

## REVIEW SUMMARY

## CARBON CYCLE

# Animals and the zoogeochimistry of the carbon cycle

Oswald J. Schmitz\*, Christopher C. Wilmers, Shawn J. Leroux, Christopher E. Doughty, Trisha B. Atwood, Mauro Galetti, Andrew B. Davies, Scott J. Goetz

**BACKGROUND:** Modern advances in remote-sensing technology are providing unprecedented opportunities to accurately measure the global distribution of carbon held in biomass within ecosystems. Such highly spatially resolved measures of biomass carbon are intended to provide an accurate inventory of global carbon storage within ecosystems. They are also needed to test the accuracy of carbon cycle models that predict how global changes that alter biogeochemical functions—such as carbon assimilation via photosynthesis, carbon losses via plant and microbial respiration, and organic matter deposition in soils and sediments—will affect net ecosystem carbon uptake and storage. Emerging ecological theory predicts that wild animals stand to play an important role in mediating these biogeochemical processes. Furthermore, many animal species roam widely across landscapes, creating a spatial dynamism that could regu-

late spatial patterning of vegetation biomass and carbon uptake and soil carbon retention. But such zoogeochimical effects are not measured by current remote-sensing approaches nor are they factored into carbon cycle models. Studies are now providing new quantitative insights into how the abundance, diversity, and movement of animal species across landscapes influence the nature and magnitude of zoogeochimical affects. These insights inform how to account for animals in remote-sensing applications and in carbon cycle models to more accurately predict carbon exchange between ecosystems and the atmosphere in the face of global environmental change.

**ADVANCES:** Zoogeochimical effects have been measured using manipulative experiments that exclude or add focal wild animal species or along landscape gradients where animal abun-

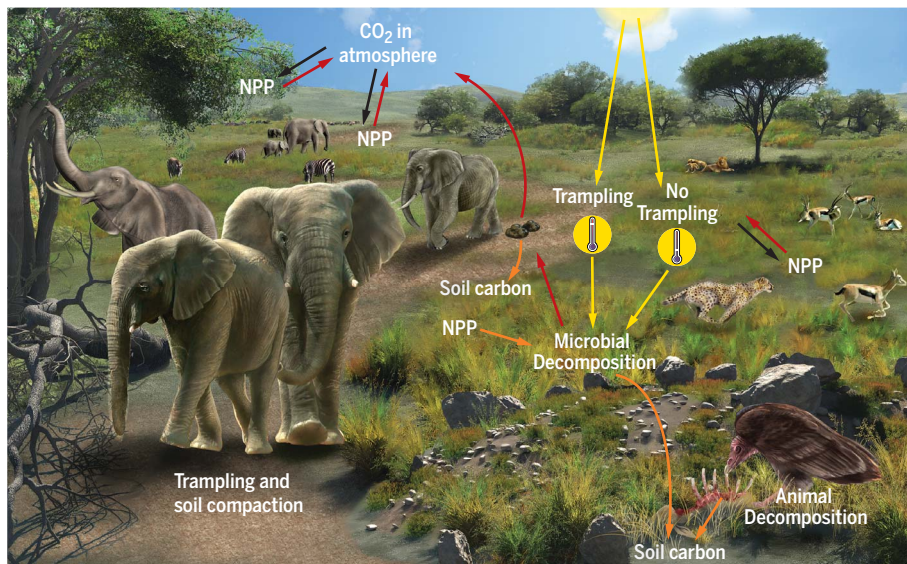
dances or diversity vary naturally. Our review of these studies, which cover a wide diversity of taxa (vertebrates and invertebrates and large- and small-bodied organisms) and ecosystems, reveals that animals can increase or decrease rates of biogeochemical processes, with a median change of 40% but ranging from 15 to 250% or more. Moreover, models that embody zoogeochimical effects reveal the potential for considerable under- or overestimates in ecosystem carbon budgets if animal effects are not considered. The key challenge, in light of these

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findings, is comprehensively accounting for spatially dynamic animal effects across landscapes. We review new developments in spatial ecosystem ecology that offer the kind of analytical guidance needed to link animal movement ecology to geospatial patterning in ecosystem carbon uptake and storage. Considerations of animal movement will require highly resolved spatially explicit understanding of landscape features, including topography, climate, and the spatial arrangement of habitat patches and habitat connectivity within and among ecosystems across landscapes. We elaborate on advances in remote-sensing capabilities that can deliver these critical data. We further review new geospatial statistical methods that, when combined with remote-sensing data and spatial ecosystem modeling, offer the means to comprehensively understand and predict how zoogeochimical-driven landscape processes regulate spatial patterns in carbon distribution.

**OUTLOOK:** There is growing interest to slow climate change by enlisting ecological processes to recapture atmospheric carbon and store it within ecosystems. Wild animal species are rarely considered as part of the solution. Instead, it is often held that managing habitat space to conserve wild animals will conflict with carbon storage. Our integrative review offers a pathway forward for deciding when and how conserving or managing a diversity of animal species could in fact enhance ecosystem carbon uptake and storage. Such understanding informs international climate and biodiversity initiatives such as those described by the United Nations Convention on Biological Diversity and national biodiversity strategies and climate action plans. All of these initiatives require better resolution of how biodiversity effects on ecosystem structure and biogeochemical functioning will become altered by global change. ■



**The myriad animal zoogeochimical effects on carbon cycling.** Animals can mediate net carbon sequestration by plants (net primary productivity, NPP) by altering CO<sub>2</sub> uptake into (black arrows) and from (red arrows) ecosystems. Herbivore grazing and tree browsing can alter the spatial distribution of plant biomass. Predators can modify herbivore impacts via predation and predator-avoidance behavior. Animal trampling compacts soils and alters soil temperatures by changing the amount of solar radiation reaching soil surfaces (yellow arrows). Animals also change the chemical quality of organic matter that enters the soil pool (orange arrows).

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Predicting and managing the global carbon cycle requires scientific understanding of ecosystem processes that control carbon uptake and storage. It is generally assumed that carbon cycling is sufficiently characterized in terms of uptake and exchange between ecosystem plant and soil pools and the atmosphere. We show that animals also play an important role by mediating carbon exchange between ecosystems and the atmosphere, at times turning ecosystem carbon sources into sinks, or vice versa. Animals also move across landscapes, creating a dynamism that shapes landscape-scale variation in carbon exchange and storage. Predicting and measuring carbon cycling under such dynamism is an important scientific challenge. We explain how to link analyses of spatial ecosystem functioning, animal movement, and remote sensing of animal habitats with carbon dynamics across landscapes.

Understanding the biogeochemical processes and feedbacks regulating carbon uptake and storage within ecosystems is key to predicting and managing atmospheric CO<sub>2</sub> concentrations and the rate and extent of climatic change (1–3). Concerted efforts, abetted by modern advances in remote-sensing technology, are providing unprecedented opportunities to accurately measure the global distribution of carbon held in biomass within ecosystems (3–5). Such highly resolved measures of spatial variation in biomass carbon are needed to provide an accurate inventory of global carbon storage within ecosystems (5, 6) and reliably test and refine carbon cycle models used to make predictions about the relationships between ecosystem structure, biogeochemical functioning, and carbon storage (2).

Contemporary carbon cycle models have largely evolved [e.g., (3, 7, 8)] under the assumption that carbon uptake and allocation to biomass is controlled by nutrient and water limitation, microbial mineralization of organic matter and weathering of geological parent material, and climate and hydrological regimes. The models account for carbon that is distributed in live plant biomass, plant detritus, and organic matter

entering soils by characterizing fundamental biogeochemical processes driving ecosystem carbon exchange and storage. These processes include carbon assimilation via photosynthesis, losses via autotrophic (plant) and heterotrophic (microbial) respiration, and organic matter deposition in soils and sediments.

Carbon cycle models typically do not, however, account for the biomass or effects of animals (herbivores and carnivores) in higher trophic levels of ecosystems. Granted, herbivores and carnivores in many ecosystems tend to be progressively less abundant (by orders of magnitude) than plants, owing to low transfer efficiencies of nutrients and carbon from plants to these higher trophic levels (5, 9, 10). The existence of such a pyramidal trophic structure has led to the reasoning that animals are entirely dependent upon the availability of plant biomass. Furthermore, their comparative rarity makes it unlikely that they will exert strong feedback control on ecosystem processes (9, 10). Hence, it may seem reasonable to assume that animals are unlikely to have substantial effects on biogeochemical processes and carbon storage, and consequentially construct the carbon budget without considering their contributions (6). But animals can cause important positive and negative feedback effects that alter the trophic structure of ecosystems (11) and, furthermore, may influence carbon cycling (9, 12) despite their comparatively low biomass representation within ecosystems. Failure to account for these feedbacks could result in under- or overestimates in the capacity of ecosystems to take up and store carbon (Fig. 1).

Until very recently, most studies measuring animal feedback effects have focused on herbivores. Numerous studies have experimentally measured the amount of plant biomass that is

removed by herbivores and attendant changes in plant species composition, inferring how such changes influence the fate of carbon in ecosystems (13). However, herbivorous and nonherbivorous animals are hypothesized to influence carbon cycling via many other mechanisms that affect ecosystem biogeochemical processes and properties directly (9, 12). These influences, which we call zoogeochemical effects, include mediation of carbon uptake via photosynthesis, autotrophic and heterotrophic respiration, and soil organic matter deposition and alteration of the physical and chemical properties of organic matter and soils and sediments.

We review here studies that have explicitly measured the zoogeochemical effects by a diversity of animal taxa (vertebrates and invertebrates and large- and small-bodied organisms) in several ecosystems globally. Additionally, animals can control the magnitude of carbon exchange with soil reservoirs, influencing both short- and long-term carbon turnover rates (Fig. 1). Such zoogeochemical effects are not measured by current remote sensing, nor are they included in carbon cycle models (2), and therefore contribute to critical uncertainties about the fate of carbon in key global reservoirs. This currently limits our ability to accurately calculate carbon budgets and predict future climate change. We show how to overcome this limitation by reviewing recent efforts to estimate the implications of changes in animal species abundance on regional carbon budgets.

