## **REVIEW AND SYNTHESIS**



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## Context matters when rewilding for climate change

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#### **Abstract**

- There is a cross-sectoral push among conservationists to simultaneously mitigate biodiversity loss and climate change, especially as the latter increasingly threatens the former. Growing evidence demonstrates that animals can have substantial impacts on carbon cycling. As such, there are increasing calls to use animal conservation and rewilding to dually overcome biodiversity loss and mitigate climate change.
- 2. Specifically, trophic rewilding—which involves restoring intact animal communities, functional roles and trophic structure within food webs, and natural ecosystem processes—utilizes a rewilding framework to simultaneously support biodiversity conservation and carbon capture and storage. Trophic rewilding is a complex conservation approach to mitigating climate change, involving accurate estimations of baseline conditions and continuous monitoring of carbon cycling and species impacts within a system. It is also predicated on garnering social support for both the reintroduction and monitoring of a species, and obtaining the animals themselves.
- 3. We are excited by the growing interest in this potential, but emphasize that a species' net impact on ecosystem carbon dynamics is context-dependent. Caution is required whenever biodiversity conservation (including rewilding), climate change mitigation, and human welfare do not readily align. Hence—similar to other nature-based solutions—these burgeoning efforts must avoid sweeping generalizations.
- 4. To bolster successful trophic rewilding, we highlight a range of social and ecological context dependencies that can vary outcomes in a rewilded carbon cycle and provide ethical considerations for successful implementation.
- 5. We conclude with an overview of the available technology to predict and monitor progress toward both biodiversity and climate mitigation goals.

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#### KEYWORDS

biodiversity, carbon cycle, carbon offset, conservation decision-making, conservation ethics, conservation prioritization, nature-based climate solutions, rewilding

#### INTRODUCTION

Scientists, policymakers and conservation practitioners are confronted with the dual challenge of mitigating climate change and biodiversity loss (Dinerstein et al., 2020; Seddon et al., 2021). Until recently, solutions to each have been routinely treated as functionally unrelated (Dinerstein et al., 2020; Malhi et al., 2022); yet this line of thought is shifting. Growing evidence shows that animals may play an important role in mitigating climate change by mediating carbon capture and storage in ecosystems, thus demonstrating potential congruence between the biodiversity and climate challenges (Cromsigt et al., 2018; Kristensen et al., 2022; Malhi et al., 2022). Hence, continuing to focus landscape conservation on protecting either animal diversity or maximizing carbon capture and storage could miss opportunities to further both goals (Schmitz et al., 2023).

One burgeoning climate change mitigation strategy is animating the carbon cycle through trophic rewilding. Animating the carbon cycle recognizes that animals, particularly large vertebrates, can have important effects on ecosystem carbon capture despite their smaller total biomass relative to other biological drivers of carbon cycling (e.g. plants or microbes; Schmitz et al., 2014, 2023). Trophic rewilding rebuilds ecosystems by restoring intact animal communities, the trophic structure of food webs, and natural ecosystem processes and services for both humans and wildlife (Carver et al., 2021; Svenning et al., 2016). Thus, Trophic Rewilding to Animate the Carbon Cycle (TRACC) leverages both animating the carbon cycle and trophic rewilding frameworks, positing that rewilding animals' functional roles in ecosystems can simultaneously further biodiversity conservation and increase carbon capture and storage in ecosystems. Although all rewilding initiatives involve species restoration and therefore restoration within a trophic level of an ecological community, trophic rewilding specifically assesses all subsequent top-down and bottom-up effects that arise following restoration.

Estimates derived from a subset of animals across diverse ecosystems reveal that animals could substantially alter an ecosystem's carbon budget by 60%-95%, relative to cases where these focal animals are absent (Schmitz & Leroux, 2020). Therefore, restoring animal populations can potentially enhance ecosystem carbon capture and storage globally by at least 6.4 billion tonnes per year (Schmitz et al., 2023). By comparison, this amount rivals that of each of the IPCC top five steps for reducing net emissions expeditiously, including a rapid transition to solar and wind technology (IPCC, 2022). Hence, the high potential of TRACC to add to the portfolio of nature-based solutions makes it an appealing way to promote wildlife conservation to overcome the dual challenges of mitigating climate change and biodiversity loss.

However, we are at a juncture where careful examination is warranted for ecologically accurate biodiversity protection using

TRACC. The few studies that quantify animal effects on ecosystem carbon cycling show promise; however, they also demonstrate the importance of considering ecological context. This is because animal effects on carbon capture and storage can vary with ecosystem type and the functional role of wildlife species in that ecosystem (Table 1; Figure 1), and the uncertainty around estimates can be high (Schmitz et al., 2023; Supporting Information). TRACC also inherently requires increasing the abundance of wildlife species on the landscape, potentially in competition with people who already live there. Therefore, as a nature-based solution, TRACC requires including human communities as part of the solution (Schmitz & Sylvén, 2023; Seddon et al., 2021).

We discuss key considerations when designing and monitoring TRACC programmes. This includes assessing and balancing social and ecological dependencies to produce ethical and scientifically defensible nature-based solutions using TRACC. We begin by (1) highlighting the context of species and of ecosystems features and (2) outlining a series of social contexts which need to be considered. We then (3) address the kinds of ethical considerations that are needed, given the potential impacts of TRACC on people and the value that rewilding projects place on wildlife. We conclude with (4) suggestions and directions for conservationists interested in trophic rewilding schemes for carbon storage. We also discuss how to optimize available technologies for appropriate monitoring strategies to better understand how a species impacts the carbon storage of a specific ecosystem.

Trophic Rewilding to Animate the Carbon Cycle is a subset of rewilding initiatives, with the deliberate aim of restoring animal populations and communities to enhance carbon capture and storage. We focus here on TRACC examples involving terrestrial megafauna (e.g., >45 kg; Martin & Klein, 1989) because they are among the most studied and most vulnerable animals to human activities (Belote et al., 2020; Dirzo et al., 2014; Ripple et al., 2014). Consequently, conservationists have heightened their investment in the rewilding of large and charismatic species. Moreover, given their biomass, density and role in ecosystem function, they often have significant impacts on carbon cycling (Kristensen et al., 2022; Malhi et al., 2022; Schmitz et al., 2018). This is not to diminish the critical importance of considering marine wildlife (Durfort et al., 2022; Saba et al., 2021), large reptiles and invertebrates (e.g. arthropods; de Miranda, 2017) for similar purposes. To that end, the concepts and principles we derive from terrestrial case studies should apply to other taxa.

We recognize that rewilding is a growing, multifaceted strategy with many different goals and socio-ecological benefits and challenges. Within such a breadth, some rewilding efforts primarily try to restore ecological function through the management and conservation of habitat and landscape connectivity, acknowledging that such efforts may have ancillary benefits of increasing carbon storage (Goswami, 2023; Lamba et al., 2023). Other rewilding programmes

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TABLE 1 Effects of animal species on ecosystem carbon uptake and storage driven by trophic impacts, illustrating context-dependency in animal effects. Orange, green, and grey squares represent net negative, positive, and neutral animal effects on ecosystem carbon budgets, respectively.

