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Natural climate solutions are being advanced to arrest climate warming by protecting and enhancing carbon capture and storage in plants, soils and sediments in ecosystems. These solutions are viewed as having the ancillary benefit of protecting habitats and landscapes to conserve animal species diversity. However, this reasoning undervalues the role animals play in controlling the carbon cycle. We present scientific evidence showing that protecting and restoring wild animals and their functional roles can enhance natural carbon capture and storage. We call for new thinking that includes the restoration and conservation of wild animals and their ecosystem roles as a key component of natural climate solutions that can enhance the ability to prevent climate warming beyond 1.5 °C.

The Paris Climate Agreement is celebrated for spurring the development of climate solutions that would hold global mean temperature rise to 1.5 °C (refs. 1,2). The proposed solutions focus on reaching net-zero fossil fuel CO_2 emissions by a complete transition to renewable energy generation by 2050, together with a halt to deforestation and land conversion to prevent the emissions of carbon already stored in ecosystems[3]. However, these solutions alone will be insufficient because the heat trapping capacity of the CO_2 that remains in the atmosphere will challenge the current efforts to hold the global mean temperature rise even to below 2 °C (refs. 3,4). To prevent this requires 'negative emissions' solutions that remove and store 500 Gt of atmospheric CO_2 between now and 2100 (~ 6.5 $GtCO_2$ yr^{-1}) (refs. 3,4).

To this end, natural climate solutions are being proposed as cost-effective and relatively safe ways to capture the excess atmospheric CO_2 and store it within terrestrial and aquatic ecosystems[5-8]. These solutions are inspired by the recognition that natural biogeochemical processes within terrestrial and marine ecosystems already remove up to 50% of all human-caused CO_2 emissions annually[9]. Natural climate solutions aim to do more, first by protecting forest, wetland, coastal and grassland ecosystems to avoid emissions of 4 $GtCO_2$ yr^{-1}, and second by restoring and managing plants, soils and sediments in these ecosystems to capture and store 5–6 $GtCO_2$ more each year[10-12]. If guidelines to avoid negative impacts are followed[8,13], such efforts could co-benefit biodiversity conservation and the provision of ecosystem

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services that support human livelihoods and welfare[12,14,15]. The current 5–6 $GtCO_2$ yr^{-1} goal is a major step forward. However, the solutions still fall short of reaching the 6.5 $GtCO_2$ yr^{-1} removal target by 0.5–1.5 $GtCO_2$ yr^{-1}. To overcome this shortfall with additional natural climate solutions requires thinking differently about biotic controls over ecosystem carbon capture and storage.

Changing the current mindset

Current natural climate solutions focus on protecting and restoring plants (primarily trees, mangroves and seagrasses), and soil and sediment microbes in ecosystems. This focus stems from the premise that these taxa are the ones that have consequential effects on ecosystem carbon capture and storage[9,16,17]. However, wild animals, especially terrestrial and marine mammals and marine fish, also can have consequential effects[18–26]. For example, intensive sampling of 650 plots of 100 m^2 in a 48,000 km^2 tropical forest region in Guyana revealed that tree and soil carbon storage increased by 3.5–4 times across a gradient from 10 to 70 tree species[26]. Yet, across a gradient from 5 to 35 mammal species within this same region, tree and soil carbon storage in the sampling plots increased 4–5 times[26]. This boost in carbon storage is attributable to a diversity of animal species with medium-to-large bodies that have a diversity of functional roles in the ecosystem. These include seed dispersal that supports the germination of large-seeded trees with carbon-dense wood, herbivory that reduces plant competition and the enhancement of soil nutrient supply and organic carbon storage[26–28]. This is one of a growing number of examples from various ecosystems showing that wild animals can substantially enhance negative emissions (Table 1).

Enlisting animal functional roles for natural climate solutions, however, requires changing the current mindset, which largely holds that wild animals need to be protected from human impacts and climate change[15]. This mindset accordingly leads to the separate allocation of landscape and seascape space for animal conservation and natural climate solutions because it sees them as competing objectives for finite spaces (see, for example, refs. 29–34). Changing the mindset to consider them as functionally interdependent creates new opportunities to increase negative emissions.

Using wild animal conservation explicitly to enhance carbon capture and storage is known as 'animating the carbon cycle'[19]. Animating the carbon cycle requires abandoning static allocations of space and creating dynamic landscapes and seascapes. To do this certainly requires protecting and restoring species presences in ecosystems. However—and this is key—it requires protecting and restoring the ability of animal species to reach ecologically meaningful densities so that as they move and interact with each other they can fulfil their functional roles across landscapes and seascapes[35–37]. To restore and protect animal functional roles in ecosystems is known as trophic rewilding[22,38,39].