A further consideration is that many animal species roam widely across landscapes (14). Animal movements create a spatial dynamism that connects geographic locations across landscapes via active transport of nutrients and seeds and temporal variation in the location and abundance of herbivores and carnivores. Disrupting animal movements can alter the spatial patterning of plant and animal biomass across landscapes and trophic controls over ecosystem functioning (14–17). These spatial effects are not embodied in conventional carbon cycle models (3, 7, 8) or carbon inventories (5). If lessons from historical losses of large migratory animals are any indication, these spatial effects need to be included because they can be large (18). It is estimated that population reductions and extinctions of large migratory mammals during ancient and more modern times in Earth's history have resulted in alterations of global methane emissions to the atmosphere by 0.8 to 34.8% (18). Attendant changes in land surface cover affecting both global atmospheric CO<sub>2</sub> concentrations and biophysical properties such as albedo or evapotranspiration have been noted as well (19, 20). Modern global environmental changes such as habitat fragmentation and land-use conversion continue to alter the composition and abundance of animal species in many ecosystems (21) and change the extent and geospatial locations of their movements across landscapes (22). Evidence shows that such loss and disruption of movement introduces the risk that ecosystems could even flip from being carbon sinks to sources (Fig. 1). To address this uncertainty, we review recent modeling efforts that can be used

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to integrate zoogeochemical effects with carbon models and budget estimates. We further discuss model developments that include animal movement ecology, using case examples to show how such integration can deepen understanding of carbon cycling in the face of global environmental changes. Ultimately, we offer insights about how to link animal spatial ecology, ecosystem modeling,

and remote sensing—the kind of integration that is needed to improve the ability to accurately predict and manage the carbon cycle across landscapes.

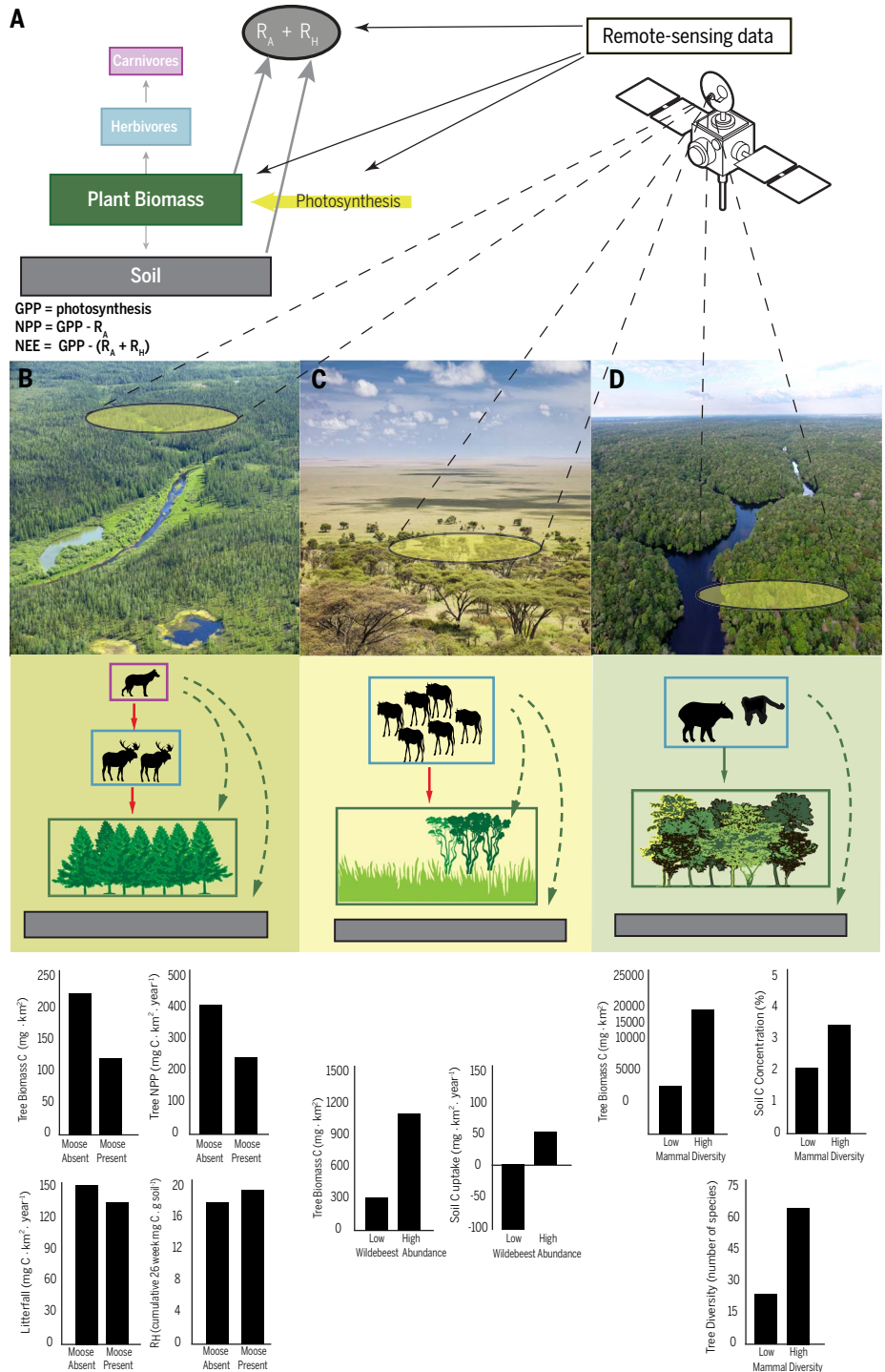
**Mechanisms and magnitudes of animal effects on ecosystem carbon balance**

Fundamentally, zoogeochemical effects become manifested as a consequence of direct and indi-

rect interactions among carnivores, herbivores, and plants within food chains in ecosystems (9, 12, 13). Herbivorous animals directly remove plant biomass, assimilate some of the embodied nutrients and carbon to build animal biomass through growth and development, and release additional carbon to the soil via egestion and to the atmosphere via respiration (9, 12). Herbivory

**Fig. 1. Remote sensing does not measure important animal controls on landscape carbon.**

**(A)** Modern remote-sensing methods measure biogeochemical processes, including plant carbon uptake via photosynthesis and autotrophic ( $R_A$ ) and heterotrophic ( $R_H$ ) respiration, and inventory standing biomass carbon across landscapes. These measures can be used to estimate landscape-scale carbon cycle processes, including GPP, NPP, and NEE, which is information used to test carbon cycle models and construct carbon budgets. These methods focus on the plant trophic level (green) and do not include the biogeochemical contributions of herbivore and carnivore trophic levels (blue and purple, respectively) that tend to be less abundant in ecosystems. Remote sensing also cannot measure carbon storage in the soil reservoir (gray). **(B to D)** Animals directly (solid arrows) and indirectly (dashed arrows) control carbon dynamics in ecosystems through trophic interactions that reduce plant and animal biomass (red arrows), which ramify to have positive indirect effects on carbon uptake and storage in plants and in soil reservoirs. Failing to account for animal effects can lead to biases in carbon accounting. Consideration of animal effects will become increasingly important as global environmental changes such as land conversion, habitat loss, and exploitation stand to alter animal abundances and impacts across landscapes. Loss of predators such as wolves from boreal forest ecosystems (B) can lead to a rise in moose herbivore abundances, leading to declines in forest tree biomass and soil carbon storage (gray box). Loss of migrating grazing wildebeest herbivores in savanna ecosystems (C) can lower grazing pressure and lower soil carbon (gray box), owing to a concomitant rise in the frequency and extents of wildfires that consume combustible standing grass and woodland biomass. Loss of large mammal frugivores and attendant reduction in dispersal of large seeds in tropical forests (D) can lead to changes in tree community composition via reduction in abundance and biomass production of carbon dense trees (trees with black shading). Data from experimental and observational analyses (as shown in the graphs) reveal that variation in animal abundances can lead to large variation in carbon exchange and storage, sometimes even causing ecosystems (e.g., savanna) to switch from being carbon sources when animals are not abundant to becoming carbon sinks when they are highly abundant. **C.** carbon. Data were obtained from the following references: (B) boreal forest (28), (C) savanna (15), and (D) tropical forest (36). [Photos (from left to right): Serg Zastavkin/Shutterstock; mdd/Shutterstock; Costa Rodrigues/Shutterstock. Images: Vertyr/Depositphotos (African tree); Sonechko/Depositphotos (trees and grasses); airin.dizain/Depositphotos (wildebeest); YurikswO/Depositphotos (moose); Cundrawan703/Depositphotos (wolf)]



leaves less plant biomass available for photosynthesis, and plant stress from herbivore damage may further decrease plant photosynthetic rates and increase rates of autotrophic respiration ( $R_A$ ) and heterotrophic respiration ( $R_H$ ), all of which could decrease net primary productivity (NPP) and alter net ecosystem carbon exchange (NEE). Herbivores may also selectively feed on different plant species, thereby potentially altering the plant diversity and carbon density of standing biomass, given that plant species vary in their capacity to fix carbon and allocate it toward structural tissue and antiherbivore defense (9, 12). Predators, through direct interactions with herbivore prey, could reverse the effects of herbivores. By reducing herbivore abundances and by causing changes in herbivore behavior and physiology, predators can have indirect effects on plant biomass, photosynthesis, and respiration, ultimately affecting NPP and NEE and fluxes of  $CO_2$  and  $CH_4$  between ecosystems and the atmosphere (12, 13). Frugivorous animals disperse consumed seeds during the course of their movement, thereby determining the spatial distribution and diversity and abundance of plant species that take up and store carbon within ecosystems. Large animals can further influence ecosystem processes by trampling and compacting or perturbing soil surfaces and sediments, which can alter surface temperatures and chemical reactions that enhance soil or sediment carbon retention or exacerbate carbon release. Finally, animals can influence soil or sediment microbial activity by altering the amount and chemical content of organic matter that becomes available to microbes for decomposition (12, 13).

Resolving the magnitude of zoogeographical effects requires the use of manipulative experiments that systematically exclude or add focal animal species or of observational studies that take advantage of variation in natural animal abundance across landscape locations. We searched (23) the published literature for studies that fit the dual criteria of (i) having measured wild-animal effects explicitly on biogeochemical processes using (ii) experimental animal removals or additions, or systematic analyses across gradients of animal abundances or diversity. Studies that met these criteria reveal that animal effects are consistent with the various hypothesized mechanisms (Fig. 2).