Animal species and ecosystem <sup>a</sup>	Animal effects on ecosystem function
Anninal species and ecosystem	Annual effects on ecosystem function
$Moose \to boreal \; forest \; vegetation \to soil$	$\blacksquare \downarrow$ primary productivity and biomass, $\downarrow$ soil organic carbon retention, $\uparrow$ wildfire
$Wolf \rightarrow Moose \rightarrow boreal\ forest\ vegetation$	$\blacksquare$ $\uparrow$ primary productivity, $\uparrow$ soil organic carbon retention, $\downarrow$ wildfire
$Elk \to prairie \ grassland \ vegetation \to soil$	↑ primary productivity, ↑ soil organic carbon retention
$Wolf \rightarrow Elk \rightarrow prairie\ grassland\ vegetation$	$\blacksquare$ $\downarrow$ primary productivity, $\downarrow$ soil organic carbon retention
$Bison \to prairie \ grassland \ vegetation \to soil$	■ ↑ primary productivity, ↑ soil organic carbon retention
$Wildebeest \rightarrow savanna\text{-}woodland\ vegetation} \rightarrow soil$	$\blacksquare\downarrow$ wildfire, $\uparrow$ soil organic carbon retention, $\uparrow$ woody biomass carbon
${\sf Savanna\ elephants} \to {\sf savanna\text{-}woodland\ vegetation}$	$\blacksquare\downarrow$ woodland biomass carbon, $\uparrow$ herbaceous vegetation carbon $\uparrow$ soil carbon retention
Forest elephants $\rightarrow$ tropical forest vegetation	■↑ forest overstorey biomass carbon density
${\sf Caribou} \to {\sf dry} \ {\sf tundra} \ {\sf heath} \ {\sf vegetation} \to {\sf soil}$	$\blacksquare$ $\downarrow$ primary productivity, $\downarrow$ soil organic carbon retention
$Caribou \to boreal \ forest \ vegetation \to soil$	$\blacksquare\downarrow$ plant standing stock, $\uparrow/\text{-}$ soil organic carbon retention
$Muskox \to wet \ tundra \ mire \ vegetation \to soil$	■ ↑ primary productivity, ↑ soil organic carbon retention
$Muskox \to dry \ tundra \ heath \ vegetation \to soil$	■ ↓ primary productivity, ↓ soil organic carbon retention
Frugivores (primates, tapirs, guans, hornbills, fruit bats) → fruits → tropical forest tree diversity	■↑ forest tree biomass carbon density

*Note*:  $\rightarrow$  = trophic interaction,  $\uparrow$  = increase in ecosystem effect,  $\downarrow$  = decrease in ecosystem effect,  $\neg$  = neutral ecosystem effect.

aim to reintroduce or promote animal populations for other socioeconomic and ecological contributions; however, these are beyond the scope of this paper.

# 2 | CONTEXT DEPENDENCY IN REWILDING THE CARBON CYCLE

Determining whether trophic rewilding as a nature-based solution—that is, TRACC—will work largely depends on understanding whether such efforts are ecologically and socially feasible. Here, we highlight some contexts necessary to consider for successful TRACC projects so that conservationists may be able to use this as an initial means to identify the context dependencies that are most relevant in their system.

#### 2.1 | The species context

In the intricate web of ecological relationships, the success of TRACC efforts hinges on a nuanced understanding of the unique roles that individual species play within ecosystems. While most TRACC initiatives focus on wildlife species, some TRACC initiatives may use domestic animals to mimic the role of wild animals in cases where wild counterparts have gone extinct (e.g. introducing cattle to mimic extinct aurochs). This is a legitimate TRACC approach if these animals are managed differently from herded livestock by allowing them to functionally mimic the movement and foraging ecology of their extinct wild counterparts, even if in some context, they are still legally treated as livestock (e.g. required vaccinations; Gordon, Manning, et al., 2021; Gordon, Pérez-Barbería, et al., 2021; Hempson

et al., 2017). As such, it is an important prerequisite to consider a species not just in terms of its taxonomic identity but more importantly in terms of its functional traits, population demographics and density, and the resident animal community assemblage to which it will be restored (Figure 2).

Understanding species' functional traits is critical to understanding their impacts on carbon cycling (Figure 2). Varied hunting or foraging styles determine how individuals impact their community and ecosystem, primarily by modulating the vegetative structure of the landscape (Bakker et al., 2016), which has carbon implications. For example, grazers generally consume fast-growing grasses, which can promote shoot production, thereby increasing carbon capture (Wilson et al., 2018). In contrast, browsers consume slow-growing shrubs and trees, which, in some systems, may limit carbon capture (Salisbury et al., 2023). Additionally, functional traits such as digestion capabilities may shape the quality and quantity of plants that are eaten and the subsequent amount of methane released (Clauss et al., 2020). Activity such as trampling may compact soil and reduce soil respiration (Schmitz et al., 2018), while wallowing can create natural fire breaks (Malhi et al., 2022), and migration across landscapes may translocate nutrients essential to plant production (Subalusky et al., 2017).

The demographics of a rewilded population can also differentially affect carbon sequestration even within the same system (Figure 2b). For example, in Kruger National Park, male elephants decreased above-ground carbon storage, while breeding herds had a nonsignificant impact (Davies & Asner, 2019). In deer species, males are known to consume more woody vegetation (Garcia et al., 2023); hence, populations with higher proportions of males could ultimately reduce carbon storage and uptake. Other demographics (e.g. age, social status) that also alter consumption rates and preferences may also have carbon capture implications.

<sup>&</sup>lt;sup>a</sup>References for case studies are presented in Supplemental Information.

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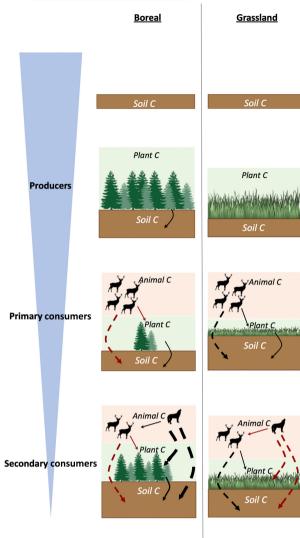


FIGURE 1 The consideration of a full trophic cascade disentangling the assumption that organismal biomass or abundance equates to the cumulative effect of carbon storage mechanisms. Demonstrating using a wolf-deer system (Wilmers & Schmitz, 2016), the greatest carbon uptake is yielded through indirect effects, disproportionate to biomass. From top to bottom and beginning with bare soil, increasing the number of trophic levels in a grassland system and in a boreal system increases soil carbon storage through indirect effects. Arrows represent direct effects (solid line), indirect effects (dashed line), negative effects (red), positive effects (black), and magnitude of effect (arrow thickness).

One of the most important decisions to make in trophic rewilding efforts is how densely populated a rewilded species should be. Different population densities of rewilded animals can have negative, positive or negligible effects on ecosystem carbon storage (Figure 2c; Berzaghi et al., 2019; Holdo et al., 2009), notwithstanding potential density-dependent risk of human-wildlife conflict. For example, forest elephants (Loxodonta cyclotis) in the Congo can have negative overconsumption and trampling effects on tree production at high densities, negligible effects at low densities and positive effects at intermediate densities due to their enhancement of forest canopy tree production via reducing competition with understorey

vegetation and promoting seed dispersal and germination (Berzaghi et al., 2019). In the Serengeti, a 20% reduction in the wildebeest population shifted the savanna from being a carbon sink to a source because reduced grazing led to more frequent and intense wildfires (Holdo et al., 2009). Thus, maximizing carbon capture using rewilded animal populations could require population control for both carbon storage and conflict mitigation, which may be antithetical to the goals of merely conserving wildlife biodiversity (e.g. prioritizing species richness). Effective TRACC solutions require deciding which species to rewild, what density is needed to balance carbon capture and other determined targets and the kind of management or stewardship needed to maintain the population at this density.

Of course, species do not exist or act alone in ecosystems, and the resident plant and animal community assemblage must also be considered (Figure 1). For instance, different mammalian herbivore assemblages can have varying impacts on carbon storage and CO<sub>2</sub> fluxes via herbivory that alters plant communities (Olofsson & Post, 2018), above-ground biomass (Metcalfe & Olofsson, 2015) and soil mixing (Kristensen et al., 2022). Further research is needed to untangle how differing community assemblages, and changes in assemblages, may impact carbon sequestration.

Not all animal traits and characteristics can be addressed or managed in a rewilding or TRACC intervention. We add the caveat that applying this ecological understanding nearly always relies on estimating average species contribution to the carbon cycle, which neglects to account for intraspecific variation (Bolnick et al., 2011; Sommer & Schmitz, 2020). The species and individual contexts provided here are not an insurmountable hurdle to successful TRACC intervention, but rather emphasize the importance of local knowledge and application.

### The ecological context

Implementing trophic rewilding as a nature-based climate solution must also account for the ecological characteristics within ecosystems and their relationship to the candidate species for rewilding (Table 1). These characteristics include trophic cascades, community composition and ecosystem or habitat type. Wild animals can have top-down feedback effects on ecosystem functions via trophic cascades (Figures 1 and 2e), in which density and trait-mediated effects at upper trophic levels can alter the amount of carbon exchanged between plants, soils and the atmosphere (Schmitz & Leroux, 2020). As described above, such roles include foraging and space use by carnivores and herbivores that, respectively, control animal and plant productivity and abundance; redistributing seeds and nutrients over vast spatial extents; and trampling, burrowing, and wallowing causing disturbance and compaction.

