton. Proc. Natl. Acad. Sci. USA *108*, 1076–1081. https://doi.org/10.1073/pnas.1010963108.

126. Boyd, P.W., and Trull, T.W. (2007). Understanding the export of biogenic particles in oceanic waters: Is there consensus? Prog. Oceanogr. *72*, 276–312. https://doi.org/10.1016/j.pocean.2006.10.007.

127. Boeuf, D., Edwards, B.R., Eppley, J.M., Hu, S.K., Poff, K.E., Romano, A.E., Caron, D.A., Karl, D.M., and DeLong, E.F. (2019). Biological composition and microbial dynamics of sinking particulate organic matter at abyssal depths in the oligotrophic open ocean. Proc. Natl. Acad. Sci. USA *116*, 11824–11832. https://doi.org/10.1073/pnas.1903080116.

128. Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D., and Amon, D.J. (2015). Whale-fall ecosystems: Recent insights into ecology, paleoecology, and evolution. Annu. Rev. Mar. Sci. *7*, 571–596. https://doi.org/10.1146/annurev-marine-010213-135144.

129. National Academies of Sciences, Engineering, and Medicine (2022). A Research Strategy for Ocean-based Carbon Dioxide Removal and Sequestration (The National Academies Press), https://nap.nationalacademies.org/catalog/26278/a-research-strategy-for-ocean-based-carbon-dioxide-removal-and-sequestration.

130. Collins, J.R., Cape, M.R., Boenish, R.E., Benitez-Nelson, C.R., Doney, S.C., Fujita, R., Gaines, S.D., Gruby, R.L., Jin, D., Kim, H.H., *et al*. (2025). The biogeochemistry of natural climate solutions based on fish, fisheries, and marine mammals: A review of current evidence, research needs, and critical assessment of readiness. Glob. Biogeochem. Cycles *39*, e2024GB008393. https://doi.org/10.1029/2024GB008393.

131. Savoca, M.S., Czapanskiy, M.F., Kahane-Rapport, S.R., Gough, W.T., Fahlbusch, J.A., Bierlich, K.C., Segre, P.S., Di Clemente, J., Penry, G.S., Wiley, D.N., *et al*. (2021). Baleen whale prey consumption based on high-resolution foraging measurements. Nature *599*, 85–90. https://doi.org/10.1038/s41586-021-03991-5.

132. Malhi, Y., Lander, T., le Roux, E., Stevens, N., Macias-Fauria, M., Wedding, L., Girardin, C., Kristensen, J.Å., Sandom, C.J., Evans, T.D., *et al*. (2022). The role of large wild animals in climate change mitigation and adaptation. Curr. Biol. *32*, R181–R196. https://doi.org/10.1016/j.cub.2022.01.041.

133. Isla, J., Serrano, E., Calleja, J.A., Hernández-Castellano, C., Alcalá-Herrera, R., Albanell, E., Alonso, C., Baraza, E., Brolly, M., Burnside, N., *et al*. (2026). High densities of large herbivores rapidly disrupt ecosystem integrity. Glob. Chang. Biol. *32*, e70964. https://doi.org/10.1111/gcb.70964.

134. Buma, B., Gordon, D.R., Kleisner, K.M., Bartuska, A., Bidlack, A., DeFries, R., Ellis, P., Friedlingstein, P., Metzger, S., Morgan, G., *et al*. (2024). Expert review of the science underlying nature-based climate solutions. Nat. Clim. Change *14*, 402–406. https://doi.org/10.1038/s41558-024-01960-0.

135. Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y.M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E., *et al*. (2023). The global biomass of wild mammals. Proc. Natl. Acad. Sci. USA *120*, e2204892120. https://doi.org/10.1073/pnas.2204892120.

136. Hengl, T., Miller, M.A.E., Križan, J., Shepherd, K.D., Sila, A., Kilibarda, M., Antonijević, O., Glušica, L., Dobermann, A., Haefele, S.M., *et al*. (2021). African soil properties and nutrients mapped at 30 m spatial resolution using two-scale ensemble machine learning. Sci. Rep. *11*, 6130. https://doi.org/10.1038/s41598-021-85639-y.

137. Svenning, J.-C., Buitenwerf, R., and Roux, E.L. (2024). Trophic rewilding as a restoration approach under emerging novel biosphere conditions. Curr. Biol. *34*, R435–R451. https://doi.org/10.1016/j.cub.2024.02.044.

138. Lovell, C., Dawson, T.P., and Pettorelli, N. (2025). Impacts of an omnivorous ungulate on plant communities and soil organic carbon. Ecol. Solut. Evid. *6*, e70079. https://doi.org/10.1002/2688-8319.70079.

