Animating the carbon cycle through trophic rewilding could provide highly effective natural climate solutions

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Abstract

Natural climate solutions are being advanced as cost-effective and safe ways to achieve net-zero emissions by protecting and enhancing carbon capture and storage in plants, and in soils and sediments in terrestrial and marine ecosystems. Current thinking holds that these solutions have the added benefit of protecting habitats and landscapes to restore and conserve animal species diversity. However this reasoning undervalues the inexorable functional role of animals in controlling the carbon cycle. We discuss the growing scientific evidence that reveals how enlisting the functional role of animals can significantly enhance natural carbon capture and storage. We call for new thinking that treats the conservation and restoration of animal species and their functional roles within ecosystems as a key way to broaden the scope of natural climate solutions and thereby help speed up the removal of CO_2 from the atmosphere to prevent climate warming beyond 1.5°C.

Main

The Paris Climate Agreement is celebrated for spurring the development of climate solutions that would ideally hold global mean temperature rise to 1.5°C[1,2]. Proposed solutions focus on reaching net-zero fossil fuel CO_2 emissions by transitioning completely to renewable energy generation by 2050, together with halting deforestation and land conversion to prevent emissions of carbon already sequestered within ecosystems[3]. But these solutions alone will be insufficient because the amount of CO_2 remaining in the atmosphere is still high-enough that the goal of holding global mean temperature rise even to 2°C is highly unlikely to be met[3,4]. Hence there is an urgent need to create new solutions focused on "negative emissions" that remove and store as much as 500 $GtCO_2$ between now and 2100 (approximately 6.5 $GtCO_2\ yr^{-1}$)[3,4].

Natural climate solutions are proposed as cost-effective and safe alternatives to technology-based solutions[4] to achieve net-zero emissions by capturing and storing carbon within terrestrial and aquatic ecosystems[5-8]. The promise of these solutions derives from the recognition that natural biogeochemical processes within terrestrial and marine ecosystems already remove up to 50% of all human-caused CO_2 emissions annually[9,10]. Natural climate solutions aim to do more, first by protecting the current uptake of 4 $GtCO_2$ yr^{-1} within forest, wetland and grassland ecosystems; and moreover, by restoring and managing plants, and soils and sediments in those ecosystems to increase their capacity to remove an additional 5-6 $GtCO_2$ each year[11-13]. Such efforts are further promoted as having co-benefits including stemming biodiversity loss and provisioning a wide range of ecosystem services that support human livelihoods and welfare, which alternative technological climate solutions are less able to provide[13-15]. While currently-proposed natural climate solutions are a major step toward achieving net-zero, they could still fall short of reaching 6.5 $GtCO_2$ yr^{-1} by between 0.5 - 1.5 $GtCO_2$ yr^{-1}. Overcoming this shortfall with the continued use of natural climate solutions requires thinking differently about biotic controls over ecosystem carbon uptake and storage.

Changing the natural climate solutions mindset

The current goal of natural climate solutions is to protect and restore plant species (primarily trees and seagrasses) and soil and sediment microbial species of ecosystems as a means of increasing ecosystem carbon sequestration. This objective is based on the premise that those species are the only organisms that have a consequential effect on ecosystem carbon uptake and storage[9,16,17]. However, wild animal species also can have consequential effects, both directly and indirectly, by mediating plant and microbial functions[18-25]. For example, within a 48,000 km^2 tropical forest region in Guyana the carbon stored in soils and trees increased by 3.5× – 4× across a gradient from 10 to 70 tree species per sampling plot[26]. Yet, within this same region, tree and soil carbon storage in sampling plots increased 4× – 5× across a gradient from 5 to 35 animal species[26]. This boost in carbon uptake with increasing animal species diversity is attributed to the diversity of animal body sizes and accordingly the diversity of functional roles of animals in that ecosystem[26,27]. These functional roles include frugivory and seed dispersal that support the reproduction of large-seeded trees with carbon dense wood; herbivory that reduces plant competition; and enhancement of organic matter recycling for soil carbon and nutrient supply and storage[26-29]. This is but one of a growing number of examples from across a variety of ecosystem types that suggest that wild animals across their ranges could increase ecosystem CO_2 uptake and storage to levels that rival and perhaps exceed the 5-6 $GtCO_2$ yr^{-1} target of current natural climate solutions (Table 1).

Taking advantage of this potential, however, requires changing the current mindset, which largely sees wild animals merely as unwitting victims of climate change, or that dedicating space for their conservation directly competes with landscape space needed to implement natural climate solutions[15]. Consequently, many current solutions aimed at addressing the dual objectives of conserving animal diversity and mitigating climate change optimize the spatial allocation for biodiversity conservation and carbon storage among separate landscape locations. Furthermore, the amount of landscape space dedicated to each objective varies with preference weightings for carbon storage vs. animal species presence[30-35]. Sometimes both objectives are implemented within the same landscape spaces[33,35] but even in these cases the two objectives are still mostly treated as though they are functionally unrelated. This spatial separation leads to missed opportunities to integrate animal conservation and restoration with natural climate solutions to increase the likelihood of holding temperature rise to 1.5ºC, and the rate at which that goal can be achieved.

