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Opinion

Can large herbivores enhance ecosystem carbon persistence?

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There is growing interest in aligning the wildlife conservation and restoration agenda with climate change mitigation goals. However, the presence of large herbivores tends to reduce aboveground biomass in some open-canopy ecosystems, leading to the possibility that large herbivore restoration may negatively influence ecosystem carbon storage. Belowground carbon storage is often ignored in these systems, despite the wide recognition of soils as the largest actively-cycling terrestrial carbon pool. Here, we suggest a shift away from a main focus on vegetation carbon stocks, towards inclusion of whole ecosystem carbon persistence, in future assessments of large herbivore effects on long-term carbon storage. Failure to do so may lead to counterproductive biodiversity and climate impacts of land management actions.

The importance of large herbivores for ecosystem carbon storage

Large herbivores are important for ecosystem biogeochemistry [1–4], including soil carbon pools [5–8]. Yet, the few remaining **semi-open grassland ecosystems** (see Glossary) with intact wild herbivore assemblages experience increasing pressure from alternative land uses, including tree planting to increase vegetation biomass for climate mitigation purposes [9–11]. This focus on vegetation biomass is reflected in ecosystem models, where a direct relationship between vegetation biomass accumulation and whole ecosystem carbon storage is often assumed, an assumption that has received recent criticism [12]. While promoting trees through planting or spontaneous regeneration is an important nature-based solution [13], concern is sometimes expressed around the permanence of woody vegetation biomass, whether because of fire and other natural disturbance regimes enhanced by climate change, or because of possible future deforestation [13,14]. Moreover, the focus on aboveground biomass and its simplistic relationship with whole ecosystem carbon stocks has led to the notion that large herbivores decrease ecosystem carbon stocks through consumption and disturbance [15–17]. However, herbaceous habitats could play an underappreciated role as reliable long-term carbon stores [18], partly due to large soil carbon stocks [8,19,20], and we still do not sufficiently understand the role large herbivores play in providing this ecosystem service.

Here, we sketch the role that large herbivores could play in building and maintaining persistent soil carbon pools, and suggest mechanisms and initial steps to constraining the potential of enhancing this ecosystem service by restoring wild herbivore assemblages at the regional or global scale.

The dominating concept: herbivores impact soils through trophic interactions

The effects of aboveground herbivory on belowground ecological processes has been assessed in a relatively large number of exclosure (fencing) experiments (reviewed in [5,21,22]). Despite a strong bias towards grassland ecosystems, they show highly variable results on soil carbon processes. The cause of these inconsistencies are likely multiple, but two relate to scale. The limited duration of most experiments (median duration of 6 years, [5]) is likely insufficient to capture ecosystem

Highlights

Grasslands are often overlooked global reservoirs of carbon, with soil carbon stocks large enough to compensate for the lower aboveground biomass carbon compared to forests.

Due to a larger fraction of ecosystem carbon stored belowground, particularly in more persistent mineral-associated fractions, grazed grassland carbon stocks may be less vulnerable to perturbations than systems with higher aboveground carbon storage.

To optimise restoration efforts to achieve both biodiversity and climate mitigation goals, we need to shift away from focusing only on building immediate carbon stocks to include carbon persistence.

Herbivores can increase the persistence of ecosystem carbon through redistributing carbon from aboveground vegetation pools vulnerable to disturbances into persistent soil pools.

This is particularly important in ancient fire-prone grasslands, but increasing disturbance frequencies across many ecosystems make herbivore restructuring of carbon pools relevant in a wider range of systems.

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changes with relatively long equilibration times [16,23], such as **soil macrofaunal community** composition [24,25] or subsoil organic matter content (mean residence time: 8280 years [26]). This may result in conclusions being made on transient conditions, for example after trophic rewilding [27], where large herbivores may be introduced in 'habitat islands' without their corresponding soil biome [28]. Moreover, in exclosure experiments, rigorous replication of the same habitat (e.g., closed canopy forest) has often been prioritised over weighted representation of main landscape habitat types (e.g., grasslands and closed canopy patches in the same biome), which hampers our ability to reliably upscale processes to inform Earth System Models. Despite these limitations, exclosure studies have provided the primary evidence base for conceptualising herbivore effects on belowground ecosystem functioning [29,30]. In terms of soil carbon storage, the popular framework by Wardle *et al.* [29] predicts that herbivores will increase soil carbon accumulation in infertile systems, such as boreal forests or dwarf shrub tundra, and decrease carbon stocks in highly fertile systems, such as many grasslands. This is mainly due to trophic responses to herbivory at the plant community level (i.e., species with less decomposable litter left behind after selective feeding at infertile sites) versus accelerating decomposition by increasing soil inputs of labile substrates (greenfall, root exudates, dung, and urine) at fertile sites [30]. Subsequent conceptual work, particularly based on empirical evidence from the tundra, has questioned whether these predictions hold at medium to long timescales, where herbivory-caused shifts between ecosystem states are commonly observed (e.g., shifts from low productivity moss/dwarf-shrub tundra to medium–highly productive herbaceous tundra [31,32]). Further, such models are based on an obsolete understanding of soil carbon ecology (see [33,34] and section 'Shifting the focus towards ecosystem **carbon persistence**').

Emerging perspective: soil impacts through non-trophic effects

Non-trophic interactions between herbivores and soil processes have recently gained attention, but remain underexplored [21,28]. They include both direct and indirect effects of herbivore behaviour, with the herbivore-driven decrease in permafrost thaw through ecosystem engineering in the Arctic as a famous example [35,36]. Direct effects also include physical soil disturbance by large animals (e.g., trampling, digging, and wallowing) causing compaction and/or **bioturbation**. Compaction by herbivores is described from the Arctic to the Tropics [21,37,38], is proportional to body size, and primarily reduces soil process rates [5,21]. By contrast, rates of bioturbation (vertical soil mixing) are inversely related to body size [39], and animal-induced bioturbation was recently shown to be significant across a range of biomes [40]. While large mammals, such as suids (e.g., wild boar), proboscideans (e.g., elephants), and equids (e.g., donkeys), can make considerable contributions to bioturbation in certain ecosystems [41–44], associated **fossorial mammals** and soil macrofauna are generally more effective bioturbation agents [28].

Recent reviews on herbivore effects on belowground carbon processes have argued that non-trophic impacts may in the long term exceed trophic effects in magnitude and scale [21,28]. Hence, a key question is whether existing trophic-based frameworks are adequate for predicting herbivore effects on long-term carbon storage in soils, in a future with increasing ecosystem perturbations [45] (Figure 1).

Shifting the focus towards ecosystem carbon persistence

A shift in perspective from a strong focus on immediate carbon stocks to a focus that factors in carbon persistence is imperative, as increases in extreme weather events and human-caused disturbances may increase the vulnerability of carbon, particularly in aboveground pools [14,45]. Disturbances, such as wildfires, have already shown strong negative effects on carbon and nutrient storage in many ecosystems [14,50,51], although the vulnerability of organic matter in grasslands is lower than in forests [15,18,20,51]. As grassland ecosystems also store more

Glossary

Bioturbation: biotic soil mixing. Large herbivores may mix soil (e.g., through digging, wallowing, or foraging) but the most effective bioturbators are often fossorial mammals and soil macrofauna (see below and Figure 1).