Other ecosystem characteristics such as climate, topography, seasonality and rainfall gradient can influence the carbon storage potential of animals. For extensive reviews on how ecosystem context can impact rewilding and/or the carbon cycle, see Malhi et al. (2022) and Kristensen et al. (2022). The effects of these

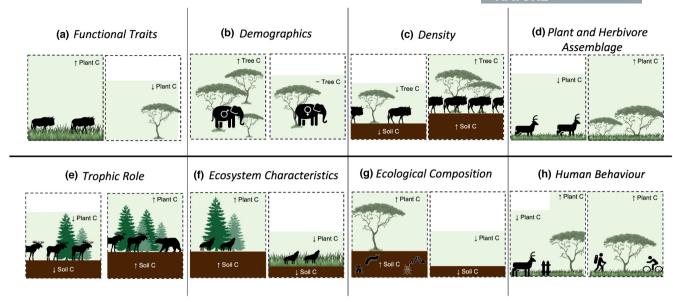


FIGURE 2 Known and potential discrepancies in carbon storage, based on system-specific contexts: (a) Species' functional traits, in which grazing or browsing could alter carbon stored in plant biomass; (b) Population demographics, in which species' sex can differentially alter the amount of plant carbon stored (Davies & Asner, 2019); (c) Animal density, where the number of animals can alter soil and tree carbon stored (Holdo et al., 2009); (d) Community composition, in which presence or absence of certain herbivore or plant species can directly affect plant carbon storage (Metcalfe & Olofsson, 2015); (e) Trophic role, where presence or absence of a predator can indirectly affect soil and plant carbon storage (Cromsigt et al., 2018); (f) Ecosystem characteristics, where system-specific effects, such as habitat type, will determine whether a species has a positive or negative impact on carbon storage (Wilmers & Schmitz, 2016); (g) Ecological composition, where soil animal communities have known effect on carbon storage in soil and in the plants (Andriuzzi & Wall, 2018; Filser et al., 2016); (h) Human behaviour, where the presence or absence of humans, as well as the type of activity occurring on the landscape, will indirectly impact plant carbon storage ecosystem characteristics.

ecosystem characteristics are magnified by trophic interactions that can alter the diversity, abundance and carbon density of plant communities, fire regimes, methane release from permafrost, carbon inputs to soil from faecal and carcass deposition, and microbial processes and chemical reactions that mediate the retention of soil carbon. Herbivores themselves can influence ecosystem fire frequency and severity by determining the quantity and quality of fuels on the landscape, thereby affecting carbon source or sink potential. As a result, trophic rewilding has been proposed as a potential tool for regulating fire and carbon loss, as climate change renders fire seasons longer and more severe (Johnson et al., 2018). The ecosystem effects of herbivores can be further mediated by predators. Predator-driven reduction in herbivore abundances and altered herbivore behaviour and physiology can have indirect effects on plant biomass, photosynthesis and respiration, ultimately affecting fluxes of CO<sub>2</sub> and CH<sub>4</sub> between ecosystems and the atmosphere.

Even a species' role itself can differ across longitude, habitats or ecosystem types (Figure 2f; Berzaghi et al., 2019; Davies & Asner, 2019). For example, savanna elephants (*Loxodonta africana*) in savanna ecosystems appear to have neutral or negative effects on carbon storage (Davies & Asner, 2019; Pellegrini et al., 2017; Sandhage-Hofmann et al., 2021), whereas forest elephants (*L. cyclotis*) in the central African rainforest play a significant role in seed dispersal, above-ground biomass and thus above-ground carbon storage (Berzaghi et al., 2019). Regional differences are not only limited to the effects of large animals or plant communities but also

extend to intra-annual weather patterns and interannual changes in climate. Carbon-relevant processes are highly dependent on local contexts, which necessitates longitudinal, holistic, regional assessments of how rewilding will impact carbon storage.

It is also noteworthy to consider that animals selectively move across the landscape, therefore stratifying nutrient subsidies (Ferraro et al., 2021), shaping plant diversity (Ellis-Soto et al., 2021) and altering the carbon density of standing vegetation within a region. Resolving such zoogeochemistry mechanisms and climate fluctuations is key for predicting the feedback between animals and elemental cycling, and become increasingly important under continued climate change (e.g. changes in seasonality, droughts and floods). Such feedbacks could be large enough that, if animal effects are ignored, conventional natural climate solutions may either miss opportunities to enhance carbon capture or fail to meet carbon capture targets.

Ecological community composition is diverse and complex; therefore, it is also necessary to consider the impacts of carbon beyond the direct management action of large animals (Figure 2g). For example, soil animal communities are rarely considered in conservation or rewilding projects despite their known effect on soil carbon turnover and storage (Andriuzzi & Wall, 2018; Filser et al., 2016). Relatedly, management to improve carbon storage might result in unintended consequences on the above-ground invertebrate community that, in turn, could decrease ecosystem function. For example, ecosystem changes can indirectly reduce pollinator diversity, leading to a decrease in plant pollination (Guy et al., 2021). Understanding the

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relationships between ecosystem characteristics, animal functional roles and carbon dynamics is crucial for comprehensive TRACC.

#### 2.3 | The social context

Few nature–society interactions can be considered one-sided. Just as animals shape ecosystems, human land use can reshape ecological communities with important implications for ecosystem functioning and conservation efforts, both of which are relevant for rewilding and carbon sequestration (Estes et al., 2011; Suraci et al., 2021; Figure 2h). For example, the restriction of wide-ranging species through fencing or deforestation can concentrate their functional impacts within a small area (Tucker et al., 2021), thereby possibly altering the sequestration of carbon by plants or nutrient cycling rates. The nature and frequency of human–wildlife interactions through land use and infrastructure, as well as through human mobility, recreation, or byproducts can determine the landscape occurrences of rewilded species and hence TRACC.

The need to consider local ecological context means enlisting local knowledge and community buy-in will be essential for successful TRACC implementation (Goswami, 2023; Schmitz & Sylvén, 2023; Takacs, 2020). It necessitates active community engagement and power-sharing in decision-making (Ainsworth et al., 2020). TRACC must therefore be responsive to social dynamics influenced by factors such as human well-being, intrinsic values, local knowledge, socio-cultural heritage and access to natural resources (Carver et al., 2021; Schulte To Bühne et al., 2022; Takacs, 2020).

In numerous cases, rewilding alone explicitly emphasizes community consent and the transformative potential of rewilding on local rural economies (Martin et al., 2021). For instance, wildlife tourism in Scotland contributes approximately £276 million annually (McVittie et al., 2017). However, these projections do not always materialize as fully realized outcomes and do not always include carbon benefits or tradeoffs. Accurate projections of the economic benefits and costs of TRACC projects must include any consideration of development for recreation and tourism, in addition to carbon offsets. These include acquisition costs, management costs, and transaction costs (Naidoo et al., 2006). Examples of associated costs to rewilding include the potential impacts on other local economies, such as the introduction of beavers potentially impacting habitat for fisheries (Gaywood, 2018) and the initial conversion costs of land for rewilding purposes (Schou et al., 2021). Moreover, rewilding often demands substantial land areas that may require fencing (Schou et al., 2021).

The costs and benefits of rewilding are not always economic, and conventional economic valuation frameworks may not adequately capture its social, political and cultural aspects (Thondhlana et al., 2020). Examination of the cost-benefit restrictions should ensure that excessive rewilding costs do not erode its comparative advantage over alternative nature-based or mitigation approaches (e.g. Naidoo et al., 2006; Reed et al., 2013; White et al., 2022). There should also be transparency in which valuations will take priority when the estimation of these tradeoffs do not yield clear solutions (Armsworth et al., 2017).

Current policies and incentives also complicate how and when trophic rewilding initiatives will benefit local communities. For example, grazing of natural areas in Denmark is subsidized through the EU's current Common Agricultural Policy. Rewilding could be a stronger economical choice if this policy included additional subsidies for natural rewilding efforts (Schou et al., 2021). However, current government policies and subsidies render year-round grazing more economically advantageous than rewilding (Schou et al., 2021). Competing land uses and the opportunity costs related to rewilding thus are not only linked to the economic and non-economic costs but also the current political policies.

