

MINI REVIEW

The Plant Ecology of Nature-based Solutions

Planning for the future: Grasslands, herbivores, and nature-based solutions

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Abstract

1. Global interest and investment in nature-based solutions (NbS) are rapidly increasing because of the potential of this approach to concurrently counter biodiversity loss, provide cost-effective measures for climate change adaptations, and maintain natural processes that underpin human health and wellbeing.
2. Recognition is growing that grasslands in many regions will protect carbon stores more effectively than forests in the warmer, drier, more fire-prone conditions of the future while also serving as hotspots for biodiversity. Yet grasslands have received less attention for their NbS potential. Despite the wide-ranging goals of this approach, many investments in nature-based solutions also have focused narrowly on using plants to meet climate pledges, often without considering plant interactions with herbivores and the abiotic environment that jointly control ecosystem functioning and underpin the success of nature-based solutions.
3. Here, we review the roles that large and small vertebrate and invertebrate herbivores play in the ability of the world's grasslands to provide nature-based solutions, with a focus on wild herbivore impacts on biodiversity and carbon storage.
4. *Synthesis.* Planning for nature-based solutions with a holistic, ecologically informed view that includes the role of herbivores and their interaction with plants and the environment will allow NbS investments to more likely achieve successful, sustainable outcomes.

KEYWORDS

above-ground, below-ground, biodiversity, carbon, climate, invertebrate, plant-herbivore interactions, vertebrate

1 | INTRODUCTION

Nature-based solutions (NbS) use natural ecosystems and processes to provide concurrent solutions to the many challenges posed by ongoing climate change and biodiversity loss (Cohen-Shacham et al., 2016). Because of their potential to provide cost-effective

climate mitigation and adaptation measures while concurrently supporting biodiversity and providing services to humans, there is increasing urgency of interest and investment in nature-based solutions in natural, restored, and artificial ecosystems around the world (Girardin et al., 2021; Seddon et al., 2020). With a focus on climate mitigation goals, 2/3 of the world's countries have made

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commitments to nature-based solutions, with the vast majority of these focused on forest protection, restoration, and afforestation, often with a sole focus on carbon (C) uptake and storage (Mo et al., 2023; Seddon et al., 2021). Despite the promise for climate mitigation (e.g. Bastin et al., 2019), the outcomes of forest management for nature-based solutions have been criticized in the scientific community for a variety of reasons, including the narrow focus on a single biome and approaches that undermine NbS biodiversity goals (e.g. Russell, 2020; Seddon et al., 2020; Veldman et al., 2019). Climate change is a key consideration for nature-based solutions. Importantly, despite critical government investment in forests to provide nature-based solutions (Seddon et al., 2021), a warmer, drier future will increasingly create conditions for fire (Senande-Rivera et al., 2022), favouring grasslands for C storage in many locations (Dass et al., 2018). Proactive planning for nature-based solutions must incorporate a foundational understanding of the ecology of plants, including their environmental constraints and interactions with herbivores.

Grasslands currently cover approximately 40% of Earth's terrestrial surface, occurring on every continent (White et al., 2000). With basal meristems near the soil surface, grasses grow well in conditions with herbivory, drought and fire (Anderson, 2006). As a result, grasslands emerged and spread millions of years ago, as Earth's climate became warmer and drier (Strömberg, 2011). Although modern grasslands often are viewed as degraded, successional habitats, many are ancient, maintained through climatic, edaphic and biotic conditions (Buisson et al., 2022; Erdős et al., 2022). From the perspective of nature-based solutions, grasslands harbour unique plant and animal biodiversity (Petermann & Buzhdygan, 2021), with more endangered plant species than forests (Staude et al., 2023). Grasslands also store roughly one third of terrestrial C, more than 90% of which is underground (Bai & Cotrufo, 2022; Watson & Verardo, 2000). Temperate grasslands, for example, hold an estimated 304 GtC compared to 159 GtC in forests, with almost 300% more C below-ground, protected from fire (295 GtC vs. 100 GtC, IPCC, 2019). In tropical savannas, grasses contribute more to soil C than do trees (Zhou, Bomfim, et al., 2023). Small natural and created grasslands also can play concurrent roles for nature-based solutions in human-dominated landscapes, including floodwater and fire management, groundwater recharge, biodiversity and recreation (Bengtsson et al., 2019; O'Connor et al., 2004; Zhou, 2014). However, with their deep, nutrient-rich soils, much of the world's grassland area has been cultivated for food production (White et al., 2000), and more recently, grasslands have been targeted for afforestation to meet climate mitigation goals (Bond et al., 2019). This loss is particularly worrisome as grasslands grow in importance for protecting biodiversity and storing C in a warmer, drier future.