Including wild animal species and their functional roles in the portfolio of natural climate solutions is known as animating the carbon cycle[19]. Animating the carbon cycle requires abandoning static allocations of space and creating dynamic landscapes and seascapes. Doing this certainly requires protecting and restoring the presence of species in ecosystems, as is currently done. 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 fully interact with each other and the systems they live in, they can fulfill their functional roles across landscapes and seascapes[36-38]. A conservation strategy focused on restoring the functional roles of animals in ecosystems is known as trophic rewilding[39,40]. Here, we explore the positive contributions that trophic rewilding could have for CO_2 removal and storage and provide an outlook on how to proceed to combine the conservation and restoration of animals with carbon sequestration.

Trophic rewilding to animate the carbon cycle

The huge dividend of restoring and conserving dynamic landscapes and seascapes to enhance negative emissions is illustrated by the 1.2 million Serengeti wildebeest. This population annually migrates throughout the 25,000 km^2 Serengeti savanna-woodland landscape, tracking lush vegetation created by seasonal, spatially-varying rainfall patterns. In the course of the migration, wildebeest consume a large fraction of grassland carbon and return it as dung that becomes incorporated by insects into soil storage reservoirs[41]. But in the early 20th century this dynamic was halted when wildebeest numbers plummeted to 300,000 animals, decimated by a disease—rinderpest—which spilled over from domestic cattle[41]. As a consequence, there were too few animals to fully graze the landscape. The increased grass fueled more frequent and intense wildfires that released carbon stored in biomass across 80% of the landscape, rendering the Serengeti a net source of CO_2 to the atmosphere[38]. Indeed, widespread near-prehistoric extinctions of other large herbivores have had similar consequences for fire regimes, the legacies of which persist today[42,43]. Although fire is an essential, natural, process in most of these systems, the loss of natural grazing increases the frequency and intensity of fires. Restoring the wildebeest population through disease management led to patchier, less frequent and cooler wildfires and gradually restored the Serengeti back to being a carbon sink. The Serengeti now annually takes up 2.1 million more tons of CO_2 than when wildebeest were at their historic low levels. Beyond their impacts on Serengeti savanna-woodland carbon, wildebeest also affect carbon cycling in the major river ecosystems that flow through the Serengeti. Specifically, their mass drowning while trying to cross the Mara River during their migrations is alone estimated to contribute ~100,000 kg of carcass-derived carbon, which represents an 18 to 191% subsidy of dissolved organic carbon to the Mara River during peak carcass-deposition time[44].

Hence, even though wild animals represent only 0.3% of carbon held in biomass globally[45], many could nonetheless have outsized control over carbon exchange between larger terrestrial and aquatic carbon reservoirs and the atmosphere[23,25]. Animals exert such control through a wide range of functional roles including foraging and movements that redistribute seeds and nutrients over vast land- and seascapes, and trampling, burrowing, and wallowing which induces disturbance and compaction. These various functions enhance the diversity, abundance and carbon density of plant communities, change fire regimes in ways that stimulate carbon sequestration, prevent massive net CH_4 release by protecting against permafrost thawing, enhance soil and sediment carbon stocks via fecal and carcass deposition, and improve soil and sediment carbon retention through influences on microbial processes and chemical reactions[19,21,22,46,47].

Estimates indicate that certain animals may already sizably increase negative emissions (Table 1) from the restoration of sea otter populations and associated trophic cascades they instigate in coastal kelp forests[48]; and from extant trophic cascades driven by wolves in boreal forests[49] and sharks on coral reefs[50]; and via muskox grazing and trampling in high arctic ecosystems (Supplementary Information). Further global accounting of sources and fates of carbon flux through marine fish populations as they migrate and interact within marine food chains[51] reveals that they currently enhance ocean CO_2 sequestration by 5.5 Gt yr^{-1} (Table 1). The contributions of all these animals alone, which together drive an estimated additional uptake of 6.06 $GtCO_2$ yr^{-1} (Table 1), remain altogether unaccounted for in current carbon budgets and natural climate solutions.

Instead, populations of these species are left to face existential threats from predator culls (sea otters, wolves), overfishing and habitat damage from trawling (sharks and marine fisheries), impediments to migrations from fencing landscapes (wildebeest, reindeer) and overharvesting. The attendant risk of losing these species is that their ecosystems could flip from being carbon sinks to sources[23,52-54]. A poignant example of a flip comes from overfishing inshore predatory fish along the northeast coast of the USA. The resultant overgrazing by exploding herbivorous saltmarsh crabs has triggered large areas of intertidal saltmarshes to die-off, leading to the erosion of tide-exposed sediments[55]. This erosion leads to the loss of hundreds of years of stored sediment carbon, as well as the loss of future CO_2-absorption potential.