Herbivore exclusion experiments show that animals can affect carbon dynamics by changing the species composition of the plant community—including tundra herbs and shrubs, saltmarsh grasses, and boreal and tropical forest trees—by selectively foraging. Individual cases show herbivore effects ramify by triggering changes in any or all of the following: above- and belowground plant biomass allocation, photosynthesis (gross primary production, or GPP) and NPP, and ecosystem respiration rates ( $R_A + R_H$ ). In some cases, such as muskox in arctic mire and geese and hares in tidal saltmarshes (Fig. 2), herbivore presence enhances  $CO_2$  uptake and carbon storage by 20 to 25% (24, 25). Large grazers furthermore can protect carbon in sediments by changing physical

and chemical processes (e.g., redox potential as a measure of organic matter decomposition and microbial carbon mineralization) via compaction from trampling (24). But in other cases—such as caribou, muskox, and geese in the arctic; marmots, mice, and invertebrates in alpine meadows; and moose in boreal forests—grazing and browsing herbivores cause a 15 to 70% decrease in  $CO_2$  uptake (Fig. 2) by altering plant community composition, photosynthetic rates, and ecosystem respiration (26–29). Some cases, such as muskox in arctic mire and barnacle geese in arctic wet meadows (Fig. 2), reveal that animals can have conflicting positive and negative effects on different biogeochemical processes and properties. For example, muskox-caused  $CH_4$  release could offset any gains in carbon storage owing to their enhancement of  $CO_2$  uptake, and barnacle geese enhance soil carbon retention despite reducing  $CO_2$  uptake by plants (25, 30).

Manipulating the trophic structure of ecosystems shows that predators can reverse the effects of herbivores (Fig. 2). In grasslands, grasshoppers cause a 17% reduction in  $CO_2$  uptake, relative to experimental controls that contain only plants. As with vertebrate herbivores, the grasshoppers modify the plant community composition, which cascades to alter NEE through changes in rates of photosynthesis and whole-ecosystem respiration (31). The addition of spider predators, which control grasshopper foraging, more than reverses the grasshopper effect by increasing  $CO_2$  uptake by 46% (Fig. 2). The net effect of predators is that the fully intact food chain causes 22% more  $CO_2$  uptake than experimental plant-only control conditions in which there are no animals. In humic lakes, zooplankton feed on methanotrophic bacteria—bacteria that consume and metabolize methane as their carbon source for energy—with the consequence that lakes emit  $CH_4$  to the atmosphere (32). The reduction of zooplankton abundance after experimental introduction of zooplanktivorous perch caused a 50% reduction in  $CH_4$  emission (Fig. 2) by releasing the bacteria from heavy consumption by zooplankton. In other experimental systems (freshwater ponds and streams), predatory stickleback fish and stonefly insects enhance carbon capture and retention by 88 to 90% (Fig. 2). Here, predation on zooplankton and macroinvertebrates increases algal  $CO_2$  uptake for production, thereby reducing the concentrations of dissolved inorganic carbon in the water column that could otherwise be released to the atmosphere (33). Food chain interactions in lakes can also modulate  $CO_2$  exchange in ways that depend on the number of predatory trophic levels present (Fig. 2). In three-trophic-level lakes containing minnow predators, zooplankton prey, and algae, minnows controlled the abundance of zooplankton, releasing algae from zooplankton grazing (34). The addition of bass predators to create a four-trophic-level system in which bass prey on minnows reversed this effect, resulting in more zooplankton and less algal biomass (34). Although lakes tend to be a net source of  $CO_2$  to the atmosphere, the three-level system emitted 27% less  $CO_2$  than the four-

level system. The strength of this effect varied, however, with the level of nutrient supply. Nutrient enrichment, which enhanced algal production, magnified the difference in  $CO_2$  exchange between the two kinds of systems. The effect of nutrient enrichment of algal production along with predator control of algal-feeding zooplankton meant that the three-level system became a net  $CO_2$  sink. The four-level system became net carbon neutral. Consequently, there was 90% less  $CO_2$  retained in the lake in the presence of bass than in their absence (Fig. 2).

Manipulative experiments have been completed within small spatial extents—most on the order of tens to hundreds of square meters but sometimes reaching up to several hectares—because of logistical constraints imposed by the need to physically control for animal presence or absence and extraneous environmental variables, and to make precise measures of carbon storage and exchange. This inevitably begs the question of whether the insights are scalable to the large spatial extents needed for management to make a difference in the carbon budget but also scalable to the extent that variation in the magnitude of biophysical environmental factors could swamp out any animal effect. Observational studies that have measured animal effects across larger spatial extents of entire ecosystems reveal that the insights about mechanisms and magnitude of effects are indeed scalable.

Grazing halos, patches largely devoid of seagrasses and macroalgae, surround many coral reef patches globally. They are large and ubiquitous enough to be detected by high-resolution remote sensing (35). Analyses in a  $\sim 10\text{-km}^2$  area near Heron Island in Australia's Great Barrier Reef revealed that predators can cause the appearance of these halos by altering foraging behavior of herbivorous fishes (35). Sharks persistently cruise hunt near the reef patches. The perceived threat of predation causes herbivorous fish to feed heavily near the coral patches, staying in close proximity to the escape cover afforded by the coral. As a consequence, the highly grazed halos have lower vegetation canopy height and cover and, hence, 24% less carbon stored in their sediments than do areas beyond the halos that have little or no grazing impact (35).

Wildebeest in the 25,000- $\text{km}^2$  Serengeti savanna-woodland were decimated by disease and poaching before the 1960s, reducing their numbers from about 1.2 million to 300,000 animals (15). In turn, the accumulated, ungrazed aboveground vegetation fueled wildfires that consumed 80% of the ecosystem annually, leading to a net release of  $CO_2$  to the atmosphere. Disease management and anti-poaching enforcement over the ensuing decades has led to wildebeest population recovery, reducing the extent and intensity of wildfires (15). Wildebeest grazing is now causing a large fraction of carbon from combustible aboveground plant biomass to be released as dung that becomes incorporated by insects into soil reservoirs that are not prone to burning. The recovered grazing regime restored the Serengeti as a net  $CO_2$  sink—estimated to be large enough today to offset all of east Africa's annual fossil fuel  $CO_2$  emissions (9)—by

facilitating carbon capture and build-up in soil reservoirs and in savanna-woodland regrowth (15).

Conserving mammal species diversity in tropical forests maintains a diversity of functional roles—including frugivory and seed dispersal that supports tree reproduction, herbivory that modulates plant production, and provisioning of organic matter for soil storage—that are all functionally related to carbon capture (36). Consequently, carbon retention in woody biomass and in soil increases by 230 to 400% across a 3.5-fold increase in mammalian species diversity (Fig. 2). This effect of animal diversity is detectable across a 48,000-km<sup>2</sup> area despite considerable background spatial variation in biophysical properties across the landscape (36).

Sea otters can enhance carbon uptake within a 12,000-km<sup>2</sup> stretch of western North American coastal marine kelp forests by 1100% via the same mechanisms observed in small-scale trophic manipulation experiments (Fig. 2). Sea otters enhance kelp biomass carbon retention by preying on sea urchins that decimate coastal marine kelp forests (37).

The gathered evidence shows that animals can have both positive and negative impacts on biogeochemical processes driving ecosystem carbon uptake and storage, with a median change of 40%, relative to conditions without the focal animal present. Hence, animal effects on ecosystems should not be assumed to be negligible. Moreover, human impacts are increasingly causing multiple animal species to be lost from ecosystems—called defaunation (21)—as a result of poaching and overfishing, culling to reduce human-wildlife conflicts, illegal trade, logging, and habitat loss due to conversion to other land uses. Humans also have restored animal species to ecosystems, with a push to restore more—called rewilding (38). Estimates of the potential effects of species losses or rewilding on regional ecosystem carbon budgets reveal that they may not be trivial and may even have unintended consequences.

**Changes in animal species and regional carbon budgets**

In neotropical forests, large carbon-dense hardwood trees make a sizeable contribution to carbon

uptake and storage. Their successful regeneration across the landscape is predicated on the presence of large frugivorous vertebrates that disperse the large seeds from such trees across long distances. But large frugivores are preferred by hunters and are thus most threatened by overhunting. Simulation analyses evaluated the effects of systematically losing large-bodied seed-dispersers, relative to random extinctions of any seed-dispersing vertebrates and found that such losses could alter the community composition of trees with different carbon storage traits (wood density, tree diameter, and tree height) with implications for aboveground carbon stored in tree biomass within the Atlantic forest region (39). The loss of trees dispersed by large-bodied frugivores (39) revealed a potential reduction in carbon storage capacity of 4 to 37% (40). Similar magnitudes of effect have been estimated for other forested regions of the Amazon (41). The erosion of carbon storage capacity via shifts in tree species composition can persist up to 100 years after defaunation (42), and smaller frugivores that are less preferred by hunters are unlikely to substitute



**Fig. 2. Animal zoogeochemical effects in ecosystems.** Experiments that exclude focal animals and observational studies across a range of focal animal species abundances reveal that animals can change the amount of carbon that is stored within ecosystems or exchanged between ecosystems and the atmosphere. Animal interventions in

biogeochemical processes can both enhance (green bars) and reduce (pink bars) the amount of carbon stored in ecosystems. Animal effects can be appreciable, ranging from 10 to 1100%, with a median change of 40%. Data were obtained from (24–37). C, carbon; R<sub>E</sub>, whole-ecosystem respiration.

the seed-dispersal services of their larger counterparts (39).

Analyses comparing effects of simulated declines of large-seeded animal-dispersed trees on carbon storage in woody biomass among African, American, Asian, and Australian tropical forests reveal that animals may not always affect ecosystem carbon balance owing to geographic differences in the dependence of tropical trees on animal seed dispersal. African, American, and South Asian forests, which have high proportions of animal-dispersed tree species, stand to lose their carbon with defaunation (43). Southeast Asian and Australian forests, alternatively, harbor trees that are less reliant on animals to disperse their seeds, and accordingly, defaunation has lesser consequences for forest carbon (43).

Wolves have been highlighted as important predators in North American terrestrial ecosystems, and their restoration has been hailed as a means to restore ecosystem functioning (38). Wolves can have an indirect effect on plant biomass, NPP, and NEE by reducing the abundances and changing the foraging behavior of large herbivores such as moose in boreal forests and elk in grasslands (44). Carbon budget analyses reveal, however, that this single species can propagate different net effects in different ecosystems. In boreal forest ecosystems, wolves control moose populations and thereby reverse the negative effects of moose on NPP and NEE (Fig. 1). Here wolf predation reduces the damage moose inflict on boreal plants—especially deciduous trees that tend to have high NPP and litter production for soil storage (Fig. 1)—thereby changing the plant community composition of the forest ecosystem in ways that enhance carbon storage in soil. Hence, culling wolves to enhance game populations could have a negative impact on carbon storage. Alternatively, in shortgrass prairie, elk stimulate NPP by enhancing nutrient cycling within the ecosystem. Wolves (along with other predators such as bears and cougars) reduce elk density and foraging, which in turn is estimated to reduce both NPP stimulation and NEE. Hence, restoration of wolves with the intention to restore grassland ecosystem functioning (38) can have negative impacts on ecosystem carbon balance. Estimates show that the strength of this effect should vary, however, with background soil-nutrient level. In nutrient-poor environments, wolf predation should reduce NEE by 78%, whereas in nutrient-richer environments, it should be reduced by 52% (44).