Here, we discuss how trophic rewilding to animate the carbon cycle can expand the portfolio of natural climate solutions. We highlight larger-bodied wild vertebrates because they are the focus of most current trophic rewilding efforts[22,24,38,39], their ecological effects can be large[21–23,40–42], they are sensitive to human exploitation and persecution, habitat loss and landscape and seascape alterations[43,44], and rewilding them requires more deliberate and challenging interventions than restoring plant biomass and diversity[45,46]. Nevertheless, our discussion applies generally to all animals[23,25]. We underline the need to consider the complexities associated with trophic rewilding to expand natural climate solutions because some species may have different effects in different ecosystems. For example, grey wolves can have positive effects in forests, but negative effects in grasslands[25]. We thus identify the kinds of research needed to better understand whether animals will be impactful within specific ecological contexts. Also, we underline the need to understand and address human societal impacts that may arise from restoring animal species to ensure the equity and sustainability of

Table 1 | Estimated animal effects on net ecosystem carbon storage and the spatial extent of ecosystems in which the animals occur

Species	Ecosystem type	Spatial extent (km^2)	Additional ecosystem CO_2 uptake ($GtCO_2$ yr^{-1})
Enhanced sinks and avoided emissions by protecting species			
Wildebeest	Savannah	2.5×10^4	0.0044 ± 0.001
Sea otter	Coastal kelp forest	1.2×10^4	0.0052 ± 0.0025
Grey wolf	Boreal forest	1.9×10^6	0.260 ± 0.134
Tiger, black-tipped reef and lemon sharks	Coral reefs	2.1×10^3	0.00074 ± 0.00037
Muskox	Arctic wet meadows	4.8×10^5	0.030 ± 0.015
Fish	Marine pelagic and inshore	3.0×10^8	5.50 ± 4.40
Subtotal			5.80
Enhanced sinks by restoring species			
African forest elephant	Tropical forest	5.4×10^5	0.013 ± 0.007
Bison	Tall and shortgrass prairie	4×10^5	0.595 ± 0.275
Baleen whales	Southern Ocean	7.9×10^6	0.00062 ± 0.0001
Subtotal			0.608
Total			6.41

The data show the added atmospheric CO_2 that could be held in ecosystems by using trophic rewilding as a natural climate solution. Additional ecosystem CO_2 uptake represents amounts of carbon storage above levels estimated or measured in the absence of the focal animal. Data sources and calculations can be found in Supplementary Appendix 1.

natural climate solutions and human welfare within human-dominated landscapes and seascapes.

Trophic rewilding to animate the carbon cycle

The dividend of creating dynamic landscapes and seascapes is illustrated by the 1.2 million Serengeti wildebeest still found in Africa. This population annually migrates throughout the 25,000 km^2 savannah–woodland landscape tracking lush vegetation created by seasonally and spatially varying rainfall. During the migration, wildebeest consume large amounts of grassland carbon and return it as dung that is incorporated by insects into soil storage[47]. In the early twentieth century this dynamic was halted when the wildebeest population plummeted to 300,000 animals, decimated by rinderpest disease transmitted from domestic cattle[47]. Consequently, there were too few animals to fully graze the landscape. The increased standing grass fuelled more frequent and intense wildfires that released carbon stored in the biomass across 80% of the landscape, which rendered the Serengeti a net source of atmospheric CO_2 (ref. 47). Similar alterations of fire regimes followed the near-prehistoric extinctions of other large herbivores, the legacies of which persist today[48,49]. Fire is an essential natural process in most of these systems, but the loss of natural grazing increases their frequency and intensity. Restoring the wildebeest population through disease management led to less frequent and intense wildfires, and gradually restored the Serengeti back to being a carbon sink. The Serengeti now stores up to 4.4 $MtCO_2$ more than when the wildebeest population was at its lowest[47]. Rewilding other species may help to avoid fire-driven carbon emissions, especially in warm-climate, grass-dominated landscapes with intermediate rainfall[49].

Wild animals contain only 0.3% of the carbon held in the biomass globally[50]. However, a synthesis of experimental studies shows that many could nonetheless exert outsized control by causing a 15–250%

difference in the amounts of carbon in plants, soils and sediments relative to the conditions in which they are absent[25]. Animal functional controls come from foraging and movements that redistribute seeds and nutrients across landscapes and seascapes, and from trampling, burrowing, wallowing and ecosystem engineering, which cause soil and sediment disturbance. These various functions enhance the diversity, abundance and carbon density of plant communities, change fire regimes in ways that stimulate carbon capture and storage, prevent massive CH_4 release by protecting against permafrost thawing, enhance soil and sediment carbon stocks via organic matter (fecal, carcass and vegetation) deposition and improve soil and sediment carbon retention by influencing microbial processes and chemical reactions[19,21–23,51,52].