Other examples show that trophic rewilding could offer more (Table 1). In the Central African Congo Basin, forest elephants once numbered more than 1 million. They functionally contribute to carbon storage in many ways; by dispersing seeds of carbon dense overstory woody species and by reducing understory plant competition by foraging and trampling understory vegetation that enables overstory trees to grow larger and store more carbon in their tissues[56]. Estimates suggest that restoring elephants to historical levels just within national parks and protected areas in the region could lead to an additional sequestration of 138 million tons of CO_2[57] (Table 1). Bison, which once numbered 30+ million and occupied 22 ecosystem types within 9.4 million km^2 of North American landscapes, now exist at 2% of their historical population size, within 1% of their historical range[58]. Restoring populations to even a fraction of the landscape—places where conflict with human activities would be minimal (i.e., 1%-16% of 6 shortgrass and tallgrass prairie regions)—is estimated to potentially add 11 million tons of CO_2 annually to prairie ecosystem reservoirs through grazing and nutrient recycling that stimulate of plant productivity (Supplementary Information).

Whales have become the popular face of animal-driven carbon storage in the ocean[59]. They play a functional role in the carbon cycle as a so-called "whale pump" in which they feed at ocean depth and release nutrients in excrement when they breath and rest in surface waters. This nutrient release supports CO_2 uptake by stimulating phytoplankton production. Moreover, carbon contained in whale carcasses sinks to the seafloor where it can be stored long-term at great ocean depths. But their populations too have been decimated by historical whaling. Estimates indicate that restoring even the five most dominant whale species of the Southern Ocean to near-historic levels has the potential to store an additional 33 million tons of ocean CO_2 per year through their stimulation of phytoplankton production and from sinking carcasses[59].

Even smaller-bodied animals can have dramatic effects on greenhouse gases. The global population of beavers (~25 kg) is currently ~ 11.1 million. Although their individual colonies and associated dams are localized on landscapes, across their geographic range in the northern hemisphere their ecosystem engineering impacts 0.9 to 1.1 million ha[60]. They are found in a variety of ecosystems and have been demonstrated to influence a number of ecosystem functions and services, including wetland CO_2 and CH_4 sequestration[60]. Estimates of their global impacts on the carbon budget range widely from causing a net sink of 174 million tons CO_2e to a net source of 300 million tons CO_2e[61]. Clearly, these numbers need to be better constrained. However, the size of the impact warrants serious consideration, especially to identify beaver conservation focused on animating the carbon cycle to prevent emissions, if not enhance sink potentials of wetlands and long-term carbon storage in beaver meadows[62].

A potential hotspot for trophic rewilding efforts could be the Arctic, where ~500 Gt of carbon is currently bound up in organic carbon-rich Yedoma permafrost[63], and where a high density of large animals are proposed as a powerful tool to prevent massive, CH_4 release due to permafrost melting[64,65]. Herds of large animals compact the snow during the winter, which lowers soil temperatures, enabling the soil to remain in a frozen state. Rewilding with a diverse herbivore assemblage adapted to live there, including reindeer, American bison and wild horses, may protect up to 80% of the Yedoma permafrost region[65]. However, successfully scaling-up current trophic rewilding efforts across this entire region still holds large uncertainties. This is because it would require building up large populations of animals over a short period of time[64] along with the need for an ecosystem regime shift from tree and shrub dominance into a steppe to ensure the production and availability of vegetation that supports the high densities of these populations[22,66].

Research needs

We still lack a synoptic understanding of the direct and indirect ways in which animals control biogeochemical cycling. We have highlighted a few species for which net emissions can be quantified. But uncertainties remain for many more already-studied species because empirical analyses have tended to measure only parts of the full complement of biogeochemical processes (i.e., biomass carbon, net primary productivity, soil and sediment respiration, animal respiration, or soil organic matter deposition, biomass carbon content of animal wastes, plant litterfall and carcasses) needed to calculate the carbon budget[23,25]. Moreover, many of the mechanisms by which animals can influence the carbon cycle operate via interactions with plants at particular life stages, but we need a much better understanding of carbon dynamics across entire plant life cycles[67]. Without these, it will be impossible to determine whether animal-driven emissions will be net negative or positive[23,25,68] which, in the latter case would require reconciling trade-offs between carbon storage and animal conservation. Also, there may be cases where the same species will have different net effects in different ecosystem types depending on the nature of their functional dependencies with other species[49,69,70]. Differences in animal species effects among ecosystem types may be further caused by disturbances and degradation that have resulted in missing animal species or their presence at low density. Generally, ecosystem types provide important context for animal effects on carbon cycling, for instance, whether the ecosystems are fire prone or contain permafrost soils.