The ability to construct carbon budgets that account for animal effects for a wider range of species is currently limited by a fragmentary understanding of the biogeochemical effects of any given animal species (Fig. 2). This is because empirical studies have tended to measure only one to a few of the full complement of zoogeological processes operating in any one system. Moreover, a given animal species can have both positive and negative impacts on different process within a system (Fig. 2). Hence, the total net effects of any particular animal species on carbon balance remain largely unknown. An important research

need is to develop more comprehensive understanding of the net effects of different, and potentially interacting, zoogeological mechanisms on ecosystem carbon balance. This will require confronting complexity due to interplay between myriad animal interactions and feedbacks. Resolving such complexity must be guided by new kinds of ecosystem models that account for animal impacts on plant and animal biomass carbon, NPP,  $R_A$ ,  $R_H$ , and soil organic matter deposition (biomass carbon content of excreta, egesta, and plant litterfall). Models embodying these zoogeological processes hold promise to offer a more complete picture of animal effects on carbon cycling.

### Ecosystem models embodying zoogeological processes

At their core, newer ecosystem models are founded on the conventional compartment structure used in classic ecosystem modeling, including soil elemental pools and plants (Fig. 3A) with the addition of herbivores and predators (45–49). The models capture the essential biogeochemical processes, including elemental uptake by plants from the abiotic environment (i.e., carbon uptake from the atmosphere and nitrogen uptake from soils) and elemental transfer and loss to and from all compartments through trophic interactions, respiration, excretion, egestion, and leaching out of the ecosystem as a result of physical processes. The models embody principles of ecological stoichiometry, namely how organisms and their interactions in ecosystems affect the balance of nutrients and energy. Typically, there is a focus on fluxes and pool sizes of nitrogen and carbon, but the focus could easily be extended to considerations of other important elements such as phosphorus. The models are formulated to obey fundamental mass-balance requirements such that, at equilibrium, elemental inputs to the ecosystem equal elemental losses from the ecosystem plus storage.

One such model has motivated systematic experimental and observational analyses exploring and comparing how two key ways that the top-down effects of predators may affect cycling and thereby modulate the amount of carbon exchanged between ecosystem reservoirs (e.g., soils and plants) and the atmosphere (49). Predators may cause cascading effects by killing and consuming their prey, thereby reducing herbivore biomass and herbivory and causing increased amounts of plant-based carbon to enter soil organic matter storage pools. The mere presence of predators within ecosystems may also cause nonconsumptive fear effects that increase respiratory costs at the expense of production owing to chronic stress (31, 50). Herbivores compensate by switching preferences from plants high in nitrogen to plants higher in soluble carbohydrate carbon (50). This alters herbivore elemental balance via altered uptake from plants and elemental release via respiration, excretion, and egestion. The herbivore diet shift alters the species composition of the plant community and the amount of carbon in senescent plant matter entering the

soil storage pool (50). Active-hunting predators generally cause consumptive effects; sit-and-wait predators cause nonconsumptive effects (50). The feedbacks from predator nonconsumptive effects may be most important to whole-ecosystem elemental stocks, production and efficiency rates, and recycling fluxes by changing the stoichiometric balance of all trophic levels (50).

When parameterized with data from long-term experimentation in meadow ecosystems (49), the model predicts that there should be a 2.5× increase in soil carbon storage across a gradient from sit-and-wait predator dominance to active-hunting predator dominance. This trend has been empirically validated using manipulative experiments and a landscape-scale survey of soil carbon retention among 15 different meadows comprised of spider predators, grasshopper prey, and three functional groups of plants represented by the carbon-dense herb goldenrod (*Solidago rugosa*), nitrogen-rich grasses, and a variety of other herbs (51). Along a gradient of shifting dominance of sit-and-wait predators to a dominance of active-hunting predators, there is a 1.7× increase in aboveground NPP driven by shifts in *Solidago* biomass and, in reasonable agreement with model predictions, a 2× increase in soil carbon retention (51). Biophysical factors such as total live-plant biomass, degree of land-use development around the fields, field age, and soil texture were not significant predictors of the trend in soil carbon retention (51).

### Incorporating spatial dynamics

Most ecosystem models used to predict carbon dynamics are spatially implicit, simply modeling exchanges between ecosystem reservoirs and the atmosphere within a fixed geographic space. But animal movement creates a spatial dynamism that connects geographic locations across landscapes (52–54). For example, beyond their impacts on Serengeti savanna-woodland carbon, migrating wildebeest also affect carbon cycling in the river ecosystems that flow through the Serengeti. Specifically, their mass drowning while trying to ford the Mara River 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 (55). Evidence suggests that the impacts of large terrestrial ungulates on carbon cycling across ecosystems into freshwater environments may be ubiquitous (56). Migratory animals have the potential for large impacts on carbon dynamics across landscapes (14, 57) because they are typically gregarious and directly redistribute large quantities of carbon across landscapes via transport and release during migration. For example, streams with migratory Pacific salmon carcasses have different riparian plant overstory and understory communities than streams without Pacific salmon driving potential differences in riparian forest carbon sequestration (58).

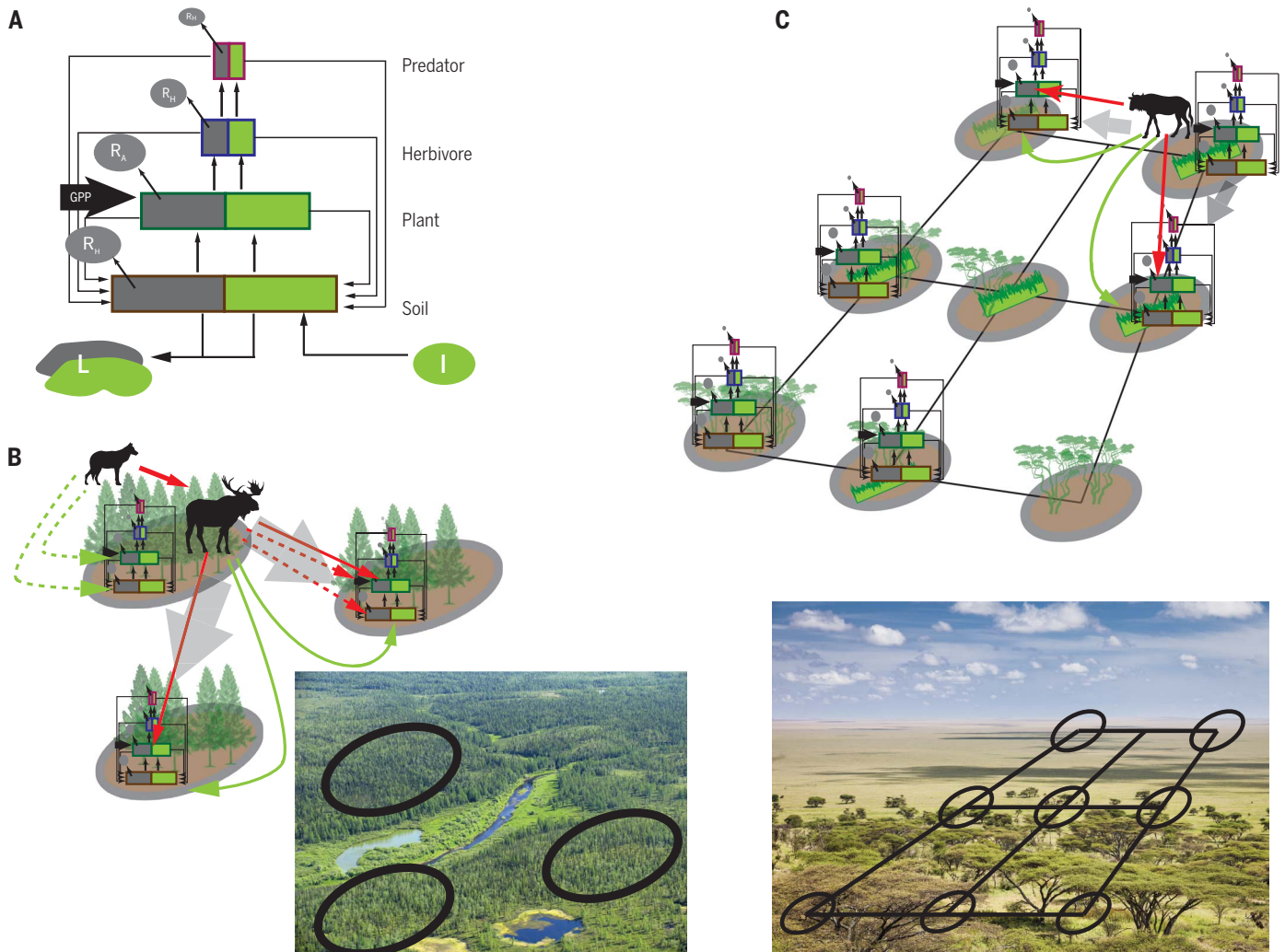
Theory of spatial ecosystem ecology (59–61) has been advanced precisely to begin predicting how animal movement between source and

recipient locations influence the nature and strength of controls over ecosystem functioning within the source and recipient locations (Fig. 3). Different spatial locations could range from different habitat patches arrayed across a landscape within a single ecosystem [e.g., forest patches separated by a developed-land matrix (62)] to different ecosystems arrayed across a broader regional landscape [e.g., grassland and woodland ecosystems (62)]. Animal movement across landscapes can subsidize recipient locations via an influx of new prey or predators, as well as

animal transported nutrients and materials such as nitrogen and phosphorus in dung and urine, or as organic matter in carcasses that are deposited in the recipient locations (59).

