Context matters when rewilding for climate change

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Abstract

There is a cross-sectoral push amongst conservation practitioners 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 and as such, there are increasing calls to use animal conservation and trophic rewilding to help dually overcome biodiversity loss and climate change. Trophic rewilding is a complex conservation approach to mitigating climate change because it requires accurate baseline estimates of carbon cycling and species impacts on a system, social support for the project, and the actual reintroduction of a species. We join the growing excitement around this potential but caution that rewilding cannot always be justified on carbon benefits alone: a species' net impact on ecosystem carbon dynamics is context dependent. The need for caution intensifies whenever biodiversity conservation (including rewilding), climate change mitigation, and human welfare do not readily align. Hence, these burgeoning efforts must avoid sweeping generalizations. To bolster reliable outcomes, we highlight the regional social and ecological context dependencies that can drastically vary outcomes in a rewilded carbon cycle and provide ethical considerations for successful implementation. We conclude with an overview of the available technology to predict and monitor progress toward both biodiversity and climate mitigation goals.

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

Manuscript Word Count: 6,397

I. Introduction

Scientists, policymakers, and conservation practitioners are confronted with the dual challenge of mitigating climate change and biodiversity loss (Dinerstein et al., 2020; Pörtner et al., 2023; Seddon et al., 2021; Smith et al., 2022). Until recently, solutions to each have been routinely treated as functionally unrelated (Dinerstein et al., 2020; Malhi et al., 2022; Smith et al., 2022; Figure 1); yet this line of thought is shifting. Growing evidence shows that animals may play an essential role in mitigating climate change by mediating ecosystem carbon capture and storage in ecosystems, 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 maximizing *either* animal diversity *or* carbon capture and storage could lead to missed opportunities to further both goals (Schmitz et al., 2023).

Nature-based solutions to climate change and biodiversity loss encompass landscape-scale conservation practices aimed at driving carbon uptake and storage through the protection and restoration of biodiversity, ecosystem processes, and ultimately ecological resilience for both people and nature (Seddon et al., 2021; Woroniecki et al., 2020). Among these nature-based efforts, a 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) utilizes both frameworks, positing that rewilding animals' functional roles in ecosystems can simultaneously further biodiversity conservation and increase carbon capture and storage in ecosystems (Figure 1).

Estimates derived from a subset of animals across diverse ecosystems reveal that animals could substantially alter an ecosystem's carbon budget by an average of 60-95% relative to cases where focal animals are absent (Schmitz & Leroux, 2020), thereby potentially enhancing 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 5 steps for reducing net emissions expeditiously, including rapid transition to solar and wind technology, reducing the conversion of natural ecosystems, enhancing carbon capture and storage in agriculture, and restoring, afforesting and reforesting ecosystem (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 everywhere to overcome the dual challenges of mitigating climate change and biodiversity loss.

However, we are at a juncture where some caution is warranted. The few studies which quantify animal effects on ecosystem carbon cycling demonstrate the importance of considering ecological context. This is because animals can either enhance or reduce ecosystem carbon capture and storage depending on ecosystem type and the functional role of wildlife species in that ecosystem (Table 1). Thus, regardless of the intention to rewild to meet carbon storage goals, biodiversity goals, or both, it is essential to understand how a focal species may impact an ecosystem's carbon budget. This involves giving significant consideration to the effects that animals at different trophic levels can have on individual, population, and community ecological processes within a specific environmental setting. TRACC also inherently requires increasing the abundance of wildlife species on the landscape, potentially in competition with people who already live there. This raises significant concerns that TRACC could conflict with human livelihoods and welfare without consideration of people on landscapes and the further commodification of nature (Seddon et al., 2021). Therefore, as a nature-based solution, TRACC requires an equal emphasis on understanding and including human communities as part of the solution (Schmitz & Sylvén, 2023).

Here we explain how to understand and balance necessary social, ecological, and social-ecological context dependencies to produce an ethical and scientifically defensible nature-based solution using TRACC We 1) highlight the context of species, of systems, and of people. We then 2) address the kinds of ethical considerations needed given the potential impacts of trophic rewilding on people and the value they place on wildlife. We conclude with 3) suggestions/directions for practitioners interested in trophic rewilding schemes for carbon storage. We also discuss how to optimize available technologies for appropriate monitoring strategies in order to better understand how a species impacts the carbon storage of a specific ecosystem.

We focus on examples of terrestrial megafauna (e.g., >45 kg; Martin & Klein, 1989) because they are among the most studied and most vulnerable animals in terms of their response to human activities (Atwood et al., 2020; Belote et al., 2020; Dirzo et al., 2014; Ripple et al., 2014). Consequently, conservation practitioners have given heightened investment and attention to trophic rewilding of large and charismatic species. This is not to dimmish 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; Schmitz & Leroux, 2020) for similar purposes. To that end, the emerging concepts and principles we derive from the terrestrial case studies should apply to these taxa as well.

II. Context Dependency in Rewilding the Carbon Cycle

Determining *if* rewilding as a nature-based solution, i.e. TRACC, will work is largely dependent on understanding whether the plan is ecologically and socially feasible. Here we highlight several of the contexts necessary to consider for successful TRACC projects.