There is a need for a concerted effort to quantify effects of many more animal species. To this end, synthetic conceptual frameworks are available to guide research on a wider range of animal species[22,23,25,68,71-74]. Integration of empirical studies with modelling are highlighted in these frameworks as key to exploring rewilding scenarios, identifying drivers across ecosystems, filling knowledge gaps, and predicting animal effects across landscapes and seascapes[25,74]. These frameworks also spell out the need to go beyond a species-centric perspective and account for animal functional traits. Such traits include body size, herbivore foraging mode (e.g., grazing, browsing, mixed-feeding) and predator hunting mode (e.g., stalking, ambush) that determine animal mobility (and the spatial extent of their movements and interactions) and the spectrum of resources that they can capture, consume and digest. The effect of species with different traits needs to be quantified and generalized because ultimately those are the species attributes that determine the nature and strength of animal impacts on vegetation structure, biogeochemsitry and soil and sediment properties of ecosystems[25,71,73-75]. Moreover, ecosystems are composed of communities of many animal species that have complementary functional traits, requiring analyses to explore potential synergistic or antagonistic effects of the different animals[69,71,73-76]. An accounting of animal effects will also need to quantify how animal population density affects the structure and functioning of ecosystems[71] and, by extension, how much carbon is taken up by ecosystems as a function of population density[23,56,74,75]. At low population density, far from population carrying capacity, species might be functionally neutral, and may only become functionally effective at higher densities[56,74]. For example, the contribution of forest elephants to increasing carbon storage is negligible at a density less than 0.25 elephants km^{-2} but increases sharply at higher densities and becomes negative when density is beyond 4 elephants km^{-2} [56]. In the Serengeti, the carbon sink increased by 15% with each increase of 100,000 wildebeest, as the population size grew back to historical levels[23].

In many cases, trophic rewilding will involve large herbivore populations, which can increase methane release[20,22]. Estimates indicate that the late Pleistocene large mammal fauna released between 120.4 - 138.5 $MtCH_4\ yr^{-1}$ (or 3.01-3.46 $GtCO_2e^{\ yr-1}$)[77]. Atmospheric methane release declined with successive large mammal extinction events, only to be fully built back up by domesticated livestock herds[76]. While completely restoring late Pleistocene herbivore species and abundances is untenable in practice[78], more moderate goals such as rewilding close to a pre-industrial 1500AD baseline are reachable[79]. But it would add 11.7 - 13.4 $MtCH_4\ yr^{-1}$ (or 292 - 335 $MtCO_2e^{\ yr-1}$) to the current release by domesticated and wild herbivores[76]. While this added positive emission is a small fraction of the estimated total negative CO_2 emissions potential (Table 1), rewilding efforts should nonetheless account for methane release to ensure that carbon budgets are accurate. This will require better quantification of release by different sizes, functional groups and densities of wild herbivores[20,22,79-81]. Keeping the methane budget balanced will inevitably require reconciling trade-offs between stock sizes and kinds of domestic livestock reared vs. densities and kinds of wild animal populations that are restored and protected[22]. But, replacing livestock with wild animals can have added benefits because they may promote ecosystem CO_2 storage that could offset current CO_2 release arising from livestock impacts to those ecosystems[e.g.,82]. This again underscores the need to account for the full effects of animals on carbon cycling.

Animating the carbon cycle can expand the global scope of natural climate solutions and biodiversity conservation

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Natural climate solutions are heavily focused on forest ecosystems[6,7,13, but see 7]. However, forest ecosystems (including plantations) only represent 14% of the 431 terrestrial and 37 marine ecosystem types occurring regionally across the globe[83,84]. Moreover, forests only cover 9% of the Earth's surface area. Wild animal species occur within all ecosystems across the globe, thus broadening the scope for implementing natural climate solutions, as well as places in which to store carbon (e.g., peatlands, permafrost, soils and deep marine sediments). Individual wild animal species also do not occur globally, but are distributed regionally[19,22], resulting in locally unique animal species compositions[79,85]. This has considerable strategic advantage because it can align regional-scale ecosystem processes with values, policies and management interventions that are usually implemented regionally within national or sub-national political jurisdictions[19,22,24,31,79,86,87]. Animating the carbon cycle projects could thus potentially relieve spatial inequities in natural climate solution projects by helping regional jurisdictions strengthen their global commitments to meet Paris agreements. The many regional strategies would create a portfolio of solutions that can meaningfully add up across the globe to help slow global temperature rise.

Animating the carbon cycle will require conserving and restoring the functional intactness of regional ecosystems, which is the fundamental goal of trophic rewilding[37,39,40]. Functional intactness within a region can be pragmatically defined to occur when the complement and density of species comprising ecological communities and their interactions match historical (pre-1500) conditions in at least two areas >10,000 km^2 within a region[79,88]. This would appear to be a daunting challenge, given that the global reach of human impacts is causing opposite trends. These trends include declines in species abundances and functional diversity[31,76], and impediments to large-scale movements and migrations that compromise ecosystem functioning[89,90], resulting in only about 2.8% of the global land surface being functionally intact to support ecosystem functioning[79]. However, there is also reason to be hopeful. Many of the listed cases in Table 1 already encompass the spatial extents needed for functional intactness, and those that do not still contribute substantially to the carbon budgets of their smaller regions, including within protected areas[e.g., 57]. Moreover, while intactness of mammal communities relative to a 1500AD baseline now only occurs in 16% of the land surface worldwide, it could be enhanced to 54% by rewilding only a few species[79], especially those kinds that complement the functional traits of existing community members[76].