Carbon persistence: the inverse likelihood of a carbon pool to suffer severe losses to major disturbances, such as wildfires, drought, or biotic pests.

Carbon use efficiency (CUE): the amount of carbon remaining in a system relative to carbon entering the system. Often defined as carbon input converted to biomass rather than returned to the atmosphere at a certain system level (e.g., whole ecosystem or soil microbes).

Ecosystem metabolism: the sum of chemical reactions synthesising and breaking down chemical compounds in an entire ecosystem from autotrophs through consumers to decomposers. Higher metabolism means a higher flow of matter through a system, but not necessarily a lower net content of matter (e.g., carbon), as long as the input (productivity) increases simultaneously.

Fossorial mammals: soil dwelling mammals adapted to digging [e.g., moles (Talpidae), prairie dogs (Sciuridae), gophers (Geomyidae), and pikas (Ochotonidae)]. They are often effective bioturbating agents, and are often associated with open herbivore-rich habitats.

Mineral-associated organic matter (MAOM): a mix of microbial- and plant-derived molecules protected by chemical sorption to mineral particles and/or in microaggregates (often defined as <63 μm and >1.6–1.85 g cm^{-3} [53]). The rest, particulate organic matter (POM), consists of less decomposed plant residues in macroaggregates or free form.

Multitrophic rewilding: trophic rewilding is the restoration of self-regulating ecosystems by introducing key ecosystem engineers, often large herbivores and/or predators. It often relies on the implicit assumption that all other relevant organisms/functions will automatically disperse into the rewilded system. Multitrophic rewilding is the proposed term for rewilding restoration at multiple trophic/ecosystem levels, for instance through soil inoculation alongside key mammal species introduction.

Non-trophic interaction: trophic interactions are the direct or indirect impact that organisms can exert on carbon under elevated CO_2 as opposed to many mid- and high-latitude forest systems [12], natural herbaceous ecosystems may be more reliable long-term carbon sinks than woody systems [12,19].

The conceptual view of soil carbon ecology has changed markedly in recent years [33,34,52–54]. The traditional view has been that soil carbon residence times are primarily a consequence of intrinsic organic matter characteristics (e.g., content of nutrients and sugars relative to cellulose and lignin, aromaticity, etc.), sometimes referred to as 'substrate decomposability' [54]. However, empirical evidence has shown that such intrinsic characteristics are insufficient to explain observations of soil carbon persistence [53–55]. The physicochemical inhibition of organic matter decomposition through surface interactions with mineral soil particles and within soil microaggregates [**mineral-associated organic matter (MAOM**)] is now widely recognised as an important mechanism for increasing soil carbon persistence at decadal–millennial timescales [20]. MAOM constitutes the majority of total soil organic matter, especially in the subsoils (below ~30 cm, [34]). This is particularly pronounced under herbaceous vegetation [20], roughly doubling the organic matter residence times in subsoils under grassy (~5400 y) relative to woody (~2800 y) vegetation [26]. The key pathway to MAOM formation is through belowground plant inputs (primarily exudates, see Box 1) processed by microbial decomposers [56–58], allowing labile organic matter to be an equally conducive substrate to long-term soil carbon storage as substrates with low decomposability [33]. While carbon stored in the MAOM-fraction is more resistant to disturbances than other ecosystem pools, carbon continuously leaves this pool [52]. Thus, maintaining a constantly high and diverse flow of matter through the soil decomposer community to replenish lost MAOM likely increases the long-term storage of carbon in persistent carbon pools, and in turn decadal-scale soil carbon persistence, even if soil respiration rates increase simultaneously [59,60] (see also section 'Increasing **ecosystem metabolism** and fertility').

Mechanisms for herbivore enhancement of ecosystem carbon persistence

To assess whether a more persistence-focused framework should change our perception of the potential role of large herbivores for climate mitigation, we need to evaluate whether large herbivores are likely to move ecosystem carbon from relatively vulnerable aboveground carbon storage towards mineral-associated soil pools. Below, we outline three potential pathways for this (Figure 2).

Increasing ecosystem metabolism and fertility

Ecosystem metabolism (the flux of matter though the system) and fertility increase disproportionally when large herbivores are present [1]. A common way of estimating organic matter turnover is through assessing heterotrophic soil effluxes of CO_2, which is often interpreted as a loss. Yet, this perception stems from agriculture, where the input of organic matter is typically relatively fixed, hence reducing carbon turnover is the only way to increase carbon storage [59,60]. In a system with no harvest export, increasing plant productivity, and in turn organic matter inputs to soils, is a common response to increased fertility [1]. A positive relationship between respiration and soil carbon pools was recently shown in both grassland [61,62] and forest ecosystems [44]. Generally, higher primary productivity tends to increase labile carbon inputs (i.e., **rhizodeposition** and animal excreta [8,61]), and the efficacy of microbial biomass production [**carbon use efficiency (CUE)]** (Figure 2) [58,63], hence the formation of microbial-derived persistent carbon [44,56–58,60,61,64,65].

Favouring herbaceous vegetation with high belowground inputs and dense root nets

Herbivore control on vegetation structure is often tightly linked to disturbances. While herbivores moderate fire regimes in grasslands [18,66], they prolong canopy openings after initial disturbances in forests [23,67]. A recent example from fire-prone savannas showed how

different organisms through food webs (e.g., decreased substrate availability to soil decomposers by selective feeding by herbivores). Non-trophic interactions circumvent the food webs (e.g., habitat niche creation by physical ecosystem engineering).
Rhizodeposition: root litter (i.e., senesced and/or abscised roots) and low-molecular weight compounds (i.e., enzymes, sugars, amino-acids, etc.) exuded by the roots to stimulate microbial activity, release nutrients, minimise physical root resistance, or other growth promoting purposes.
Semi-open grassland ecosystem: ancient grassland systems have historically hosted herds of large herbivores, while many of them are also prone to seasonal fires. The most famous examples are tropical savannas and temperate steppes/prairies, but we emphasise that large herbivores often thrive in, and help sustain, mosaic landscapes with woody patches and open areas in other biomes as well.
Soil macrofaunal community: strict definitions of soil macrofauna vary, but we use the term to describe fauna larger than 2 mm in diameter. Important groups are earthworms (Lumbricina), ants (Formicidae), termites (Isoptera), and dung-beetles (Scarabaeidae). Many are very effective soil engineers, and some are closely linked to large herbivores.

