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Review

The role of large wild animals in climate change mitigation and adaptation

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SUMMARY

Two major environmental challenges of our time are responding to climate change and reversing biodiversity decline. Interventions that simultaneously tackle both challenges are highly desirable. To date, most studies aiming to find synergistic interventions for these two challenges have focused on protecting or restoring vegetation and soils but overlooked how conservation or restoration of large wild animals might influence the climate mitigation and adaptation potential of ecosystems. However, interactions between large animal conservation and climate change goals may not always be positive. Here, we review wildlife conservation and climate change mitigation in terrestrial and marine ecosystems. We elucidate general principles about the biome types where, and mechanisms by which, positive synergies and negative trade-offs between wildlife conservation and climate change mitigation are likely. We find that large animals have the greatest potential to facilitate climate change mitigation at a global scale via three mechanisms: changes in fire regime, especially in previously low-flammability biomes with a new or intensifying fire regime, such as mesic grasslands or warm temperate woodlands; changes in terrestrial albedo, particularly where there is potential to shift from closed canopy to open canopy systems at higher latitudes; and increases in vegetation and soil carbon stocks, especially through a shift towards below-ground carbon pools in temperate, tropical and sub-tropical grassland ecosystems. Large animals also contribute to ecosystem adaptation to climate change by promoting complexity of trophic webs, increasing habitat heterogeneity, enhancing plant dispersal, increasing resistance to abrupt ecosystem change and through microclimate modification.

Introduction

The decline in abundance and geographic range of wild animals is one of the most striking features of human-induced environmental change[1]. Total global wild mammal biomass (in carbon units) is now estimated to be seven teragrams (Tg; 10^6 tonnes) carbon, a factor of six smaller than its value (40 Tg) in the Late Pleistocene, 100,000 years ago[2], and this decline continues at a rapid rate[3]. Meanwhile, total human biomass has increased to 60 Tg carbon, and domesticated livestock biomass to 100 Tg[2]. The decline in the quantity and functional diversity of wild animals leads to elevated extinction rates in other species groups[4], and affects the functioning of whole ecosystems[5,6]. The current and near-future decline in wild animals is largely a result of habitat loss and degradation, overexploitation, eutrophication, exotic species proliferation and climate change, as well as interactions between these drivers, and cascading effects through trophic webs[7–9].

There is growing interest in policy opportunities that align biodiversity conservation and recovery with climate change mitigation and adaptation agendas[10]. One such alignment is through nature-based solutions to climate change: solutions that involve people working with nature, both for direct mitigation of climate change and for facilitating adaptation by ecosystems or local human communities[11]. Nature-based solutions have gained policy traction in international climate change and biodiversity negotiations, but most of the evidence for nature-based solutions, and thus the proposed interventions, has focused on managing the major reservoirs of biosphere carbon in vegetation and soil via avoided deforestation and forest degradation, reforestation and the restoration of peatlands and coastal ecosystems[12]. The potential contribution of large animal wildlife in this arena has received little attention. In parallel, in the conservation agenda there has been new momentum around protecting, restoring and rewilding ecosystems, emphasising multitrophic

complexity — the diversity of species, functions and interactions on multiple trophic levels — and the role of animals in generating and maintaining key ecosystem functions[13,14]. Large wild animals are often a particular focus of conservation strategy and public awareness, because of their charisma and ability to attract funding[15], as well as their capacity to act as umbrella and ambassador species for a suite of ecosystem protection benefits[16]. Finding interventions that simultaneously meet biodiversity conservation and climate change mitigation and adaptation agendas will require a systematic examination of the interactions between vegetation-, animal-, ecosystem-, and climate-centred interventions. Some of these interactions may be negative and involve trade-offs, but an examination of opportunities within these two environmental agendas can help bring to light interventions that align and may be mutually reinforcing[17].

In this review, we examine and synthesise our knowledge of how large wild animals can influence ecosystem-based mitigation of, and adaptation to, climate change, whether in beneficial or detrimental ways. Our review spans terrestrial and marine systems, reflecting the functional connections between the realms and the practical benefits of coordinated management and conservation interventions[18]. Our overarching goal is to provide an evidence base to help integrate the wildlife conservation and climate change agendas and identify when and if there is a potential for synergistic outcomes. We focus on three questions: How does the presence of large animals influence the climate change mitigation and adaptation potential of ecosystems? Are there underlying biogeographical patterns and principles that determine the magnitude and type of influence by large animals on ecosystem processes? Are there opportunities to align the climate change mitigation and adaptation and wildlife conservation and restoration agendas?

We focus on the role of large wild animals. Much of the pertinent literature refers to 'megafauna', often defined as animals with adults larger than a given threshold mass (45 to 1000 kg for herbivores and 15 to 100 kg for carnivores[19]). These thresholds are linked to the observation that terrestrial herbivores above a given mass can alter vegetation on a landscape scale by changing ecosystem structure, disturbing woody vegetation and consuming large amounts of foliage, and altering the biogeochemical pathways from autotrophs to decomposers[13]. Large carnivores, in turn, influence ecosystems by affecting the abundance and activity of small-medium herbivores through direct consumption or behavioural changes[20,21]. In many ecosystems, however, the largest herbivorous animals are below these threshold mass values, but influence ecosystem structure and composition because of key traits or size-reduction of overall trophic structure[22]. For example, giant tortoises in island systems [9], parrot fish in reef systems[23], and large birds or beavers in freshwater systems[24] may be amongst the largest extant herbivores in their ecosystems, and through particular behaviours or high abundance exert influences on ecosystem structure and composition[25]. Thus, in line with the suggestion that body size is insufficient to capture the varied eco-evolutionary impacts of megafauna[19], we employ the term 'large animals' to collectively refer to large herbivores and carnivores in terrestrial continental ecosystems, as well as smaller size classes in non-terrestrial or non-continental ecosystems when those species are among the larger animals in their ecosystems and are the major drivers of ecosystem structure and composition[9,19]. We discuss mainly wild rather than domestic animals, while recognising that in some cases domestic animals (e.g., roaming cattle in rangelands) can replicate some aspects of wildlife function.

In the context of natural systems, we define 'climate change mitigation' as actions that result in a reduction in the Earth's surface radiative budget, through changing atmospheric greenhouse gas concentrations or surface or atmospheric albedo. Large animals may directly impact climate mitigation through their greenhouse gas emissions and indirectly impact climate mitigation through their influences on primary producers, soils, biogeochemical cycles, other fauna, and abiotic disturbance regimes, all of which affect ecosystem function, carbon stocks and radiative properties (Figure 1). 'Climate change adaptation' refers to the capacity of a biome to respond effectively to climate change pressure through resistance, resilience or transformation (Figure 2). Biome resistance is system persistence and maintenance of current conditions, the 'status quo', despite climate change[26,27]. Biome resilience refers to the capacity of a system to return to its initial state following a disturbance[26–28]. Biome transformation is a shift from one biome type to another (some species may go extinct, some may colonise), which may either enhance or decrease aspects of ecosystem function or species composition; this is a fundamental, system-wide reorganisation. There is an inherent tension between the desirability of biome resistance or resilience and biome transformation[29]. Resistance or resilience are usually preferable under moderate climate change pressure, with an emphasis on slowing down rates of ecosystem change and maintaining composition and function. Under higher levels of climate change, if maintaining or strengthening ecosystem processes is deemed a priority, it may be more pragmatic to facilitate biome transformation (e.g. by facilitating immigration of better adapted species or varieties). Large animals may promote climate change adaptation in natural systems through their influences on primary producers, soils, biogeochemical cycles, other fauna and abiotic disturbance regimes (Figure 2). They may also impact local microclimate, habitat connectivity, propagule dispersal rates and ecosystem composition.