The success of nature-based solutions will benefit from biologically informed management approaches (Seddon et al., 2020), infusing strategies and investments with an ecological understanding of plant-herbivore interactions and the dependence of their functioning on current and future conditions (Berzaghi et al., 2022;

Pringle et al., 2023; Xu et al., 2023). Here, we draw from the literature to examine factors such as the role of vertebrate and invertebrate herbivore diversity, density, dietary preferences, and species identity on two focal NbS goals, biodiversity maintenance and soil C storage (Kristensen et al., 2022; Seddon et al., 2020). We focus on grasslands because they are often excluded from NbS planning, yet they have substantial C storage potential (Plaza et al., 2018), and they are home to rapidly declining plant (Staude et al., 2023), mammal (Atwood et al., 2020; Ripple et al., 2015), bird (Rosenberg et al., 2019) and arthropod (Seibold et al., 2019) species. We highlight the role of climatic and edaphic conditions in mediating the outcome of plant-herbivore interactions, pointing to important context-dependence for NbS planning. Although livestock grazing is increasing globally (Godde et al., 2018), and Earth's livestock biomass far surpasses the mass of wild mammalian herbivores (Greenspoon et al., 2023), the potential role of domestic grazers in conservation of diversity and soil carbon have been reviewed extensively (e.g. Bai & Cotrufo, 2022; Byrnes et al., 2018; Fraser et al., 2022; Garnett et al., 2017; McSherry & Ritchie, 2013; Olff & Ritchie, 1998; Zhang et al., 2020), so while included, livestock are not the focus of the current review.

2 | NATURE-BASED SOLUTIONS: BIODIVERSITY

2.1 | Herbivore effects on diversity of plants

Maintaining and restoring species-rich assemblages of plants and animals is a widespread conservation goal, but whether NbS diversity goals are supported or undermined by herbivores depends on the outcome of their interactions with plants. In grasslands, herbivores can have a surprisingly wide range of effects on plant diversity, depending on body size, feeding preferences, density, and the abiotic environment (Jia et al., 2018; Lundgren et al., 2024; Olff & Ritchie, 1998). Spatial heterogeneity can maintain plant diversity (Tilman, 1994), and both large and small vertebrate and invertebrate herbivores can create and maintain spatial heterogeneity via selective consumption and deposition of dung or urine with stoichiometry that varies by body size (le Roux et al., 2020; Tuomi et al., 2019; Wang et al., 2021). Below-ground, root herbivores can reduce plant diversity by altering resource competition (Crawford et al., 2021).

Plant diversity effects also can depend on environments and herbivore diversity. Across rainfall and fertility gradients, large bodied herbivores, particularly under intensive grazing, tend to maintain plant diversity in high fertility environments but reduce diversity at low fertility (Jia et al., 2018; Proulx & Mazumder, 1998), whereas small herbivores do not consistently impact plant diversity across a fertility gradient (Bakker et al., 2006). These interactions of climate, fertility, or grazing intensity with plant diversity may arise from herbivore impacts on limiting resources such as light. In grasslands where the loss of herbivores leads to a decline in light

at ground level, plant diversity also declines (Borer et al., 2014), with greatest losses of native plant species (Seabloom et al., 2015) especially in grasslands with an evolutionary history of grazing (Price et al., 2022). Important for nature-based solutions, herbivores tend to reach higher densities and strongly suppress plant diversity in restorations (Xu et al., 2023). In depauperate herbivore communities or where herbivores share dietary preferences, herbivores can create skewed abundance distributions in which plant diversity is suppressed (Kempel et al., 2015; Knops et al., 2000). In contrast, where dietary preferences are complementary, herbivores maintain a more even plant species abundance distribution, supporting greater plant diversity (Kempel et al., 2015; Koerner et al., 2018; Ritchie & Olff, 1999).

Plant restoration and diversity maintenance rely on seed production and dispersal, and herbivores play a central role via seed dispersal and consumption. For example, seeding is frequently used for restoration to achieve NbS plant diversity goals (Shaw et al., 2020), but insects, birds and mammals can consume seeds at high rates (Linabury et al., 2019), causing greater seed mortality of larger seeded species (Celi-Diez et al., 2004; Palmer et al., 2022). Limitations on dispersal distance of seeds also is a major force constraining plant diversity in natural and managed grasslands (Makoto & Wilson, 2019; Seabloom et al., 2003), and dispersal of many plant species relies on the composition of the animal community. For example, with increasing size of mammalian seed dispersers, seed dispersal distance increases whereas damage to seeds from granivory declines (Jia et al., 2018; Karimi et al., 2020). Depauperate animal communities or behavioural avoidance by larger bodied animals of, for example, edge habitats in human-dominated landscapes can determine plant species composition by reducing the average size of seeds arriving (Razafindratsima et al., 2021). Thus, both large and small bodied animals play a central role in achieving long-term success of nature-based solutions via seed survival and dispersal.