The Context of the Species

Trophic rewilding focuses on the processes and functions of wildlife species within the ecosystem they will occupy after translocation, and TRACC expands upon this focus by honing in on how a species' attributes and functions specifically impact the carbon cycle. As such, it is an important prerequisite to consider a species' functional traits, population demographics, and population density, as well as the resident animal community assemblage, prior to determining whether the species should be introduced as a nature-based solution.

Understanding species' functional traits is critical to understanding its impacts on carbon cycling because it sheds light on how a species interacts with members of its ecological community (Figure 3A). 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). For example, grazers generally consume fast-growing grasses, which can promote shoot production, thereby increasing carbon capture. In contrast, browsers consume slow-growing shrubs and trees, which, in some systems, may limit carbon capture (Salisbury et al., 2023). Additional functional traits such as digestion may shape the quality and quantity of plant types that are eaten and the ensuing amount of methane released (Clauss et al., 2020) Trampling during daily movements may compact soil (Schmitz et al., 2018), wallowing can create natural fire breaks

(Malhi et al., 2022), and migration across landscapes may translocate nutrients essential to plant growth (Subalusky et al., 2017).

The demographics of a rewilded population can also differentially affect carbon sequestration even within the same system (Figure 3B). In Kruger National Park, male and female elephants (*Loxodonta africana*) had different impacts on local tree dynamics (Abraham et al., 2021) and, at certain densities, male elephants decreased aboveground carbon storage, while breeding herds had a nonsignificant impact (Davies & Asner, 2019). In deer species, males are known to consume more woody vegetation than females (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) may also impact consumption rates and preferences, ultimately impacting nutrient deposition and, potentially ecosystem carbon uptake.

Different populations of rewilded animals can turn ecosystems from net carbon sinks into net sources (Figure 3C). For example, the density of forest elephants (*Loxodonta cyclotis*) in the Congo can have negative, positive, and negligible effects on carbon storage depending on species density: negative effects due to their damaging effect on tree production at high densities, negligible effects at low densities, and positive due to their enhancement of forest canopy tree production at medium densities (Berzaghi et al., 2019). In the Serengeti, a 20% reduction of 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). Maximizing carbon capture using rewilded animal populations may require strategic population control, which may seem antithetical to the goals of conserving wildlife biodiversity (e.g. prioritizing species richness). Practitioners must decide which species to rewild, what animal density is needed to reach carbon capture 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 an ecosystem, and the resident plant and animal community assemblage must be considered as the rewilded species' impacts on carbon uptake and sequestration could be amplified or reduced (Figure 3D). Different mammalian herbivore assemblages in the Arctic had varying impacts on CO_2 fluxes via herbivory (Metcalfe & Olofsson, 2015). Herbivore community assemblages can also impact soil mixing (Kristensen et al., 2022), aboveground biomass (Metcalfe & Olofsson, 2015), plant communities (Olofsson & Post, 2018), and other metrics which impact carbon capture and storage. Further research is needed to untangle how differing community assemblages, and changes to assemblages, may impact carbon sequestration.

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. In other words, the average will not capture variable contributions to the carbon cycle if trait responses among individuals are not identical (e.g., dependent on physiological or behavioral states; Bolnick et al., 2011; Ovadia & Schmitz, 2002; Schmitz & Trussell, 2016; Sommer & Schmitz, 2020).

The Context of the System

Implementing trophic rewilding as a nature-based climate solution must also account for the ecological nuances within ecosystems as a whole and the relationship to the candidate species for rewilding. These nuances include trophic cascades, community composition, and ecosystem or habitat type.

First and foremost, wild animals can have top-down feedback effects on ecosystem functions via trophic cascades (Figure 2; Figure 3E), in which density and trait-mediated effects at upper trophic levels can alter the amount of carbon exchanged between plants, soils, and the atmosphere. These feedbacks arise from a wide range of animal functional roles that propagate along trophic chains to impact the biophysical properties of ecosystems and the functioning of plants and soils (Cromsigt et al., 2018; Malhi et al., 2022; Schmitz et al., 2018; Schmitz & Leroux, 2020). 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. The effects of these functions 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 and sediments from fecal and carcass deposition, and microbial processes and chemical reactions that mediate the retention of soil carbon. But the role a species plays can differ among different habitats or ecosystem types (Figure 3F). For example, savanna elephants (*L. africana)* in the grassland ecosystem of the Serengeti appear to have neutral or negative effects on carbon storage (Davies & Asner, 2019; Pellegrini et al., 2017; Sandhage-Hofmann et al., 2021) while the forest elephant (*L. cyclotis*) in the central African rainforest plays a significant role in seed dispersal, aboveground biomass and thus aboveground carbon storage (Berzaghi et al., 2019).

Other ecosystem characteristics such as climate, topography, seasonality, and rainfall gradient can influence the carbon storage potential of animals (Malhi et al., 2022, Kristensen et al., 2022). These considerations will be increasingly important under continued climate change (e.g., changes in seasonality, droughts, floods, etc.). These impacts can be large enough that, if ignored, conventional natural climate solutions could either miss opportunities to enhance carbon capture or fail to meet carbon capture targets (Schmitz & Leroux, 2020).