Large animals influence the climate change mitigation and adaptation potential of ecosystems

Below, we outline the key processes and mechanisms through which large wild herbivores and carnivores potentially influence climate change mitigation and adaptation in marine and terrestrial systems (Figures 1 and 2), and summarise what the literature indicates about the net effect on climate change mitigation and adaptation (Table 1 and Supplemental information). We note that most direct effects on ecosystem structure and biogeochemical cycling discussed below are through herbivores, but in many cases herbivore effects are modified by the presence and abundance of carnivores. The role of predator–prey interactions and ecosystem 'trophic intactness' in climate change mitigation and adaptation is touched on in several of the following sections, but discussed most explicitly under 'Ecosystem complexity and heterogeneity'.

Carbon stocks in living organisms

In total, terrestrial and marine animals (including invertebrates and vertebrates) hold two petagrams (Pg; 10^9 tonnes) carbon,

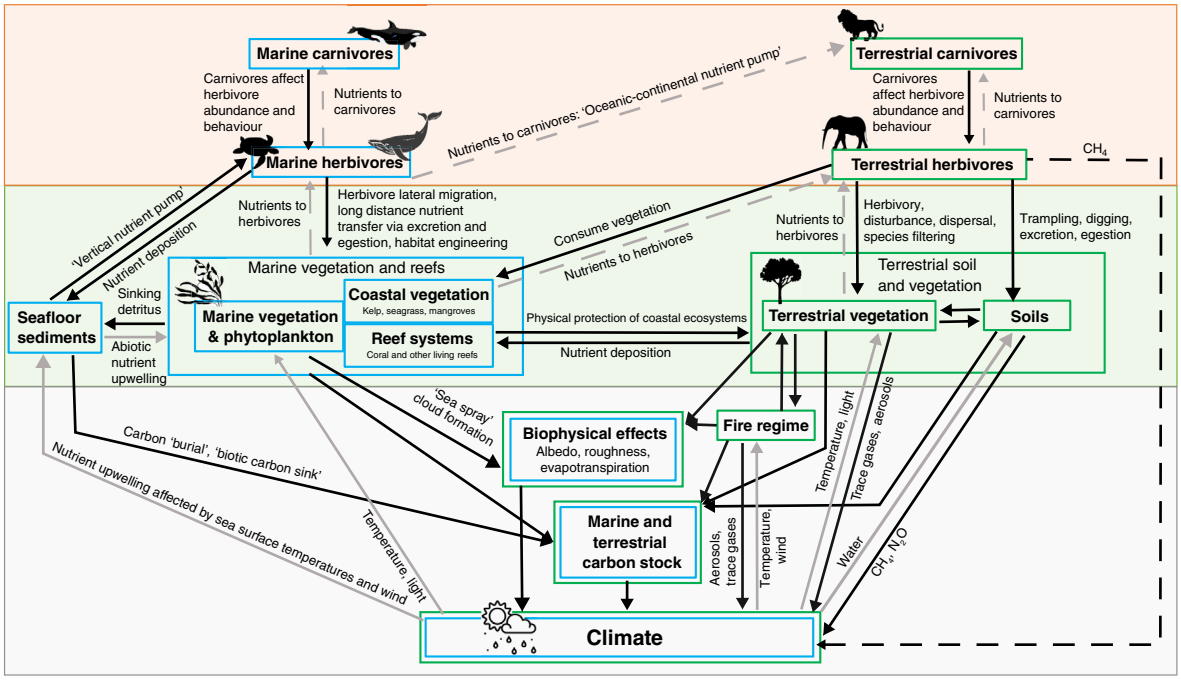


Figure 1. Climate change mitigation.
The key interactions that determine the potential contribution of large animals to climate change mitigation. Terrestrial large animals influence climate by altering the properties of surface vegetation and soils, influencing vegetation mortality and species composition, which can in turn affect ecosystem-wide biophysical characteristics, change disturbance regimes (especially fire regimes), and alter soil properties and biogeochemical cycling through excretion, trampling and digging. There is also a direct atmospheric effect through methane emissions. Coastal and reef large animals influence ecosystems through grazing and other analogous processes to terrestrial herbivores, but in the open ocean this directly influences vertical nutrient exchange and hence phytoplankton productivity. Large terrestrial and marine carnivores influence these processes through their influence on herbivore abundance and behaviour. Several interactions between terrestrial and marine ecosystems, most notably biogeochemical cycling, are also influenced by animals (solid black arrow: animals mitigate climate change; dashed black arrow: animals exacerbate climate change; solid grey arrow: a direct impact from climate; dashed grey arrow: interactions affected by climate-driven changes in species type, abundance or behaviour).

of which arthropods account for 1 Pg carbon, fish 0.7 Pg carbon and wild mammals and birds only 0.009 Pg[2]. Hence, the total carbon stored in wild mammals and birds is equivalent to roughly eight hours of current anthropogenic fossil fuel emissions, and the total amount stored in all wild animals is equivalent to about two months of emissions. Thus, in most cases, the carbon stock in wild animals is negligible, and it is appropriate to focus instead on the effects of animals on the much more substantial autotroph, soil, sediment, and deep ocean stocks.

Around 80% (450 Pg carbon) of the carbon stocks in all living organisms (~550 Pg) are in vegetation biomass, of which around 320 Pg (~70%) is in lignified tissue[2]. For comparison, current anthropogenic emissions are around 10 Pg carbon per year[30], and to limit global warming to below 1.5 °C (or 2 °C), future cumulative net global emissions need to remain below 120 Pg carbon (or 374 Pg CO_2); this is the median remaining carbon budget as of 2020[31]. Hence, one of the most profound impacts that large herbivores can have on biosphere carbon stocks, and therefore climate change mitigation, is through their impact on vegetation structure in woody communities (Figure 1)[32–35].

In open-canopy terrestrial ecosystems, large herbivores may lower above-ground carbon stocks through consumption and physical disturbance[33,36]. Alternatively, they may optimise biomass production through changes in vegetation community composition, short-term compensatory growth responses by grazed vegetation, particularly belowground[37–40] or long-term increases in soil fertility and ecosystem metabolism[37,41,42]. In closed-canopy ecosystems, such as tropical forests, large herbivores may increase aboveground tree biomass by up to 26–60 tonnes/hectare[43] by reducing competition from juvenile trees and favouring dispersal of large-seeded tree species, which tend to be long-lived with high wood density and high biomass[44]. The effects of large herbivores in any of these ecosystems may be modified by a number of less direct impacts on vegetation community structure, including filtering of community composition through seed dispersal and selective browsing, changes in fire regime and enhancement of nutrient cycling[42,45]. Animal-mediated acceleration of terrestrial nutrient recycling is most pronounced in regions where the litter decay pathway is limited by abiotic factors, such as cold or arid conditions[46]. Most of these processes scale with animal size, with large animals having larger day ranges and longer gut residence times[41,47,48]. In addition, large herbivores may change vegetation carbon stocks by accelerating biome transformation (e.g. by introducing seeds of more productive species or by shifting the competitive advantage in favour of resource competitors through increased soil nutrient availability)[40,41].