2.2 | Herbivore effects on diversity of (wild) animals

The approach to achieving biodiverse grasslands often involves restoring plant communities with the assumption that restored areas will be colonized by and support a more diverse animal community (Dixon, 2009; Guiden et al., 2021; Seddon et al., 2021). Unfortunately, this assumption is not well-supported by research (except under specific interventions, Neff et al., 2020). Instead, the larger landscape context (e.g. dispersal corridors) or management of the system (e.g. fire, mowing, or grazing to achieve C storage, food production, etc.) are more powerful forces suppressing colonization or persistence of vertebrate and invertebrate biodiversity (Guiden et al., 2021). Where colonization can occur, grazing by either domestic or wild herbivores can support diverse, abundant bird (Boyce et al., 2021) and butterfly (Bussan, 2022) assemblages; however, the abundance and taxonomic diversity of above- and below-ground arthropods

and smaller mammals (Filazzola et al., 2020; Foster et al., 2014; Schieltz & Rubenstein, 2016; van Klink et al., 2015; Vandegehuchte et al., 2017; Zhou, Xiang, et al., 2023) is often reduced, particularly in low fertility grasslands (Andriuzzi & Wall, 2017; Bardgett & Wardle, 2003). Growing evidence suggests that, although domestic grazing can maintain plant species diversity, arthropod diversity may decline with grazing, haying, or mowing because plant biomass (consistent with C and energy capture) is more important than plant diversity for supporting arthropod diversity (Borer et al., 2012) or because of habitat homogenization (Gossner et al., 2016; Prather & Kaspari, 2019). Importantly, the grazing effects on animal diversity appear to depend on grazing intensity, with low to moderate grazing promoting animal diversity (Guan et al., 2023). Thus, landscape connectivity and habitat heterogeneity as well as nutritional provisioning and maintenance of sufficient plant biomass (Guiden et al., 2021; Schmitz et al., 2018) are critical multi-scale considerations for meeting NbS diversity goals.

3 | NATURE-BASED SOLUTIONS: CARBON SEQUESTRATION

3.1 | Herbivore effects on plant biomass

Grassland vegetation is the conduit for C uptake and storage in grasslands, and biomass production can be stimulated by herbivory as well as nutrient-rich urine and faecal inputs above-ground (Dobson et al., 2022; Geremia et al., 2019; le Roux et al., 2020; Tuomi et al., 2019) and root-feeding invertebrates below-ground (Johnson et al., 2016). Nonetheless, wild vertebrate and invertebrate herbivores can cause up to 60% net reductions of plant biomass above-ground (Borer et al., 2020; Detling, 1988; Peters et al., 2006; Risch et al., 2013; Staver et al., 2021) and below-ground (Seabloom et al., 2018; Zaret et al., 2023). Particularly important for nature-based solutions is that herbivores reduce restored vegetation even more than native biomass (Xu et al., 2023). However, herbivore impacts depend on factors including plant nutritional quality and defences as well as herbivore size, density, and diet. Dietary preferences often vary among even closely related herbivore species, with greater community-wide diversity of animal body size, feeding traits, and plant traits (e.g. digestibility, chemistry) supporting greater biomass consumption (Branson, 2022; Deraison et al., 2015; Lebbink et al., 2024; Pansu et al., 2022; Potter et al., 2022). Moderate herbivory by large ungulates and invertebrates can provide concurrent benefits to nature-based solutions by reducing grass biomass, promoting diversity of flowering plants (e.g. Beck et al., 2015; Tschardt & Greiler, 1995), reducing fire frequency and intensity (e.g. Rouet-Leduc et al., 2021), and enhancing soil C with dung input (Kristensen et al., 2022). This conversion of 'fire vulnerable' above-ground biomass to 'protected' below-ground C storage (Rouet-Leduc et al., 2021; Sandhage-Hofmann et al., 2021), is likely to become an increasingly important benefit of grassland herbivory to nature-based solutions.