Ecological community composition is diverse and complex, and it is also necessary to consider the impacts of carbon beyond the direct management action of large animals (Figure 3G). 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 in a system might result in unintended consequences on the 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 (Pringle et al. 2021). Management with a singular focus on carbon capture and storage can encourage monoculture production (e.g., eucalyptus farms) within ecosystems, thereby maximizing carbon storage but minimizing ecological diversity and function (Seddon et al., 2021).

The Social Context

The context dependency within a system is also influenced by variation in human social (e.g., culture, religion, ethics, politics) and economic context that impacts landscape use (Figure 3H). 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 capture and storage (Berti & Svenning, 2020; Estes et al., 2011; Schmitz et al., 2018; Suraci et al., 2021). For instance, regional fragmentation and isolation through fencing or deforestation can confine animal populations or restrict their movements. The restriction of large-ranging species will concentrate their functional impacts within a small area and exert a lot of pressure compared to individuals of the same species in undisturbed habitats that can operate across larger ranges. This will have affects across the ecosystem, including the carbon sequestration by plants (Wall et al., 2021; Xu et al., 2021). Such consideration for how fragmentation and isolation will impact the carbon cycle is particularly important when considering wildlife connectivity across private and public lands (Kauffman et al., 2021). Animals can also vary in the directionality of their response to disturbances based on real or perceived anthropogenic pressures such as mortality, recreation, and hunting (Kays et al., 2017; Naidoo & Burton, 2020; Smith et al., 2019; Suraci et al., 2021; Venter et al., 2016; Wilson et al., 2021). For instance, individuals from a large mammalian species may respond to human disturbance in opposite ways depending on how frequently they interact with humans (e.g., within a heavily-visited land trust versus a remote area of a national park) (Bateman & Fleming, 2017; Reilly et al., 2017).

III. Creating ethical TRACC solutions

Complex, and sometimes differing, ecological contexts and values surround biodiversity conservation and, subsequently, rewilding and carbon storage. Trophic rewilding to animate the carbon cycle (TRACC) can only be an appropriate nature-based solutions when the project, at the bare minimum, does not exclude impacted humans from the decision-making processes, or else the conserved landscape entirely (Schmitz & Sylvén, 2023; Takacs, 2020). Animal-focused carbon offset projects, which emulate existing offset projects such as REDD+, risk neglecting human rights, particularly of local and indigenous communities (Raftopoulos, 2016). Often this is because the sites designated for carbon credits may have already been allocated and thereby closed off to human activities or access (Beymer-Farris & Bassett, 2012; Brockington, 2002; Büscher & Whande, 2007). The critiques of fortress conservation are long (Brockington, 2002; Büscher &

Ramutsindela, 2016; Goldman & Riosmena, 2013; Hartter & Goldman, 2011);this cannot happen for rewilding.

Equitable TRACC projects require community involvement and power-sharing (e.g., Ainsworth et al., 2020; Ernoul et al., 2018). This means embracing and adapting to dynamic social contexts shaped by human welfare, intrinsic values, local knowledge, sociocultural heritage, and access to natural resources (Carver et al., 2021; Corlett, 2016; Schulte To Bühne et al., 2022; Takacs, 2020). Key to this is recognizing and respecting aspects of socio-cultural importance to local economies (e.g., food and other artisanal production) and balancing trade-offs among different economic opportunities whenever they arise. Examples include investments in climate-smart farming and compensation schemes for existing economic opportunities that might be supplanted to allocate landscape space for carbon capture (Boedhihartono et al., 2018; Chami et al., 2022). Governance structures can support projects by coordinating with communities to ensure regional carbon finance equity and developing plans to monitor and evaluate the outcome of rewilding initiatives carried about by communities.

Like all conservation programs, TRACC is inherently ethical and requires all participants to balance the interests, needs, and functions of humans, animals, and ecosystems. Lee et al., *(2021)* outline the kinds of interwoven ethical issues that are at stake in determining the outcome of rewilding efforts: human rights, animal welfare, environmental justice, intrinsic values, and ecosystem functionality. To ensure that local communities do not bear the brunt of negative impacts, Human Rights Impact Assessments, or similar approaches, could be employed as deliberate measures to link human rights and TRACC endeavors. While human rights assessments are typically conducted at the local level, policies and management strategies for mitigating atmospheric buildup are often implemented regionally, within sub-national jurisdictions such as states or provinces (Dulal et al., 2012; Venter & Koh, 2012).

It is important to note that many conservation projects often rely on implicit and unquestioned ethical norms and values (Ferraro et al., 2023), focusing primarily on financial and environmental cost-benefit implications, rather than considering the broader range of issues outlined above. This approach fails to recognize conservation and stewardship practices alongside human virtues, as well as the valuation of animals as purposeful, sentient beings rather than abstract taxonomic entities (Schmitz & Sylvén, 2023; Sommer & Ferraro, 2022; Wallach et al., 2018). TRACC can adopt an eco-centric perspective, moving away from an anthropocentric lens (Carver et al., 2021) and ensuring that humans and animals are not treated merely as means to an end. Effectively navigating these ethical complexities necessitates 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, rather than imposing predetermined solutions (Ferraro et al., 2021; Nelson, 2021).