With the right enabling conditions in place, animal populations can also bounce back rapidly[91]. Since the mid-20th century, select European mammal and bird species have staged a remarkable comeback both in numbers and distribution in response to stronger continental legislation, active conservation measures, rapidly increasing conservation area networks (e.g., Natura 2000[92]), reduced hunting, favourable policies and land use developments, and strong financial support from the public and private sectors[91-94]. This includes large carnivores such as the gray wolf as well as large herbivores, such as the European bison. Similar kinds of policy, legislative and conservation measures could rapidly (by mid-century) rebuild populations of marine animals as well[95]. Such restoration programs will, however, need to find consensus on proper baselines for animal numbers that align with natural ecosystem processes[79].

High potential species

Large herbivores such as bison, reindeer, moose, wildebeest, zebra, buffalo and elephants are strong candidate species for immediate consideration in new animating the carbon cycle projects. They are important for terrestrial ecosystems, via their direct effects on vegetation structure and productivity, on soils, on numerous dependent species (e.g., the high diversity of dung-associated animals and fungi) and on plant dispersal, thereby influencing the climate-resilience of vegetation and enhancing climate mitigation by moderating fire regimes, increasing albedo and enhancing stable soil carbon build-up[68,72,73,96]. As well, carbon uptake and storage could be enhanced by reducing market-hunting losses of a number of larger tropical vertebrates including old- and new-world primates, tapirs, black-fronted piping guan, hornbills, and old-world fruit bats. Collectively, they play a key role in shaping tropical forest tree community structure and forest biomass carbon by dispersing and enhancing germination success of large seeds produced by carbon dense tree species[28,29]. Protecting and enhancing populations of predatory fish such as jacks and sharks could play a significant role in the amount of blue carbon stored in mangroves and seagrass meadows[96]. These predators induce trophic cascades that reduce the foraging impacts of their herbivore prey and reduce bioturbation effects of prey that would otherwise release organic carbon from sediments[97]. Rebuilding whale populations globally has large potential to increase ocean primary productivity[98]. Large reptiles, including crocodilians, snakes, marine turtles, river turtles and tortoises, are currently not at all accounted for in global estimates of carbon in animal biomass[45]. Their roles in ecosystem processes, including seed dispersal, nutrient flow, predation, scavenging, grazing and trampling and compaction, are similar to mammals, and could be similar in magnitude[99]. But their effects on carbon uptake and storage have been woefully understudied[99].

Animating the carbon cycle requires human-nature coexistence across landscapes and seascapes

The area of intact and effectively protected landscape and seascape space required to maintain a habitable climate, functional biodiversity and ecosystems, and human wellbeing is not yet well established[31]. However, growing evidence indicates that the sizeable effects of animals on regional carbon budgets result from the ability of these animals to roam and interact across functionally intact spatial extents of 10^5 - 10^8 km^2 (Table 1). Globally, however, only 11% of the areas that are considered to be functionally intact (based on a 1500AD baseline), or which could be candidates for restoring intactness, occur in protected areas[79,88]. The remaining spaces needed to animate the carbon cycle are inhabited by people (e.g., for bison rewilding[58]). Hence, efforts to animate the carbon cycle through trophic rewilding will need to ensure the welfare of the local communities that live within these ecosystems will not be jeopardized[13,100]. Indeed, many animal conservation initiatives have failed to consider human values and tolerance, land tenure rights, and participatory decision-making and governance as part of conservation planning[100]. Without such considerations, rewilding landscapes to animate the carbon cycle could create risks that restored and protected animal species come into conflict with people by threatening their livelihoods, property and personal safety[101]. The conflict in turn could instigate loss of political support, retaliatory killing or habitat destruction that undermines animating the carbon cycle initiatives, begging further questions about whether hunting might be used strategically as a tool to engage local communities to manage overabundant animals for purposes of enhancing carbon storage[102]. Clearly, the success of animating the carbon cycle as a natural climate solution rests on respecting and accounting for the social complexities that play a decisive role in conservation success, including human welfare, intrinsic values, cultural heritage and ancestral knowledge, and access to natural resources (e.g. land tenure)[31,40,100,101].

Working within the complex interplay between climate, biodiversity and human social systems coupled as a socio-ecological system demands embracing a dynamic landscape and seascape perspective even further. This involves seeking ways for wild animals and humans to coexist across landscapes, rather than keeping people separate from nature as is common practice in algorithms that apportion landscape spaces for biodiversity and carbon storage[e.g.,25-29]. Dynamic "coexistence landscapes" create the stage for people and animals to share spaces, but this needs to be done in ways that enable each to continually respond and adapt to one-another[100,101]. Achieving coexistence means that people and animals can live according to their biological and social natures, adjusting their behavior as they learn from experience, and pursue their own interests within the social-ecological context of the landscape[100,101]. Coexistence landscapes can then allow for many more opportunities for humans to remain on the landscapes and make a living there than other nature-based solutions, which tend to be more exclusionary such as afforestation and reforestation that emphasize forest production over local human welfare. Achieving such coexistence requires drawing and building on local knowledge in parity with ecological and social science knowledge. This can effect cultural and institutional changes and governance structures that create tolerable levels of risk, thereby ensuring the persistence of wildlife populations and their functional roles, as well as the livelihoods and welfare of local communities[100,101]. Local communities thus need to be involved from design to implementation for successful rewilding programs.