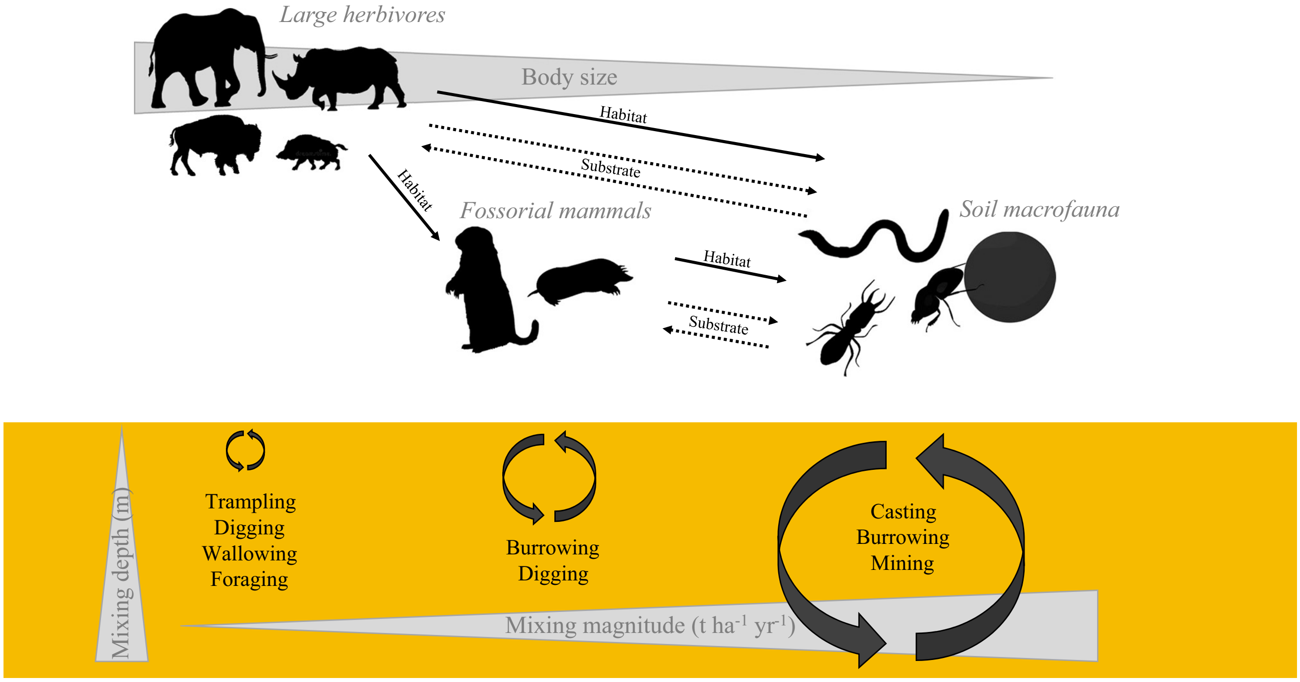

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Figure 1. Interactions between large herbivores, fossorial animals, and soil macrofauna, and the hypothesised generalised consequences for soil bioturbation. Main behaviours responsible for bioturbation are listed under each animal group, where the hypothesised generalised mixing depth and magnitude scales with the circular double-arrow. Unbroken arrows between animal groups indicate where larger animals create habitats for smaller animals, while broken arrows indicate when groups of animals provide substrate (feed) for one another. To estimate soil-mixing rates based on large herbivore communities, one should include co-occurrences between specific large animals, specific fossorial mammals, and specific soil fauna in a species distribution and trait database (e.g., [46,47]). Soil mixing characteristics (depth and rate) would need to be estimated for each animal or animal group. Quantification of long-term soil mixing can be achieved by diffusion modelling of sediment luminescence characteristics [40,48], while recent advances have been made in using remote sensing to estimate burrowing densities and depth [49].

Box 1. Herbivore fire-risk reduction and increased soil carbon storage

In fire-prone ecosystems, such as savannas and boreal forests, large herbivores can moderate fire severity, primarily through consumption and restructuring of the vegetation [18,50,68,92]. This reduces fuel loads and/or breaks its spatial continuity, particularly in the understory and ground layers where most fires ignite and spread [15]. Pyrogenic carbon is not the focus here, but we note that herbivores may increase production of persistent pyrogenic carbon, as pyrogenic carbon production is inversely related to fire residence time (lower in grazed systems), and positively related to the graminoid:woody cover ratio [100]. A recent series of simulations from California showed that all studied climate scenarios, except the most optimistic one (representative concentration pathway 2.6), showed substantially higher persistence of ecosystem carbon when stored in grasslands rather than forests, primarily due to a higher belowground carbon (C)-storage that is less vulnerable to disturbances [19]. This is pertinent as more frequent extreme weather events are expected to drive an increase in disturbance frequencies and severities in many regions of the world [14,45].

When herbivores graze the North American prairies, they can induce fine root growth [80] and increase root exudation from grasses leading to increased microbial biomass [62,79]. Microbial residues and plant exudates are effective substrates for persistent soil organic matter (SOM) formation in the mineral-associated organic matter (MAOM) fraction [56–58]. A recent substrate labelling study showed that 46% of root exudates ended up in MAOM compared to only 9% of the root biomass. Instead, 20% of the root litter ended up in the particulate organic matter (POM) fraction [57]. Yet, while grazing-induced increases in SOM are consistent across some grassland systems, studies from managed pastures indicate some context dependencies (photosynthetic pathway, soil texture, precipitation, and grazing intensity) that require further exploration [22] (Figure I).

To understand these effects at the ecosystem scale, Holdo *et al.* [50] assessed the annual ecosystem C-stock increase across protected Serengeti savannas after the wildebeest populations grew back following a virus epidemic in East Africa in the 1960s. They estimate that the avoided carbon emissions from wildfires and additional carbon sequestered corresponded to 10^6 Mg less carbon in the atmosphere per year, which is roughly equal to the annual greenhouse gas emissions from ~500 000 EU citizens emitting ~2 tonnes of carbon per capita [101]. The majority of the carbon stock change in the Serengeti savanna occurred in the soil.