Data are available to derive a first approximation of the contribution of several animals to the current net ecosystem carbon balance (NECB) (Table 1). The NECB quantifies the net rate of carbon storage in ecosystems due to carbon fixation by plants and autotrophic and heterotrophic CO_2 respiration (net ecosystem productivity), as well as by additional losses, which include CH_4 emissions directly from the animals, soils and sediments of ecosystems[53]. Estimates (Supplementary Appendix 1) reveal that these animals enhance the NECB by protecting ecosystems to avoid emissions or by increasing the ecosystem carbon capture and storage (Table 1). Their enhancement of the NECB arises from different mechanisms, which include fire suppression by wildebeest[47], trophic cascades caused by sea otters in coastal kelp forests[54], wolves in boreal forests[55], sharks on coral reefs[56] and grazing and trampling by muskox in high Arctic ecosystems[23]. Although the estimated annual contributions of each taxon (that is, millions of tons of CO_2) is minuscule compared with the global carbon budget (that is, billions of tons of CO_2), their combined 0.300 $GtCO_2$ annual boost in storage could nevertheless come close to making up the low end of the estimated 0.5–1.5 $GtCO_2$ yr^{-1} shortfall range. Accounting for the estimated annual 5.5 Gt contributions of global marine fish as they migrate and interact within marine food chains[57] could help to exceed the entire shortfall target (Table 1).

Trophic rewilding of other species could offer even more annual storage (Table 1). In the Central African Congo Basin and parts of East Africa, forest elephants once numbered more than one million. They control carbon storage by dispersing seeds of carbon-dense overstory woody species, and by foraging and trampling understory vegetation, which enables overstory trees, released from competition, to grow larger and produce more carbon-dense biomass[58]. Restoring elephants just within the national parks and protected areas in the region could enhance the annual CO_2 storage by an estimated 13 $MtCO_2$ (Table 1). Bison, which once numbered over 30 million and occupied 22 ecosystem types within 9.4 million km^2 of the North American landscapes, now exist at 2% of their historical numbers, restricted to 1% of their historical range[59]. Restoring populations to even a fraction of the landscape—places where conflict with humans would be minimal (that is, 1–16% of six shortgrass and tallgrass prairie regions)—could add an estimated 595 $MtCO_2$ annually to prairie ecosystem storage primarily by reducing soil emissions (Supplementary Appendix 1).

Whales have become popular candidates for animal-driven ocean carbon storage[60,61]. They control the carbon cycle via the so-called 'whale pump', which involves feeding at ocean depth and released nutrients in the excrement as they breathe and rest in surface waters, which thereby stimulates phytoplankton production. Their migrations also translocate nutrients across vast geographical spaces and subsidize carbon capture in nutrient poor waters[60,61], although the magnitude of that effect remains uncertain[61]. Carbon in whale carcasses sinks to the seafloor where it is stored long-term at great ocean depths. However, whale populations were decimated by historical whaling. NECB estimates (Table 1) indicate that to protect and restore the five dominant Southern Ocean species (blue whale, fin whale, humpback whale, southern right whale and Antarctic minke whale) to near-historic levels[61] could conservatively add 0.6 million tons of ocean CO_2 storage,

and perhaps more if estimates of the magnitude of whale-subsidized phytoplankton production are improved (Supplementary Appendix 1).

Even smaller-bodied animals can have notable effects. The global population of beavers is currently ~11.1 million, due to conservation efforts the twentieth century[62]. Their ecosystem engineering impacts 0.9–1.1 Mha across the northern hemisphere, and alters wetland CO_2 and CH_4 flux[62]. Estimates of their global impacts range widely from causing a net sink of 174 $MtCO_2e$ to a net source of 300 $MtCO_2e$ (ref. 62). Although the accuracy of the estimates must be improved, the magnitude of the effects on the NECB warrants serious attention[63].

Trophic rewilding could be impactful in the Arctic where ~500 Gt of organic carbon is stored in the Yedoma permafrost[64], and where high densities of large animals could prevent massive CH_4 release from permafrost melting[65,66]. Herds of large animals compact snow, which keeps soil in a frozen state. Rewilding with a diverse herbivore assemblage adapted for cold conditions, which including muskox, reindeer, American bison and wild horses, could protect up to 80% of the Yedoma region[66]. It remains uncertain whether trophic rewilding this entire region would be successful because it requires building up large populations of animals in a short time[65,67]. It also requires a dramatic shift from tree and shrub dominance to grassland steppe to provide enough vegetation to support high densities of these animals[68].

Negative emissions solutions need to be sustained for the next 100+ years to help avert a 1.5–2 °C rise in global mean temperature[3]. The highlighted terrestrial species live for between 20.6 and 65 years, and whales between 50 and 200 years (AnAge database in ref. 69). Thus, enacting policies to rewild and protect even several generations of these species' populations can accordingly ensure that their contributions to negative emissions are sustained over the critical 100-year timeline.