In some cases, rewilding a species into an ecosystem may lead to carbon storage and/or sequestration with no downside social costs or ethical issues. However, rewilding the same species into other ecosystems could decrease carbon capture or risk human-wildlife conflict, thereby requiring trade-off decisions between carbon and rewilding goals. Trade-off decisions require weighing the marginal carbon benefits (or costs) of rewilding against the socio-cultural and welfare opportunities for local communities. The decision about whether to proceed with a project requires the explicit engagement of all partners, including local communities, regional governance, conservation NGOs, and investors (Ainsworth et al., 2020).

IV. A Path Forward

Determining if TRACC will work is dependent upon creating solutions which simultaneously address biodiversity loss and climate change mitigation *and* which leverage the points that we have elaborated upon above: ecological accuracy and the incorporation of human rights and the inherent value of all involved. After initial assessment and project design, it comes down to the action itself: actually reintroducing a species.

Yet, *how* exactly do we go about executing a rewilded carbon cycle? We emphasize that the question centers upon measuring carbon; projects must track the carbon cycle before, during, and after the introduction of a species. Blending the ecological and ethical nuances that we describe above, we contend that longevity and transparency must lay the foundation for such projects. TRACC must ensure that the introduction of a species fosters long-term, stable carbon storage, and sequestration amidst balancing socio-ecological contexts. Below, we highlight the technology that is accessible to achieve this and further describe the research and/or management potential for carrying out a relevant project.

Assessing and Monitoring TRACC

Leveraging TRACC for nature-based solutions requires accurate carbon measurements that, in turn, provide scientifically defensible long-term project outcomes. We emphasize the necessity for baseline estimates prior to rewilding and measurements following reintroductions in order to monitor and evaluate the species' impact on the system. Additionally, monitoring must assess more than standing plant or animal biomass (as currently emphasized by carbon offset and rewilding projects, respectively). It must include direct estimates of carbon storage in different parts of the ecosystem, fluxes between carbon pools through gasses, the projects economic value, and its social impacts over time (i.e., it requires estimating net ecosystem carbon balance; Schmitz et al. 2023). Previous reviews have provided extensive detail as to how to assess and monitor the movement of nutrients by animals, including impacts on carbon sequestration (Abraham et al., 2022; Ellis-Soto & Ferraro et al., 2021; Schmitz & Sylvén, 2023; Supplemental Appendix 1). Here we provide a few new technologies and methods to consider.

Currently, a new fleet of satellites allows us to estimate methane emissions including TROPOMI with a pixel resolution of $7km^2$. 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 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 $30m^2$ (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 $25m^2$ 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 high-resolution 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 & Ferraro 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 trap cameras (Dumortier et al., 2019; Stoy et al., 2021). For instance, recent work was able to obtain hourly, daily, and seasonal 'methane footprints' at $20m^2$ resolution of a herd of American bisons (*Bison bison*) by combining as atmospheric conditions measured from eddy covariance, with animal occupancy measured by trap cameras, bison body mass, and daily hay intake (Stoy et al., 2021). This methodology was even able to detect the influence of animal behavior (resting, moving, foraging) through the methane emissions detected from the eddy covariance. A similar methodology expanded using individual animal locations derived from GPS collars as opposed to estimates from cameras, improving the spatial accuracy and decreasing methane emissions uncertainty (Dumortier et al., 2021). 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 belowground carbon will still require field-based *in situ* measurements as belowground biomass carbon can be substantially greater than aboveground biomass carbon in some ecosystems.

Combining on-the-ground empirical studies with mathematical or statistical modeling 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 modeling. Advancements in ecology allow us to estimate species space-use (Jetz et al., 2004), movement speed (Hirt et al., 2017), and to some extent stoichiometry (Allgeier et al., 2020). Agent-based modeling provides a means to simulate and anticipate ecosystem processes based on species traits, density, and management (Ferraro et al., 2022; 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 ought to 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. Lastly, adaptive management may be needed if project goals and targets are not being met. It 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). Various levels of governance, practitioners, and local communities could apply adaptive management (König et al., 2020). Successful human-wildlife systems, including social buy-in, require the collaboration and engagement of various stakeholders from practitioners to local residents.

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. Differentiating itself from broad conservation or broad rewilding projects, TRACC uniquely and simultaneously requires social buy-in, ecological baseline estimates, and the introduction of a species into a landscape in which it will likely interact with humans. 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. 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.