139. Vanak, A.T., Shannon, G., Thaker, M., Page, B., Grant, R., and Slotow, R. (2012). Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. Ecography *35*, 315–321. https://doi.org/10.1111/j.1600-0587.2011.07213.x.

140. Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., de Semboli, B., Mbenzo, V., *et al*. (2007). Forest elephant crisis in the Congo Basin. PLoS Biol. *5*, e111. https://doi.org/10.1371/journal.pbio.0050111.

141. Braulik, G.T., Taylor, B.L., Minton, G., Notarbartolo Di Sciara, G., Collins, T., Rojas-Bracho, L., Crespo, E.A., Ponnampalam, L.S., Double, M.C., and Reeves, R.R. (2023). Red-list status and extinction risk of the world's whales, dolphins, and porpoises. Conserv. Biol. *37*, e14090. https://doi.org/10.1111/cobi.14090.

142. Bush, E.R., Whytock, R.C., Bahaa-el-din, L., Bourgeois, S., Bunnefeld, N., Cardoso, A.W., Dikangadissi, J.T., Dimbonda, P., Dimoto, E., Edzang Ndong, J., *et al*. (2020). Long-term collapse in fruit availability threatens Central African forest megafauna. Science *370*, 1219–1222. https://doi.org/10.1126/science.abc7791.

143. Lee, P.C., and Graham, M.D. (2006). African elephants *Loxodonta africana* and human-elephant interactions: implications for conservation. Int. Zoo Yearb. *40*, 9–19. https://doi.org/10.1111/j.1748-1090.2006.00009.x.

144. Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba'a, R., Abitsi, G., Ambahe, R.D., and Amsini, F. (2013). Devastating decline of forest elephants in Central Africa. PLoS One *8*, e59469.

145. Ngcobo, J.N., Nedambale, T.L., Nephawe, K.A., Sawosz, E., and Chwalibog, A. (2018). The future survival of African elephants: implications for conservation. Int. J. Avian Wildl. Biol. *3*, 379–384.

146. Turkalo, A.K., Wrege, P.H., and Wittemyer, G. (2017). Slow intrinsic growth rate in forest elephants indicates recovery from poaching will require decades. J. Appl. Ecol. *54*, 153–159. https://doi.org/10.1111/1365-2664.12764.

147. Brodie, J.F., Bello, C., Emer, C., Galetti, M., Luskin, M.S., Osuri, A., Peres, C.A., Stoll, A., Villar, N., and López, A.-B. (2022). Defaunation impacts on the carbon balance of tropical forests. Conserv. Biol. *39*, e14414. https://doi.org/10.1111/cobi.14414.

148. Macias-Fauria, M., Jepson, P., Zimov, N., and Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? Philos. Trans. R. Soc. B Biol. Sci. *375*, 20190122. https://doi.org/10.1098/rstb.2019.0122.

149. Zerbini, A.N., Clapham, P.J., and Wade, P.R. (2010). Assessing plausible rates of population growth in humpback whales from life-history data. Mar. Biol. *157*, 1225–1236. https://doi.org/10.1007/s00227-010-1403-y.

150. Xu, C., Silliman, B.R., Chen, J., Li, X., Thomsen, M.S., Zhang, Q., Lee, J., Lefcheck, J.S., Daleo, P., Hughes, B.B., *et al*. (2023). Herbivory limits success of vegetation restoration globally. Science *382*, 589–594. https://doi.org/10.1126/science.add2814.

151. Huang, R.M., Maré, C., Guldemond, R.A.R., Pimm, S.L., and van Aarde, R.J. (2024). Protecting and connecting landscapes stabilizes populations of the Endangered savannah elephant. Sci. Adv. *10*, eadk2896. https://doi.org/10.1126/sciadv.adk2896.

152. Perdok, A.A., de Boer, W.F., and Stout, T.A.E. (2007). Prospects for managing African elephant population growth by immunocontraception: a review. Pachyderm *42*, 95–105.

153. Seddon, N., Smith, A., Smith, P., Key, I., Chausson, A., Girardin, C., House, J., Srivastava, S., and Turner, B. (2021). Getting the message right on nature-based solutions to climate change. Glob. Chang. Biol. *27*, 1518–1546. https://doi.org/10.1111/gcb.15513.

154. Chami, R., Cosimano, T., Fullenkamp, C., Berzaghi, F., Español-Jiménez, S., Marcondes, M., and Palazzo, J. (2022). The value of nature to our health and economic well-being: A framework with application to elephants and whales. In Economic Challenges for Europe After the Pandemic, L. Paganetto, ed. (Springer Proceedings in Business and Economics), pp. 117–162.