However, the contributions that these highlighted species can make remain unaccounted or not well attributed in the global carbon budget and natural climate solutions. Instead, populations of these species face existential threats from predator culls (sea otters and wolves), overfishing and habitat damage from trawling (sharks and marine fisheries), impediments to migrations from fencing landscapes (wildebeest and reindeer), killing for damage control (beavers) and overharvesting. Losing these species risks ecosystems switching from being carbon sinks to carbon sources[23,43,44,68]. A poignant example of a switch comes from overfishing inshore predatory fish along the northeast coast of the USA. The resultant overgrazing by exploding herbivorous saltmarsh crabs triggered large areas of intertidal saltmarshes to die off, which led to the erosion of tide-exposed sediments and with it the loss of hundreds of years of stored sediment carbon, as well as the loss of future CO_2 capture[70].

Research needs

The combined contributions of hundreds-to-thousands of marine fish species to global ocean carbon storage[26] underlines the value of expanding consideration to a wider diversity of animal species. Granted, numerous studies already report on the effects of many animal species[23,25]. However, these studies only consider animal impacts on one or a few parts of the carbon cycle (that is, storage in the vegetation biomass, soil organic carbon deposition, fluxes (such as net primary productivity), or soil and sediment respiration). This precludes estimating the NECB for these species.

Many animal effects are measured on single life stages of plants. A better understanding of how different animals benefit or harm plants across entire plant life cycles (for example, frugivory and seed dispersal, germination and the establishment of seed release in dung, and herbivory that affects seedling, sapling and mature tree competition and development) is needed to understand net animal effects[71]. The effects of a species can also vary across space. For example, some migratory whales feed in polar regions during part of the year, which drives the whale pump and deep ocean carbon storage there.

They migrate to the tropics at other times where they feed very little and merely release nutrients as waste from the metabolism of their body stores. Also, animal species were shown to have different net effects on ecosystems under different biophysical conditions, such as different rainfall regimes or soil textures[42,72]. As well, they can have different impacts in different ecosystem types, such as the positive effects of wolves in boreal forests but negative effects in grasslands[55], or the positive effects of elephants in tropical forests but neutral or negative effects in savannah[42,73–75]. Animal effects may vary with their population density. For example, the amount of carbon stored in the Serengeti increased linearly by 15% with every increase of 100,000 animals[47]. However, animal effects may also be non-linear. At a low population density, species might be functionally neutral, and may only become functionally effective at higher densities[75]. For instance, the effect of forest elephants on carbon storage is negligible at densities less than 0.25 km^{-2} but becomes increasingly positive at higher densities, and even becomes negative at densities beyond 4 km^{-2} (ref. [75]).

Synthetic conceptual frameworks can guide empirical research on a wider range of animal species[25,76,77]. Integrating empirical studies with modelling is necessary to identify drivers across ecosystems, fill knowledge gaps and predict animal effects[25,78]. Taking functional traits rather than a species perspective can enhance prediction because ultimately these are the attributes that determine the nature and strength of animal impacts on vegetation structure, biogeochemistry and soil and sediment properties[25,76–79]. Such traits include body size, herbivore foraging mode (for example, grazing, browsing and mixed-feeding) and predator hunting mode (for example, stalking and ambush) that determine the spatial extent of animal movements and interactions, as well as the spectrum of resources that animals capture, consume and digest. Moreover, ecosystems are composed of many species that interact within and between trophic compartments[25,39]. An important challenge is to account for the potential synergistic or antagonistic effects that arise from interactions between a rewilded species and the other species among trophic compartments[76–80]. To account for the spatial variation in carbon cycling within ecosystems and across landscape also requires scaling from the local animal, plant and microbial physiological process through to behaviour and species interactions[81,82]. For example, to understand how the hunting modes of the predators of a herbivore species influence its physiological demands for different nutrients (carbohydrate C versus protein N) and foraging preference for plant species with different C:N ratios can lead to reliable predictions about the magnitude of the herbivore-induced changes in carbon storage across a landscape gradient[83,84].

Not all species will have positive effects on the NECB[25,42]. The negative effects could be substantial and reduce the ecosystem carbon capture and storage by an average of 65% relative to the conditions in which the animals are absent[25]. Thus, to account for animal effects is necessary to avoid overestimating the carbon storage capacity for currently proposed natural climate solutions. This further means that trophic rewilding could sometimes come into conflict with natural climate solutions. To reconcile the conflict requires balancing the trade-off between the goals of natural climate solutions and the goals of animal conservation, which include protecting species diversity and other kinds of animal-driven ecosystem services that also support human welfare and well-being[15].