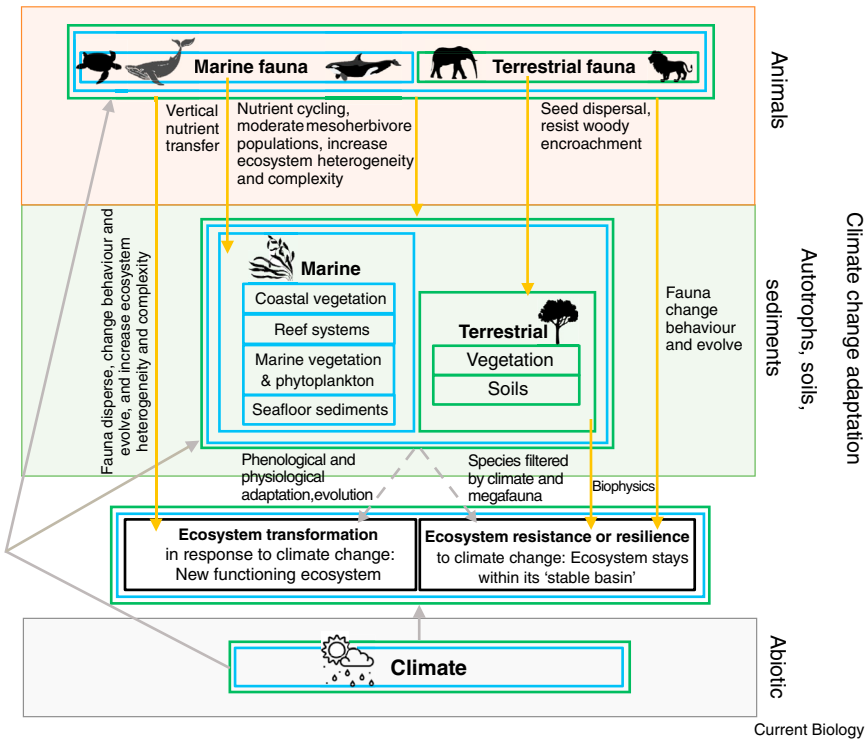


Figure 2. Climate change adaptation.
The key interactions that determine the potential contribution of large animals to climate change adaptation potential of ecosystems, whether resistance, resilience or transformative adaptation. Large animals influence ecosystem adaptation by altering the primary producer community and ecosystem structure, as well as through changes in their own behaviour, migration and dispersal and through evolution (solid grey arrow: a direct impact from climate; dashed grey arrow: interactions affected by climate-driven changes in species type, abundance or behaviour).

In marine systems, the carbon stocks in living autotrophs are generally less significant for climate change mitigation, because of their smaller spatial extent, shorter lifetimes leading to quick transfer to the marine sediment carbon stock, debated capacity for long-term carbon storage, limited ability to sequester carbon directly, and overall smaller quantity[49]. Marine autotrophs account for ~1 Gt (1 x 10^9 tonnes) carbon out of ~6 Gt carbon in all marine biomass; this may be compared with 450 Gt in terrestrial autotrophs out of ~470 Gt C in terrestrial biomass[2]. Although the carbon stocks in marine autotrophs are lower than in terrestrial systems, they are still important, and marine large wildlife can influence autotroph carbon stocks in coastal regions through top-down control mechanisms[50,51].

Carbon stocks in persistent reservoirs

Terrestrial soil organic matter provides climate mitigation and adaptation services via erosion control, water and nutrient retention[52] and carbon storage (globally ~2770 Pg carbon in the top 3 m[53]). The impact of large animals on soil carbon stocks varies, partly due to differences between biomes and scales, herbivore assemblages and densities and soil community adaptation (Figure 1 and Tables 1 and S1)[6,54–57]. For example, herbivores can help preserve soil carbon by maintaining permafrost in the Arctic[58], maintaining below-ground carbon in fire-prone ecosystems[59,60], stabilising soil carbon through soil mixing[61] and through the activities of their associated soil macrofauna (e.g. earthworms, dung beetles[62–64]). Large herbivores may also promote accumulation of new carbon in soils by selective feeding on more palatable vegetation, leaving behind litter with low bioavailability for decomposers[45], by increasing nutrient availability[42,65,66], or through community shifts towards grazing-tolerant species with compensatory responses to grazing leading to increased belowground carbon-allocation and stabilisation[53,56,66–69]. Large herbivores may also enhance long-term ecosystem carbon storage via enhancing the persistence to perturbation, primarily through securing a larger portion of total ecosystem carbon in resistant soil pools without compromising overall ecosystem carbon storage[59,70–73].

Marine sediments store more carbon than terrestrial soils (total global carbon in the top 1 m: marine sediments ~2300 Pg[74], terrestrial soils ~ 1486 Pg[53]). The persistent reservoirs of carbon in marine systems may be divided into those in coastal and benthic systems, and those in open ocean. In coastal and benthic ecosystems (seagrass meadows, mangroves and kelp forests), animal herbivory, disturbance and top-down control of benthic communities are likely to influence sediment carbon stocks, much as they do in terrestrial systems[49,75–77]. However, the spatial extent of these systems is limited, as is the evidence for the direction and magnitude of the net effect. In open ocean waters, the carbon stock in living phytomass is relatively small[2]. However, phytoplankton is responsible for around 40% of Earth's primary production[78], and the flux of organic debris from the surface into the deep ocean (the ocean biotic carbon sink), where it is largely isolated from the short-term global carbon cycle, can be an important climate mitigation process[79,80]. Similarly, carbon stored in macroalgal biomass and exported to deep ocean ecosystems is also thought to be a valuable long-term carbon sink[81,82]. Large animals (mammals and mesopelagic fish) affect this marine carbon sink by stimulating plankton and macroalgal productivity through nutrient enrichment[51,83], transferring nutrients up from deep waters and the downward transfer of matter through carcasses and excreta (Figure 1)[84].

Soil trace gas emissions

Methane (CH_4) is thought to be the second most important greenhouse gas. Although it is ~200 times less abundant than atmospheric CO_2, methane is ~84 times more efficient at trapping radiation on decadal timescales (20 year average Global Warming Potential[85]) and ~28 times more efficient on a 100-year timescale). Wetland ecosystems, especially in the tropics, are the largest natural sources of atmospheric methane, which is produced during microbial anaerobic metabolism[86]. In wetlands, herbivores can drive a shift from shrubs and trees to grasses and forbs with dense and diffuse root nets. In seasonally

Table 1. Variation between biomes in the influence of large animals.