Similar to conservation projects, TRACC efforts necessitate a deep understanding and contextualization of local power dynamics (Margulies & Karanth, 2018). Species can symbolize specific entities, including state intervention or coercion, which can provoke retaliatory responses, hostility and resentment (Naughton-Treves & Treves, 2005). In particular, large-bodied vertebrates often serve as symbols of government or state authority (Margulies & Karanth, 2018). In the United States, wolves have become emblematic of federal government actions that restrict the autonomy of local, place-based communities that oppose wolf reintroduction (Dickman & Hazzah, 2016; Wilson, 1997). Rewilding efforts, including TRACC, need to not only consider animals themselves but also address the underlying social, economic, and cultural factors contributing to local communities' values and hence potential resistance to a project (Dickman & Hazzah, 2016; Margulies & Karanth, 2018; Naughton-Treves & Treves, 2005).

Many of these concerns can be effectively addressed by conducting a thorough needs assessment and participating in extensive community consultation during the initial stages of the project. A regional assessment can help fill the social and biological gaps, ensuring ecological accuracy while involving local communities. Decisions that reconcile trade-offs require balancing the benefits and drawbacks of coexisting with wildlife, the incremental carbon benefits, costs of rewilding itself, and the socio-cultural and welfare opportunities for local communities. These decisions would also weigh the intensive management and intangible costs compared to other carbon sequestration projects—such as potential reductions in land access privileges, including hunting, logging, crop production, grazing and the potential impact on landowners' knowledge-alongside the prospects for hydrological, coastal and nutrient restoration (Falcón & Hansen, 2018; Schou et al., 2021). Sustaining ongoing projects requires continuous follow-up through integrative and adaptive management approaches as well as social evaluations, and fostering the collaboration between various levels of governance and local communities (König et al., 2020; Sandom & Wynne-Jones, 2019).

#### 2.4 | The ethical context

Like all conservation programmes, TRACC is inherently ethical as it is motivated by the normative values that (1) wild, intact ecosystems are good and (2) humans ought to address anthropogenic climate change (Ferraro et al., 2023). Further, it requires that all participants

balance the interests, needs and functions of humans, animals and ecosystems together. Human rights, animal welfare, environmental justice, intrinsic values and ecosystem functionality represent some of the interwoven ethical issues that are at stake in determining the outcome of rewilding efforts (Lee et al., 2021), and thus also apply to TRACC endeavours.

Conservation science is underpinned by ethical norms and values that are often not critically examined by conservationists (Ferraro et al., 2023; Pyron & Mooers, 2022) and are primarily driven by consequentialist thinking (Ferraro et al., 2021). To some, TRACC may seem similarly consequentialist—driven by the desire to combat climate change for humankind's persistence on the planet. Indeed, many conservation projects focus primarily on financial and environmental cost-benefit implications, rather than considering the broader range of issues outlined above. These cost-benefit approaches often do not consider conservation and stewardship practices alongside human virtues, and do not value animals beyond their identity as taxonomic entities (Schmitz & Sylvén, 2023; Sommer & Ferraro, 2022; Wallach et al., 2018). Yet, TRACC, like all rewilding, is inherently an ecocentric perspective, one that acknowledges the intrinsic value of ecosystems and their components, emphasizing the interconnectedness of all elements within an ecosystem, and ensures that humans and animals are not treated merely as means to ends (Carver et al., 2021; Schulte To Bühne et al., 2022). It is an important recognition that rewilding projects that aim to create intact and healthy ecosystems, which may help mitigate climate change, are created in a way that respects and appreciates the intrinsic value of nature and individual animals. Importantly, a shift away from an anthropocentric framework does not preclude opportunity for any human intervention (i.e. the human-mediated reintroduction or conservation of animals), nor does it preclude human benefit (i.e. carbon containment). Rather, ecocentrism in TRACC promotes sustainable and responsible interactions with the environment that benefits those within the environment. Further, it demands action for climate change that underscores how the well-being of ecosystems and individuals within are worth protecting.

Beyond careful ethical consideration for non-human animals involved in rewilding, Human Rights Impact Assessments (HRIA), or their equivalency, should be used across TRACC programs as an intentional effort to link human rights and wildlife carbon offsets to ensure local communities do not bear the brunt of wildlife's negative impacts. This is particularly important, given growing concern that rewilding initiatives could encourage removing people from landscapes slated for rewilding, an action which would be unjust (Fletcher et al., 2021). Many rewilding scholars explicitly state that rewilding must incorporate humans within nature (Carver et al., 2021), a sentiment which we wholeheartedly support. An example of successful integration, and consideration, of ethics in rewilding can be found in Lee et al. (2021) who critically and thoroughly explore the ethical realities of grizzly rewilding in California; and we argue this kind of assessment must be undertaken for each proposed rewilding scheme.

We advocate for a cumulative approach which weighs all parts of a context rather than seeking to simply rank which species or

system is more or less important to the carbon cycle. Complex, and sometimes differing, ecological contexts and human values surround biodiversity conservation and carbon storage (see the IPBES, 2023). Without each of these full considerations, we risk a disconnect between the generalizations advertised in carbon offset programs, conservationists' implementations, ecological accuracy, and social and ethical impacts. Effectively navigating these ethical complexities requires greater collaboration with experts in human and environmental ethics, enabling well-informed and ethically sound decisions that foster coexistence between humans and wildlife in a given landscape (Ferraro et al., 2021; Lee et al., 2021; Nelson et al., 2021).

#### CREATING TRACC SOLUTIONS 3

With active consideration of the context dependencies described above, TRACC can be implemented at local and regional scales. While some TRACC initiatives may require the translocation of animals, benefits from TRACC may also be seen in efforts focused on broader ecosystem restoration goals (such as climate-resilient ecosystems), which can ultimately create habitat for the recolonization of animals. Likewise, conservation programmes, either aimed at conserving ecosystems or specific animals, may also see TRACC benefits (Lamba et al., 2023). The decision about whether to proceed with a project requires trade-off decisions between carbon and rewilding goals and the explicit engagement of all partners, including local communities, regional governance, conservation NGOs, and investors (Ainsworth et al., 2020).

At its core, TRACC centres upon reintroducing a species to enhance carbon capture and storage. Yet, how exactly do we go about creating a rewilded carbon cycle? It requires collaboration between conservation practitioners and scientists and begins with estimating carbon flux and storage potential within ecosystems to determine the feasibility of using trophic rewilding as a climate change solution in addition to existing priorities and values for human land uses. If feasible, then projects must define carbon storage goals and accurately measure carbon embodied in soil, plant, and animal biomass (as currently emphasized by carbon offset and rewilding projects, respectively) as well as carbon fluxes between the pools and the atmosphere (Schmitz et al., 2023). Monitoring before, during, and after the species introduction is needed to evaluate whether TRACC goals are being achieved. Detailed guidance on how to assess and monitor animal effects on the movement and storage of carbon in ecosystems is provided in Abraham et al. (2023) and Ellis-Soto et al. (2021) and Supporting Information. In addition, there are a few new technologies and methods to consider.

Currently, a new fleet of satellites, including TROPOMI with a pixel resolution of 7km<sup>2</sup>, allows the direct measurement of methane emissions. This has already been used to quantify human methane emissions from oil-producing basins (Zhang et al., 2020) and livestock (Scarpelli et al., 2020), and could be used to track methane release from large aggregations of wild ruminants. The launch of the

Carbon Mapper satellite in 2023 offers measures of methane and carbon dioxide emissions at fine spatial resolutions of 30 m<sup>2</sup> (https:// carbonmapper.org) and could build upon methodological advances and algorithms from the TROPOMI mission. Both satellites could be calibrated and validated with in situ measurements of flux towers and eddy covariance towers. Other available remote sensing satellite imagery includes nearly globally available Light Detection And Ranging (Lidar) data from the Global Ecosystem Dynamics Investigation (GEDI) that can provide 25m<sup>2</sup> resolution insights into forest structure and above-ground biomass density (Hancock et al., 2019). This will provide unprecedented opportunities to study how megafauna shape the environment at the landscape scale (Davies & Asner, 2019). Besides near global LIDAR, local to regional estimates of carbon through airplane (Asner et al., 2014) and highresolution satellite imagery (e.g. Planet tasking; Csillik et al., 2019) could be coupled with species habitat use to estimate the impact of megafauna on the carbon cycle (sensu Ellis-Soto et al., 2021).