Trophic rewilding of large herbivores will increase methane release[20,22] unless it occurs with modest reductions in domestic livestock. Estimates indicate that the late Pleistocene large mammal fauna directly released between 120.4 and 138.4 $\text{MtCH}_4 \text{ yr}^{-1}$ (or 3.37–3.88 $\text{GtCO}_2\text{e yr}^{-1}$, assuming CH_4 has 28× more heat trapping capacity than CO_2) into the atmosphere; this does not count for waste or other releases due to animal impacts on ecosystems[40]. The methane release declined dramatically with successive large mammal extinction events, being replaced by CH_4 emissions from domesticated livestock[40]. Today, livestock represent ~92% of the methane release by

herbivores; this sector's overall contribution to the methane budget is also ~16% greater than it was in the Pleistocene. Although completely restoring late Pleistocene herbivore species and abundances is untenable in practice[45], more moderate goals, such as rewilding close to a pre-industrial 1500–1800 AD baseline, are reachable[46], especially if accompanied by modest reductions in livestock. Assuming the habitat and sufficient plant production were available, to restore wildlife to 1800 AD levels would add an additional 11.7 $\text{MtCH}_4 \text{ yr}^{-1}$ (or 327.6 $\text{MtCO}_2\text{e yr}^{-1}$) to the current average release of ~128 $\text{MtCH}_4 \text{ yr}^{-1}$ by domesticated herbivores and 11 $\text{MtCH}_4 \text{ yr}^{-1}$ by wild herbivores[40]. This added CH_4 release would be overwhelmed by animal-driven gains in carbon storage generally. Nevertheless, CH_4 release should be accounted to ensure the NECB estimate for a given ecosystem is accurate (for example, Supplementary Appendix 1). This could include exploring how predators might help avoid CH_4 emissions by reducing densities of their herbivore prey. Keeping a balanced methane budget will inevitably require a trade-off between maintaining domestic livestock herds versus rewilding different abundances and kinds of wild animal populations[85,86]. However, to replace livestock with wild animals can offset the current CO_2 release that arises from livestock impacts on those ecosystems (for example, ref. [86]).
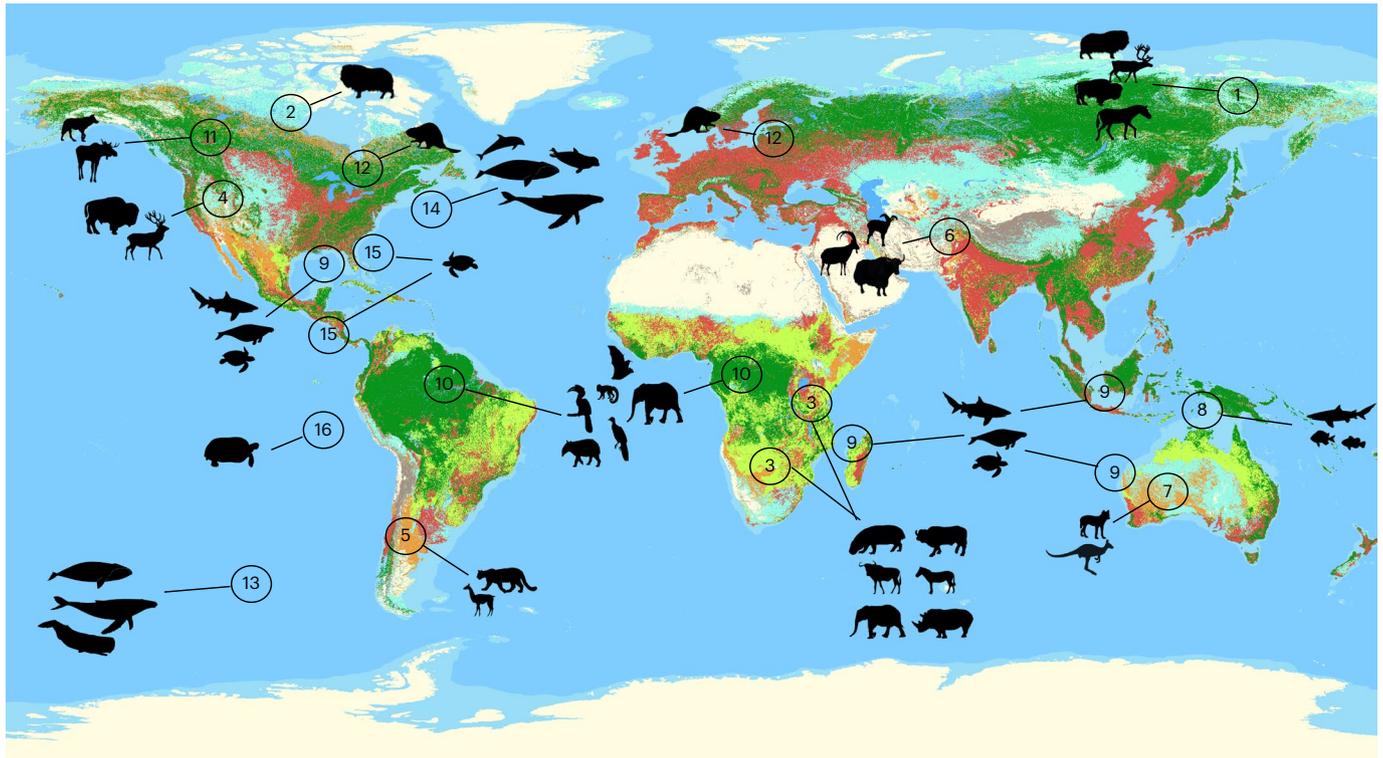
Expanding natural climate solutions