This theory predicts that animal subsidies via movement of live animals and transport of nutrients and material into recipient locations can cause a switch in ecosystem functioning, from being controlled predominantly by nutrient supply to largely being controlled by animal effects (59). Empirical synthesis of field experiments and observational studies support the prediction

that animal subsidies can cause switches in trophic control in recipient locations. The strongest, persistent effects came from an influx of nutrients and herbivores (versus influx of predators) into recipient locations (16). These kinds of animal movements and nutrient translocations can be represented in spatial ecosystem theory in a variety of ways, ranging from consideration of landscapes organized as mosaics of multiple patches to lattices parameterized for realistic landscapes (Fig. 3, B and C). In its simplest form, animal effects across landscapes can be



**Fig. 3. Ecosystem modeling to accommodate animal feedbacks and spatial dynamics.** (A to C) General nonspatial ecosystem models (A) consider soil, plant, herbivore, and predator trophic compartments arranged as biomass pyramids. The models account for fluxes of nitrogen (green) and carbon (gray) due to trophic exchange between trophic compartments. The models further include CO<sub>2</sub> uptake by plants (GPP), autotrophic respiration ( $R_A$ ), heterotrophic respiration ( $R_H$ ) recycling fluxes from each trophic compartment to soil, weathering inputs (I) to soil, and leaching (L) from soil. As such, they respect mass-balance requirements of ecosystem functioning. The models can be made spatially explicit by considering landscapes either in terms of patch (B) or lattice (C) configurations, with ecosystem trophic structure and functioning prevalent at each location. Within spatial locations, animals drive ecosystem functioning via direct effects (solid arrows) such as trophic interactions (red arrows) and indirect effects (dashed arrows) mediated

by trophic interactions that can enhance carbon storage in biomass within plant and abiotic compartments. Animals also connect different spatial locations through movement (gray arrows) from source to recipient locations. During such movements, they translocate nutrients to recipient locations (green arrows) or consume nutrients (nitrogen and carbon) contained within biomass in recipient locations (solid red arrows). They thereby can control the amount of biomass carbon that eventually enters and is retained in the soil compartment within a spatial location by changing organic matter inputs and heterotrophic respiration. Net ecosystem carbon exchange and storage is quantified by summing carbon pool sizes and fluxes across the spatial locations. [Photos (left to right): Serg Zastavkin/Shutterstock; mdd/Shutterstock. Images: Vertyr/Depositphotos (African tree); Sonechko/Depositphotos (trees and grasses); airin.dizain/Depositphotos (wildebeest); YurikswO/Depositphotos (moose); Cudrawan703/Depositphotos (wolf)]

represented with distance decay functions [e.g., (63)] or dispersal kernels [e.g., (64)]. More mechanistic representations of animal movement can be built into spatially explicit theory in continuous time with reaction-diffusion equations (65) and in discrete-time with integrodifference equations [e.g., (66)] to characterize the changing influence of animals away from source areas.

An example of the promise of incorporating animal movement effects comes from a parameterized lattice model, representative of the entire Serengeti savanna-woodland landscape (67). The modeled landscape was divided into 10 km-by-10 km cells, to account for grass and woodland distribution based on spatial empirical data on these vegetation groups. The modeling evaluated how movement between cells and feeding by grazing versus browsing herbivores within them could affect the landscape distribution of grass and woodland relative to biophysical drivers of plant distribution such as wildfire and rainfall (67). Simulations revealed that browsers and fire together cause a decline in woodland cover and tree biomass, a negative effect that would intensify if grazers were absent, because large amounts of combustible grass biomass would remain standing across the landscape. Migratory movement in response to rainfall patterns determines grazer presence across the landscape. Hence, grazers play an important role in mediating the strength of impact of fire and browsers across the entire landscape by reducing fuel as they respond to rainfall-driven grass production across the landscape. This creates a feedback that exerts strong effects on spatial patterns of woodland patches (67), thereby explaining the observed measures of landscape-scale variation in carbon capture and storage (15).

### Opportunity to link remote sensing with animal movement and zoogeographical effects

The impacts of animal movement on the global carbon cycle still need to be predicted and quantified. Movement underlies behavioral decisions about where to forage and seek shelter that impact NPP and NEE (68) at multiple scales, ranging from the habitat patch to the home range to migratory destinations. Fundamentally, considerations of animal movement will require a highly resolved spatially explicit understanding of landscape features, including topography, climate, habitat structure, and the spatial arrangement of habitat patches and habitat connectivity within and among ecosystems across landscapes.

Modern remote-sensing technology can deliver highly spatially resolved data on functional and structural properties of vegetation within ecosystems. Light detection and ranging (LIDAR) (69–71), in particular, can provide full three-dimensional characterization of habitat structure, including vertical profiles of cover, biomass, and carbon density, as well as underlying surface topography and integrative metrics of vertical biomass profiles like foliage height diversity (4, 72). When combined with image data, such as those from the Landsat series of satellites,

LIDAR data can provide detailed insight into the topography and spatial arrangement of habitat patches across landscapes (73, 74), which can be related to the spatial distribution and movement of animal species across a landscape (75, 76). Nevertheless, airborne or satellite remote-sensing methods with broad geographic scope (2, 77) are limited in their ability to detect and quantify animal biomass and animal effects, especially nutrient inputs and carbon storage in soil. This underscores the need to develop greater synergy in the use of on-the-ground sampling and remote-sensing methods (2, 78).

As a complement to remote sensing, on-the-ground surveys of animal abundance using spatial capture-recapture approaches (79) and plot sampling of soil biogeochemistry [e.g., (36)] can advance understanding of the dynamism driving the spatially explicit effects of animals. New geospatial statistical methods reveal the promise of quantitatively characterizing biogeochemical landscapes using spatial nutrient and carbon distribution modeling. Outputs from such models could provide the kinds of key data layers (80, 81) needed for spatial ecosystem models to connect animal movements, spatial animal biomass, trophic interactions, and carbon cycling to fundamental landscape attributes (nutrition) that motivate why and where animals move across landscapes [e.g., (67)].

The spatial mapping of biogeochemical landscapes, in combination with data from modern biologging devices (82), offers the means to test predictions of spatial ecosystem models about the net effects of animal movement on nutrient and carbon dynamics in terms of landscape attributes that motivate their movement behavior and interactions with other species. Biologging involves the use of remote sensors that can continuously measure most aspects of an animal's state (e.g., location, behavior, caloric expenditure, and interactions with other animals) and external environment (e.g., temperature, salinity, and depth). Modern technology, such as accelerometers sampling at 16 Hz or faster, can be used to determine the behavior of individual animals (e.g., feeding), whereas Fastloc GPS allows for sub-minute spatial sampling over long time scales (82). This technology facilitates linking measures of animal physiology (and hence nutrient demand) to foraging and movement behavior that is motivated by spatially heterogeneous resource supplies. In addition to landscape context, the spatial distribution of many herbivore prey species is influenced by their fear from perceived predation (34, 49). Ambush predators will often use cover (e.g., areas of higher carbon) to stalk prey, leading prey to disproportionately avoid those areas [e.g., (35, 83)]. Thus, monitoring predator interactions with their prey can offer an understanding of the indirect effects of predators on carbon cycling mediated by herbivore spatial responses to predator presence.

The promise of using remote sensing and on-the-ground sampling to provide the kind of synergy we call for is illustrated by a series of studies combining on-the-ground data on African elephant densities with LIDAR-derived measure-

ments of woody vegetation. Elephants are a dominant driver of vegetation change and treefall in African ecosystems (84–87). Moreover, sex-specific elephant density data revealed that bull elephants, but not breeding herds, surpassed abiotic controls as the dominant driver of change in aboveground carbon stocks, which decreased only where bull densities exceeded 0.5 bulls km<sup>-2</sup> (87). Effects of bull elephants are, however, landscape dependent, leading to decreases in carbon along rivers, at mid-elevations, and on steeper slopes. By contrast, carbon density mostly increases across the rest of the landscape regardless of elephant densities. Data collected from a companion-exclusion experiment further confirmed the dominant role of elephants in driving carbon change, with significantly slower carbon gains occurring only where elephants had access to woody vegetation.

This elephant study, along with examinations of wildebeest impacts in savanna (15, 67), provides a blueprint for the new kinds of multi-pronged research that is needed to understand and predict landscape-scale effects of animals. Such research begins with animal enclosure experiments to measure rates of the full complement of zoogeographical processes [GPP, R<sub>A</sub>, R<sub>II</sub>, and organic matter (litter, excreta and egesta) deposition rates and leaching losses]. These measures can be used to parameterize ecosystem models and predict how much carbon should be distributed among different biomass pools, especially in soil and plants. Model predictions can then be tested via systematic sampling of carbon density within plots in the vicinity of the enclosure experiments. It is noteworthy that the strength of animal effects can covary or interact with the effects of biophysical properties across landscapes—including soil type, soil moisture, and soil nutrients—to influence plant biomass (88–90). This calls for landscape-scale experiments that replicate enclosures along landscape biophysical gradients to disentangle variation arising from animal effects from variation due to local biophysical conditions (88–90). The location of experimental sites can be informed by remotely sensed characterization of biophysical conditions, including landforms and vegetation structure [e.g., (87, 88)] and statistical distribution models of soil nutrient concentrations (80, 81). Studies involving multiple animal species should consider using nested experimental designs—modeled after the African KLEE, UHURU, and GLADE experiments—that use fencing to selectively exclude animal species across landscape nutrient and rainfall gradients (90). Movement analyses in combination with remotely sensed biophysical conditions can facilitate understanding of pathways by which animal subsidies flow across landscapes. These data, along with animal population surveys along those pathways, enable an accounting of the per capita rates of animal-mediated spatial exchange of nutrient and carbon among areas across landscapes. This information can be input as model parameters to refine predictions and tests of spatial variation in biomass carbon (Fig. 3).



## Conservation and management implications

There is growing interest to actively enlist natural ecological processes to recapture atmospheric carbon and store it within ecosystems (91, 92). Proposed solutions focus on managing plants and microbes, owing to the huge role they play in forming carbon sinks within ecosystems (91–93). Conserving or managing wild animal species to control carbon exchange between ecosystems and the atmosphere is rarely considered as part of the portfolio of natural carbon-recapture solutions. The thinking, in fact, often holds that managing habitat space to conserve wild animals within ecosystems will conflict with allocating space to capture and store carbon, or, if both can happen in the same locations, they are, nonetheless, functionally unrelated (94–96). The evidence presented here shows that failing to quantitatively account for the positive and negative zoogeochanical effects of animals can mean missed opportunities to enhance carbon uptake by ecosystems or failure to achieve carbon management targets.

Attention has also turned to the prospect of compensating for the functional losses of wild animals using domestic livestock (90, 97). Indeed, methane emissions from modern cattle production are estimated to now fully compensate for estimated methane emission loss due to historical large mammal extinctions (18). But grazing cattle do not always compensate directly for functional losses of similarly sized modern wild herbivore grazers (90, 98). The magnitude of cattle effects varies with biophysical conditions of landscapes, including soil texture, moisture and nutrient status, and wet versus dry climates (98, 99). Cattle exclusion experiments reveal that heavy cattle grazing uniformly reduces ecosystem carbon uptake and soil storage as well as increases carbon fluxes from ecosystems to the atmosphere (99, 100). This effect is opposite to that of similarly sized wild grazers such as Serengeti wildebeest and North American elk. Although grazing intensity could be managed to align with biophysical conditions in ways that encourage grassland carbon sequestration (97, 98), the effects would still be highly localized given livestock herding practices. Hence, such management could not replicate the kind of grazing impact exerted by wild animals that migrate in large herds across the vast spatial scales of landscapes. Moreover, cattle cannot at all compensate for loss of browsing herbivores that affect savanna woody vegetation (89) or for browsing herbivores and frugivores residing in forest ecosystems, where much of the defaunation is happening. Hence, mounting evidence that large wild animals can control ecosystem carbon dynamics argues for considering the effects of their losses via defaunation as much as deforestation (21, 97) when accounting for human impacts on the global carbon cycle.