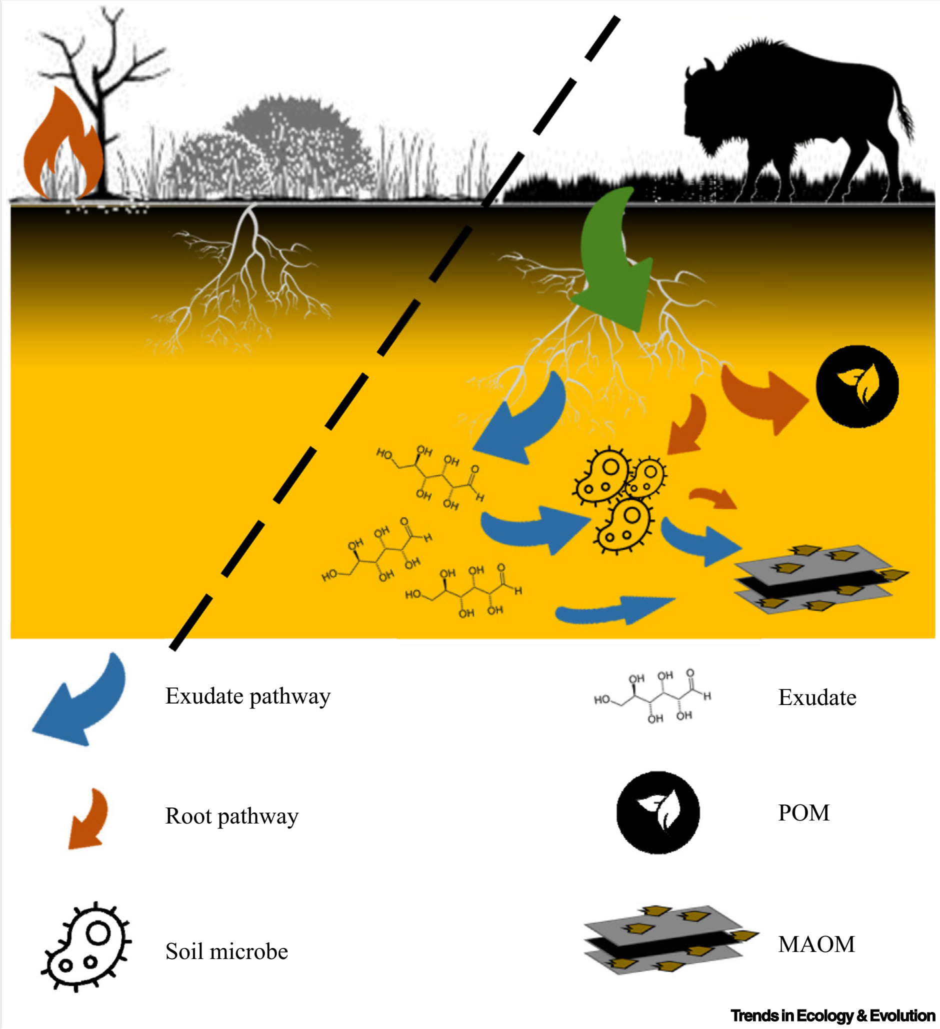
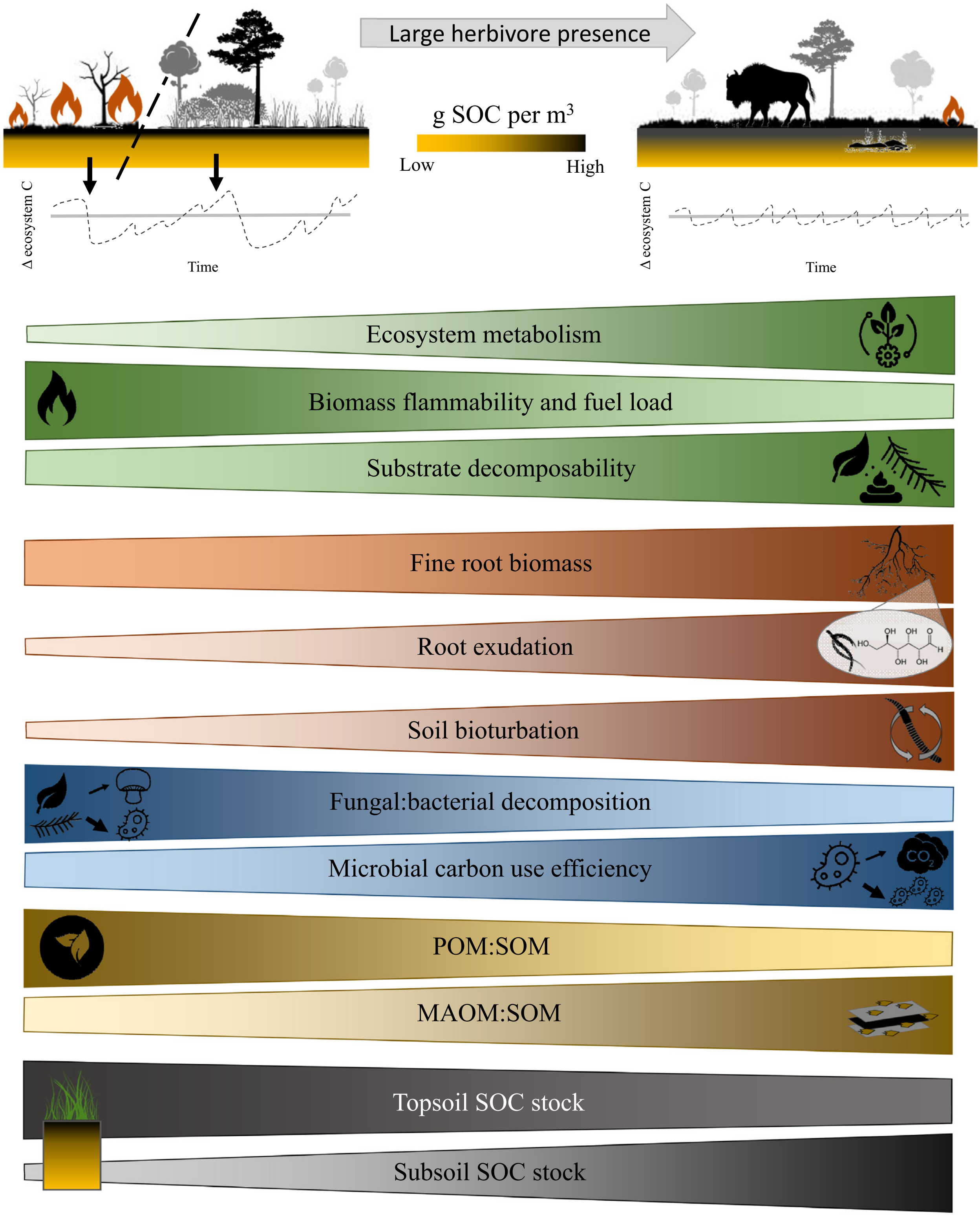


Figure I. Pathways for formation of POM and MAOM from rhizodeposition enhanced by herbivore presence.

aboveground biomass lost in areas with high elephant densities was gained in less vulnerable soil pools [8]. Understanding such interactions are important as neither consumption by herbivores nor fire result in a total loss from the system, but a redistribution of a fraction into persistent soil pools [8,15] (Box 1).

In tropical [50], temperate [67–69], and arctic [31,70] grasslands, herbivore presence promotes fast-growing, highly productive herbaceous vegetation. Grassland species have the highest root: shoot biomass allocation across ecosystems [71]. As herb-dominated systems also have dense and relatively deep root distribution profiles [72,73], a large proportion of the soil volume is part of the rhizosphere, the zone of active exchange of matter between plants, soil community, and mineral matrix. Hence, a considerable fraction of carbon allocated belowground in grasslands forms microaggregates with, and is sorbed to, mineral surfaces forming MAOM [34,74,75]. This can increase the subsoil carbon stock beyond what is stored in soils under woody vegetation in



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the same landscape, and hence increase the overall ecosystem carbon persistence without compromising total carbon storage [8,75–77] (Box 1).

Herbivores can directly stimulate plant productivity [78] and allocation of carbon to roots and associated microbes in high intensity grazing areas (grazing lawns) [62,79,80], which can further increase carbon storage belowground [57,62]. After a certain amount of revisits by large grazers, lawns are too compacted to sustain productivity, which leads herbivores to temporarily abandon them to natural restoration by soil engineers (see next section 'Soil mixing and processing by associated fauna'). Hence, there seems to be a plot–scale cyclicity, where short-grass dominated grazing lawns are gradually compacted and abandoned followed by an invasion by soil engineers loosening the soil and shifting the vegetation towards long grasses, until herbivores eventually return and convert it back to a grazing lawn [37]. The time needed for regeneration in natural systems is why high-density pastures are likely insufficient representations of natural herbivore-rich ecosystems [81].