Satellites are not the only opportunity to quantify faunal impact on the carbon cycle. Eddy covariance towers are used to measure gas exchange in ecosystems and can allow disentangling methane emissions from animals and carbon dioxide exchanges from plant-soil exchange. This subsequently allows for constructing ecosystem budgets that account for species effects on the carbon cycle through production of greenhouse gasses. This has already proved successful with large herbivores methane emissions by coupling atmospheric measurements from eddy-covariance matrix with animal locations obtained from GPS collars or camera traps (Dumortier et al., 2019; Stoy et al., 2021). This methodology can also detect the influence of animal behaviour (resting, moving and foraging) through the methane emissions detected from the eddy covariance. Further, such methane footprints obtained from animals can be validated using artificial source experiments (Dumortier et al., 2019). Such eddy-covariance towers are increasingly reduced in cost, and large-scale networks of flux towers, such as the National Ecological Observatory Network (NEON) sites or the FLUXNET network (https://fluxnet.org/), could be target areas for detailed studies of megafauna influence on the carbon cycle through the installation of trap cameras or collaring of individual animals. Remote sensing from satellite or airplane imagery and eddy covariances could be used to detect to quantify the contribution of populations, herds, and individual animals, particularly megafauna; while radar technologies could quantify the contribution of mass migration of birds and insects on the carbon cycle (Bauer et al., 2019; Dokter et al., 2018; Hu et al., 2016; Stepanian et al., 2020). However, these technologies can only provide measurements down to the ground surface.

Measuring below-ground carbon will require field-based in situ measurements as below-ground biomass carbon can be substantially greater than above-ground biomass carbon in some ecosystems. Combining on-the-ground empirical studies with mathematical or statistical modelling offers a way to rigorously explore the potential climate benefits of rewilding by examining scenarios involving animals that are key functional drivers of ecosystem

carbon capture, as illustrated by (Berzaghi et al., 2019). Empirically, this can be executed through exclosure plots that provide controls following species introduction, or enclosure plots that manipulate the introduced species' density, etc. (Forbes et al., 2019).

By integrating the suite of species traits, described above, we can develop mechanistic models of animal movement (Hirt et al., 2018) and estimate predator-prey food web architecture (Brose et al., 2019; Hirt et al., 2020) that could be expanded into carbon cycle modelling (Schmitz & Leroux, 2020). Quantitative allometric approaches further support estimating species space-use (Jetz et al., 2004), movement speed (Hirt et al., 2017), and to some extent stoichiometric impacts on ecosystems (Allgeier et al., 2020). Agentbased modelling and other spatially explicit, bio-inspired models provide a means to simulate, anticipate, and weigh the costs and benefits of ecosystem processes based on species traits, density, management and policy decisions (Ferraro et al., 2022; Reed et al., 2013; Somveille & Ellis-Soto, 2022) as well as how anthropogenic change may alter zoogeochemical impacts (Abraham et al., 2023).

In conjunction with monitoring and evaluation, reporting should be openly accessible in order to share information about project successes and/or failures. This requires a willingness to discuss and possibly revise the project to meet the existing goals and targets, or re-engage in design to refine the goals and targets. Given the lack of information about time frames of TRACC interventions, this will be critical in providing frames of reference for future projects.

Lastly, adaptive management may be needed if project goals and targets are not being met. Missed targets may necessitate altered monitoring, changes in wildlife management, socio-ecological conflict resolution, or even sunsetting a project that originally seemed feasible (which, ethically, should include partners helping local communities identify, develop and transition to alternative economic and welfare opportunities). Ultimately, we posit that the strongest pathway to successfully a TRACC is to have a cyclical, communicative interplay between research and management in order to safeguard resilient ecosystems and human rights.

#### CONCLUSION

Animating the carbon cycle through rewilding represents a promising way to mitigate climate change and biodiversity loss. Broadening the scope of climate solutions to encompass wildlife can potentially accelerate the time frame for removing carbon from the atmosphere as well as maintain current storage. This is particularly true if we actively capitalize on existing chances to safeguard and swiftly restore species populations, as well as maintain the functional integrity of ecosystems. In systems where rewilding does not result in immediate carbon sequestration, there can be indirect benefits such as building resilient ecosystems. Our summary and contextualization in this paper can be broadly relevant to all rewilding projects, though TRACC requires specific social buy-in, ecosystem baseline estimates, and species introductions which will likely interact with humans. While the potential of TRACC is exciting, it does not negate

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the need to reduce anthropogenic carbon emissions including the decarbonization of energy production. Within larger TRACC efforts, there needs to be more long-term studies on how animals impact the carbon budget. This requires research and management to leverage appropriate technology in order to quantify animal roles in the carbon cycle. Projects must be sensitive to local socio-ecological contexts—identifying appropriate locations for conserving biodiversity and land towards carbon capture as well as addressing the needs of people living on the land. Sometimes rewilding initiatives, climate mitigation, and human welfare will align. At other times they will not be mutually-reinforcing, requiring reconciliation of difficult trade-offs. Therefore, we caution that careful consideration and regionally specific project assessment is needed to ethically execute rewilding schemes. Specifically, economists quantifying the impact of TRACC should consider these factors when initiating a project.

We share the excitement that rewilding to animate the carbon cycle can expand the geographic scope of natural climate solutions, but ultimately recognize that it is but one of many climate stabilization wedges. Like all such wedges, the crux of its optimized potential leans on a feedback-loop of transparency and accuracy between research and management.

#### **AUTHOR CONTRIBUTIONS**

Mary K. Burak conceived the original idea for the manuscript. Kristy M. Ferraro and Kaggie D. Orrick redesigned and structured future iterations. Mary K. Burak, Kristy M. Ferraro, Kaggie D. Orrick, and Oswald J. Schmitz led editing of the manuscript. All authors contributed critically to writing the manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

No new data were created or analysed for this publication. Data sharing is not applicable.

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#### REFERENCES

- Abraham, A. J., Duvall, E., Ferraro, K., Webster, A. B., Doughty, C. E., le Roux, E., & Ellis-Soto, D. (2023). Understanding anthropogenic impacts on zoogeochemistry is essential for ecological restoration. *Restoration Ecology*, 31, e13778. https://doi.org/10.1111/rec.13778
- Ainsworth, G. B., Redpath, S. M., Wilson, M., Wernham, C., & Young, J. C. (2020). Integrating scientific and local knowledge to address conservation conflicts: Towards a practical framework based on lessons learned from a Scottish case study. *Environmental Science & Policy*, 107, 46–55. https://doi.org/10.1016/j.envsci.2020.02.017
- Allgeier, J. E., Wenger, S., & Layman, C. A. (2020). Taxonomic identity best explains variation in body nutrient stoichiometry in a diverse marine animal community. *Scientific Reports*, 10(1), 13718. https://doi.org/10.1038/s41598-020-67881-y
- Andriuzzi, W. S., & Wall, D. H. (2018). Soil biological responses to, and feedbacks on, trophic rewilding. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 373(1761), 20170448. https://doi.org/10.1098/rstb.2017.0448
- Armsworth, P. R., Jackson, H. B., Cho, S.-H., Clark, M., Fargione, J. E., Iacona, G. D., Kim, T., Larson, E. R., Minney, T., & Sutton, N. A. (2017). Factoring economic costs into conservation planning may not improve agreement over priorities for protection. *Nature Communications*, 8(1), 2253. https://doi.org/10.1038/s41467-017-02399-y
- Asner, G. P., Knapp, D. E., Martin, R. E., Tupayachi, R., Anderson, C. B., Mascaro, J., Sinca, F., Chadwick, K. D., Higgins, M., Farfan, W., Llactayo, W., & Silman, M. R. (2014). Targeted carbon conservation at national scales with high-resolution monitoring. *Proceedings of the National Academy of Sciences of the United States of America*, 111(47), E5016–E5022. https://doi.org/10.1073/pnas.1419550111
- Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W. M., Sandom, C. J., Asner, G. P., & Svenning, J.-C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proceedings of the National Academy of Sciences of the United States of America, 113(4), 847–855. https://doi.org/10.1073/pnas.1502545112
- Bauer, S., Shamoun-Baranes, J., Nilsson, C., Farnsworth, A., Kelly, J. F., Reynolds, D. R., Dokter, A. M., Krauel, J. F., Petterson, L. B., Horton, K. G., & Chapman, J. W. (2019). The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography*, 42(5), 861–875. https://doi.org/10.1111/ecog.04083
- Belote, R. T., Faurby, S., Brennan, A., Carter, N. H., Dietz, M. S., Hahn, B., McShea, W. J., & Gage, J. (2020). Mammal species composition reveals new insights into Earth's remaining wilderness. Frontiers in Ecology and the Environment, 18(7), 376–383. https://doi.org/10.1002/fee.2192
- Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., & Doughty, C. E. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience*, 12(9), 725–729. https://doi.org/10.1038/s41561-019-0395-6
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Volker, H. W. R., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192.
- Brose, U., Archambault, P., Barnes, A. D., Bersier, L.-F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., ... Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, 3(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x
- Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S. R., Nelson, C., Gann, G. D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W. J., Davis, J., Sinclair, A., Bekoff, M., ... Soulé, M. (2021). Guiding principles for