Acknowledgements: We thank J. Monk and A. Dobson for their insightful feedback on an earlier draft of this paper. This work was supported by the National Science Foundation Graduate Research Fellowship to KMF (DGE-1752134) and MKB (DGE-1122492). Any opinion, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Figures

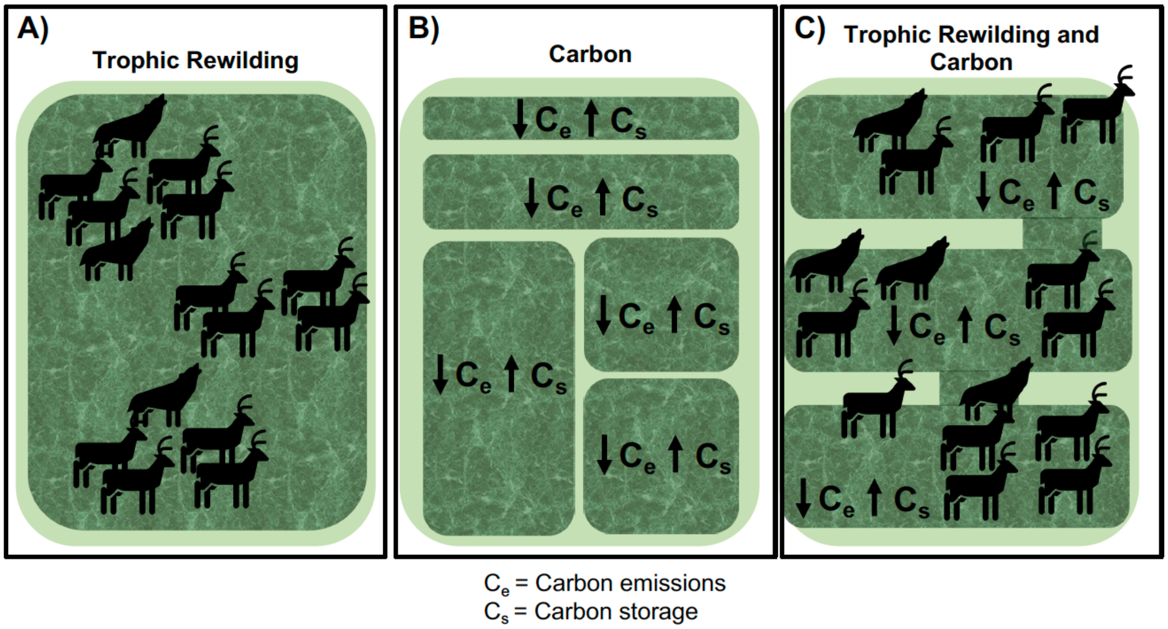

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Figure 1. A theoretical depiction of nature-based solutions which separately prioritize (A) the composition of target species of interest or (B) carbon storage in the landscape, whereas (C) TRACC can prioritize both at the landscape scale.