Soil mixing and processing by associated fauna

Large animals can expose a larger fraction of the organic matter in soils to organo–mineral interaction through vertical soil mixing, either through their own activity [41–44] or the activity of associated fossorial mammals or soil fauna [28,82,83] (Figure 1). The highest known soil mixing rates are reported in open or semi-open ecosystems historically associated with large herds of herbivores (savannas and grasslands [40]), but we lack good quantification of soil mixing rates in many systems. Both invertebrate and vertebrate soil engineers are important and integrated agents in megafauna-rich ecosystems [37,82,84–86]. Hence, the habitat niche creation for many effective bioturbators is closely linked to large herbivores, and the sustainability of some of these ecosystems depends on bioturbation to loosen up soils after megafauna compaction [37]. While a large part of the soil community is relatively insensitive to dispersal barriers, soil macrofauna take much longer to adjust to shifts in the aboveground subsystem, as they depend on active or passive vector dispersal [25]. Apart from the increased exposure of organic matter to mineral soil through physical mixing, soil fauna play a dominant role for overall ecosystem functioning [87]. In the Arctic, where it has been proposed that large herbivores played a major role in prehistoric times in shaping ecosystems [88,89], the soil community is currently not adapted to large herbivore-rich systems, which may have functional repercussions [89]. For example, experimental introduction of soil-mixing earthworms in the Arctic has shown that they can effectively alleviate plant nutrient limitations and increase greening [90]. Moreover, such geophagous fauna can be effective soil engineers and bioreactors for enhancing carbon persistence [33,91]. Introducing soil-mixing animals alongside associated large herbivores has also been suggested as an effective fire control [92]. Therefore, co-introduction of critical soil fauna needs to be considered in megafauna restoration efforts (**multitrophic rewilding**), if large animals are introduced in areas detached from ecosystems where soil fauna could naturally disperse from [28].

Upscaling to estimate herbivore enhancement of ecosystem carbon persistence

Modelling efforts to upscale herbivore effects to the ecosystem level have been called for in recent syntheses [3,4,23]. Ideally, process-based models integrating plant/soil-focused and animal-

Figure 2. Hypotheses about the responses to herbivore presence, primarily based on findings from grasslands. The colour saturation and thickness variation of the wedges indicates the expected relative variation between generalised ecosystems with/without herbivores at natural densities in similar landscapes. Green wedges represent large scale ecosystem processes, primarily aboveground; red wedges represent mechanisms actively transporting C into soils; blue wedges represent key microbial ecological variables; yellow wedges represent partitioning into soil organic carbon pools of different persistence; and black wedges represent SOC stocks (tC ha^{-1}). Imperative for assessing herbivore effects on long term ecosystem C persistence are the altered depth distribution of soil organic matter, and the shift in POM:MAOM ratio upon herbivore introduction. Abbreviations: C, carbon; MAOM, mineral-associated organic matter; POM, particulate organic matter; SOC, soil organic carbon; SOM, soil organic matter; tC ha, tonnes of carbon per hectare.

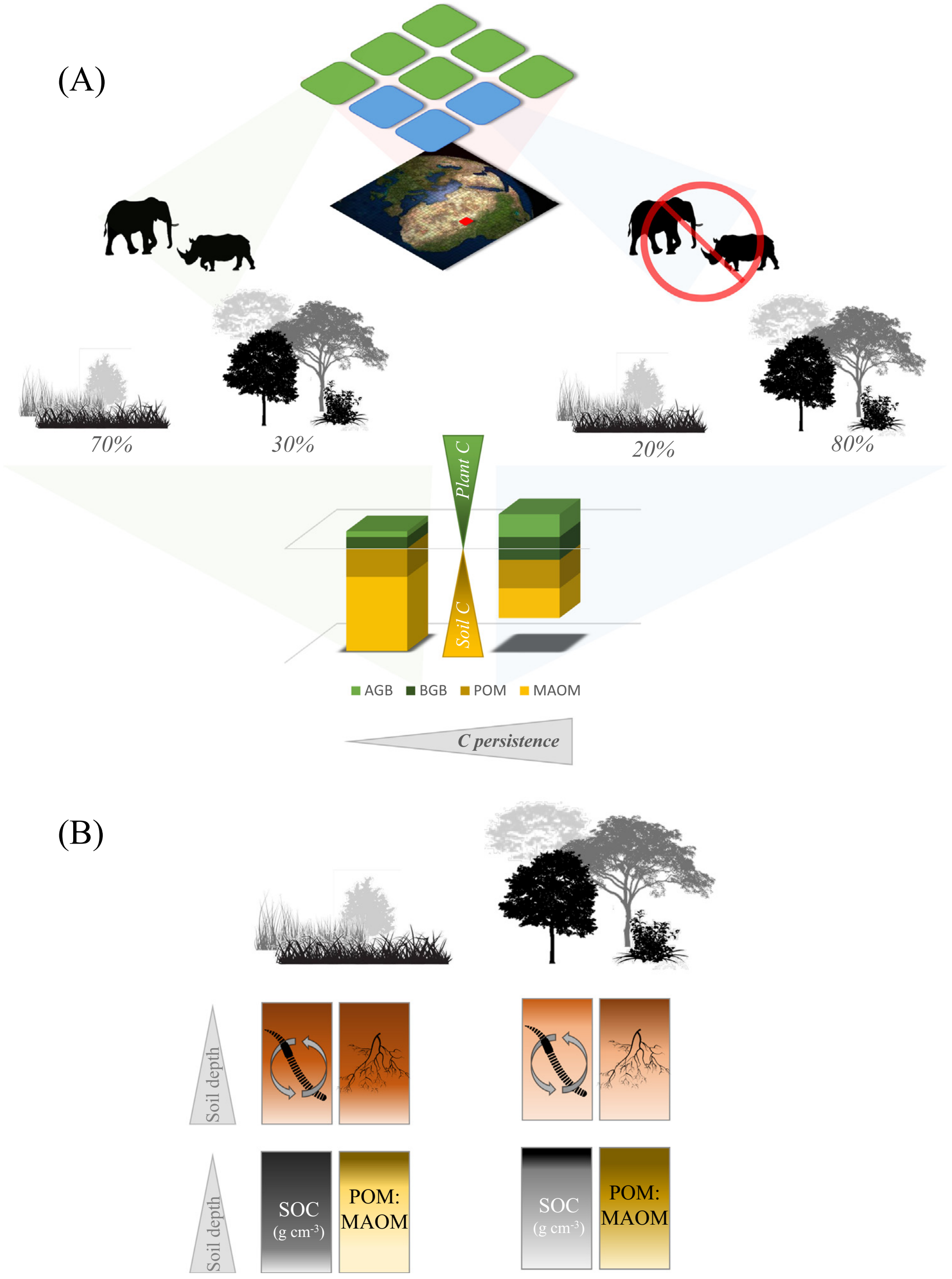

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Figure 3. Upscaling the herbivore effects on ecosystem carbon storage above- and belowground. (A) A sketch of a possible first step allometric modelling approach to upscale the effects of herbivores on ecosystem carbon storage in different pools along the carbon persistence continuum [aboveground vegetation biomass (AGB) < belowground vegetation biomass (BGB) < particulate soil organic matter (POM) < mineral-associated soil organic matter (MAOM)]. While the aboveground vegetation biomass-C can be estimated based on the relative distribution of plant functional types (e.g., graminoids, shrubs, and trees) in each pixel, we lack the necessary knowledge to reliably extend such carbon stock estimates belowground. (B) The four most essential variables to be able to make reasonable predictions about long-term shifts in ecosystems C-persistence: soil mixing (top left), fine root density (top right), tonnes soil organic carbon (tSOC per m^3, bottom left) and the ratio of particulate organic matter to mineral-associated organic matter (POM:MAOM, bottom right). The saturation of the