	Tundra (Figure 3)		Temperate woodland (Figure 3)		Savanna (Figure 3)		Desert, arid systems (Figure 2)		Tropical wet forest (Figure 2)		Temperate grassland (Figure 2)		Boreal forest (Figure 2)		Seagrass (Figure 4)		Tidal marsh		Kelp forest (Figure 4)		Coral reef		Deep sea, open ocean (Figure 4)	
Mitigation (M)/ Adaptation (A)	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A	M	A
Vegetation/ autotroph structure and carbon stock above and below-ground	↓	↑	↓	↑	↓	↑	↓	↑	↑	↑	~	↑	↓	↑	↓	~	↓	~	↓	~	~	↑	↑	?
Carbon storage in soil, sediments and deep waters	↑	↑	↑	↑	+/-	+/-	+/-	+/-	↑	↑	↑	↑	↓	↓	+/-	~	↓	~	~	~	~	~	↑	↑
Soil trace gas emissions	↑	~	↑	~	↑	~	+/-	~	+/-	~	↑	~	+/-	~	?	?	↓	~	~	~	~	~	~	~
Animal trace gas emissions	↓	~	↓	~	↓	~	~	~	~	~	↓	~	↓	~	~	~	~	~	~	~	~	~	~	~
Surface albedo	↑	↑	↑	↑	↑	↑	↑	↑	~	~	↑	↑	↑	↑	~	~	~	~	↓	~	~	~	↓	↓
Atmospheric albedo	~	~	~	~	↑	↑	~	~	~	~	~	~	~	~	~	~	~	~	~	~	~	~	?	?
Other biophysical properties	~	↑	~	+/-	~	↓	+/-	+/-	~	~	~	~	~	↑	~	~	~	~	~	~	~	↑	↑	↑
Fire regime	?	?	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	/	/	/	/	/	/	/	/	/	/
Riparian geomorphology and flooding regimes	+/-	↑	+/-	↑	+/-	↑	~	↑	?	?	+/-	↑	+/-	↑	/	/	/	/	/	/	/	/	/	/
Vegetation/ autotroph filtering and dispersal	Climate change adaptation is strongly, positively affected by large animal presence via vegetation/autotroph filtering and dispersal in most biomes. Adaptation effects spill over to mitigation effects by reducing risk of ecosystem breakdown under climate stress																							
Ecosystem complexity (biodiversity, trophic diversity)	Climate change adaptation is strongly, positively affected by large animal presence via increased ecosystem complexity in most biomes. Adaptation effects spill over to mitigation effects by reducing risk of ecosystem breakdown under climate stress																							

The positive or negative mitigation or adaptation impacts of wild animals that could feasibly be present or be introduced and occur at functionally relevant densities on the timescale of a century in the given biome. Feasibility here refers to the practical aspects of large animal recovery, excluding animals that are effectively or globally extinct, and including considerations of human societal acceptance. Notes on the cells of this table are available in Table S1. (Symbols: ↑: strong positive mitigation or adaptation effect; ↑: weak positive mitigation or adaptation effect; ↓: weak negative mitigation or adaptation effect; ~: the impact has been studied, and information to date suggests it is small/negligible; +/-: the impact has been studied and there are clear processes in both positive and negative directions, but the direction of the net effect is not known; ?: lacking information, little studied or poorly understood.)

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waterlogged soils, these grass and forb-dominated systems have higher transpiration rates and drier topsoil compared to systems dominated by woody plants[87], which can reduce methane production. However, some of the reduction in methane radiative forcing (the change in energy flux in the atmosphere caused by methane) may be negated by increased CO_2 emissions. Herbivores may also increase methane emissions from permanently waterlogged soils through grazing-induced disruption of plant control on stomatal conductance[88]. Thus, existing evidence suggests that herbivores may increase methane emissions from permanently waterlogged soils and may decrease methane emissions from seasonally waterlogged soils. In cold biomes, herbivores reduce winter snow cover through trampling and foraging. This activity exposes soil microbial communities to cold winter temperatures, which reduces their activity[89,90] and creates drier soil conditions during the spring thaw[91], both of which result in lower methane and N_2O emissions (N_2O is a greenhouse gas ~265 times more potent than CO_2[85])[92,93]. Animals also add nitrogen to the soil system, via defecation and urination, which can increase pulse N_2O production (Figure 1)[88].

Direct animal methane emissions

Methane is a by-product of the microbial breakdown of carbohydrates (mainly cellulose) in the digestive tracts of herbivores (Figures 1 and 2). This process is particularly important for ruminants, which host large populations of bacteria and protozoans in their rumens[94]. The quantity of methane produced per individual animal depends on size, diet, and digestive physiology, with hindgut fermenter herbivores (pigs, horses) emitting considerably less methane than ruminants of similar size[22,95]. Globally, wild mammals are estimated to emit ~13 Tg methane yr^{-1}, but these emissions may have been as high as 140 Tg methane yr^{-1} prior to the Late Pleistocene extinctions[96]. Domesticated animals emit ~115 Tg methane yr^{-1} [86]. Hence, animals account for a significant proportion (wild: ~2.2%; domestic: ~20%) of total global methane emissions (~600 Tg methane yr^{-1} [86]). This means that increases in large animal wildlife where large animals were previously absent could result in an increase in methane emissions. However, any wildlife-related effects are likely to be modest in comparison to global methane emissions from domesticated animals.

Albedo

Beyond affecting greenhouse gas concentrations, the other major climate mitigation service that ecosystems can provide is through increasing surface or atmospheric albedo. In general, terrestrial herbivores increase surface albedo by reducing woody cover through browsing[7,58,97–100] and exposing bare ground, grass or snow, which have higher albedo than closed-canopy woody vegetation (Figure 1)[101,102]. The contrast in albedo is most stark at high latitudes, where snow increases the albedo of open vegetation relative to closed canopies, resulting in a strong net surface cooling effect in the spring/autumn seasons of moderate solar irradiation and high snow cover[101]. For example, it is estimated that the extinction of mammoths and other Arctic megafauna, and the resulting expansion of *Betula* shrubs, increased regional temperatures in Siberia and Beringia by up to 1°C[103]. In addition to climate change mitigation, increasing albedo can also support local climate change adaptation, by reducing local surface temperatures (Figure 2).

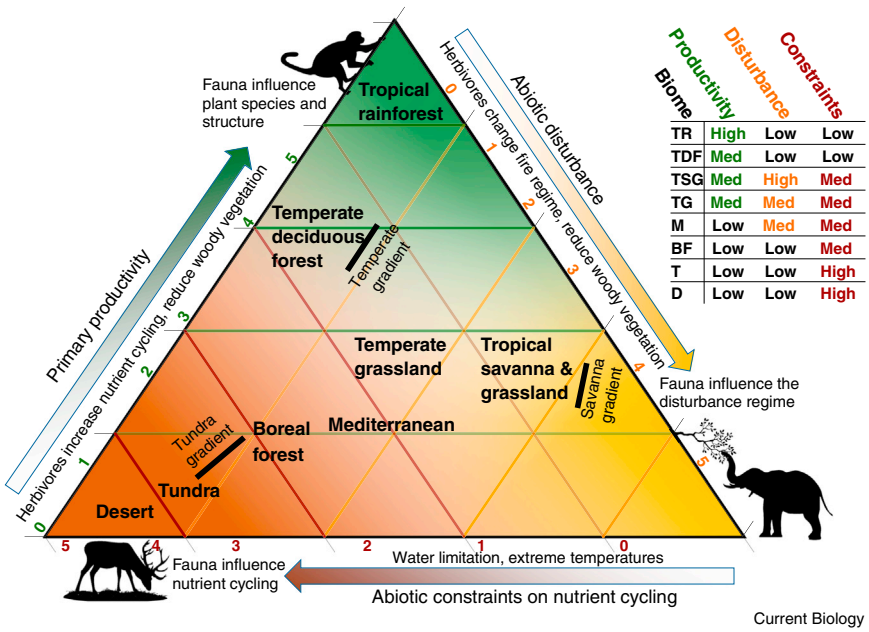
Animal impacts not only affect the vegetation's direct reflective properties, they also affect the Earth's atmospheric albedo[104]. Specifically, when large animals affect tree cover, this also impacts evapotranspiration[105], which, in turn, can impact fire regime and dustiness. Atmospheric dust and aerosols directly cool the climate by scattering solar radiation, and affect the number and size of cloud condensation nuclei, which impacts cloud cover, type and duration and tends to result in more reflective and long-lived clouds[106] and higher atmospheric albedo.