3.2 | Herbivore effects on soil C content, stability and persistence

Herbivore effects on soil C is an area of divergent results and active research. Nonetheless, some generalities are emerging. Exclusion of large herbivores generally increases soil C pools (Forbes et al., 2019), enhancing the formation of mineral associated organic matter (MAOM; Kristensen et al., 2022). However, excluding wild and domestic herbivores can increase interannual fluctuation in soil C pools by 30%–40% (Naidu et al., 2022), and edaphic nutrients can strongly mediate C accumulation (Sitters, Wubs, et al., 2020) across a wide range of grassland conditions. Importantly, NbS soil C goals appear to benefit most when herbivore densities and grazing intensity are controlled by the environment. Light to moderate grazing by cattle or large wild mammals can retain or increase soil C, whereas heavy grazing, above the environmental carrying capacity, generally reduces soil C pools (Conant et al., 2017; Forbes et al., 2019; Hyvarinen et al., 2023; Schmitz et al., 2018; Sitters, Kimuyu, et al., 2020; Zhang et al., 2023; Zhou et al., 2017). Herbivorous arthropods also can play key roles in soil C accumulation (Culliney, 2013; Quirion et al., 2021). Leafcutter ants, for example, are estimated to contribute more to soil C and fertility in the New World tropics than any other animal group (Farji-Brener & Tadey, 2009). Below-ground, soil decomposers and their functions tend to decline with increasing herbivore body size and climate severity, impacting soil C sequestration (Andriuzzi & Wall, 2017); however, there is greater uncertainty about the impacts of root herbivores on soil C dynamics (Gan & Wickings, 2020).

The identity, size, and diversity of herbivores also determine the magnitude and direction of impacts on soil C storage. Although livestock are not a focus of this review, these more well-studied systems are illustrative, here. For example, sheep grazing can cause minimal impact or loss of soil C (Chang et al., 2018; Su et al., 2023), whereas yak grazing can reduce soil C by more than 20% (Ma et al., 2022; Su et al., 2023). In mixed grazing, plant diversity and dietary preference can control soil C effects. For example, dietary preferences of sheep (preference for forbs) and cattle (consume more grass) can promote greatest soil C storage under mixed grazing in a high diversity pasture, whereas sheep alone cause C loss (Chang et al., 2018). Similarly, cattle grazing can induce nearly 14% increases in soil C (Su et al., 2023) to 40% reductions (Sitters, Kimuyu, et al., 2020), depending, in part, on the local assemblage, density, and dietary diversity of domestic and wild herbivores (Sitters, Kimuyu, et al., 2020). Important context for grazing and C storage, however, is that the global livestock supply chain is estimated to account for nearly 15% of anthropogenic C emissions (Garnett et al., 2017). Although concurrent considerations of both C emissions and C storage remain a pressing knowledge gap, estimates suggest that emissions from the livestock supply chain under most conditions and management practices substantially outstrip C storage (Garnett et al., 2017).

4 | CRITICAL INTERACTIONS AND DEPENDENCIES

Grazing intensity, climate and soil chemical and physical properties jointly determine both soil C storage and plant diversity. For example, grazing intensity has differing impacts on soil C storage depending on the local climatic regime, with soil C increasing with air temperature and seasonality under low intensity grazing, but high intensity grazing inducing the opposite effect along the same climatic gradient (e.g. Abdalla et al., 2018; Maestre et al., 2022; Sitters, Kimuyu, et al., 2020). Grazing also interacts with soil nutrients to determine soil C storage, with grazed and fertilized conditions inducing higher soil microbial activity, plant growth, and soil C pools (Chang et al., 2018; Sitters, Wubs, et al., 2020). Plant diversity is often reduced under high intensity grazing, particularly in areas with low soil fertility (Proulx & Mazumder, 1998; Sanaei et al., 2023), suggesting greatest negative impacts of grazing intensity on NbS goals in low fertility regions. Additionally for vertebrate and invertebrate herbivores that move long distances, landscape management and connectivity may determine plant diversity and the movement and storage of soil C (Maguire et al., 2015; Schmitz et al., 2018). Thus, planning for the success of nature-based solutions requires careful consideration of the interactions of grazing type and intensity with site spatial, climatic, and edaphic conditions.

5 | OPPORTUNITIES, CHALLENGES AND FUTURE DIRECTIONS

Given globally declining biodiversity and increasing atmospheric C, it is increasingly important to invest in sustainable nature-based solutions that tackle both crises (Girardin et al., 2021; Seddon et al., 2020). Multi-factor solutions are effective investments, but these rely on a foundational understanding of the ecology of plants, including interactions with their herbivores and the climatic and edaphic environment. We end by summarizing emergent messages from this review to inform the design and implementation of sustainable approaches.