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focused approaches as well as the interaction with disturbances should be developed [93,94]. While few attempts have been made to include herbivores in ecosystem models [94,95], we know of no modelling studies including both herbivore and fire effects. Moreover, the representation of soil processes in many existing ecosystem models remains overly simplistic [12,96]. A more holistic model-representation of SOM dynamics was recently developed, for the first time directly considering vertical transport of soil carbon by bioturbators [97,98], with first tests showing high SOM stock sensitivity to soil engineer population dynamics [97]. Until sufficient data and understanding to develop process-based models is available, it is worth developing more simple models based on allometric relationships between large herbivore presence/absence in different ecoregions and the consequent carbon storage in different ecosystem carbon pools. A practical way to approach the incorporation of carbon persistence in ecosystem models that seek to assess the interaction between herbivory and disturbances, may be to categorise ecosystem carbon into crude persistence classes along a continuum of increasing persistence in the order of aboveground plant biomass (AGB) < belowground plant biomass (BGB) < POM < MAOM. To validate such models, depth resolved data on SOC stocks partitioned into POM and MAOM is required, in addition to more readily available estimates of above- and belowground vegetation biomass. Root distribution profiles and soil mixing rates would further improve the mechanistic inferences (Figure 3). The ability of large herbivores to increase ecosystem metabolism, and soil fertility was recently upscaled to the planetary level using allometric modelling [1]. Such models have also revealed important differences between grassland (increase) and forests (decrease) carbon storage in soils in response to fire [51] and increasing atmospheric CO_2 concentrations [12].

We emphasise the potentially large context dependencies that eventually need to be reflected in model construction. Soil carbon responses to grazing depend on abiotic variables (climate, soil texture and mineralogy, topography, and hydrology) as well as biotic variables, notably herbivore assemblies, densities and history, and dominant plant traits (e.g., photosynthetic pathway and growth form) [6,22,62,99]. For example, a meta-analysis of mainly temperate pastures found a negative relationship between herbivory pressure and soil carbon storage in systems dominated by C3-species, while the opposite relationship was found for C4-dominated systems [22]. Similarly, moderate grazing treatments had the highest SOC stocks in Tibetan pastures [99]. Yet, the underlying mechanisms remain unclear, as does the degree to which such findings can be extended to natural ecosystems. One obvious difference is the intermittent nature of herbivory in natural systems due to herbivore population dynamics and migration patterns, which makes consistent overgrazing unlikely [81]. Moreover, a recent estimate from the Arctic suggested that large herbivore reproduction rates may be a main bottleneck to upscaling large herbivore effects on ecosystems [36].

Concluding remarks

By maintaining a narrow focus on visible aboveground vegetation carbon stocks, we risk making ineffective management decisions to counteract biodiversity decline and climate change. Understanding the role that large herbivores may play in enhancing ecosystem carbon persistence, by reducing the flammability of aboveground carbon and shifting carbon storage from vulnerable pools towards more persistent soil pools at the biome scale, is crucial to balancing the ecosystem services provided by semi-open herbivore-rich systems against potential services from alternative land-uses, such as afforestation. We need to shift our focus away from building immediate carbon

colours in each soil profile in (B) indicates a hypothesised depth-distribution of the variables under grassy and woody vegetation in the same landscape. Depth resolved SOC and POM:MAOM would be the first step, while soil mixing rates (see Figure 1), and root/rhizosphere distributions would aid the mechanistic understanding of vertical C-translocation in soils (see also Figure 2). Abbreviation: C, carbon.

Outstanding questions

Can large herbivores move ecosystem carbon towards more persistent pools? Applying the suggested carbon persistence continuum could be helpful. Depth-resolved data on SOM stocks and fractionation into POM and MAOM is particularly scarce. Data from exclosures placed along natural habitat gradients (e.g., from open herbaceous habitats into closed-canopy woody habitats) would allow better upscaling in space and time, as effects may vary between woody and herbaceous systems.

How do herbivore–disturbance interactions impact projections of carbon losses under trophic rewilding scenarios? The integration of herbivore–disturbance regulation of carbon budgets is warranted in ecosystem models. Development is particularly needed on soil dynamics, but due to the slow changes in soil carbon pools (decades to millennia), the best possible validation data may be obtained from chronosequences of ‘time since herbivore (re)introduction’ in ongoing rewilding areas.

What are the functional consequences of links between functional guilds (e.g., large herbivores × fossorial mammals × soil fauna)? These could occur through trophic interactions (i.e., modification of feed/substrate availability), but particularly non-trophic interactions need further attention (e.g., physical habitat niche creation). ‘Omics’ data from soils inside and outside exclosures could assess the effects on the soil community and functions.

How do herbivore assemblages influence ecosystem carbon storage? Initial studies from savannas indicates that carbon stock reduction by a single herbivore functional type may be negated by the presence of others in concert.

How do natural herbivore fluctuations in the spatiotemporal use of landscape resources influence ecosystem carbon storage? Due to natural migration, population dynamics, and selective use of certain habitats for resting, feeding, etc., landscape resources are not used homogeneously over space and time, but we have limited understanding of the consequences for carbon storage.

stocks to also include carbon persistence, as increased persistence may be needed to secure long-term carbon sequestration in a world of more frequent and severe perturbations.

Questions to be examined in future research efforts are summarised later (see Outstanding questions). Interactions between engineers at multiple levels of the ecosystem are of key importance to understand the full potential of megafauna-rich systems for biodiversity and climate change mitigation purposes. This knowledge is also needed to assess the feasibility of multitrophic rewilding. The long-term carbon storage in mineral-associated forms needs to be quantified in exclosure experiments and across herbivory intensity gradients to capture the landscape scale variation in carbon pool characteristics along the suggested carbon persistence continuum. Finally, upscaling with ecosystem models is crucial for assessing the potential of herbivores to contribute to climate change mitigation through increasing carbon persistence at ecosystem to global scales.

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Declaration of interests

No interests to declare.