- rewilding. Conservation Biology, 35(6), 1882–1893. https://doi.org/10.1111/cobi.13730
- Clauss, M., Dittmann, M. T., Vendl, C., Hagen, K. B., Frei, S., Ortmann, S., Müller, D. W. H., Hammer, S., Munn, A. J., Schwarm, A., & Kreuzer, M. (2020). Review: Comparative methane production in mammalian herbivores. *Animal*, 14, s113-s123. https://doi.org/10.1017/S1751731119003161
- Cromsigt, J. P. G. M., te Beest, M., Kerley, G. I. H., Landman, M., le Roux, E., & Smith, F. A. (2018). Trophic rewilding as a climate change mitigation strategy? *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 373(1761), 20170440. https://doi.org/10.1098/rstb.2017.0440
- Csillik, O., Kumar, P., Mascaro, J., O'Shea, T., & Asner, G. P. (2019). Monitoring tropical forest carbon stocks and emissions using planet satellite data. *Scientific Reports*, 9(1), 17831. https://doi.org/10.1038/s41598-019-54386-6
- Davies, A. B., & Asner, G. P. (2019). Elephants limit aboveground carbon gains in African savannas. *Global Change Biology*, 25(4), 1368–1382. https://doi.org/10.1111/gcb.14585
- de Miranda, E. B. P. (2017). The plight of reptiles as ecological actors in the tropics. *Frontiers in Ecology and Evolution*, *5*, 159. https://doi.org/10.3389/fevo.2017.00159
- Dickman, A. J., & Hazzah, L. (2016). Money, myths and man-eaters: Complexities of human-wildlife conflict. In F. M. Angelici (Ed.), Problematic wildlife (pp. 339–356). Springer International Publishing. https://doi.org/10.1007/978-3-319-22246-2\_16
- Dinerstein, E., Joshi, A. R., Vynne, C., Lee, A. T. L., Pharand-Deschênes, F., França, M., Fernando, S., Birch, T., Burkart, K., Asner, G. P., & Olson, D. (2020). A "global safety net" to reverse biodiversity loss and stabilize Earth's climate. *Science Advances*, 6(36), eabb2824. https://doi.org/10.1126/sciadv.abb2824
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401-406. https://doi.org/10.1126/science.1251817
- Dokter, A. M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W. M., La Sorte, F. A., Robinson, O. J., Rosenberg, K. V., & Kelling, S. (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nature Ecology & Evolution*, 2(10), 1603–1609. https://doi.org/10.1038/s41559-018-0666-4
- Dumortier, P., Aubinet, M., Lebeau, F., Naiken, A., & Heinesch, B. (2019).
  Point source emission estimation using eddy covariance: Validation using an artificial source experiment. Agricultural and Forest Meteorology, 266-267, 148-156. https://doi.org/10.1016/j.agrformet.2018.12.012
- Durfort, A., Mariani, G., Tulloch, V., Savoca, M. S., Troussellier, M., & Mouillot, D. (2022). Recovery of carbon benefits by overharvested baleen whale populations is threatened by climate change. Proceedings of the Royal Society B: Biological Sciences, 289(1986), 20220375. https://doi.org/10.1098/rspb.2022.0375
- Ellis-Soto, D., Ferraro, K. M., Rizzuto, M., Briggs, E., Monk, J. D., & Schmitz, O. J. (2021). A methodological roadmap to quantify animal-vectored spatial ecosystem subsidies. *Journal of Animal Ecology*, 90(7), 1605–1622.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., ... Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, 333(6040), Article 6040. https://doi.org/10.1126/science.1205106
- Falcón, W., & Hansen, D. M. (2018). Island rewilding with Giant tortoises in an era of climate change. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 373*(1761), 20170442. https://doi.org/10.1098/rstb.2017.0442
- Ferraro, K. M., Ferraro, A. L., & Sommer, N. R. (2021). Challenges facing cross-disciplinary collaboration in conservation ethics. *Conservation Science and Practice*, 3(11), e523. https://doi.org/10.1111/csp2.523

- Ferraro, K. M., Schmitz, O. J., & McCary, M. A. (2022). Effects of ungulate density and sociality on landscape heterogeneity: A mechanistic modeling approach. *Ecography*, 2022, e06039. https://doi.org/10.1111/ecog.06039
- Ferraro, K. M., Ferraro, A. L., Andis Arietta, A. Z., & Sommer, N. R. (2023).

  Revisiting two dogmas of conservation science. *Conservation Biology*, 37, e14101. https://doi.org/10.1111/cobi.14101
- Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., Uvarov, A. V., Berg, M. P., Lavelle, P., Loreau, M., Wall, D. H., Querner, P., Eijsackers, H., & Jiménez, J. J. (2016). Soil fauna: Key to new carbon models. *The Soil*, 2(4), 565–582. https://doi.org/10.5194/soil-2-565-2016
- Fletcher, M.-S., Hamilton, R., Dressler, W., & Palmer, L. (2021). Indigenous knowledge and the shackles of wilderness. *Proceedings. National Academy of Sciences. United States of America*, 118, e2022218118.
- Forbes, E. S., Cushman, J. H., Burkepile, D. E., Young, T. P., Klope, M., & Young, H. S. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, 33(9), 1597–1610. https://doi.org/10.1111/1365-2435.13376
- Garcia, F., Alves Da Silva, A., Ruckstuhl, K., Neuhaus, P., Coelho, C., Wang, M., Sousa, J. P., & Alves, J. (2023). Differences in the diets of female and male red deer: The meaning for sexual segregation. *Biology*, 12(4), 540. https://doi.org/10.3390/biology12040540
- Gaywood, M. J. (2018). Reintroducing the Eurasian beaver Castor fiber to Scotland. Mammal Review, 48(1), 48–61. https://doi.org/10.1111/ mam.12113
- Gordon, I. J., Manning, A. D., Navarro, L. M., & Rouet-Leduc, J. (2021).
  Domestic livestock and rewilding: Are they mutually exclusive?
  Frontiers in Sustainable Food Systems, 5, 550410.
- Gordon, I. J., Pérez-Barbería, F. J., & Manning, A. D. (2021). Rewilding lite: Using traditional domestic livestock to achieve rewilding outcomes. Sustainability, 13, 3347.
- Goswami, V. R. (2023). Wild animals enhance climate solutions across social-ecological systems. *Trends in Ecology & Evolution*, 38(10), 913–915. https://doi.org/10.1016/j.tree.2023.08.002
- Guy, T. J., Hutchinson, M. C., Baldock, K. C. R., Kayser, E., Baiser, B., Staniczenko, P. P. A., Goheen, J. R., Pringle, R. M., & Palmer, T. M. (2021). Large herbivores transform plant-pollinator networks in an African savanna. *Current Biology*, 31(13), 2964–2971.e5. https://doi. org/10.1016/j.cub.2021.04.051
- Hancock, S., Armston, J., Hofton, M., Sun, X., Tang, H., Duncanson, L. I., Kellner, J. R., & Dubayah, R. (2019). The GEDI simulator: A largefootprint waveform lidar simulator for calibration and validation of spaceborne missions. *Earth and Space Science*, 6(2), 294–310. https://doi.org/10.1029/2018EA000506
- Hempson, G. P., Archibald, S., & Bond, W. J. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports*, 7, 17196.
- Hirt, M. R., Jetz, W., Rall, B. C., & Brose, U. (2017). A general scaling law reveals why the largest animals are not the fastest. *Nature Ecology* & *Evolution*, 1(8), 1116–1122. https://doi.org/10.1038/s4155 9-017-0241-4
- Hirt, M. R., Grimm, V., Li, Y., Rall, B. C., Rosenbaum, B., & Brose, U. (2018). Bridging scales: Allometric random walks link movement and biodiversity research. *Trends in Ecology & Evolution*, 33(9), 701–712. https://doi.org/10.1016/j.tree.2018.07.003
- Hirt, M. R., Tucker, M., Müller, T., Rosenbaum, B., & Brose, U. (2020). Rethinking trophic niches: Speed and body mass colimit prey space of mammalian predators. *Ecology and Evolution*, 10(14), 7094–7105. https://doi.org/10.1002/ece3.6411
- Holdo, R. M., Sinclair, A. R. E., Dobson, A. P., Metzger, K. L., Bolker, B. M., Ritchie, M. E., & Holt, R. D. (2009). A disease-mediated trophic cascade in the serengeti and its implications for ecosystem C. *PLoS Biology*, 7(9), e1000210. https://doi.org/10.1371/journal.pbio.1000210
- Hu, G., Lim, K. S., Horvitz, N., Clark, S. J., Reynolds, D. R., Sapir, N., & Chapman, J. W. (2016). Mass seasonal bioflows of high-flying insect