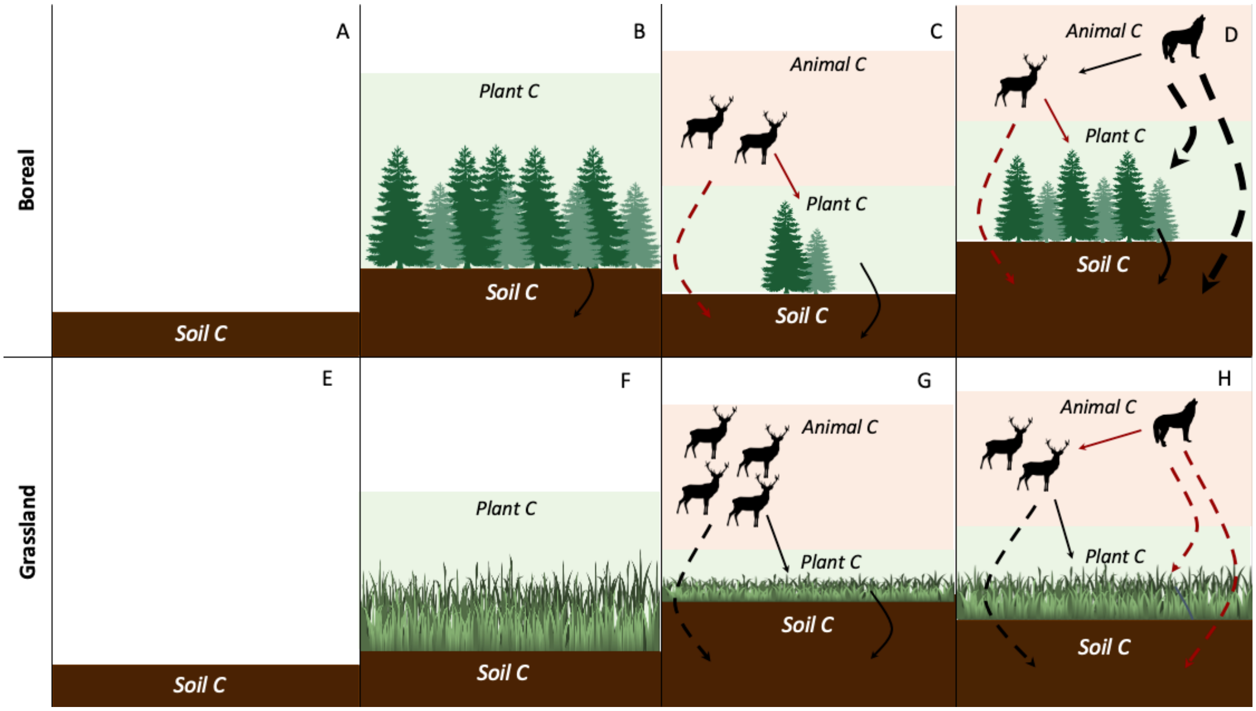

Figure 2. The consideration of a full trophic cascade disentangling the assumption that organismal biomass or abundance equates to the cumulative effect of carbon storage mechanisms. Demonstrating using a wolf-deer system (Wilmers and Schmitz 2016), the greatest carbon uptake is yielded through indirect effects, disproportionate to biomass. From left to right, increasing the number of trophic levels in a boreal system (A-D) and in a grassland system (E-H) 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).

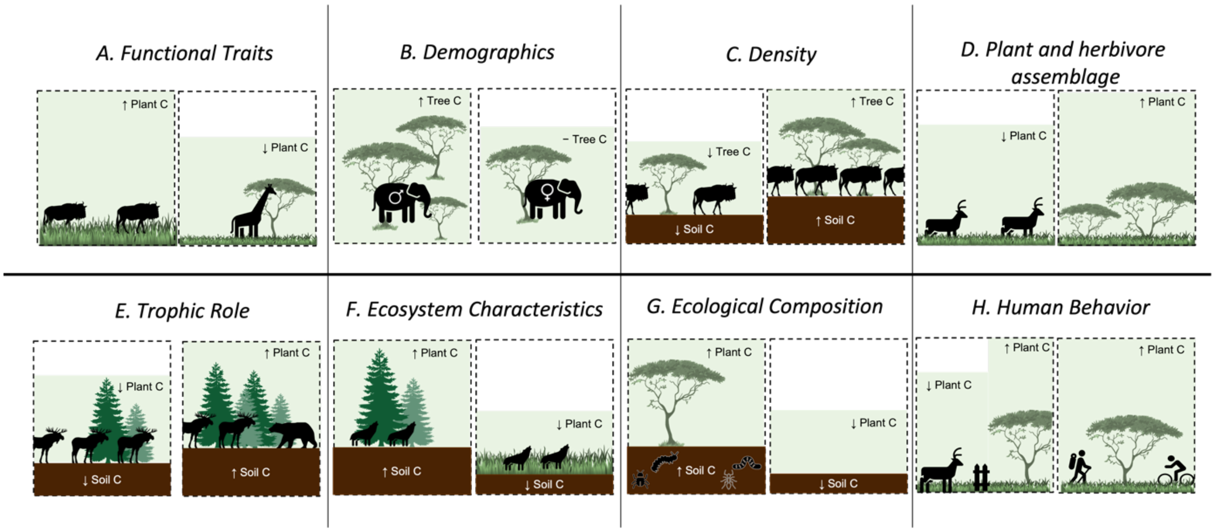

Figure 3. Known and potential discrepancies in carbon storage, based on system-specific contexts: (A) Species' functional traits, in which grazing or browsing could alter carbon stored in plant biomass; (B) Population demographics, in which species' sex can differentially alter the amount of plant carbon stored (Davies and 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 and 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 behavior, 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.

Tables

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 gray squares represent net negative, positive, and neutral animal effects on ecosystem carbon budgets, respectively.

Animal species and ecosystem[1]	**Animal effects on ecosystem function**
Moose → boreal forest vegetation → soil	■ ↓ primary productivity and biomass, ↓ soil organic carbon retention, ↑ wildfire
Wolf → Moose → boreal forest vegetation	■ ↑ primary productivity, ↑ soil organic carbon retention, ↓ wildfire
Elk → prairie grassland vegetation → soil	■ ↑ primary productivity, ↑ soil organic carbon retention
Wolf → Elk → prairie grassland vegetation	■ ↓ primary productivity, ↓ soil organic carbon retention
Bison → prairie grassland vegetation → soil	■ ↑ primary productivity, ↑ soil organic carbon retention
Wildebeest → savanna-woodland vegetation →soil	■ ↓ wildfire, ↑ soil organic carbon retention, ↑ woody biomass carbon
Savanna elephants → savanna-woodland vegetation	■ ↓ woodland biomass carbon, ↑ herbaceous vegetation carbon ↑ soil carbon retention
Forest elephants → tropical forest vegetation	■ ↑ forest overstory biomass carbon density
Caribou → dry tundra heath vegetation → soil	■ ↓ primary productivity, ↓ soil organic carbon retention
Caribou → boreal forest vegetation → soil	■ ↓ plant standing stock, ↑/– soil organic carbon retention
Muskox → wet tundra mire vegetation → soil	■ ↑ primary productivity, ↑ soil organic carbon retention
Muskox → dry tundra heath vegetation → soil	■ ↓ primary productivity, ↓ soil organic carbon retention
Frugivores (primates, tapirs, guans, hornbills, fruit bats) → fruits → tropical forest tree diversity	■ ↑ forest tree biomass carbon density

→ = trophic interaction, ↑ = increase in ecosystem effect, ↓ = decrease in ecosystem effect, – = neutral ecosystem effect.