Natural climate solutions focus largely on forest ecosystems[5–7,12] (but see refs. [7,87]). However, forests (which include plantations) represent 14% of the 431 terrestrial and 37 marine ecosystem worldwide[88,89] and only cover 9% of the Earth's surface. As wild animal species occur in all ecosystems, there is much scope to expand locations for natural climate solutions. Furthermore, individual wild animal species do not occur globally, but are distributed regionally[19,22], which results in locally unique animal species compositions[46,90]. This has considerable strategic advantage because it can align regional-scale ecosystem processes with human values, policies and management interventions that are usually implemented within national or subnational political jurisdictions[46,91,92].

Many large animal species other than those we highlight (Table 1) have a high potential to expand natural climate solutions (Fig. 1). These candidate species were selected based on their documented functional roles in ecosystems (Supplementary Appendix 2). However, their impact on the NECB cannot yet be estimated owing to a lack of measurements. To estimate the NECB for these species begins by characterizing their function within a general ecosystem trophic compartment framework, as illustrated in Supplementary Table 1. The framework illuminates the pathways through which the animal species could control carbon uptake and storage, and which carbon fluxes and biomass pools must be measured.

To expand natural climate solutions via trophic rewilding will require conserving and restoring the functional intactness of ecosystems[39]. Pragmatically, functional intactness occurs when the kinds and density of species that comprise ecological communities and their movements and interactions match historical (prior to widespread land transformation) conditions in at least two areas >10,000 km^2 within a region[46,93]. This may seem daunting given humans are causing declines in species abundances and functional diversity[30,93], and impeding large-scale movements[94,95]. Consequently, only about 2.8% of the global land surface is sufficiently functionally intact to support ecosystem functioning[46]. However, there is reason to be hopeful. Although the intactness of mammal communities relative to historical baselines only occurs in 16% of the worldwide land area, it could rise to 54% by rewilding only a few species[46], especially ones with functional traits that complement those of species already present[80].

Furthermore, with the right enabling conditions, animal populations can rebound rapidly[96]. The abundance and geographical distribution of many European mammals and birds has increased remarkably since the mid-twentieth century due to stronger

Fig. 1 | Global distribution of candidate animal species and ecosystems for which there is a high potential to expand natural climate solutions through trophic rewilding. The candidate species could protect current carbon stores or enhance carbon capture and storage. Colours represent different ecosystem types as identified in the table below the map. Candidate animal functions and ecosystem effects were identified based on published studies that identified their potential impacts on carbon cycling, as described in Supplementary Appendix 2 and Supplementary Table 1. Basemap from ref. 119. 'Animal icons from PhyloPic.

1. Yedoma: muskox, caribou, bison, horse. 2. Tundra: muskox. 3. Savannah: hippo, buffalo, wildebeest, zebra, elephant, white rhino.

4. Grassland: bison, elk. 5. Arid alpine: puma, vicuna. 6. Mountain grassland: bharal, ibex, yak. 7. Shrubland: dingo, kangaroos.

8. Coral reef: tiger, reef and lemon sharks, coral reef herbivorous fish. 9. Seagrass: tiger shark, dugongs, sea turtles.

10. Old and New World tropical forests: elephants, Old- and New-world primates, tapirs, black-fronted piping guan, hornbills, fruit bats.

11. Boreal forest: wolf, moose. 12. Boreal and temperate wetlands: beaver. 13. Southern Ocean: blue, fin, humpback, right, minke and sperm whales. 14. Gulf of Maine: right, humpback, fin, sei and pilot whales, white-sided, common and harbour porpoises, harbour and grey seals.

15. Beaches: logger head and green sea turtles. 16. Semi-arid shrubland: tortoise.

	Animal function and ecosystem effects	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Protecting C stores	*Foraging: herbivory*																
	Shrub cover	−	−														
	Albedo	+	+														
	Wildfire extent			−													
	Foraging: predation																
	Stability of soil and/or sediment C storage					+			+			+					
	Trampling and/or disturbance																
	Albedo	+	+		+												
	Soil compaction	+	+	+	+												
	Soil CO_2 release	−	−	−	−		−										
	Soil CH_4 release	−	−														
	Stability of soil and/or sediment C storage			+	+		+										
Enhancing C capture and storage	*Foraging: herbivory*																
	Net primary production		+		+						+						
	Above-ground plant biomass C				+												
	Foraging: predation																
	Net primary production								+	+		+					
	Plant abundance				+				+	+							
	Above-ground plant biomass C										+		+				
	Soil and/or sediment organic C inputs																
	C storage pool size			+	+		+	+	+			+	+	+	+		
	Nutrient inputs																
	Net primary production													+	+	+	+
	Seed dispersal																
	Tree germination and abundance										+						+
	Above-ground plant biomass C										+						