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- migrants. Science, 354(6319), 1584-1587. https://doi.org/10.1126/ science.aah4379
- IPBES. (2023). The nature futures framework, a flexible tool to support the development of scenarios and models of desirable futures for people, nature and Mother Earth, and its methodological guidance, version July 2023. IPBES Secretariat, https://doi.org/10.5281/zenodo.8171339
- IPCC. (2022). Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H. -O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, 3056 pp. https://doi.org/10.1017/9781009325844
- Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. Science, 306(5694), 266-268. https://doi.org/10. 1126/science.1102138
- Johnson, C. N., Prior, L. D., Archibald, S., Poulos, H. M., Barton, A. M., Williamson, G. J., & Bowman, D. M. J. S. (2018). Can trophic rewilding reduce the impact of fire in a more flammable world? Philosophical Transactions of the Royal Society B, 373, 20170443.
- König, H. J., Kiffner, C., Kramer-Schadt, S., Fürst, C., Keuling, O., & Ford, A. T. (2020). Human-wildlife coexistence in a changing world. Conservation Biology, 34(4), 786-794. https://doi.org/10.1111/cobi.13513
- Kristensen, J. A., Svenning, J.-C., Georgiou, K., & Malhi, Y. (2022). Can large herbivores enhance ecosystem carbon persistence? Trends in Ecology & Evolution, 37(2), 117-128. https://doi.org/10.1016/j.tree. 2021.09.006
- Lamba, A., Teo, H. C., Sreekar, R., Zeng, Y., Carrasco, L. R., & Koh, L. P. (2023). Climate co-benefits of tiger conservation. Nature Ecology & Evolution, 7(7), 1104-1113. https://doi.org/10.1038/ s41559-023-02069-x
- Lee, A., Laird, A., Brann, L., Coxon, C., Hamilton, A., Lawhon, L., Martin, J., Rehnberg, N., Tyrrell, B., Welch, Z., Hale, B., & Alagona, P. (2021). The ethics of reintroducing large carnivores: The case of the California grizzly. Conservation and Society, 19(1), 80. https://doi. org/10.4103/cs.cs\_20\_131
- Malhi, Y., Lander, T., le Roux, E., Stevens, N., Macias-Fauria, M., Wedding, L., Girardin, C., Kristensen, J. Å., Sandom, C. J., Evans, T. D., Svenning, J.-C., & Canney, S. (2022). The role of large wild animals in climate change mitigation and adaptation. Current Biology, 32(4), R181-R196. https://doi.org/10.1016/j.cub.2022.01.041
- Margulies, J. D., & Karanth, K. K. (2018). The production of humanwildlife conflict: A political animal geography of encounter. Geoforum, 95(October), 153-164. https://doi.org/10.1016/j.geofo rum.2018.06.011
- Martin, A., Fischer, A., McMorran, R., & Smith, M. (2021). Taming rewilding-From the ecological to the social: How rewilding discourse in Scotland has come to include people. Land Use Policy, 111(December), 105677. https://doi.org/10.1016/j.landusepol. 2021.105677
- Martin, P. S., & Klein, R. G. (1989). Quaternary extinctions: A prehistoric revolution. University of Arizona Press.
- McVittie, A., Bryce, R., Glass, J., Woolvin, A., Carver, S., Fisher, M., McMorran, R., & Sedee, C. (2017). A review of the social, Economic and Environmental Benefits and Constraints Linked to Wild Land in Scotland. No. 919. Scottish Natural Heritage.
- Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO<sub>2</sub> exchange during the peak of the growing season. Oikos, 124(12), 1632-1638. https://doi.org/10.1111/oik.02085
- Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006). Integrating economic costs into conservation planning. Trends in Ecology & Evolution, 21(12), 681-687. https://doi. org/10.1016/j.tree.2006.10.003
- Naughton-Treves, L., & Treves, A. (2005). Socio-ecological factors shaping local support for wildlife: Crop-raiding by elephants and other

- wildlife in Africa. In R. Woodroffe, S. Thirgood, & A. Rabinowitz (Eds.), People and wildlife (pp. 252-277). Cambridge University Press. https://doi.org/10.1017/CBO9780511614774.017
- Nelson, M. P., Batavia, C., Brandis, K. J., Carroll, S. P., Celermajer, D., Linklater, W., Lundgren, E., Ramp, D., Steer, J., Yanco, E., Wallach, A. D., & Wallach, A. D. (2021). Challenges at the intersection of conservation and ethics: Reply to Meyer et al. 2021. Conservation Biology, 35, 373-377.
- Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society, B: Biological Sciences, 373(1761), 20170437. https://doi.org/10.1098/rstb.2017.0437
- Pellegrini, A. F. A., Pringle, R. M., Govender, N., & Hedin, L. O. (2017). Woody plant biomass and carbon exchange depend on elephantfire interactions across a productivity gradient in African savanna. Journal of Ecology, 105(1), 111-121. https://doi.org/10.1111/1365-2745.12668
- Pyron, R. A., & Mooers, A. Ø. (2022). The normative postulate problem: Hidden values in ecology, evolution, and conservation. Biological Conservation, 270, 109584.
- Reed, M. S., Hubacek, K., Bonn, A., Burt, T. P., Holden, J., Stringer, L. C., Beharry-Borg, N., Buckmaster, S., Chapman, D., Chapman, P. J., Clay, G. D., Cornell, S. J., Dougill, A. J., Evely, A. C., Fraser, E. D. G., Jin, N., Irvine, B. J., Kirkby, M. J., Kunin, W. E., ... Worrall, F. (2013). Anticipating and managing future trade-offs and complementarities between ecosystem services. Ecology and Society, 18(1), 5. https://www.jstor.org/stable/26269256
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science, 343(6167), 1241484. https://doi.org/10.1126/scien ce.1241484
- Saba, G. K., Burd, A. B., Dunne, J. P., Hernández-León, S., Martin, A. H., Rose, K. A., Salisbury, J., Steinberg, D. K., Trueman, C. N., Wilson, R. W., & Wilson, S. E. (2021). Toward a better understanding of fish-based contribution to ocean carbon flux. Limnology and Oceanography, 66(5), 1639-1664. https://doi.org/10.1002/lno. 11709
- Salisbury, J., Hu, X., Speed, J. D. M., Iordan, C. M., Austrheim, G., & Cherubini, F. (2023). Net climate effects of moose browsing in early successional boreal forests by integrating carbon and albedo dynamics. Journal of Geophysical Research: Biogeosciences, 128(3), e2022JG007279. https://doi.org/10.1029/2022JG007279
- Sandhage-Hofmann, A., Linstädter, A., Kindermann, L., Angombe, S., & Amelung, W. (2021). Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass. Global Change Biology, 27(19), 4601-4614. https://doi.org/10.1111/ gcb.15779
- Sandom, C. J., & Wynne-Jones, S. (2019). Rewilding a country: Britain as a study case. In J. T. du Toit, N. Pettorelli, & S. M. Durant (Eds.), Rewilding (pp. 222-247. Ecological Reviews). Cambridge University Press. https://doi.org/10.1017/9781108560962.012
- Scarpelli, T. R., Jacob, D. J., Octaviano Villasana, C. A., Ramírez Hernández, I. F., Cárdenas Moreno, P. R., Cortés Alfaro, E. A., García García, M. Á., & Zavala-Araiza, D. (2020). A gridded inventory of anthropogenic methane emissions from Mexico based on Mexico's national inventory of greenhouse gases and compounds. Environmental Research Letters, 15(10), 105015. https://doi.org/10. 1088/1748-9326/abb42b
- Schmitz, O. J., & Leroux, S. J. (2020). Food webs and ecosystems: Linking species interactions to the carbon cycle. Annual Review of Ecology, Evolution, and Systematics, 51(1), 271-295. https://doi.org/10.1146/ annurev-ecolsys-011720-104730
- Schmitz, O. J., & Sylvén, M. (2023). Animating the carbon cycle: How wildlife conservation can be a key to mitigate climate change.