In marine systems, large animals can also impact atmospheric albedo. Specifically, animals can increase nutrient cycling and thereby potentially affect the productivity and extent of phytoplankton[107]. Phytoplankton, in turn, potentially affects cloud properties either by emission of dimethyl sulfide (DMS), which is oxidised to sulfur dioxide and can then condense to form sulfate aerosol particles[108–110] (but see[111]), or by increasing sea spray aerosol fluxes[112]. Aerosol particles have a direct cooling effect on climate by scattering solar radiation and act as cloud condensation nuclei (Figure 1). A phytoplankton–aerosol–cloud interaction has been observed in the Southern Ocean, most notably in productive summer months, though the pattern shows significant seasonal and spatial variation[109,113]. However, increased phytoplankton density and cover have also been linked to decreased ocean surface albedo and increased sea surface temperature, amplifying warming in the Arctic[114,115]. Overall, whether large animal fertilisation has significant effects on marine atmospheric aerosol concentrations remains to be assessed.

Fire regime

Fire and subsequent recovery are part of the natural dynamics of many ecosystems, but net anthropogenic increases in the area and intensity of fire have resulted in a net release of ~0.4 Pg carbon to the atmosphere annually[116]. Fire also contributes other climate warming agents to the atmosphere, such as N_2O and black (light-absorbing) aerosols[117]. These increases in carbon, N_2O and other aerosols are likely to continue as, together with land-use change, climate change is lengthening the fire season in many tropical, subtropical, Mediterranean and boreal regions, as well as increasing atmospheric water vapour deficits and aridity that favour intense fires, particularly in forests[118].

Depending on herbivore type, population density, and feeding patterns[60], herbivores can reduce fire spread and intensity in ecosystems by reducing fuel biomass and fuel continuity by consuming vegetation, digging and trampling the soil[119,120] and forming trails and wallows which act as natural fire breaks (Figure 1)[121]. Browsers can also lower the frequency of crown fires if they break-up vertical fuel continuity and remove potential fuel ladders[120]. Herbivores can also reduce fire risk in previously unburnt (non-fire-adapted) systems, for example by reducing the biomass of grasses spreading into shrublands[122–125]. In some systems, herbivores can facilitate a shift towards open and more flammable grassy systems[119,126], increasing fire frequency (which may lower tree cover) but also decreasing fire intensity (thereby reducing catastrophic fire and increasing spatial heterogeneity in woody cover[127]).



Biome	Productivity	Disturbance	Constraints
TR	High	Low	Low
TDF	Med	Low	Low
TSG	Med	High	Med
TG	Med	Med	Med
M	Low	Med	Med
BF	Low	Low	Med
T	Low	Low	High
D	Low	Low	High

Figure 3. Environmental axes affecting the influence of large animals.
The location of biomes along three environmental axes: primary productivity, abiotic disturbance, and abiotic constraints on nutrient cycling (low (0) to high (5)). The position of each of the biomes on the three axes is also indicated in the table at the right: tropical rainforest (TR), temperate deciduous forest (TDF), tropical savanna and grassland (TSG), temperate grassland (TG), Mediterranean (M), boreal forest (BF), tundra (T), and desert (D). Biome position on these three axes influences the magnitude and type of impact fauna have within the biome. The three gradients from Figure 4 are shown here as black lines.

Ecosystem biophysical properties

Animal-driven changes in terrestrial vegetation structure and species composition can change the locally experienced microclimate, influencing climate change adaptation (Figure 2). These effects include changes in surface roughness, which affects the rate of turbulent transfer of heat or water vapour from the surface; canopy conductance, linked to the ecophysiological properties of trees and herbaceous vegetation; rainwater interception and evapotranspiration rates; and sub-canopy microclimate, such as shade, humidity, maximum or minimum temperatures and frost exposure[105]. The aerodynamic surface roughness effects appear most significant in semi-wooded ecosystems and tend to saturate after tree canopy closure[105]. Overall, an animal-driven transition from closed broadleaf forest to more open canopy cover in temperate or tropical conditions would be expected to decrease surface roughness, increase canopy aerodynamic resistance, decrease canopy conductance, decrease evapotranspiration rates (trees have deeper roots and high interception) and decrease shade. These are all surface warming effects. In boreal and Arctic regions, however, animals would be expected to drive an opening up of closed-canopy, shallow-rooted coniferous forest or shrub to deeper-rooted grassland, which would increase canopy conductance and evapotranspiration rates, likely leading to net surface cooling and drying. In the marine environment, animal-driven changes to ecosystem structure and community composition enhance rates of coral-reef accretion and bioerosion, which can reduce their ability to dissipate wave energy and track sea-level rise[50,128,129], and can increase turbulent mixing of waters and associated nutrient supply. The vertical movement of large marine animals may also have a direct impact on turbulent mixing and transport of nutrients in thermally stratified ocean waters[130].

Riparian geomorphology and flood regimes

Riparian zones can ameliorate predicted climate change-linked increases in flood severity by distributing flood waters over a larger portion of the landscape and slowing downstream water movement[131]. Water residing in the landscape also provides thermal refugia for plants and wildlife[132]. Large animals modify riparian habitats by eating vegetation, physical disturbance and building dams[133]. Depending on the biome and the animal functional group, animal activity can increase or decrease water residence, and slow or accelerate water movement. For example, catchment-scale studies in the USA, Australia and East Africa have shown that grazing can increase upstream erosion and downstream flood risk[134–136]. In contrast, beavers and hippos slow water movement, both reducing flood risk and increasing carbon storage[135,137–139]. However, the carbon-storage potential of animals slowing landscape water movement should be balanced against other effects on catchment biogeochemistry, including methane emissions which can increase substantially[136,140,141].

Vegetation community dispersal and filtering

The role of large animals in shaping vegetation communities through increasing seed dispersal is particularly important in the context of climate change adaptation, especially in fragmented ecosystems in anthropogenic landscapes (Figure 2)[34,47]. Herbivores can reduce the density and diversity of seeds, seedlings and saplings[142,143], or increase diversity and density by promoting a heterogeneous environment with greater local and landscape-level plant propagule pools, and by enhancing dispersal rates[47,144,145]. Herbivores can filter species through their impacts on seeds, reducing seed production in some species and facilitating seedling recruitment in others[146,147]. They can also enable seed dormancy breaking, dispersal and subsequent early establishment through deposition of seeds in dung[146]. In some contexts, this may facilitate ecosystem resistance to climate change (e.g. by preventing encroachment of new species such as woody shrubs in the tundra[148,149]). In other contexts, the facilitated dispersal of climate-adapted species and variants, together with creation of disturbance and heterogeneity, may facilitate ecosystem transformation[47].