Carbon storage is only one among a larger portfolio of land uses. Hence, there will inevitably be conflicts over priorities for land allocation (94). In such cases, it would be helpful to quan-

tify the marginal gains or losses of animal effects to assist in adjudicating trade-off decisions about how much land to allocate for carbon storage. Such analyses [e.g., (15, 36)] can help quantify the marginal returns for conserving targeted abundances of animals. For instance, in the Serengeti savannah-woodland ecosystem, carbon storage increases by 15% for every 100,000 additional wildebeest that live within the ecosystem, with diminishing returns as the population size reaches its carrying capacity. Across the existing range of mammal diversity, the tropical forest of Guyana stores, on average, 10 to 15% more carbon for each of the 60-plus mammal species that are conserved. There is a need to expand the scope of this kind of research, measuring zoogeochanical effects across landscape gradients in focal animal abundances. Data from such studies can generate important quantitative insight about the relationships between rates of change in animal abundance and rates of change in ecosystem carbon storage.

## Conclusions

We have shown the many ways in which zoogeochanical effects can control ecosystem carbon storage and exchange across broad landscapes. Consequently, animals should be considered as an integral part of the portfolio of natural carbon-recapture solutions. Without such consideration, there may be serious inaccuracies in both carbon cycle models and anticipated global changes, which may lead to ineffective policy formulation for natural carbon storage. We challenge researchers to better represent how movement and abundances of animals may affect changes to the carbon cycle and how this will affect our future climate. Motivating tests and refinement of new spatial ecosystem models that consider animal feedbacks within trophic biomass pyramids through the integration of landscape-scale experiments, cutting-edge remote-sensing technology, and statistical models and data layers representing spatial biophysical conditions of landscapes offers a clear path to meet such an exciting challenge.

## REFERENCES AND NOTES

- R. A. Houghton, Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.* **35**, 313–347 (2007). doi: [10.1146/annurev.earth.35.031306.140057](https://doi.org/10.1146/annurev.earth.35.031306.140057)
- D. Schimel *et al.*, Observing terrestrial ecosystems and the carbon cycle from space. *Glob. Chang. Biol.* **21**, 1762–1776 (2015). doi: [10.1111/gcb.12822](https://doi.org/10.1111/gcb.12822); pmid: [25472464](https://pubmed.ncbi.nlm.nih.gov/25472464/)
- G. B. Bonan, S. C. Doney, Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science* **359**, eaam8328 (2018). doi: [10.1126/science.aam8328](https://doi.org/10.1126/science.aam8328); pmid: [29420265](https://pubmed.ncbi.nlm.nih.gov/29420265/)
- S. J. Goetz, R. O. Dubayah, Advances in remote sensing technology and implications for measuring and monitoring forest carbon stocks and change. *Carbon Manag.* **2**, 231–244 (2011). doi: [10.4155/cmt.11.18](https://doi.org/10.4155/cmt.11.18)
- Y. M. Bar-On, R. Phillips, R. Milo, The biomass distribution on Earth. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 6506–6511 (2018). doi: [10.1073/pnas.1711842115](https://doi.org/10.1073/pnas.1711842115); pmid: [29784790](https://pubmed.ncbi.nlm.nih.gov/29784790/)
- C. Le Quéré *et al.*, Global carbon budget 2017. *Earth Syst. Sci. Data* **10**, 405–448 (2018). doi: [10.5194/essd-10-405-2018](https://doi.org/10.5194/essd-10-405-2018)
- M. Heimann *et al.*, Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO<sub>2</sub>: First results of a model intercomparison

- study. *Global Biogeochem. Cycles* **12**, 1–24 (1998). doi: [10.1029/97GB01936](https://doi.org/10.1029/97GB01936)
- S. Zaehele *et al.*, Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment studies. *New Phytol.* **202**, 803–822 (2014). doi: [10.1111/nph.12697](https://doi.org/10.1111/nph.12697); pmid: [24467623](https://pubmed.ncbi.nlm.nih.gov/24467623/)
- O. J. Schmitz *et al.*, Animating the carbon cycle. *Ecosystems (N. Y.)* **17**, 344–359 (2014). doi: [10.1007/s10021-013-9715-7](https://doi.org/10.1007/s10021-013-9715-7)
- S. Leroux, M. Loreau, in *Trophic Ecology: Bottom-Up and Top-Down Interactions Across Aquatic and Terrestrial Systems*, T. C. Hanley, K. J. La Pierre, Eds. (Cambridge Univ. Press, 2015) pp. 3–27.
- J. A. Estes *et al.*, Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011). doi: [10.1126/science.1205106](https://doi.org/10.1126/science.1205106); pmid: [21764740](https://pubmed.ncbi.nlm.nih.gov/21764740/)
- T. B. Atwood *et al.*, Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Chang.* **5**, 1038–1045 (2015). doi: [10.1038/nclimate2763](https://doi.org/10.1038/nclimate2763)
- A. J. Tanentzap, D. A. Coomes, Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biol. Rev. Camb. Philos. Soc.* **87**, 72–94 (2012). doi: [10.1111/j.1469-185X.2011.00185.x](https://doi.org/10.1111/j.1469-185X.2011.00185.x); pmid: [21635684](https://pubmed.ncbi.nlm.nih.gov/21635684/)
- S. Bauer, B. J. Hoyer, Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552 (2014). doi: [10.1126/science.1242552](https://doi.org/10.1126/science.1242552); pmid: [24700862](https://pubmed.ncbi.nlm.nih.gov/24700862/)
- R. M. Holdo *et al.*, A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol.* **7**, e1000210 (2009). doi: [10.1371/journal.pbio.1000210](https://doi.org/10.1371/journal.pbio.1000210); pmid: [19787022](https://pubmed.ncbi.nlm.nih.gov/19787022/)
- D. C. Allen, J. S. Wesner, Synthesis: Comparing effects of resource and consumer fluxes into recipient food webs using meta-analysis. *Ecology* **97**, 594–604 (2016). doi: [10.1890/15-1109.1](https://doi.org/10.1890/15-1109.1); pmid: [27197387](https://pubmed.ncbi.nlm.nih.gov/27197387/)
- C. L. Atkinson, K. A. Capps, A. T. Rugenski, M. J. Vanni, Consumer-driven nutrient dynamics in freshwater ecosystems: From individuals to ecosystems. *Biol. Rev. Camb. Philos. Soc.* **92**, 2003–2023 (2017). doi: [10.1111/brv.12318](https://doi.org/10.1111/brv.12318); pmid: [28008706](https://pubmed.ncbi.nlm.nih.gov/28008706/)
- F. A. Smith *et al.*, Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 874–879 (2016). doi: [10.1073/pnas.1502547112](https://doi.org/10.1073/pnas.1502547112); pmid: [26504225](https://pubmed.ncbi.nlm.nih.gov/26504225/)
- C. E. Doughty, A. Wolf, C. B. Field, Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming? *Geophys. Res. Lett.* **37**, L15703 (2010). doi: [10.1029/2010GL043985](https://doi.org/10.1029/2010GL043985)
- S. A. Zimov *et al.*, Steppe-tundra transition: A herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* **146**, 765–794 (1995). doi: [10.1086/285824](https://doi.org/10.1086/285824)
- R. Dirzo *et al.*, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014). doi: [10.1126/science.1251817](https://doi.org/10.1126/science.1251817); pmid: [25061202](https://pubmed.ncbi.nlm.nih.gov/25061202/)
- M. A. Tucker *et al.*, Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**, 466–469 (2018). doi: [10.1126/science.aam9712](https://doi.org/10.1126/science.aam9712); pmid: [29371471](https://pubmed.ncbi.nlm.nih.gov/29371471/)
- We searched the published literature using two search engines: Google Scholar and ISI Web of Science. We searched with the following key words: animals and carbon cycling, animals and biogeochemistry, animals and ecosystem carbon balance, wild herbivores, and carbon cycling. We filtered out studies that did not examine effects of wild animals. We filtered out studies that simulated animal effects (e.g., vegetation clipping). We then filtered out studies that were not experimental or systematic (i.e., studies needed to exclude animals or animal abundance had to vary across landscapes). Finally, we filtered out studies that did not report on direct measures of biogeochemical processes or properties (e.g., biomass carbon, NPP, NEE, respiration, and biophysical impacts).
- K. Elschot, J. P. Bakker, S. Temmerman, J. van de Koppel, T. J. Bouma, Ecosystem engineering by large grazers enhances carbon stocks in a tidal salt marsh. *Mar. Ecol. Prog. Ser.* **537**, 9–21 (2015). doi: [10.3354/meps11447](https://doi.org/10.3354/meps11447)
- J. M. Falk, N. M. Schimidt, T. R. Christensen, L. Ström, Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environ. Res. Lett.* **10**, 045001 (2015). doi: [10.1088/1748-9326/10/4/045001](https://doi.org/10.1088/1748-9326/10/4/045001)
- S. M. P. Cahoon, P. F. Sullivan, E. Post, J. M. Welker, Large herbivores limit CO<sub>2</sub> uptake and suppress carbon cycle responses to warming in West Greenland. *Glob. Change Biol.* **18**, 469–479 (2012). doi: [10.1111/j.1365-2486.2011.02528.x](https://doi.org/10.1111/j.1365-2486.2011.02528.x)