- Environment: Science and Policy for Sustainable Development, 65(3), 5–17. https://doi.org/10.1080/00139157.2023.2180269
- Schmitz, O. J., Raymond, P. A., Estes, J. A., Kurz, W. A., Holtgrieve, G. W., Ritchie, M. E., Schindler, D. E., Spivak, A. C., Wilson, R. W., Bradford, M. A., Christensen, V., Deegan, L., Smetacek, V., Vanni, M. J., & Wilmers, C. C. (2014). Animating the carbon cycle. *Ecosystems*, 17(2), 344–359. https://doi.org/10.1007/s10021-013-9715-7
- Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., & Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science*, *362*(6419), eaar3213. https://doi.org/10.1126/science.aar3213
- Schmitz, O. J., Sylvén, M., Atwood, T. B., Bakker, E. S., Berzaghi, F., Brodie, J. F., Cromsigt, J. P. G. M., Davies, A. B., Leroux, S. J., Schepers, F. J., Smith, F. A., Stark, S., Svenning, J.-C., Tilker, A., & Ylänne, H. (2023). Trophic rewilding can expand natural climate solutions. *Nature Climate Change*, 13(4), 324–333. https://doi.org/10.1038/s41558-023-01631-6
- Schou, J. S., Bladt, J., Ejrnæs, R., Thomsen, M. N., Vedel, S. E., & Fløjgaard, C. (2021). Economic assessment of rewilding versus agri-environmental nature management. *Ambio*, 50(5), 1047–1057. https://doi.org/10.1007/s13280-020-01423-8
- Schulte To Bühne, H., Pettorelli, N., & Hoffmann, M. (2022). The policy consequences of defining rewilding. *Ambio*, 51(1), 93–102. https://doi.org/10.1007/s13280-021-01560-8
- Seddon, N., Smith, A., Smith, P., Key, I., Chausson, A., Girardin, C., House, J., Srivastava, S., & Turner, B. (2021). Getting the message right on nature-based solutions to climate change. *Global Change Biology*, 27(8), 1518–1546. https://doi.org/10.1111/gcb.15513
- Sommer, N. R., & Ferraro, K. M. (2022). An interest-based rights ethic for wildlife management and applications to behavioral training. Conservation Science and Practice, 4(3), e616. https://doi.org/10. 1111/csp2.616
- Sommer, N. R., & Schmitz, O. J. (2020). Differences in prey personality mediate trophic cascades. *Ecology and Evolution*, 10(17), 9538–9551. https://doi.org/10.1002/ece3.6648
- Somveille, M., & Ellis-Soto, D. (2022). Linking animal migration and ecosystem processes: Data-driven simulation of propagule dispersal by migratory herbivores. *Ecology and Evolution*, 12(10), e9383. https://doi.org/10.1002/ece3.9383
- Stepanian, P. M., Entrekin, S. A., Wainwright, C. E., Mirkovic, D., Tank, J. L., & Kelly, J. F. (2020). Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. Proceedings of the National Academy of Sciences of the United States of America, 117(6), 2987–2992. https://doi.org/10.1073/pnas. 1913598117
- Stoy, P. C., Cook, A. A., Dore, J. E., Kljun, N., Kleindl, W., Brookshire, E. N. J., & Gerken, T. (2021). Methane efflux from an American bison herd. *Biogeosciences*, 18(3), 961–975. https://doi.org/10.5194/bg-18-961-2021
- Subalusky, A. L., Dutton, C. L., Rosi, E. J., & Post, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences of the United States of America*, 114(29), 7647–7652. https://doi.org/10.1073/pnas.1614778114
- Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L. M., Forrester, T., Green, A. M., Haight, J., Harris, N. C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P. E., Lewis, J. S., McInturff, A., ... Wilmers, C. C. (2021). Disturbance type and species life history predict mammal responses to humans. Global Change Biology, 27(16), 3718–3731. https://doi.org/10.1111/gcb.15650
- Svenning, J.-C., Pedersen, P. B. M., Donlan, C. J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D. M., Sandel, B., Sandom, C. J., Terborgh, J.

- W., & Vera, F. W. M. (2016). Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences of the United States of America*, 113(4), 898–906. https://doi.org/10.1073/pnas.1502556112
- Takacs, D. (2020). Whose voices count in biodiversity conservation? Ecological democracy in biodiversity offsetting, REDD+, and rewilding. *Journal of Environmental Policy & Planning*, 22(1), 43–58. https://doi.org/10.1080/1523908X.2019.1661234
- Thondhlana, G., Redpath, S. M., Vedeld, P. O., Van Eeden, L., Pascual, U., Sherren, K., & Murata, C. (2020). Non-material costs of wildlife conservation to local people and their implications for conservation interventions. *Biological Conservation*, 246, 108578.
- Tucker, M. A., Busana, M., Huijbregts, M. A. J., & Ford, A. T. (2021). Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. *Ecography*, 44(6), 897–906. https://doi.org/ 10.1111/ecog.05210
- Wallach, A. D., Bekoff, M., Batavia, C., Nelson, M. P., & Ramp, D. (2018).
  Summoning compassion to address the challenges of conservation.
  Conservation Biology, 32(6), 1255–1265. https://doi.org/10.1111/cobi.13126
- White, T. B., Petrovan, S. O., Booth, H., Correa, R. J., Gatt, Y., Martin, P. A., Newell, H., Worthington, T. A., & Sutherland, W. J. (2022). Determining the economic costs and benefits of conservation actions: A decision support framework. *Conservation Science and Practice*, 4(12), e12840. https://doi.org/10.1111/csp2.12840
- Wilmers, C. C., & Schmitz, O. J. (2016). Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere*, 7(10), e01501. https://doi.org/10.1002/ecs2.1501
- Wilson, C. H., Strickland, M. S., Hutchings, J. A., Bianchi, T. S., & Flory, S. L. (2018). Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. Global Change Biology, 24(7), 2997–3009.
- Wilson, M. A. (1997). The wolf in yellowstone: Science, symbol, or politics? Deconstructing the conflict between environmentalism and wise use. *Society & Natural Resources*, 10(5), 453-468. https://doi.org/10.1080/08941929709381044
- Zhang, Y., Gautam, R., Pandey, S., Omara, M., Maasakkers, J. D., Sadavarte, P., Lyon, D., Nesser, H., Sulprizio, M. P., Varon, D. J., Zhang, R., Houweling, S., Zavala-Araiza, D., Alvarez, R. A., Lorente, A., Hamburg, S. P., Aben, I., & Jacob, D. J. (2020). Quantifying methane emissions from the largest oil-producing basin in the United States from space. Science. *Advances*, 6(17), eaaz5120. https://doi.org/10.1126/sciadv.aaz5120

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Supporting Information S1.** Mechanisms of animal species effects on carbon cycling within focal ecosystems.

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