conservation legislation and action, rapid increases in conservation area networks (for example, Natura 2000[97]), favourable land use policy and development, and strong financial support[96–98]. In the tropics, carbon storage could be enhanced by reducing market-hunting losses of many vertebrates, such as primates, tapirs, black-fronted piping guan, hornbills and fruit bats[27,28]. Similar kinds of legislation, policy, conservation funding and action could lead to rapid (by the mid twenty-first century) increases in marine animal populations[99]. However, any measure requires achieving a consensus on baselines and targets for animal species and numbers that align with the desired levels of natural ecosystem processes[100].

Including human–nature coexistence

The area of intact and effectively protected landscape and seascape space required to maintain a habitable climate, functional biodiversity and ecosystems, and human well-being is not yet well established[30]. Evidence suggests that large vertebrate effects on the NECB are substantial because they occur over spatial extents of 10^3–10^8 km^2 (Table 1). Globally, however, only 11% of such large spaces occur in protected areas[46,93]. The remaining available spaces are inhabited by people (for example, for American bison rewilding[59]), which necessitates working with local communities to address the social complexities that play a decisive role in conservation success. This requires engaging local communities in participatory planning and decision-making and subsequent governance to acknowledge and respect local peoples' knowledge, values and tolerance of rewilded species, and cultural heritage, land-tenure rights and access to natural resources[101]. Without such considerations, conflicts can arise if rewilded species threaten peoples' livelihoods, property and personal safety[102], which potentially instigates the loss of political support (for example, ref. 103), retaliatory killing or habitat destruction that undermines the potential solutions.

Working at the nexus of climate solutions, biodiversity conservation and human communities demands embracing a dynamic landscape and seascape perspective even further. This involves seeking ways for wild animals and humans to coexist across landscapes and seascapes, rather than separating people from nature, as has been a common practice in proposals to apportion spaces for biodiversity and carbon storage (for example, refs. 29–33). Creating dynamic 'coexistence landscapes' enables people and animals to share spaces, but in ways that enable each to continually respond and adapt to the other[102,104]. To achieve coexistence means that people and animals can live according to their biological and social natures, adjust their behavior as they learn from experience and pursue their own interests within the social–ecological context of the landscape or seascape[102,104]. This creates opportunities for humans to continue to make a living in their traditional places than more exclusionary natural climate solutions, such as afforestation and reforestation, which emphasize forest production over local human welfare. To achieve coexistence also requires drawing and building on local knowledge in parity with ecological and social science knowledge. This could effect changes in culture, institutions and governance structures that are needed to ensure the persistence of animal populations and their functional roles, as well as the livelihoods and welfare of local communities over the next 100+ years[102,104].

Policy implications

Natural climate solutions are becoming fundamental to achieve the goals of the Paris Climate Agreement while creating added opportunity to enhance biodiversity conservation. Indeed, the UN Climate Action Summit[105], the IPCC Sixth Assessment Report[106] and Target 8 in the draft UN Convention on Biological Diversity's Post-2020 Global Diversity Framework[107] recognize the importance of using natural climate solutions to enhance biodiversity conservation. However, none consider the obverse that biodiversity–especially animal diversity–can enhance climate solutions. Hence, current natural climate solutions largely focus on protecting forests and grasslands, and restoring forests, agricultural lands and grasslands, and wetlands through reforestation, plantations, agriculture management, and restoration of degraded coasts and peatlands[10]. These solutions overlook the fact that animals in these ecosystems may be necessary for the success of such solutions by already creating environmental heterogeneity, supplying nutrients, reducing fire risks, stabilizing soils and enhancing plant dispersal and germination[21,49,108].

To consider trophic rewilding as a natural climate solution has much to offer. The estimated additional 6.41 GtCO$_2$ yr^{-1} of negative emissions driven by the kinds of animals highlighted here (Table 1) could already meet 64% of the current global natural climate solutions target of 10 GtCO$_2$ yr^{-1}, although some of this might be implicitly included already in natural climate solutions that protect the habitats of these species. Nevertheless, expanding climate solutions to include animals can help shorten the time horizon over which 500 GtCO$_2$ is drawn out of the atmosphere, especially if current opportunities to protect and rapidly recover species populations and the functional intactness of landscapes and seascapes are seized on.