[1] References for case studies are presented in Supplemental Information.

Table

Abraham, A. J., Duvall, E., Ferraro, K., Webster, A. B., Doughty, C. E., le Roux, E., & Ellis-Soto, D. (2022). Understanding anthropogenic impacts on zoogeochemistry is essential for ecological restoration. *Restoration Ecology*. https://doi.org/10.1111/rec.13778

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*(3). https://doi.org/10.1111/rec.13778

Abraham, J. O., Goldberg, E. R., Botha, J., & Staver, A. C. (2021). Heterogeneity in African savanna elephant distributions and their impacts on trees in Kruger National Park, South Africa. *Ecology and Evolution*, *11*(10), 5624–5634. https://doi.org/10.1002/ece3.7465

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

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*, *111*(47). https://doi.org/10.1073/pnas.1419550111

Atwood, T. B., Valentine, S. A., Hammill, E., McCauley, D. J., Madin, E. M. P., Beard, K. H., & Pearse, W. D. (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, *6*(32), eabb8458. https://doi.org/10.1126/sciadv.abb8458

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*, *113*(4), 847–855. https://doi.org/10.1073/pnas.1502545112

Bateman, P. W., & Fleming, P. A. (2017). Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biological Conservation*, *211*, 10–19. https://doi.org/10.1016/j.biocon.2017.05.003

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

Berti, E., & Svenning, J. (2020). Megafauna extinctions have reduced biotic connectivity worldwide. *Global Ecology and Biogeography*, *29*(12), 2131–2142. https://doi.org/10.1111/geb.13182

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

Beymer-Farris, B. A., & Bassett, T. J. (2012). The REDD menace: Resurgent protectionism in Tanzania’s mangrove forests. *Global Environmental Change*, *22*(2), 332–341. https://doi.org/10.1016/j.gloenvcha.2011.11.006

Boedhihartono, A. K., Bongers, F., Boot, R. G. A., van Dijk, J., Jeans, H., van Kuijk, M., Koster, H., Reed, J., Sayer, J., Sunderland, T., Turnhout, E., van Vianen, J., & Zuidema, P. A. (2018). Conservation Science and Practice Must Engage With the Realities of Complex Tropical Landscapes. *Tropical Conservation Science*, *11*, 194008291877957. https://doi.org/10.1177/1940082918779571

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Volker HW, 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.

Brockington, D. (2002). *Fortress conservation: The preservation of the Mkomazi Game Reserve, Tanzania*. Indiana University Press.

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

Büscher, B., & Ramutsindela, M. (2016). Green violence: Rhino poaching and the war to save Southern Africa’s peace parks. *African Affairs*, *115*(458), 1–22.

Büscher, B., & Whande, W. (2007). Whims of the Winds of Time? Emerging Trends in Biodiversity Conservation and Protected Area Management. *Conservation and Society*, *5*(1), 22–43.

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

Chami, R., Cosimano, T., Fullenkamp, C., & Nieburg, D. (2022). Toward a Nature-Based Economy. *Frontiers in Climate*, *4*, 855803. https://doi.org/10.3389/fclim.2022.855803

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

Corlett, R. T. (2016). The Role of Rewilding in Landscape Design for Conservation. *Current Landscape Ecology Reports*, *1*(3), 127–133. https://doi.org/10.1007/s40823-016-0014-9

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

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

Dumortier, P., Gourlez De La Motte, L., Andriamandroso, A. L. H., Aubinet, M., Beckers, Y., Bindelle, J., De Cock, N., Lebeau, F., & Heinesch, B. (2021). Beef cattle methane emission estimation using the eddy covariance technique in combination with geolocation. *Agricultural and Forest Meteorology*, *297*, 108249. https://doi.org/10.1016/j.agrformet.2020.108249

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. https://doi.org/10.1111/1365-2656.13538

Ernoul, L., Wardell-Johnson, A., Willm, L., Béchet, A., Boutron, O., Mathevet, R., Arnassant, S., & Sandoz, A. (2018). Participatory mapping: Exploring landscape values associated with an iconic species. *Applied Geography*, *95*, 71–78. https://doi.org/10.1016/j.apgeog.2018.04.013

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

Ferraro, K. M., Schmitz, O. J., & McCary, M. A. (2022). Effects of ungulate density and sociality on landscape heterogeneity: A mechanistic modeling approach. *Ecography*, ecog.06039. https://doi.org/10.1111/ecog.06039

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. *SOIL*, *2*(4), 565–582. https://doi.org/10.5194/soil-2-565-2016

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

Goldman, M. J., & Riosmena, F. (2013). Adaptive capacity in Tanzanian Maasailand: Changing strategies to cope with drought in fragmented landscapes. *Global Environmental Change*, *23*(3), 588–597.