155. Gómez-Baggethun, E., and Ruiz-Pérez, M. (2011). Economic valuation and the commodification of ecosystem services. Prog. Phys. Geogr. Earth Environ. *35*, 613–628. https://doi.org/10.1177/0309133311421708.

156. Fenichel, E.P., Dean, M.F., and Schmitz, O.J. (2024). The path to scientifically sound biodiversity valuation in the context of the Global Biodiversity Framework. Proc. Natl. Acad. Sci. USA *121*, e2319077121. https://doi.org/10.1073/pnas.2319077121.

157. Ury, J., Kotchen, M.J., and Schmitz, O.J. (2024). Trading off nature for nature-based solutions: The bioeconomics of forest management for wildlife, timber, and carbon. Ecosphere *15*, e4963. https://doi.org/10.1002/ecs2.4963.

158. Wauchope, H.S., zu Ermgassen, S.O.S.E., Jones, J.P.G., Carter, H., Schulte to Bühne, H., and Milner-Gulland, E.J. (2024). What is a unit of nature? Measurement challenges in the emerging biodiversity credit market. Proc. R. Soc. B Biol. Sci. *291*, 20242353. https://doi.org/10.1098/rspb.2024.2353.

159. Keany, J.M., Burns, P., Abraham, A.J., Jantz, P., Makaga, L., Saatchi, S., Maisels, F., Abernethy, K., and Doughty, C.E. (2024). Using multiscale lidar to determine variation in canopy structure from African forest elephant trails. Remote Sens. Ecol. Conserv. *10*, 655–667. https://doi.org/10.1002/rse2.395.

160. Zeng, Y., Lamba, A., Teo, H.C., and Koh, L.P. (2026). Limitations of carbon markets for biodiversity conservation. Nat. Rev. Biodivers. *2*, 335–344. https://doi.org/10.1038/s44358-026-00150-4.

161. Collins, J., Boenish, R., Fujita, R., Rader, D., and Moore, L. (2022). Natural climate solutions in the open ocean: scentific knowledge and opportunities surrounding four potential pathways for carbon dioxide removal or avoided emissions (Environmental Defense Fund), https://www.edf.org/sites/default/files/2022-10/Natural%20Climate%20Solutions%20in%20the%20Open%20Ocean.pdf.

162. Mariani, G., Cheung, W.W.L., Lyet, A., Sala, E., Mayorga, J., Velez, L., Gaines, S.D., Dejean, T., Troussellier, M., and Mouillot, D. (2020). Let more big fish sink: Fisheries prevent blue carbon sequestration — half in unprofitable areas. Sci. Adv. *6*, eabb4848. https://doi.org/10.1126/sciadv.abb4848.

163. Sun, Y.-Y., Faturay, F., Lenzen, M., Gössling, S., and Higham, J. (2024). Drivers of global tourism carbon emissions. Nat. Commun. *15*, 10384. https://doi.org/10.1038/s41467-024-54582-7.

164. Buckley, R.C., Zhong, L., and Gössling, S. (2026). Ecotourism caught in decarbonisation politics. npj Clim. Action *5*, 38. https://doi.org/10.1038/s44168-026-00366-2.

165. O'Connor, S., Campbell, R., Cortez, H., and Knowles, T. (2009). Whale Watching Worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare (Economists at Large), https://www.mmc.gov/wp-content/uploads/whale_watching_worldwide.pdf.

166. Ylänne, H., and Stark, S. (2025). Can large animals direct the fate of the vast arctic soil carbon reserves — a review. Environ. Res. Commun. *7*, 022004. https://doi.org/10.1088/2515-7620/adb7be.

167. Roberts, N.J., Harihar, A., Zhou, X., She, W., and Jiang, G. (2025). Global tiger density linked with forest carbon stock, top-down and bottom-up. Glob. Chang. Biol. *31*, e70191. https://doi.org/10.1111/gcb.70191.

168. Spracklen, D.V., Chapman, P.J., Fletcher, T., Lane, J.V., Nilsen, E.B., Perks, M., Schofield, L., and Scott, C.E. (2025). Wolf reintroduction to Scotland could support substantial native woodland expansion and associated carbon sequestration. Ecol. Solut. Evid. *6*, e70016. https://doi.org/10.1002/2688-8319.70016.

169. Schmitz, O.J.J., and AlMealla, R.K.K. (2026). Integrating megafauna into blue carbon strategies: dugongs could enhance seagrass carbon storage. Front. Mar. Sci. *13*, 1816090. https://doi.org/10.3389/fmars.2026.1816090.