Ecosystem complexity and heterogeneity

Protecting, restoring, or introducing functionally diverse large wild herbivores and carnivores in marine and terrestrial biomes is expected to increase species diversity and ecosystem complexity. This increase is driven directly through their

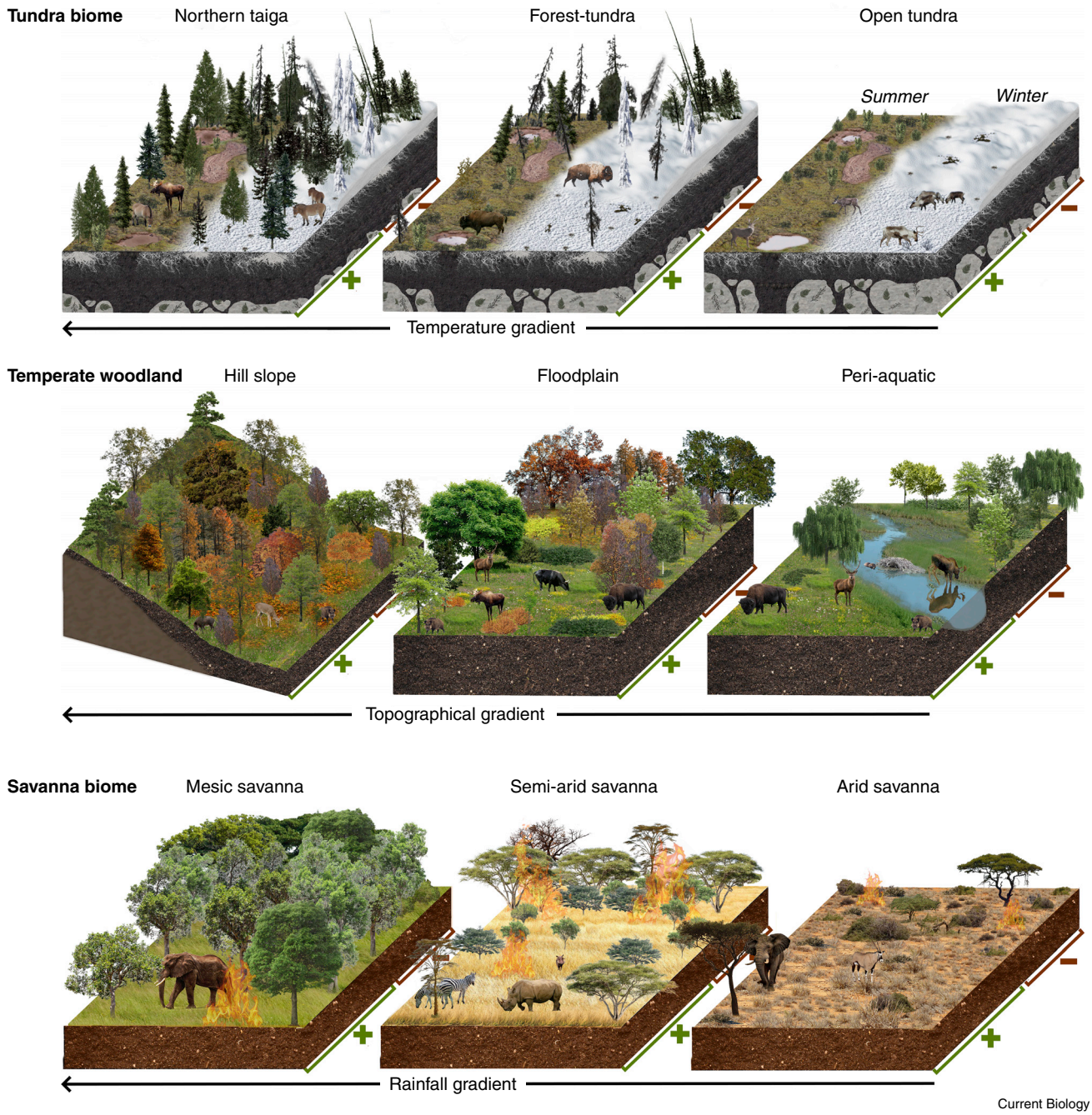


Figure 4. Variation in large animal effects along terrestrial environmental gradients.
Environmental gradients in three terrestrial biomes, representing idealized ecosystems rather than specific case studies, with necessary simplifications of the nuanced processes and local ecological variation that are described below and in the associated literature (Tables 1 and S1). The three gradients show hypothesised future trajectories with (foreground, +) and without (background, -) large herbivores. The role of carnivores is implicit but not shown. These three environmental gradients are marked as black lines in the environmental space in Figure 3. (Further explanation is available in the Supplemental information.)

presence, but also indirectly through their impacts on primary producers and predator/prey and competition interactions, and the impacts these changes have on faunal species diversity and composition[75]. Large animals can also increase physical heterogeneity and patchiness in a system, for example by disturbing vegetation, turning over soil, undertaking local and long-distance migration and creating biotic microhabitats in their living bodies, corpses and dung. Such heterogeneity creates microhabitats that may facilitate landscape-scale climate change resilience (although robust evidence for such effects is lacking) and facilitate transformative adaptation by allowing new species to establish (Figure 2)[150].

A key aspect of ecosystem complexity is trophic complexity or 'intactness', and specifically the presence of carnivores. Large

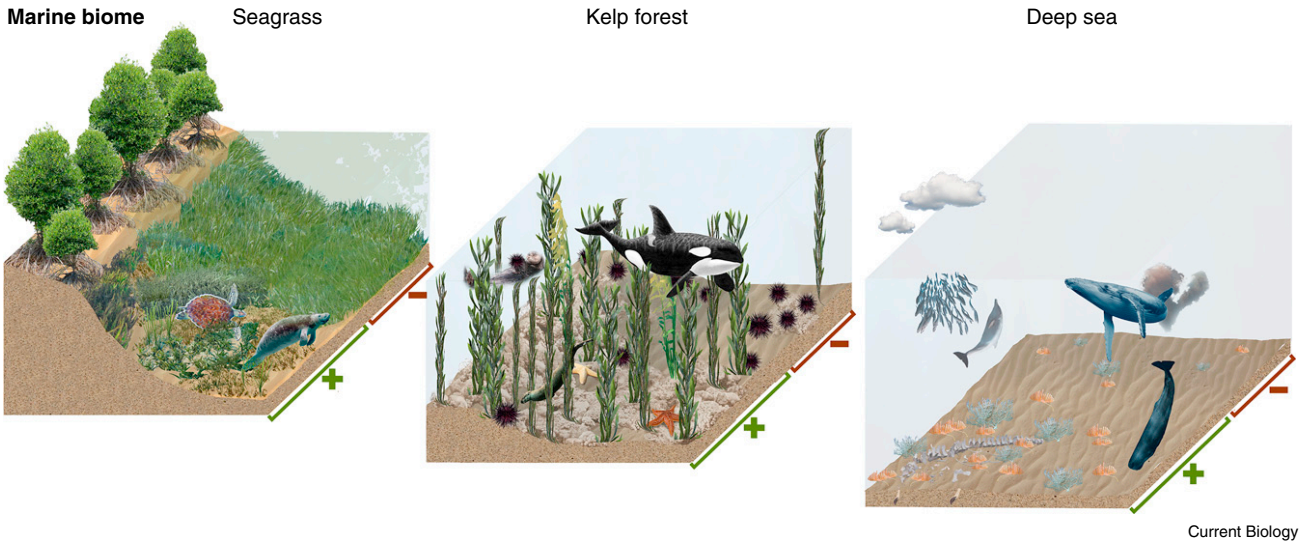


Figure 5. Variation in large animal effects across marine biomes.
Hypothesised future trajectories of key marine biomes, two coastal systems and one pelagic, which do not necessarily represent a gradient from the shore, with (foreground, +) and without (background, -) marine megafauna. (Further explanation is available in the Supplemental information.)