Policy Implications

Natural climate solutions are becoming a fundamental part of the overall global effort to achieve the goals of the Paris Agreement on climate change, while at the same time creating added opportunity to enhance biodiversity conservation. Indeed, the UN Climate Action Summit in September 2019[103] and more recently the IPCC Sixth Assessment Report[104] actively promote natural climate solutions as vital to reduce the risk of exceeding 2ºC while establishing climate-resilient societies. Still, the proposed solutions focus narrowly on protecting forests and grasslands and their associated uptake and storage of 4 $GtCO_2yr^{-1}$, as well as manage and restore working lands (forested, agricultural and grassland areas), and wetland areas that are being heavily impacted by humans to promote an additional 4-6 $GtCO_2yr^{-1}$ uptake. This additionality would be accomplished through reforestation, plantations, agriculture management, and restoration of degraded coasts and peatlands[11,104]. Although the timeline for achieving this goal ranges widely from the highly ambitious 2030 to a more modest 2100, the analyses have nonetheless provided a key carbon uptake benchmark for policy and scientific studies[11,12,13,104].

However, these proposed solutions ignore the wider potential of including less human-dominated (natural) ecosystems including the open ocean. As well, other goals, such as Target 8 in the draft UN Convention on Biological Diversity Post-2020 Global Diversity Framework[105] recognizes the importance of using natural climate solutions for the purpose of protecting biodiversity, but does not consider the obverse, that biodiversity—especially animal diversity—can be an important driver of climate solutions. As we demonstrate here, natural climate solutions that include a focus on natural ecosystems and their functionality have much to offer. The additionality of at least 6.44 $GtCO_2yr^{-1}$ of negative emissions driven by just the 10 kinds of animals considered here (Table 1) could already meet 64% of the global natural climate solutions target. When included as part of current proposed natural climate solutions, this additionality could help shorten the time horizon over which 500 $GtCO_2$ could be sequestered, especially given the opportunity to rapidly recover species populations and functional intactness of landscapes and seascapes[79,91,95]. This will, however, require reconsideration of how to achieve the global target through measures that protect and restore animal populations, and their functional roles within ecosystems over the long-term[31].

Take the case of marine fisheries as an example. While fish make up only a fraction of the living biomass in the ocean[45], their significant impact on long-term carbon storage in the ocean and their relatively short recovery times make them ideal candidates for animating the carbon cycle. Although not all of the sequestration capacity from fisheries species can be recovered because of the growing dependence on fish for human consumption, rebuilding overfished stocks, which represent 40% of the fisheries species, could add substantially to carbon burial in the ocean. Data on the recovery potential of marine life indicates that species abundances, and ecosystem structure and functioning, could be substantially restored by 2050 through sustainable fisheries and marine conservation that deliberately account for carbon cycle effects[47]. Such carbon targets could be incorporated into other global initiatives that have already gained traction, such as protecting 30% of the ocean by 2030[106] in the territorial waters (Exclusive Economic Zones, EEZ) and by excluding fishing from High Seas, to create "a fish bank" for the world. Analyses suggest that doing this would recover at least an additional 0.31-0.52 $GtCyr^{-1}$ of active and passive carbon fluxes to long-term (100's of yr) deep ocean storage currently lost due to marine fisheries[47,51].

As well, it requires rethinking rules and procedures of already well-established governance programs intended to reduce emissions and enhance carbon storage. In particular, in 2013 the UNFCCC COP 19 launched a specific financial mechanism REDD+ to avoid emissions as well as sustainably manage tropical forests for biodiversity and carbon storage in developing countries. Indeed, REDD+ is recognized as a key process in Article 5 of the Paris Agreement. However, throughout the tropics forest animal populations continue to be depleted by unstainable market-hunting, leading forests to become devoid of larger animals, so-called "empty forests"[107]. As already mentioned, these large mammal and bird species often play a critical role in dispersing seeds and enhancing productivity of larger more carbon rich tree species, such as in Amazonian forests where these species represent 1% of tree species diversity but are responsible for 50% of carbon storage and productivity[108]. REDD+ policy guidance for implementation both internationally and nationally has failed to recognize this critical functional role of animals[107]. Failing to draw connections between animals and tropical forest carbon storage, and thus implicitly fostering the attendant emptying of forests, creates an inexorably high risk that REDD+ projects will fail to reach their carbon uptake and storage goals. Mitigating this risk will require including an accounting of animal functional 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 (e.g., no-take zones, quotas, seasonal restrictions) by working in close collaboration with local hunters and resource users to devise ways to explicitly avoid loss of animal diversity as part of the biodiversity safeguards of REDD+.