Consider marine fisheries as an example. Although fish make up only a fraction of the living biomass in the ocean[50], their significant impact on long-term ocean carbon storage and their relatively short recovery times make them good candidates, even given that the storage capacity of fisheries species cannot be fully recovered because of the dependence on fish for food security[109–111]. However, rebuilding over-fished stocks, which represent 40% of the fisheries species, could add substantially to ocean carbon storage. The abundances of exploited species and their ecosystems could be substantially restored by 2050 through fisheries and marine conservation, which accounts for carbon cycle effects[52]. Attention specifically needs to focus on mesopelagic fish, the group with the most important contributions to the marine fish carbon flux[57]. Interest in exploiting these fish is growing despite large knowledge gaps about the fishing effects on these species, on carbon cycling and on existing pelagic fisheries. Hence, institutions such as the Ocean Panel (https://oceanpanel.org/about-ocean-panel/) strongly recommend refraining from exploiting mesopelagic fish until science fills the knowledge gaps.

Recommendations to introduce fishing-related carbon mitigation targets into global initiatives have also gained traction. These include protecting 30% of the ocean by 2030[106], protecting territorial waters (Exclusive Economic Zones) and the High Seas 30×30 target agreed in the *High Ambition Coalition of Biodiversity Beyond National Jurisdiction*[112] and signed by 23 countries plus the EU-27. To create a worldwide 'fish bank' by excluding fishing from the high seas and marine protected areas[113] could have rapid, positive impacts on the biomass of fish assemblages and on the density and individual size of all taxa, which together positively affect carbon capture and storage. Applying the natural climate solutions hierarchical approach[114]–to 'protect, manage and restore for climate mitigation'–can provide guidance for implementation.

Trophic rewilding for natural carbon solutions requires rethinking rules and procedures of the existing governance intended to reduce emissions and enhance carbon storage. In particular, the UNFCCC (United Nations Framework Convention on Climate Change) Committee of Parties 19 launched REDD+ (reducing emissions from deforestation and forest degradation) to avoid emissions and manage tropical forests for biodiversity and carbon storage in developing countries. REDD+ is recognized as a key process in Article 5 of the Paris Agreement[115]. However, tropical forest animal populations continue to be depleted by market hunting, which results in forests devoid of larger mammals and birds, so-called 'empty forests'[116]. Yet these animals play a critical role in dispersing seeds and enhancing the productivity of carbon-rich tree species. In Amazonian forests, such tree species represent 1% of tree diversity, but store 50% of the forest carbon[117]. REDD+ guidance for implementation, both internationally and nationally, has

failed to recognize this critical functional role of animals and thereby creates risks that REDD+ projects may fail to reach their carbon capture and storage goals. To mitigate this risk requires deliberately accounting for animal impacts in the design, monitoring, reporting and verification procedures for carbon offsets. As well, there is a need to establish alternative rules, regulations and implementation mechanisms (for example, no-take zones, quotas and seasonal restrictions) by working closely with local hunters and resource users to avoid loss of animal diversity as part of the biodiversity safeguards of REDD+. Appropriately valuing carbon offsets produced by animals could change the policy narrative owing to the potential to attract significant, alternative revenue streams to finance conservation, compensate losses from human–animal conflict and help communities transition to a sustainable use of landscapes and seascapes[118].

Conclusions

Simultaneously meeting the UNFCCC, Convention on Biological Diversity, and Sustainable Development goals requires rapid actions enacted on a scope and spatial scale that has not yet been attempted[30]. Trophic rewilding to expand natural climate solutions represents such an action to help meet these goals. It can relieve global inequities in the deployment of natural climate solution projects and thereby help regional jurisdictions strengthen their commitments to meet the Paris Agreement[115]. The regional solutions together would create a portfolio that can meaningfully add across the globe to help slow global temperature rise. Supporting such efforts scientifically will require changes in the thinking and execution of research on Earth and ecosystem science to embrace and quantify animal controls on the entirety of the carbon cycle. It further requires a change in policy thinking to recognize that trophic rewilding can be an instrumental part of natural climate solutions. There is some urgency on both fronts because we are losing populations of many animal species just as we are discovering how much they functionally impact carbon capture and storage. Thus, to ignore animals leads to missed opportunities to enhance the scope, spatial extent and range of ecosystems that can be enlisted to help hold climate warming to within 1.5 °C.

Data availability

All the data used in this study are included in this Perspective (and its Supplementary Information).

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Author contributions

O.J.S. and M.S. conceived the study. O.J.S. wrote the first draft and conducted the calculations presented in the Supplementary Information. All the authors provided technical and scholarly input and reviewed and revised drafts of the manuscript.

Competing interests

M.S., F.J.S. and A.T. are employed by environmental non-governmental organizations with interests in funding and implementing rewilding programmes for natural climate solutions. They provided technical expertise on applying trophic rewilding and carbon science to climate and conservation policy, and human–nature coexistence. The other authors declare no competing interests.

Additional information