Plants are embedded in a web of interactions with their herbivores and their environment. Management actions fostering C storage by plants and soils while supporting a diverse foodweb (Foster et al., 2014) will arise from a whole systems perspective. A singular focus on one outcome (e.g. C storage) can lead to management choices (e.g. monoculture forest planting) that are neither sustainable nor supportive of other goals for nature-based solutions (e.g. biodiversity, Seddon et al., 2020). Pragmatically, planning for sustainable, cost-effective approaches requires knowledge of likely plant-herbivore interactions that will emerge following conservation or restoration actions. For example, many biodiversity outcomes benefit from grazing but cannot be achieved by haying or mowing (Gossner et al., 2016; Prather & Kaspari, 2019). Key knowledge gaps remain for informing nature-based solutions. In particular, the current rapid decrease in above-ground invertebrates world-wide (Eggleton, 2020; Sánchez-Bayo & Wyckhuys, 2019) underscores the

urgent need to understand the role of invertebrates, both above- and below-ground, including their diversity, interactions, and feedbacks to plants and larger herbivores that impact both plant diversity and long-term C storage.

An emergent theme is that *low to moderate herbivory arising from herbivore densities supported by the local environment* is, under many conditions, consistent with achieving biodiversity and carbon goals (Maestre et al., 2022; Staver et al., 2021). In this context, rewilding or the use of domestic livestock to replace services provided by wild mammals lost from a system, is being increasingly adopted in some regions to restore plant-herbivore interactions (Bakker & Svenning, 2018). Some nature-based solution goals may be achieved through rewilding if herbivore biomass is determined by environmental resources rather than artificially predetermined stocking rates (Fløjgaard et al., 2022). Nonetheless, substantial evidence that wild and domestic animals differently affect plant and animal diversity and soil C calls for a place-based and data-driven approach to protecting and restoring animal-plant interactions to achieve NbS goals (Hart et al., 2023; Hempson et al., 2017; Pringle et al., 2023). Lifecycle analyses of C emissions and sequestration for the domestic livestock supply chain within regions will be a critical component of this work toward sustainable nature-based solutions (Garnett et al., 2017).

Many effects of herbivores on plant and animal diversity and soil C depend on the biotic (e.g. plant diversity, herbivore identity, density and composition, vegetation/habitat connectivity) and abiotic (e.g. climate, soils) context for magnitude, and in some cases, direction. Depending on site-level climate and soils, for example, high grazing intensity can increase or reduce plant diversity and soil C storage (Maestre et al., 2022), and dominant grass species also can determine herbivore effects on soil C dynamics (Abdalla et al., 2018; McSherry & Ritchie, 2013). Attention to context, particularly the role of herbivores and local climate trends, in implementation of nature-based solutions will help achieve success (Fuhlendorf et al., 2018). Although *plant-herbivore interactions are context dependent*, knowledge of the key biotic and abiotic dependencies, combined with planning for known plant-herbivore interactions, can help support the success of sustainable solutions.

The Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) highlight the link between biodiversity loss and climate change. Both global assessments have urged immediate, substantial efforts to reduce human impacts, including conservation and restoration as mitigation strategies (IPBES, 2019; IPCC, 2019; Pörtner et al., 2021). Yet the majority of NbS actions currently focus narrowly on forest protection and restoration for C uptake (Mo et al., 2023; Seddon et al., 2021), often to the detriment of biodiversity and without consideration of other biomes and opportunities (Fargione et al., 2018). Recognizing every opportunity for C storage and climate change mitigation, particularly where biodiversity goals can also be achieved, is critical in a time of crisis for both. Despite covering more than a third of Earth's ice-free land surface (White et al., 2000) and harbouring far more endangered

plant species than forests (Staude et al., 2023), *grasslands are under-appreciated* in many considerations of nature-based solutions. Yet, with attention to key species interactions, they can be managed to be complementary to forests, serving as 'global reservoirs of C' (e.g. Kristensen et al., 2022) that, under a wide range of conditions, can be consistent with sustainable protection for plant (Maestre et al., 2022) and animal (Schieltz & Rubenstein, 2016) biodiversity. By moving C from vulnerable above-ground to more persistent below-ground C pools, herbivores also can considerably contribute to C storage in a drier, warmer, and more fire prone future.

AUTHOR CONTRIBUTIONS

Elizabeth T. Borer conceived and structured the paper, drafted text for most sections, and finalized the text in all sections. Anita C. Risch drafted the carbon sections and edited other sections. Both authors read and approved the final manuscript.

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