Conclusions

Simultaneously meeting the UNFCCC, Convention on Biological Diversity, and the Sustainable Development goals together requires rapid actions enacted on a scope and spatial scale that has not yet been attempted[31]. Animating the carbon cycle through trophic rewilding represents such an action that holds promise to help meet these goals. Doing so, however, requires a change in conceptual thinking and execution of research in Earth and ecosystem science to embrace and quantify the controls animals exert on carbon cycling. It also requires a change in mindset in policy that restoration and conservation of animal species has potential to be an instrumental part of natural climate solutions. There is some urgency on both fronts because we are losing populations of many animal species at the very time that we are discovering the degree to which their functioning in ecosystems can impact carbon capture and storage. Thus ignoring their impacts 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.

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Table 1: Estimates of animal effects on carbon storage across the spatial extent of ecosystems in which the animals occur. The data reveal the potential for Animating the Carbon Cycle to be considered a key part of Natural Climate Solutions. Additional Ecosystem CO_2 uptake represents amounts of carbon storage above levels estimated or measured in the absence of the focal animal.

Species	**Ecosystem type**	Spatial extent (km^2)	Additional Ecosystem CO_2 uptake (Gt yr^{-1})
	Restoration	*successes*	
Wildebeest	Savanna	2.5 x 10^4	**0.021** ±0.004
Sea otters	Coastal kelp forest	1.2 x 10^4	**0.005** ±0.001
Subtotal			**0.026**
	Extant	*uptake*	
Wolves	Boreal forest	1.9 x 10^6	**0.518** ±0.135
Sharks	Coral reefs	1.9 x 10^6	**0.006** ±0.002
Muskox	Arctic wet meadows	4.8 x 10^5	**0.037** ±0.015
Fish	Marine pelagic and inshore	3.0 x 10^8	**5.50** ±4.40
Subtotal			**6.061**
	Restoration	*potential*	
Forest Elephants	Tropical forest	3.6 x 10^4	**0.138** ±0.012
Bison	Tall and shortgrass prairie	4 x 10^5	**0.011** ±0.002
Baleen whales	Southern Ocean	7.9 x 10^6	**0.033** ±0.013
Beaver	Freshwater ponds	1 x 10^4	**0.174** ±0.056
Subtotal			**0.356**
Total			**6.44**

Data sources: Wildebeest (ref. 41), Sea Otters (ref. 48), wolves (ref. 19), sharks and muskox (supplemental material), fish (ref. 51), Forest elephants (ref. 56, 57), bison (supplemental material), baleen whales (ref 59), beaver (ref. 61).

Data sources and calculations used to estimate the additional ecosystem carbon capture and storage in the presence of animal species.

Muskox in arctic mire and wetland

Muskox can alter ecosystem carbon capture and storage through grazing and trampling.

CO_2 exchange

Average Net Ecosystem Exchange of CO_2 (NEE) 2011-2013 (data: Falk et al. Table 4)

Control (with Muskox): -340.6* mg CO_2 m^{-2} h^{-1} average CV = 30%
Muskox Exclosure: -281.6 mg CO_2 m^{-2} h^{-1} average CV = 50%
Net difference: -59 mg CO_2 m^{-2} h^{-1}

*(-) signifies carbon uptake

Sampling season (=~ growing season) June-September = 100 d = 2400 h (Falk et al. Table 1).

Net carbon uptake = -59 mg CO_2 m^{-2} h^{-1} x 2400 h = 141,600 mg CO_2 m^{-2} = 141.6 g CO_2 m^{-2}

Area of arctic mire or arctic wetland (Data: Raynolds 2019 Table 3 [CAVM habitat G4, W1,W2,W3])

483,000 km^2 = 4.83×10^{11} m^2

Muskox range distribution (Data: Cuyler et al. 2020 Fig. 1)

Muskox occupy ~ 60% of CAVM habitat G4, W1,W2,W3 habitat locations.

NEE = -141.6 g CO_2 m^{-2} x 0.6 x 4.83×10^{11} m^2 = 410.35×10^{11} = -4.1×10^{13} g CO_2 $season^{-1}$

NEE = -4.1×10^{13} g CO_2 $season^{-1}$ x 0.27 gC/gCO_2 = -1.107×10^{13} gC yr^{-1} = -11.07 TgC yr^{-1}

Methane exchange

Average CH_4 Flux 2011-2013 (data: Falk et al. Figure 2)

Control (with Muskox): 3.33 mg CH_4 m^{-2} h^{-1}
Muskox Exclosure: 2.8 mg CH_4 m^{-2} h^{-1}
Net difference: 0.53 mg CO_2 m^{-2} h^{-1}

Net CH_4 Flux = 0.53 mg CH_4 m^{-2} h^{-1} x 2400 h = 1272 mg CH_4 m^{-2} $season^{-1}$