References

1. Enquist, B.J. *et al.* (2020) The megabiota are disproportionately important for biosphere functioning. *Nat. Commun.* 11, 699
2. Malhi, Y. *et al.* (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci. U. S. A.* 113, 838–846
3. Schmitz, O.J. *et al.* (2018) Animals and the zoogeochemistry of the carbon cycle. *Science* 362, eaar3213
4. Schmitz, O.J. and Leroux, S.J. (2020) Food webs and ecosystems: linking species interactions to the carbon cycle. *Annu. Rev. Ecol. Evol. Syst.* 51, 271–295
5. Forbes, E.S. *et al.* (2019) Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Funct. Ecol.* 33, 1597–1610
6. Sitters, J. *et al.* (2020) Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. *Nat. Sustain.* 3, 360–366
7. Sitters, J. *et al.* (2020) Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Glob. Chang. Biol.* 26, 2060–2071
8. Sandhage-Hofmann, A. *et al.* (2021) Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass. *Glob. Chang. Biol.* 27, 4601–4614
9. Bond, W.J. (2016) Ancient grasslands at risk. *Science* 351, 120–122
10. Pausas, J.G. and Bond, W.J. (2019) Humboldt and the reinvention of nature. *J. Ecol.* 107, 1031–1037
11. Veldman, J.W. *et al.* (2015) Where tree planting and forest expansion are bad for biodiversity and ecosystem services. *Bioscience* 65, 1011–1018
12. Terrer, C. *et al.* (2021) A trade-off between plant and soil carbon storage under elevated CO2. *Nature* 591, 599–603
13. Girardin, C.A.J. *et al.* (2021) Nature-based solutions can help cool the planet - if we act now. *Nature* 593, 191–194
14. Anderegg, W.R.L. *et al.* (2020) Climate-driven risks to the climate mitigation potential of forests. *Science* 368, eaaz7005
15. Pausas, J.G. and Bond, W.J. (2020) On the three major recycling pathways in terrestrial ecosystems. *Trends Ecol. Evol.* 35, 767–775
16. Tanentzap, A.J. and Coomes, D.A. (2012) Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biol. Rev.* 87, 72–94
17. Davies, A.B. and Asner, G.P. (2019) Elephants limit aboveground carbon gains in African savannas. *Glob. Chang. Biol.* 25, 1368–1382
18. Johnson, C.N. *et al.* (2018) Can trophic rewilding reduce the impact of fire in a more flammable world? *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20170443
19. Dass, P. *et al.* (2018) Grasslands may be more reliable carbon sinks than forests in California. *Environ. Res. Lett.* 13, 074027
20. Lugato, E. *et al.* (2021) Different climate sensitivity of particulate and mineral-associated soil organic matter. *Nat. Geosci.* 14, 295–300
21. Andriuzzi, W.S. and Wall, D.H. (2017) Responses of belowground communities to large aboveground herbivores: meta-analysis reveals biome-dependent patterns and critical research gaps. *Glob. Chang. Biol.* 23, 3857–3868
22. McSherry, M.E. and Ritchie, M.E. (2013) Effects of grazing on grassland soil carbon: a global review. *Glob. Chang. Biol.* 19, 1347–1357
23. Leroux, S.J. *et al.* (2020) Herbivore impacts on carbon cycling in boreal forests. *Trends Ecol. Evol.* 35, 1001–1010
24. Klein, A. *et al.* (2020) Invasive lumbricid earthworms in North America—different life histories but common dispersal? *J. Biogeogr.* 47, 674–685
25. Thakur, M.P. *et al.* (2020) Towards an integrative understanding of soil biodiversity. *Biol. Rev.* 95, 350–364
26. Shi, Z. *et al.* (2020) The age distribution of global soil carbon inferred from radiocarbon measurements. *Nat. Geosci.* 13, 555–559
27. Svenning, J.C. *et al.* (2016) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci. U. S. A.* 113, 898–906