27. R. van Der Wal *et al.*, Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Glob. Chang. Biol.* **13**, 539–545 (2007). doi: [10.1111/j.1365-2486.2006.01310.x](https://doi.org/10.1111/j.1365-2486.2006.01310.x)
28. P. F. McInnes, R. J. Naiman, J. Pastor, Y. Cohen, Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**, 2059–2075 (1992). doi: [10.2307/1941455](https://doi.org/10.2307/1941455)
29. A. C. Risch, A. G. Haynes, M. D. Busse, F. Filli, M. Schütz, The responses of soil CO<sub>2</sub> fluxes to progressively excluding vertebrate and invertebrate herbivores depends on ecosystem type. *Ecosystems* (N. Y.) **16**, 1192–1202 (2013). doi: [10.1007/s10021-013-9676-x](https://doi.org/10.1007/s10021-013-9676-x)
30. S. Sjögersten, R. van der Wal, S. J. Woodin, Habitat type determines herbivory controls over CO<sub>2</sub> fluxes in a warmer Arctic. *Ecology* **89**, 2103–2116 (2008). doi: [10.1890/07-1601.1](https://doi.org/10.1890/07-1601.1); pmid: [18724721](https://pubmed.ncbi.nlm.nih.gov/18724721/)
31. M. S. Strickland, D. Hawlena, A. Reese, M. A. Bradford, O. J. Schmitz, Trophic cascade alters ecosystem carbon exchange. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 11035–11038 (2013). doi: [10.1073/pnas.1305191110](https://doi.org/10.1073/pnas.1305191110); pmid: [23776213](https://pubmed.ncbi.nlm.nih.gov/23776213/)
32. S. P. Devlin, J. Saarenheimo, J. Syväranta, R. I. Jones, Top consumer abundance influences lake methane efflux. *Nat. Commun.* **6**, 8787 (2015). doi: [10.1038/ncomms9787](https://doi.org/10.1038/ncomms9787); pmid: [26531291](https://pubmed.ncbi.nlm.nih.gov/26531291/)
33. T. B. Atwood *et al.*, Predator-induced reduction of freshwater carbon dioxide emissions. *Nat. Geosci.* **6**, 191–194 (2013). doi: [10.1038/ngeo1734](https://doi.org/10.1038/ngeo1734)
34. D. E. Schindler, S. R. Carpenter, J. J. Cole, J. F. Kitchell, M. L. Pace, Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* **277**, 248–251 (1997). doi: [10.1126/science.277.5323.248](https://doi.org/10.1126/science.277.5323.248)
35. T. B. Atwood *et al.*, Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Front. Ecol. Evol.* **6**, 110 (2018). doi: [10.3389/fevo.2018.00110](https://doi.org/10.3389/fevo.2018.00110)
36. M. Sobral *et al.*, Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. *Nat. Ecol. Evol.* **1**, 1670–1676 (2017). doi: [10.1038/s41559-017-0334-0](https://doi.org/10.1038/s41559-017-0334-0); pmid: [28993614](https://pubmed.ncbi.nlm.nih.gov/28993614/)
37. C. C. Wilmers, J. A. Estes, M. Edwards, K. L. Lairde, B. Konar, Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Front. Ecol. Environ.* **10**, 409–415 (2012). doi: [10.1890/110176](https://doi.org/10.1890/110176)
38. J.-C. Svenning *et al.*, Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 898–906 (2016). doi: [10.1073/pnas.1502556112](https://doi.org/10.1073/pnas.1502556112); pmid: [26504218](https://pubmed.ncbi.nlm.nih.gov/26504218/)
39. C. Bello *et al.*, Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105 (2015). doi: [10.1126/sciadv.1501105](https://doi.org/10.1126/sciadv.1501105); pmid: [26824067](https://pubmed.ncbi.nlm.nih.gov/26824067/)
40. L. Culot, C. Bello, J. L. F. Batista, H. T. Z. do Couto, M. Galetti, Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. *Sci. Rep.* **7**, 7662 (2017). doi: [10.1038/s41598-017-08222-4](https://doi.org/10.1038/s41598-017-08222-4); pmid: [28794422](https://pubmed.ncbi.nlm.nih.gov/28794422/)
41. C. A. Peres, T. Emilio, J. Schietti, S. J. M. Desmoulière, T. Levi, Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 892–897 (2016). doi: [10.1073/pnas.1516525113](https://doi.org/10.1073/pnas.1516525113); pmid: [26811455](https://pubmed.ncbi.nlm.nih.gov/26811455/)
42. M. D. de Paula *et al.*, Defaunation impacts on seed survival and its effect on the biomass of future tropical forests. *Oikos* **127**, 1526–1538 (2018). doi: [10.1111/oik.05084](https://doi.org/10.1111/oik.05084)
43. A. M. Osuri *et al.*, Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* **7**, 11351 (2016). doi: [10.1038/ncomms11351](https://doi.org/10.1038/ncomms11351); pmid: [27108957](https://pubmed.ncbi.nlm.nih.gov/27108957/)
44. C. C. Wilmers, O. J. Schmitz, Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere* **7**, e01501 (2016). doi: [10.1002/ecs2.1501](https://doi.org/10.1002/ecs2.1501)
45. S. R. Hall, J. B. Shurin, S. Diehl, R. M. Nisbet, Food quality, nutrient limitation of secondary production, and the strength of trophic cascades. *Oikos* **116**, 1128–1143 (2007). doi: [10.1111/j.0030-1299.2007.15875.x](https://doi.org/10.1111/j.0030-1299.2007.15875.x)
46. S. J. Leroux, M. Loreau, Consumer-mediated recycling and cascading trophic interactions. *Ecology* **91**, 2162–2171 (2010). doi: [10.1890/09-0133.1](https://doi.org/10.1890/09-0133.1); pmid: [20715638](https://pubmed.ncbi.nlm.nih.gov/20715638/)
47. M. Loreau, *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis* (Princeton Univ. Press, 2010).
48. R. D. Bassar *et al.*, Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). *Am. Nat.* **180**, 167–185 (2012). doi: [10.1086/666611](https://doi.org/10.1086/666611); pmid: [22766929](https://pubmed.ncbi.nlm.nih.gov/22766929/)
49. S. J. Leroux, O. J. Schmitz, Predator-driven elemental cycling: The impact of predation and risk effects on ecosystem stoichiometry. *Ecol. Evol.* **5**, 4976–4988 (2015). doi: [10.1002/ece3.1760](https://doi.org/10.1002/ece3.1760); pmid: [26640675](https://pubmed.ncbi.nlm.nih.gov/26640675/)
50. D. Hawlena, O. J. Schmitz, Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am. Nat.* **176**, 537–556 (2010). doi: [10.1086/656495](https://doi.org/10.1086/656495); pmid: [20846014](https://pubmed.ncbi.nlm.nih.gov/20846014/)
51. O. J. Schmitz, R. W. Buchkowski, J. R. Smith, M. Telthorst, A. E. Rosenblatt, Predator community composition is linked to soil carbon retention across a human land use gradient. *Ecology* **98**, 1256–1265 (2017). doi: [10.1002/ecsy.1794](https://doi.org/10.1002/ecsy.1794); pmid: [28273334](https://pubmed.ncbi.nlm.nih.gov/28273334/)
52. D. G. Jenkins *et al.*, Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.* **16**, 415–425 (2007). doi: [10.1111/j.1466-8238.2007.00312.x](https://doi.org/10.1111/j.1466-8238.2007.00312.x)
53. M. A. Tucker, T. J. Ord, T. L. Rogers, Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. *Glob. Ecol. Biogeogr.* **23**, 1105–1114 (2014). doi: [10.1111/geb.12194](https://doi.org/10.1111/geb.12194)
54. E. G. Ofstad, I. Herfindal, E. J. Solberg, B.-E. Sæther, Home ranges, habitat and body mass: Simple correlates of home range size in ungulates. *Proc. Biol. Sci.* **283**, 20161234 (2016). doi: [10.1098/rspb.2016.1234](https://doi.org/10.1098/rspb.2016.1234); pmid: [28003441](https://pubmed.ncbi.nlm.nih.gov/28003441/)
55. A. L. Subalusky, C. L. Dutton, E. J. Rosi, D. M. Post, Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 7647–7652 (2017). doi: [10.1073/pnas.1614778114](https://doi.org/10.1073/pnas.1614778114); pmid: [28630330](https://pubmed.ncbi.nlm.nih.gov/28630330/)
56. E. S. Bakker, J. F. Pagès, R. Arthur, T. Alcoverro, Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. *Ecography* **39**, 162–179 (2016). doi: [10.1111/ecog.01651](https://doi.org/10.1111/ecog.01651)
57. C. E. Doughty *et al.*, Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 868–873 (2016). doi: [10.1073/pnas.1502549112](https://doi.org/10.1073/pnas.1502549112); pmid: [26504209](https://pubmed.ncbi.nlm.nih.gov/26504209/)
58. M. D. Hocking, J. D. Reynolds, Impacts of salmon on riparian plant diversity. *Science* **331**, 1609–1612 (2011). doi: [10.1126/science.1201079](https://doi.org/10.1126/science.1201079); pmid: [21442794](https://pubmed.ncbi.nlm.nih.gov/21442794/)
59. S. J. Leroux, M. Loreau, Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecol. Lett.* **11**, 1147–1156 (2008). doi: [10.1111/j.1461-0248.2008.01235.x](https://doi.org/10.1111/j.1461-0248.2008.01235.x); pmid: [18713270](https://pubmed.ncbi.nlm.nih.gov/18713270/)
60. M. Loreau, N. Mouquet, R. D. Holt, Meta-ecosystems: A theoretical framework for a spatial ecology. *Ecol. Lett.* **6**, 673–679 (2003). doi: [10.1046/j.1461-0248.2003.00483.x](https://doi.org/10.1046/j.1461-0248.2003.00483.x)
61. F. Massol *et al.*, Linking community and ecosystem dynamics through spatial ecology. *Ecol. Lett.* **14**, 313–323 (2011). doi: [10.1111/j.1461-0248.2011.01588.x](https://doi.org/10.1111/j.1461-0248.2011.01588.x); pmid: [21271282](https://pubmed.ncbi.nlm.nih.gov/21271282/)
62. I. Gounand, E. Harvey, C. J. Little, F. Altermatt, Meta-Ecosystems 2.0: Rooting the theory into the field. *Trends Ecol. Evol.* **33**, 36–46 (2018). doi: [10.1016/j.tree.2017.10.006](https://doi.org/10.1016/j.tree.2017.10.006); pmid: [29102408](https://pubmed.ncbi.nlm.nih.gov/29102408/)
63. M. W. McCoy, M. Barfield, R. D. Holt, Predator shadows: Complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos* **118**, 87–100 (2009). doi: [10.1111/j.1600-0706.2008.16878.x](https://doi.org/10.1111/j.1600-0706.2008.16878.x)
64. J. M. Morales, T. A. Carlo, The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* **87**, 1489–1496 (2006). doi: [10.1890/0012-9658\(2006\)87\[1489:TEOPDA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1489:TEOPDA]2.0.CO;2); pmid: [16869425](https://pubmed.ncbi.nlm.nih.gov/16869425/)
65. R. S. Cantrell, C. Cosner, *Spatial Ecology Via Reaction-Diffusion Equations* (Wiley Series in Mathematical and Computational Biology, Wiley, 2003).
66. S. Dewhurst, F. Lutscher, Dispersal in heterogeneous habitats: Thresholds, spatial scales, and approximate rates of spread. *Ecology* **90**, 1338–1345 (2009). doi: [10.1890/08-0115.1](https://doi.org/10.1890/08-0115.1); pmid: [19537553](https://pubmed.ncbi.nlm.nih.gov/19537553/)
67. R. M. Holdo, R. D. Holt, J. M. Fryxell, Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecol. Appl.* **19**, 95–109 (2009). doi: [10.1890/07-1954.1](https://doi.org/10.1890/07-1954.1); pmid: [19323175](https://pubmed.ncbi.nlm.nih.gov/19323175/)
68. W. M. Getz, D. Saltz, A framework for generating and analyzing movement paths on ecological landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 19066–19071 (2008). doi: [10.1073/pnas.0801732105](https://doi.org/10.1073/pnas.0801732105); pmid: [19060192](https://pubmed.ncbi.nlm.nih.gov/19060192/)
69. M. A. Lefsky, W. B. Cohen, G. G. Parker, D. J. Harding, Lidar remote sensing for ecosystem studies. *Bioscience* **52**, 19–30 (2002). doi: [10.1641/0006-3568\(2002\)052\[0019:LRSEFS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0019:LRSEFS]2.0.CO;2)
70. K. T. Vierling, L. A. Vierling, W. A. Gould, S. Martinuzzi, R. M. Clawges, Lidar: Shedding new light on habitat characterization and modeling. *Front. Ecol. Environ.* **6**, 90–98 (2008). doi: [10.1890/070001](https://doi.org/10.1890/070001)
71. K. M. Bergen *et al.*, Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions. *J. Geophys. Res. Biogeosci.* **114**, 1–13 (2009). doi: [10.1029/2008.JG000883](https://doi.org/10.1029/2008.JG000883)
72. H. Tang, R. Dubayah, Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2640–2644 (2017). doi: [10.1073/pnas.1616943114](https://doi.org/10.1073/pnas.1616943114); pmid: [28223505](https://pubmed.ncbi.nlm.nih.gov/28223505/)
73. M. C. Hansen *et al.*, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013). doi: [10.1126/science.1244693](https://doi.org/10.1126/science.1244693); pmid: [24233722](https://pubmed.ncbi.nlm.nih.gov/24233722/)
74. A. B. Davies, G. P. Asner, Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends Ecol. Evol.* **29**, 681–691 (2014). doi: [10.1016/j.tree.2014.10.005](https://doi.org/10.1016/j.tree.2014.10.005); pmid: [25457158](https://pubmed.ncbi.nlm.nih.gov/25457158/)
75. S. J. Goetz *et al.*, Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* **91**, 1569–1576 (2010). doi: [10.1890/09-1670.1](https://doi.org/10.1890/09-1670.1); pmid: [20583698](https://pubmed.ncbi.nlm.nih.gov/20583698/)
76. R. Kays, M. C. Crofoot, W. Jetz, M. Wikelski, Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aad2478 (2015). doi: [10.1126/science.aad2478](https://doi.org/10.1126/science.aad2478); pmid: [26068858](https://pubmed.ncbi.nlm.nih.gov/26068858/)
77. M. M. Bustamante *et al.*, Toward an integrated monitoring framework to assess the effects of tropical forest degradation and recovery on carbon stocks and biodiversity. *Glob. Chang. Biol.* **22**, 92–109 (2016). doi: [10.1111/gcb.13087](https://doi.org/10.1111/gcb.13087); pmid: [26398052](https://pubmed.ncbi.nlm.nih.gov/26398052/)
78. W. Turner *et al.*, Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* **18**, 306–314 (2003). doi: [10.1016/S0169-5347\(03\)00070-3](https://doi.org/10.1016/S0169-5347(03)00070-3)
79. J. Royle, R. B. Chandler, R. Sollmann, B. Gardner, *Spatial Capture-Recapture* (Academic Press, 2014).
80. K. Sitters, C. L. Atkinson, N. Guelzow, P. Kelly, L. L. Sullivan, Spatial stoichiometry: Cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* **124**, 920–930 (2015). doi: [10.1111/oik.02392](https://doi.org/10.1111/oik.02392)
81. S. J. Leroux *et al.*, Stoichiometric distribution models: Ecological stoichiometry at the landscape extent. *Ecol. Lett.* **20**, 1495–1506 (2017). doi: [10.1111/ele.12859](https://doi.org/10.1111/ele.12859); pmid: [29027338](https://pubmed.ncbi.nlm.nih.gov/29027338/)
82. C. C. Wilmers *et al.*, The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology* **96**, 1741–1753 (2015). doi: [10.1890/14-1401.1](https://doi.org/10.1890/14-1401.1); pmid: [26378296](https://pubmed.ncbi.nlm.nih.gov/26378296/)
83. A. T. Ford *et al.*, Large carnivores make savanna tree communities less thorny. *Science* **346**, 346–349 (2014). doi: [10.1126/science.1252753](https://doi.org/10.1126/science.1252753); pmid: [25324387](https://pubmed.ncbi.nlm.nih.gov/25324387/)
84. G. P. Asner, S. R. Levick, Landscape-scale effects of herbivores on treefall in African savannas. *Ecol. Lett.* **15**, 1211–1217 (2012). doi: [10.1111/j.1461-0248.2012.01842.x](https://doi.org/10.1111/j.1461-0248.2012.01842.x); pmid: [22863324](https://pubmed.ncbi.nlm.nih.gov/22863324/)
85. G. P. Asner, N. Vaughn, I. P. J. Smit, S. Levick, Ecosystem-scale effects of megafauna in African savannas. *Ecography* **39**, 240–252 (2015). doi: [10.1111/ecog.01640](https://doi.org/10.1111/ecog.01640)
86. P. J. Mograbi *et al.*, Humans and elephants as treefall drivers in African savannas. *Ecography* **40**, 1274–1284 (2017). doi: [10.1111/ecog.02549](https://doi.org/10.1111/ecog.02549)
87. A. B. Davies, A. Gaylard, G. P. Asner, Megafaunal effects on vegetation structure throughout a densely wooded African landscape. *Ecol. Appl.* **28**, 398–408 (2018). doi: [10.1002/eap.1655](https://doi.org/10.1002/eap.1655); pmid: [29178395](https://pubmed.ncbi.nlm.nih.gov/29178395/)
88. E. S. Bakker *et al.*, Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 847–855 (2016). doi: [10.1073/pnas.1502545112](https://doi.org/10.1073/pnas.1502545112); pmid: [26504223](https://pubmed.ncbi.nlm.nih.gov/26504223/)
89. R. M. Pringle, K. M. Prior, T. M. Palmer, T. P. Young, J. R. Goheen, Large herbivores promote habitat specialization and beta diversity of African savanna trees. *Ecology* **97**, 2640–2657 (2016). doi: [10.1002/ecsy.1522](https://doi.org/10.1002/ecsy.1522); pmid: [27859102](https://pubmed.ncbi.nlm.nih.gov/27859102/)
90. J. R. Goheen *et al.*, Conservation lessons from large-mammal manipulations in East African savannas: The KLEE, UHURU, and GLADE experiments. *Ann. N. Y. Acad. Sci.* **1429**, 31–49 (2018). doi: [10.1111/nyas.13848](https://doi.org/10.1111/nyas.13848); pmid: [29752729](https://pubmed.ncbi.nlm.nih.gov/29752729/)