Net CH_4 Flux = 1272 mg CH_4 m^{-2} $season^{-1}$ x 0.6 x 4.83 x 10^{10} m^2 = 3.69 x 10^{10} g CH_4 $season^{-1}$
Net CH_4 Flux = 3.69 x 10^{10} g CH_4 $season^{-1}$ x 0.75 gC/gCH_4 = 2.76 x 10^{10} gC yr^{-1}

Net carbon uptake = *1.107 x 10^{13} gC yr^{-1} – 2.76 x 10^{10} gC yr^{-1}* ***= 11.1 TgC yr^{-1}***

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Bison in prairie grasslands

Bison can alter carbon capture and storage by stimulating vegetation productivity

Tallgrass prairie

Average NPP during peak growing season (Knapp et al. Fig. 2)

Grazed NPP = 20 umol m^{-2} s^{-1} CV = 22%
Ungrazed NPP = 12.8 umol m^{-2} s^{-1} CV = 25%

Grazed NPP = 8.8 x 10^{-4} g m^{-2} s^{-1}
Ungrazed NPP = 5.7 x 10^{-4} g m^{-2} s^{-1}
Net difference = 3.1 x 10^{-4} g m^{-2} s^{-1}

Conversion: 60 sec/min x 60 min/hr x 12 hr/day growing x 100 days/season = 4.32 x 10^6 s/season

Grazed NPP = 3.1 x 10^{-4} g m^{-2} s^{-1} x 4.32 x 10^6 s/season = 13.4 x10^2 g m^{-2}

Area of tallgrass available for restoration 35,475 km^2 (assuming 10% of area recovered over the next 100 years Data: Sanderson et al. 2008 Table 2).

Total area NPP = 13.4 x10^2 g m^{-2} x 10^6 m^2/ km^2 x 35,475 km^2 = 4.75 x 10^{11} g per area
NEP = 1/6 NPP = 7.9 x 10^{10} gC per area

Shortgrass prairie

Average NPP during peak growing season (Frank and McNaughton Fig. 2)

NPP difference between grazed and ungrazed plots = 89.1 g m^2 vegetation biomass

Assume 50% carbon in biomass

NPP difference = 44.5 g m^2 C per growing season

Area of shortgrass available for restoration 360,884 km^2 (assuming recovery of 16% Central shortgrass prairie, 1% Central and Southern mixed grasslands, 16% of Northern fescue grasslands, 31% of Northern mixed grasslands, and 15% of Southern shortgrass prairie over the next 100 years Data: Sanderson et al. 2008 Table 2)

Total area NPP = 44.5 g m^{-2} x 10^6 m^2/ km^2 x 360,884 km^2 = 1.6 x 10^{13} g per area
NEP = 1/6 NPP = 2.6 x 10^{12} gC per area

Total NEP (shortgrass + tallgrass) = 2.68 *x 10^{12} gC per restoration area*

References

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Knapp A.K. et al. 1999. The keystone role of bison in North American Tallgrass prairie. *BioScience* 49: 39-50

Sanderson, E.W. et al. 2008. The ecological future of North American Bison: Conceiving long-term large scale conservation of wildlife. *Conservation Biology* 22: 252-266.

Sharks in coral reef seagrass beds

Sharks influence sediment carbon storage by limiting the spatial extent of herbivory and sediment bioturbation emanating outward from coral reefs (halo effect, Madin et al. 2019a).

Around these reefs, organic carbon storage in upper (0-5 cm) sedimentary depths over the last 40 years is estimated to amount to 125.9 Mg ha^{-1} when sharks are present, and reduces to 39.8 Mg ha^{-1} when sharks are absent (Atwood et al. 2018; Figure 4a) for a net effect due to sharks of 86.1 Mg ha^{-1}. In lower (5-14 cm) sedimentary depths, organic carbon storage over the last 100 years is estimated to amount to 100 Mg ha^{-1} when sharks are present, and reduces to 50.1 Mg ha^{-1} when sharks are absent (Atwood et al. 2018; Figure 4b) with a net effect due to sharks of 49.9 Mg ha^{-1}. This amounts to 2.15 Mg C ha^{-1} yr^{-1} at upper sediment depths and 0.499 Mg C ha^{-1} yr^{-1} at lower depths or a total of 2.65 Mg C ha^{-1} yr^{-1} at a coral reef.

The total reef reserve areas that protect sharks and their interactions amounts to 1.9 x 10^6 km^2 (Madin et al. 2019b). There is, however, a 60% chance that a halo effect will be created by shark presence producing halo areas within 0.005% of the reserve area (Madin et al. 2019b), or 57 km^2 carbon storage area. This results in a total of 1.5 x 10^{12} g (0.0015 Gt) of carbon storage.

References

Atwood, T.B. et al. 2018. Predators Shape Sedimentary Organic Carbon Storage in a Coral Reef Ecosystem. *Frontiers in Ecology and Evolution* 6:110.

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