28. Andriuzzi, W.S. and Wall, D.H. (2018) Soil biological responses to, and feedbacks on, trophic rewilding. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20170448
29. Wardle, D.A. *et al.* (2004) Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633
30. Bardgett, R.D. and Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84, 2258–2268
31. Van Der Wal, R. (2006) Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos* 114, 177–186
32. Olofsson, J. and Post, E. (2018) Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20170437
33. Prescott, C.E. and Vesterdal, L. (2021) Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. *For. Ecol. Manag.* 498, 119522
34. Jackson, R.B. *et al.* (2017) The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. *Annu. Rev. Ecol. Evol. Syst.* 48, 419–445
35. Beer, C. *et al.* (2020) Protection of permafrost soils from thawing by increasing herbivore density. *Sci. Rep.* 10, 4170
36. Macias-Fauria, M. *et al.* (2020) Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philos. Trans. R. Soc. B Biol. Sci.* 375, 20190122
37. Howison, R.A. *et al.* (2017) Biotically driven vegetation mosaics in grazing ecosystems: the battle between bioturbation and biocompaction. *Ecol. Monogr.* 87, 363–378
38. Tuomi, M. *et al.* (2021) Stomping in silence: conceptualizing trampling effects on soils in polar tundra. *Funct. Ecol.* 35, 306–317
39. Haussmann, N.S. (2017) Soil movement by burrowing mammals: a review comparing excavation size and rate to body mass of excavators. *Prog. Phys. Geogr.* 41, 29–45
40. Gray, H.J. *et al.* (2020) Depth-dependent soil mixing persists across climate zones. *Proc. Natl. Acad. Sci. U. S. A.* 117, 8750–8756
41. Don, A. *et al.* (2019) Simulated wild boar bioturbation increases the stability of forest soil carbon. *Biogeosciences* 16, 4145–4155
42. Haynes, G. (2012) Elephants (and extinct relatives) as earthmovers and ecosystem engineers. *Geomorphology* 157–158, 99–107
43. Lundgren, E.J. *et al.* (2021) Equids engineer desert water availability. *Science* 372, 491–495
44. Liu, Y. *et al.* (2020) Wild boar grubbing causes organic carbon loss from both top- and sub-soil in an oak forest in central China. *For. Ecol. Manag.* 464, 118059
45. IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press
46. Lundgren, E.J. *et al.* (2021) Functional traits of the world's late Quaternary large-bodied avian and mammalian herbivores. *Sci. Data* 8, 17
47. Soria, C.D. *et al.* (2021) COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology* 102, e03344
48. Román-Sánchez, A. *et al.* (2019) Bioturbation and erosion rates along the soil-hillslope conveyor belt, part 2: quantification using an analytical solution of the diffusion–advection equation. *Earth Surf. Process. Landf.* 44, 2066–2080
49. Grigusova, P. *et al.* (2021) Area-wide prediction of vertebrate and invertebrate hole density and depth across a climate gradient in Chile based on UAV and machine learning. *Drones* 5, 86
50. Holdo, R.M. *et al.* (2009) A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol.* 7, e1000210
51. Pellegrini, A.F.A. *et al.* (2018) Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553, 194–198
52. Kleber, M. *et al.* (2021) Dynamic interactions at the mineral–organic matter interface. *Nat. Rev. Earth Environ.* 2, 402–421
53. Lavallee, J.M. *et al.* (2020) Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Glob. Chang. Biol.* 26, 261–273
54. Lehmann, J. and Kleber, M. (2015) The contentious nature of soil organic matter. *Nature* 528, 60–68
55. Lehmann, J. *et al.* (2020) Persistence of soil organic carbon caused by functional complexity. *Nat. Geosci.* 13, 529–534
56. Sokol, N.W. and Bradford, M.A. (2019) Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nat. Geosci.* 12, 46–53
57. Villarino, S.H. *et al.* (2021) Plant rhizodeposition: a key factor for soil organic matter formation in stable fractions. *Sci. Adv.* 7, eabd3176
58. Geyer, K. *et al.* (2020) Assessing microbial residues in soil as a potential carbon sink and moderator of carbon use efficiency. *Biogeochemistry* 151, 237–249
59. Janzen, H.H. (2006) The soil carbon dilemma: shall we hoard it or use it? *Soil Biol. Biochem.* 38, 419–424
60. Sanderman, J. *et al.* (2017) Greater soil carbon stocks and faster turnover rates with increasing agricultural productivity. *SOIL* 3, 1–16
61. Stoner, S.W. *et al.* (2021) Soil organic matter turnover rates increase to match increased inputs in grazed grasslands. *Biogeochemistry* 156, 145–160
62. Wilson, C.H. *et al.* (2018) Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. *Glob. Chang. Biol.* 24, 2997–3009
63. Qiao, Y. *et al.* (2019) Global variation of soil microbial carbon-use efficiency in relation to growth temperature and substrate supply. *Sci. Rep.* 9, 5621
64. Zhu, X. *et al.* (2020) The soil microbial carbon pump: from conceptual insights to empirical assessments. *Glob. Chang. Biol.* 26, 6032–6039
65. Wang, C. *et al.* (2021) Large-scale importance of microbial carbon use efficiency and necromass to soil organic carbon. *Glob. Chang. Biol.* 27, 2039–2048
66. Rouet-Leduc, J. *et al.* (2021) Effects of large herbivores on fire regimes and wildfire mitigation. *J. Appl. Ecol.* Published online September 5, 2021. https://doi.org/10.1111/1365-2664.13972
67. Kowalczyk, R. *et al.* (2021) Do large herbivores maintain open habitats in temperate forests? *For. Ecol. Manag.* 494, 119310
68. O'Connor, R.C. *et al.* (2020) Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. *Ecology* 101, e02935
69. Freitag, M. *et al.* (2021) Post-Soviet shifts in grazing and fire regimes changed the functional plant community composition on the Eurasian steppe. *Glob. Chang. Biol.* 27, 388–401
70. Reinecke, J. *et al.* (2021) Effects of large herbivore grazing on relics of the presumed mammoth steppe in the extreme climate of NE-Siberia. *Sci. Rep.* 11, 12962
71. Qi, Y. *et al.* (2019) Plant root–shoot biomass allocation over diverse biomes: a global synthesis. *Glob. Ecol. Conserv.* 18, e00606
72. Schenk, H.J. and Jackson, R.B. (2002) The global biogeography of roots. *Ecol. Monogr.* 72, 311–328
73. Bardgett, R.D. *et al.* (2014) Going underground: root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* 29, 692–699
74. Cotrufo, M.F. *et al.* (2019) Soil carbon storage informed by particulate and mineral-associated organic matter. *Nat. Geosci.* 12, 989–994
75. Jobbágy, E.G. and Jackson, R.B. (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10, 423–436
76. Conant, R.T. *et al.* (2017) Grassland management impacts on soil carbon stocks: a new synthesis. *Ecol. Appl.* 27, 662–668
77. Jackson, R.B. *et al.* (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418, 623–626
78. Frank, D.A. *et al.* (2016) Ungulate control of grassland production: grazing intensity and ungulate species composition in Yellowstone Park. *Ecosphere* 7, e01603
79. Hamilton, E.W. *et al.* (2008) Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biol. Biochem.* 40, 2865–2873
80. Frank, D.A. *et al.* (2002) Consumer control of grassland plant production. *Ecology* 83, 602–606

81. Augustine, D.J. and McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manag.* 62, 1165–1183
82. Fahnestock, J.T. and Detling, J.K. (2002) Bison-prairie dog–plant interactions in a North American mixed-grass prairie. *Oecologia* 132, 86–95
83. Reichman, O.J. and Seabloom, E.W. (2002) The role of pocket gophers as subterranean ecosystem engineers. *Trends Ecol. Evol.* 17, 44–49
84. Bacher, M.G. *et al.* (2018) The impact of cattle dung pats on earthworm distribution in grazed pastures. *BMC Ecol.* 18, 59
85. Li, X. *et al.* (2021) A facilitation between large herbivores and ants accelerates litter decomposition by modifying soil microenvironmental conditions. *Funct. Ecol.* 35, 1822–1832
86. Sandom, C.J. *et al.* (2014) High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* 111, 4162–4167
87. Briones, M.J.I. (2018) The serendipitous value of soil fauna in ecosystem functioning: the unexplained explained. *Front. Environ. Sci.* 6, 149
88. Zimov, S.A. *et al.* (2012) Mammoth steppe: a high-productivity phenomenon. *Quat. Sci. Rev.* 57, 26–45
89. Willerslev, E. *et al.* (2014) Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506, 47–51
90. Blume-Werry, G. *et al.* (2020) Invasive earthworms unlock Arctic plant nitrogen limitation. *Nat. Commun.* 11, 1766
91. Angst, G. *et al.* (2021) Plant- or microbial-derived? A review on the molecular composition of stabilized soil organic matter. *Soil Biol. Biochem.* 156, 108189
92. Kelly, L.T. *et al.* (2020) Fire and biodiversity in the Anthropocene. *Science* 370, eabb0355
93. Weisberg, P.J. *et al.* (2006) Modelling of large herbivore–vegetation interactions in a landscape context. In *Large Herbivore Ecology, Ecosystem Dynamics, and Conservation* (Danell, K. *et al.*, eds), pp. 348–382, Cambridge University Press
94. Dangal, S.R.S. *et al.* (2017) Integrating herbivore population dynamics into a global land biosphere model: plugging animals into the Earth system. *J. Adv. Model. Earth Syst.* 9, 2920–2945
95. Berzaghi, F. *et al.* (2018) Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential of vegetation models. *Ecography* 41, 1934–1954
96. Luo, Y. *et al.* (2016) Toward more realistic projections of soil carbon dynamics by Earth system models. *Glob. Biogeochem. Cycles* 30, 40–56
97. Flores, O. *et al.* (2021) KEYLINK: towards a more integrative soil representation for inclusion in ecosystem scale models - II: model description, implementation, and testing. *PeerJ* 9, e10707
98. Deckmyn, G. *et al.* (2020) KEYLINK: towards a more integrative soil representation for inclusion in ecosystem scale models. I. review and model concept. *PeerJ* 8, e9750
99. Xiang, M. *et al.* (2021) Heavy grazing altered the biodiversity–productivity relationship of alpine grasslands in Lhasa river valley, Tibet. *Front. Ecol. Evol.* 9, 455
100. Saiz, G. *et al.* (2015) Pyrogenic carbon from tropical savanna burning: production and stable isotope composition. *Biogeosciences* 12, 1849–1863
101. Friedlingstein, P. *et al.* (2020) Global carbon budget 2020. *Earth Syst. Sci. Data* 12, 3269–3340