Hancock, S., Armston, J., Hofton, M., Sun, X., Tang, H., Duncanson, L. I., Kellner, J. R., & Dubayah, R. (2019). The GEDI Simulator: A Large-Footprint Waveform Lidar Simulator for Calibration and Validation of Spaceborne Missions. *Earth and Space Science*, *6*(2), 294–310. https://doi.org/10.1029/2018EA000506

Hartter, J., & Goldman, A. (2011). Local responses to a forest park in western Uganda: Alternate narratives on fortress conservation. *Oryx*, *45*(01), 60–68. https://doi.org/10.1017/S0030605310000141

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., 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/s41559-017-0241-4

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 migrants. *Science*, *354*(6319), 1584–1587. https://doi.org/10.1126/science.aah4379

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, Cambridge, UK and New York, NY, USA, 3056 pp., doi: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

Kauffman, M. J., Cagnacci, F., Chamaillé-Jammes, S., Hebblewhite, M., Hopcraft, J. G. C., Merkle, J. A., Mueller, T., Mysterud, A., Peters, W., Roettger, C., Steingisser, A., Meacham, J. E., Abera, K., Adamczewski, J., Aikens, E. O., Bartlam-Brooks, H., Bennitt, E., Berger, J., Boyd, C., … Zuther, S. (2021). Mapping out a future for ungulate migrations. *Science*, *372*(6542), 566–569. https://doi.org/10.1126/science.abf0998

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas? *Journal of Applied Ecology*, *54*(1), 242–252. https://doi.org/10.1111/1365-2664.12700

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

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

Martin, P. S., & Klein, R. G. (1989). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press.

Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO_2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085

Naidoo, R., & Burton, A. C. (2020). Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. *Conservation Science and Practice*, *2*(10). https://doi.org/10.1111/csp2.271

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

Ovadia, O., & Schmitz, O. J. (2002). Linking individuals with ecosystems: Experimentally identifying the relevant organizational scale for predicting trophic abundances. *Proceedings of the National Academy of Sciences*, *99*(20), 12927–12931. https://doi.org/10.1073/pnas.192245499

Pellegrini, A. F. A., Pringle, R. M., Govender, N., & Hedin, Lars. O. (2017). Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. *Journal of Ecology*, *105*(1), 111–121. https://doi.org/10.1111/1365-2745.12668

Pörtner, H.-O., Scholes, R. J., Arneth, A., Barnes, D. K. A., Burrows, M. T., Diamond, S. E., Duarte, C. M., Kiessling, W., Leadley, P., Managi, S., McElwee, P., Midgley, G., Ngo, H. T., Obura, D., Pascual, U., Sankaran, M., Shin, Y. J., & Val, A. L. (2023). Overcoming the coupled climate and biodiversity crises and their societal impacts. *Science*, *380*(6642), eabl4881. https://doi.org/10.1126/science.abl4881

Raftopoulos, M. (2016). REDD+ and human rights: Addressing the urgent need for a full community-based human rights impact assessment. *The International Journal of Human Rights*, *20*(4), 509–530. https://doi.org/10.1080/13642987.2015.1115266

Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation*, *207*, 117–126. https://doi.org/10.1016/j.biocon.2016.11.003

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), 1241484–1241484. https://doi.org/10.1126/science.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

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., 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., & 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., 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

Schmitz, O. J., & Trussell, G. C. (2016). Multiple stressors, state-dependence and predation risk — foraging trade-offs: Toward a modern concept of trait-mediated indirect effects in communities and ecosystems. *Current Opinion in Behavioral Sciences*, *12*, 6–11. https://doi.org/10.1016/j.cobeha.2016.08.003

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

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

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology*, *100*(7). https://doi.org/10.1002/ecy.2724

Smith, P., Qin, Z., Lovelock, C. E., Joly, C. A., Kalantari, Z., Destouni, G., & Duguma, L. (2022). Decarbonizing through nature. *One Earth*, *5*(5), 449–451. https://doi.org/10.1016/j.oneear.2022.05.001

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*, *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*, *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*, *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

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*(1), 12558. https://doi.org/10.1038/ncomms12558

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., Henley, M., Vollrath, F., Maisels, F., Ferwerda, J., & Douglas-Hamilton, I. (2021). Human footprint and protected areas shape elephant range across Africa. *Current Biology*, *31*(11), 2437-2445.e4. https://doi.org/10.1016/j.cub.2021.03.042

Wilson, A. A., Ditmer, M. A., Barber, J. R., Carter, N. H., Miller, E. T., Tyrrell, L. P., & Francis, C. D. (2021). Artificial night light and anthropogenic noise interact to influence bird abundance over a continental scale. *Global Change Biology*, *27*(17), 3987–4004. https://doi.org/10.1111/gcb.15663

Woroniecki, S., Wendo, H., Brink, E., Islar, M., Krause, T., Vargas, A.-M., & Mahmoud, Y. (2020). Nature unsettled: How knowledge and power shape ‘nature-based’ approaches to societal challenges. *Global Environmental Change*, *65*, 102132. https://doi.org/10.1016/j.gloenvcha.2020.102132

Xu, W., Dejid, N., Herrmann, V., Sawyer, H., & Middleton, A. D. (2021). Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *Journal of Applied Ecology*, *58*(4), 690–698. https://doi.org/10.1111/1365-2664.13806

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