carnivores influence carbon budgets and surface albedo because they moderate herbivore populations[151], although they have limited impact on the largest herbivores[21] or on mass migratory species[134,152]. In systems with herbivores that are vulnerable to predation, large carnivores may reduce overall vegetation consumption, potentially resulting in a net increase in vegetation biomass and carbon stocks[22]. On the other hand, predation of mesoherbivores can increase food resources for large herbivores and result in overall increased animal biomass[21], as, for example, in Yellowstone, where the increase in bison compensated for the (partially) wolf-induced decrease in elk[134]. The same dynamics can be at play in marine systems. For example, a study comparing kelp carbon dynamics with and without sea otter predation in North America estimated that otter predation was linked to a one-time increase of 4.4–8.7 Tg carbon sequestration in living kelp biomass over an area of 5.1 x 10^{10} m^2 [153]. Similarly, predators in seagrass habitats can prevent overgrazing and bioturbation, avoiding the loss of living carbon stores and disturbed sediments[154,155]. Without marine megafauna, phase shifts and algal blooms may be more likely to occur as a result of losing top-down control mechanisms[154], or reduced foraging and turnover rates[156,157]. In addition to the direct consumptive effects, carnivores also alter herbivore behaviour and distribution, and the location and intensity of herbivore impact, in both terrestrial[158] and marine systems[159]. Fear of predation can intensify herbivore impact in areas perceived by prey animals as relatively safe, while alleviating it in areas perceived as risky[158]. Overall, complex and heterogeneous systems are likely to be more resilient to climate change because of their capacity to facilitate ecological network re-wiring, and mitigate phenological mismatches and loss of interaction partners[160]. Habitat heterogeneity and species diversity and functional redundancy are also likely to facilitate the continued provision of ecological functions and services under a changing climate[161].

Biogeographical patterns and principles determining the influence of large animals on climate-change-relevant ecosystem processes

There is a large and diverse body of evidence supporting the concept that large animals influence the climate change mitigation and adaptation potential of ecosystems. However, the magnitude and nature of herbivore impacts varies biogeographically. In biomes where high aridity and low temperatures constrain nutrient cycling[162,163], herbivores tend to accelerate nutrient cycling[20] and suppress plant biomass production[164] and plant reproduction[33] (Figure 3). In biomes of intermediate productivity and moderate climatic limitation, abiotic disturbances are significant and interact with herbivores to shape community structure and function. The most widespread disturbance agent in these systems is fire, but other agents include wind, flooding, mass movements and pathogens. In very high productivity systems, animals have limited direct impact on vegetation biomass and structure, as herbivore impacts are negated by rapid compensatory regrowth and plants can develop tall canopies inaccessible to large herbivores (Figure 3). However, herbivores still have indirect, longer-term effects through seed dispersal, lateral nutrient transfer (e.g. oceanic-continental nutrient pump), community composition and demographic filtering (Figure 1). Thus, in any particular ecosystem, the net effect of large animal wildlife on climate change mitigation and adaptation depends on the sum and interaction of the processes described above and on the underlying local trends caused by rapid global change.

Based on these patterns, we illustrate how the predicted effects of large animals could play out in three terrestrial ecosystems (Figure 4 and Table 1) and three marine ecosystems (Figure 5 and Table 1). The tundra biome (Figure 4) is an example of a system where abiotic constraints (cold) limit ecosystem function. When large herbivores are present in these areas, they constrain woody plant encroachment and enhance

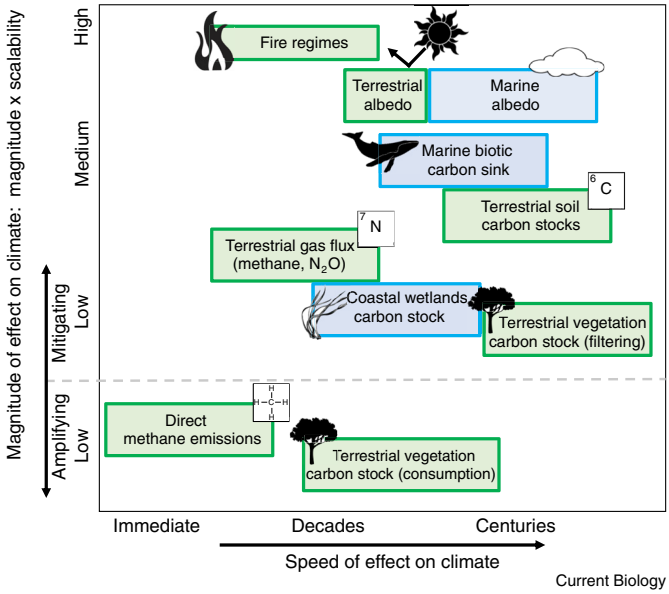


Figure 6. The magnitude and speed of potential climate mitigation effects.
A schematic of the distribution of wildlife-mediated climate mitigation actions in terms of magnitude of potential impact (a product of magnitude of local effect and scalability of the intervention), and the speed at which climate-relevant effects would appear. Box position on the x-axis represents the time at which effects might begin, not the total temporal span of an effect. Placement of each mechanism is approximate and intended to show the magnitude and scalability relative to other mechanisms. Optimal interventions are in the upper middle, where they have high scalability and are likely to have noticeable effects by the mid-21st century. Note that these phenomena affect each other and any intervention would be expected to simultaneously affect multiple factors (Figure 1). As the mitigation effects arise from interventions aimed at individual ecosystem features, this figure provides a summary of the detailed, ecosystem-level descriptions of these processes in Tables 1 and S1.

forb and graminoid (flowering plants, including grasses, sedges and rushes) plant communities[165]. This mitigates climate warming through increased albedo, lower methane to CO_2 emission ratio, increased soil carbon storage and reduced snowpack insulation, which preserves permafrost. Overall, the tundra biome shows some of the strongest climate change mitigation and adaptation effects from large animal wildlife (Table 1), and given the positive feedback between large herbivore presence and the grazer carrying capacity of these systems[40], climate mitigation potential in this biome may be substantially underestimated[58].

Although clearly ecologically distinct from tundra systems, the open ocean also has strong abiotic constraints. In this biome large animals affect climate change mitigation and adaptation through distinct mechanisms: through their role as a nutrient source for abyssal benthic ecosystems and surface waters[130], by enhancing the ocean biotic carbon pump, and possibly by contributing to cloud formation and atmospheric albedo[110,166] (Figure 5).

The temperate woodland biome (Figure 4) is an example of a high-productivity system. The ratio of closed to open vegetation communities in these landscapes, and hence the landscape's carbon storage, as well as the stability and dynamics of the floodplain and peri-aquatic systems, partly depend on the large herbivore and predator guild assemblages, abundance, spatial preferences and interactions[70,133,167,168]. In productive coastal marine systems, much like the productive terrestrial systems, large animals shape the autotroph community and carbon stocks through grazing, disturbance and nutrient cycling[169–173] (Figure 5). The savanna biome (Figure 4) is an example of a biome where large animal impact varies along a rainfall gradient. Herbivores reduce woody plant survival, recruitment and biomass[32], reduce fuel loads and break up fuel layer continuity[174]. Large animals may also reduce woody expansion, lowering above-ground vegetation carbon stocks, but also promoting a shift to higher carbon storage belowground in the semi-arid and mesic conditions of this biome[175–177]. In summary, the position of a biome along the environmental axes of abiotic constraints, abiotic disturbance, and primary productivity, (Figure 3), represented by the tundra and open ocean, savanna, and temperate woodland and coastal biomes, respectively (Figures 4 and 5), affects the magnitude and type of influence large animals may have on climate-change-relevant ecosystem processes.