91. B. W. Griscom *et al.*, Natural climate solutions. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 11645–11650 (2017). doi: [10.1073/pnas.1710465114](https://doi.org/10.1073/pnas.1710465114); pmid: [29078344](https://pubmed.ncbi.nlm.nih.gov/29078344/)
92. R. A. Houghton, A. A. Nassikas, Negative emissions from stopping deforestation and forest degradation, globally. *Glob. Chang. Biol.* **24**, 350–359 (2018). doi: [10.1111/gcb.13876](https://doi.org/10.1111/gcb.13876); pmid: [28833909](https://pubmed.ncbi.nlm.nih.gov/28833909/)
93. U. Stockmann *et al.*, The knowns, known unknowns and unknowns of sequestration of soil organic carbon. *Agric. Ecosyst. Environ.* **164**, 80–99 (2013). doi: [10.1016/j.agee.2012.10.001](https://doi.org/10.1016/j.agee.2012.10.001)
94. E. Nelson *et al.*, Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 9471–9476 (2008). doi: [10.1073/pnas.0706178105](https://doi.org/10.1073/pnas.0706178105); pmid: [18621703](https://pubmed.ncbi.nlm.nih.gov/18621703/)
95. B. B. N. Strassburg *et al.*, Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conserv. Lett.* **3**, 98–105 (2010). doi: [10.1111/j.1755-263X.2009.00092.x](https://doi.org/10.1111/j.1755-263X.2009.00092.x)
96. C. D. Thomas *et al.*, Reconciling biodiversity and carbon conservation. *Ecol. Lett.* **16** (suppl. 1), 39–47 (2013). doi: [10.1111/ele.12054](https://doi.org/10.1111/ele.12054); pmid: [23279784](https://pubmed.ncbi.nlm.nih.gov/23279784/)
97. G. P. Hempson, S. Archibald, W. J. Bond, The consequences of replacing wildlife with livestock in Africa. *Sci. Rep.* **7**, 17196 (2017). doi: [10.1038/s41598-017-17348-4](https://doi.org/10.1038/s41598-017-17348-4); pmid: [29222494](https://pubmed.ncbi.nlm.nih.gov/29222494/)
98. M. E. McSherry, M. E. Ritchie, Effects of grazing on grassland soil carbon: A global review. *Glob. Chang. Biol.* **19**, 1347–1357 (2013). doi: [10.1111/gcb.12144](https://doi.org/10.1111/gcb.12144); pmid: [23504715](https://pubmed.ncbi.nlm.nih.gov/23504715/)
99. D. Xiong, P. Shi, X. Zhang, C. B. Zou, Effects of grazing exclusion on carbon sequestration and plant diversity in grasslands of China—A meta-analysis. *Ecol. Eng.* **94**, 647–655 (2016). doi: [10.1016/j.ecoleng.2016.06.124](https://doi.org/10.1016/j.ecoleng.2016.06.124)
100. G. Zhou *et al.*, Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: A meta-analysis. *Glob. Chang. Biol.* **23**, 1167–1179 (2017). doi: [10.1111/gcb.13431](https://doi.org/10.1111/gcb.13431); pmid: [27416555](https://pubmed.ncbi.nlm.nih.gov/27416555/)

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## Animals and the zoogeochemistry of the carbon cycle

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### Animals count

Flux across the carbon cycle is generally characterized by contributions from plants, microbes, and abiotic systems. Animals, however, move vast amounts of carbon, both through ecosystem webs and across the landscape. Schmitz *et al.* review the different contributions that animal populations make to carbon cycling and discuss approaches that allow for better monitoring of these contributions.

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