Aligning climate change mitigation and adaptation with conservation and restoration

Large animals and climate change mitigation

We show in the first section of the review ('Large animals influence the climate change mitigation and adaptation potential of ecosystems') that there is not a ubiquitous positive synergy between large animal conservation and climate change mitigation, and there are many areas where the climate change mitigation potential of large animals is unclear, or species or context-dependent. However, we also show that there are some biomes and mechanisms of large animal influence on climate, where there seems to be consensus that ecologically functionally important populations of large wild animals are likely to beneficially impact climate change mitigation. Specifically, the mechanism–biome pairs where it appears animals can have the greatest climate change mitigation impacts are: previously low-flammability biomes with a new or intensifying fire regime, such as mesic grassy biomes, arid biomes where grasses are invading (Figure 4) or warm temperate woodlands (Figure 4); surface albedo impacts in systems where there is potential to shift from closed canopy to open canopy systems, especially at higher latitudes with long periods of snow on the ground (Figure 4); and through ecosystem carbon stabilisation through a shift towards belowground carbon pools in temperate, sub-tropical and tropical grassland ecosystems (Figure 4 and Table 1).

Large animals and ecosystem adaptation to climate change

While the climate mitigation benefits of large animals can be nuanced and context-specific (Table 1), there is a larger body of evidence on how large animals can make major contributions to ecosystem adaptation to climate change. The main mechanisms through which large animals influence climate change adaptation are: first, impacts on vegetation structure and linked biophysical properties of ecosystems, plant dispersal and

increases in ecosystem complexity and habitat heterogeneity. Specifically, some animal-induced changes in vegetation structure can moderate local microclimates by increasing surface evaporative cooling, aerodynamic roughness, shade, and environmental and microclimate heterogeneity. Second, wildlife-facilitated dispersal and establishment of plants can enhance plants' ability to track changing climates. Third, heterogeneous habitats have more microhabitats and microclimates above- and belowground where species may persist, at least temporarily, despite climate change. Habitat heterogeneity may also moderate fire regimes. Finally, complex multitrophic ecosystems are more likely to show resilience of ecosystem processes to environmental change, because of greater redundancy in trophic pathways and a mixture of top-down and bottom-up controls on ecosystem composition and function[178]. It is important to note that there is a need for greater understanding of the contexts in which large animals enhance ecosystem resistance and resilience to climate change, and where they enhance transformative adaptation, and which of these outcomes is more desirable under different degrees of local climate change.

Magnitude and timescale of climate change mitigation and adaptation effects

A key difference between consideration of climate mitigation versus adaptation is one of scale. In most cases (e.g. carbon sequestration, trace gas emissions), the climate change mitigation potential of an ecosystem intervention is only tangible if it is scalable to regional or global scales[12,179,180]. Thus, the significance of climate mitigation is a function of both the local magnitude of the climate mitigation effect and the potential for the ecosystem intervention to be scaled. Climate mitigation interventions that are prioritized should have the potential to provide substantial beneficial mitigation outcomes on a short to medium timescale, i.e. the next few decades to half-century, the timescale of reaching peak warming under IPCC 1.5°C and 2°C scenarios[181]. The positive mitigation interventions most likely to have high magnitude of impact and potential for scalability are those affecting fire regime, terrestrial and marine albedo, and terrestrial carbon stocks (Figure 6). Importantly, climate adaptation actions are not so contingent on scalability: adaptation yields tangible benefits even if only occurring at the local scale, although the larger the area it is applied to, the more significant a contribution it can make to safe-guarding biodiversity under climate change, for example by increasing metapopulation size and spatial connectivity[131].

Although this review has identified a number of potential 'win–win' climate change and animal conservation interventions, there are also important biodiversity conservation and restoration outcomes that are not linked to, or that run counter to, climate change mitigation or adaptation. While it is important to highlight synergies where they exist, it is also important to recognize that the responsibility for tackling climate change does not lie with the natural world, and a misalignment with climate change mitigation or adaptation efforts does not suggest a biodiversity conservation goal should be abandoned[182]. Moreover, it is fundamentally important to consider local human community requirements and welfare when considering conservation interventions, including identifying direct benefits to human communities from wildlife, such as reduction of catastrophic fire or flood, as well as strategies for minimisation of human–wildlife conflict. Thus, when prioritising conservation action, it is important to evaluate projects on a wide range of metrics, including climate change mitigation and adaptation, biodiversity conservation and restoration, ecosystem services protection and enhancement and Sustainable Development Goals.

Outlook

There are several areas where the climate benefits of large animals are potentially substantial, but more research is needed to understand the key processes and magnitude of effects. For example, fertilization of phytoplankton productivity by large marine animals may increase the biotic carbon sink, aerosol generation rates and cloud regimes, but a clear empirical demonstration of such effects remains elusive[49]. Similarly, large marine animals may have positive effects on benthic carbon stocks[76,183], but again there is a lack of clear evidence. In terrestrial systems, there is evidence that large animals can limit the spread of novel fire regimes (e.g. fire in tundra peatlands, or in humid tropical forests) and reduce thawing of permafrost, but more evidence is needed to determine whether large animals can reduce the climate change-induced risk of carbon emissions from these processes at scales significant to the Earth system. Soil carbon effects of large animals are also poorly quantified, especially away from temperate open ecosystems, and in deep root inputs and mineral associations[53,184]. In addition, non-trophic effects, such as compaction and bioturbation by animals and their associated soil fauna, may have important climate change mitigation or adaptation effects[62,73], but are poorly understood. Finally, in both terrestrial and marine ecosystems, understanding the consequence of large animals for ecosystem adaptation (resistance, resilience or transformation) is a priority for research, including the direct effects on microclimate, ecosystem functions, and stability.

The complexity of ecosystem interactions and the large number of outstanding research questions highlight a clear need to build a more solid evidence base by establishing protocols for monitoring conservation interventions. Many animal restoration and protection initiatives are being established with claims of providing synergistic biodiversity and climate benefits. This is an opportunity to establish rigorous and hypothesis-focused evaluation of which interventions are effective, and which contexts provide a high probability of successful outcomes[185,186]. In addition to empirical studies focused on building the evidence base, a logical step forward would be the development of models incorporating both biodiversity and climate change measures, as well as realistic representations of large animal impacts. The first generation of Earth system models that incorporate animals have begun to appear, e.g.[187], but these models do not yet effectively simulate the key processes and dynamic feedback effects we outline in this paper. These are needed to reliably explore the climate change mitigation and adaptation outcomes of restoration scenarios with and without large wild animals on the timescales of decades to centuries.

Climate change and biodiversity decline are the two major environmental challenges of our time, and they are interwoven. The linkages between these two challenges are usually only explored through the lens of vegetation; animals tend to be largely invisible in our framing and in explicit modelling of Earth system function. We have explored how one particularly

vulnerable and functionally important type of animal (large animal wildlife) can influence climate change mitigation and adaptation. This holistic and multitrophic view of ecosystem functioning provides additional evidence for the importance of maintaining and restoring large wildlife diversity and abundance.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.01.041.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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