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Ruminating on soil carbon: Applying current understanding to inform grazing management

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Abstract

Among options for atmospheric CO_2 removal, sequestering soil organic carbon (SOC) via improved grazing management is a rare opportunity because it is scalable across millions of globally grazed acres, low cost, and has high technical potential. Decades of scientific research on grazing and SOC has failed to form a cohesive understanding of how grazing management affects SOC stocks and their distribution between particulate (POM) and mineral-associated organic matter (MAOM)—characterized by different formation and stabilization pathways—across different climatic contexts. As we increasingly look to grazing management for SOC sequestration on grazinglands to bolster our climate change mitigation efforts, we need a clear and collective understanding of grazing management's impact on pathways of SOC change to inform on-the-ground management decisions. We set out to review the effects of grazing management on SOC through a unified plant ecophysiology and soil biogeochemistry conceptual framework, where elements such as productivity, input quality, soil mineral capacity, and climate variables such as aridity co-govern SOC accumulation and distribution into POM and MAOM. To maximize applicability to grazingland managers, we discuss how common management levers that drive overall grazing pattern, including timing, intensity, duration, and frequency can be used to optimize mechanistic pathways of SOC sequestration. We discuss important research needs and measurement challenges, and highlight how our conceptual framework can inform more robust research with greater applicability for maximizing the use of grazing management to sequester SOC.

KEYWORDS
adaptive grazing, conceptual framework, ecophysiology, grazing management, soil organic carbon

1 | INTRODUCTION

Grazing animals are influential controls on the estimated 30% of our total soil organic carbon (SOC) stocks held in the two-thirds of agricultural lands grazed globally (Dondini et al., 2023). Mismanagement of domesticated grazing animals, along with land-use change, has historically led to significant SOC loss on grazed lands (Sanderman et al., 2017). This SOC deficit has created a renewed interest in the use of improved grazing management to help sequester SOC as a part of atmospheric carbon (C) drawdown efforts (Bai & Cotrufo, 2022;

Paustian et al., 2016). However, the literature examining grazing impacts on SOC report mixed outcomes, ranging from large SOC gains to SOC losses, spanning different management approaches and climatic contexts (McSherry & Ritchie, 2013). Synthesizing the influence of grazing management on pathways of SOC change within current SOC formation and stabilization frameworks, and how effects vary across climatic variables, is an important next step in optimizing management for SOC sequestration.

Traditionally, most studies have inferred grazing impacts on SOC based on dichotomous experimental manipulations in which SOC outcomes are compared between "presence" or "absence" of grazing, and "grazing" is considered a homogeneous function (Piñeiro et al., 2009, 2010). However, grazing management is incredibly variable regionally, temporally, and among producers of different backgrounds, demographics, and operation sizes. Therefore, these studies are more helpful in illustrating SOC response in the *absence* of grazing than they are for understanding SOC response *from* grazing. The other commonly studied experimental grazing dichotomy is "light" versus "heavy" grazing, defined simplistically in terms of total animal units (AUs), a metric used to standardize across livestock of different classes according to similar dry matter intake needs, or stocking rate (total AUs/total grazed area; Abdalla et al., 2018). These approaches to assessing the impact of grazing management on SOC have failed to converge into a cohesive mechanistic understanding and have resulted in significant variability across the literature in both the direction and magnitude of SOC changes from grazing management practices. We propose two primary factors contributing to this:

1. Grazing management varies widely along gradients of timing, intensity, frequency, and duration, which combine with stocking rate to create an overall grazing pattern, driving plant ecophysiology, and SOC outcomes. However, these factors of grazing pattern remain under-represented and often ill-defined in the literature, and we posit that by influencing grazing outcomes, they can explain some of the large variability observed in the direction and magnitude of SOC changes from grazing (Laca, 2009).

2. Climate, edaphic, and plant ecophysiology factors act as master mediators of SOC response to grazing (Abdalla et al., 2018; Bai & Cotrufo, 2022; McSherry & Ritchie, 2013). Grazing is the most widely applied agricultural activity globally, spanning climate gradients from tropical to desert, and land types, which we define together here as grazinglands, encompassing managed pastures and native grasslands and rangelands (Rangelands ATLAS, 2021) where optimal grazing approaches for SOC likely vary (Deng et al., 2023). The interaction between grazing management and unique environmental factors is complex and has hindered identification of generalizable mechanisms underlying grazing-induced SOC change (Derner & Schuman, 2007), which are necessary for informing context-dependent management to optimize SOC sequestration in grazinglands. Arguably, poorly managed

grazing leads predictably to loss of plant diversity and productivity, and to soil erosion which compromises soil health and SOC storage (Byrnes et al., 2018; Conant & Paustian, 2002); while well-managed grazing can support plant diversity and productivity, driving positive SOC outcomes (Franzluebbers et al., 2012; Schuman et al., 2002). However, what constitutes "good management" depends on climate and plant ecophysiology variables (Taboada et al., 2011).

To date, little has been done to synthesize our understanding of how grazing influences mechanisms of SOC formation. In their conceptual framework, Piñeiro et al. (2010) summarized three pathways by which grazing controls SOC formation: net primary production (NPP), nitrogen (N) cycling, and decomposition. Since then, scientific understanding of SOC formation and stabilization has developed significantly. SOC is now broadly categorized into particulate (POM) or mineral-associated organic matter (MAOM), which exhibit distinct formation pathways, soil functionalities, turnover rates, and responses to management interventions (Cotrufo & Lavallee, 2022; Lavallee et al., 2020). Additionally, climate is an overarching control on SOC storage (Davidson & Janssens, 2006), and on POM and MAOM distribution (Hansen et al., 2024). Here, we review the effects of grazing on SOC using a novel conceptual framework, which integrates the mechanisms by which grazing pattern influences pathways of SOC formation and stabilization through ecophysiological changes derived from alteration of ecosystem functioning and structure (Figure 1). With this framework, we intend to align scientific understanding on the ways in which grazing influences SOC, which can inform context-specific optimization of grazing management for SOC sequestration in grazinglands across climates.

Broadly defined, grazing is a type of herbivory, or defoliation of plant tissue, typically leaves, by animals ranging from arthropods to elephants. Here, we focus on ruminant livestock because of their global dominance among herbivores, agricultural importance, and scale of SOC influence, although the ecophysiology and SOC pathways discussed will largely overlap with other types of herbivory. Grasslands and rangelands worldwide evolved being grazed by large herbivores (Bråthen et al., 2021). However, shifts from native herbivory toward largely fenced, domesticated, and managed livestock grazing coincide with SOC losses generally. While cattle and native grazers like bison share important functional traits and behaviors (Allred et al., 2011), the human mismanagement of grazed cattle on small scales can create unique behaviors, which drive SOC outcomes. Currently, the biomass of domesticated cattle on Earth far surpasses that of other native grazers (Bar-On et al., 2018). While some work suggests that contemporary livestock numbers vastly exceed historical baselines (Barnosky, 2008), recent re-appraisals contend that contemporary livestock numbers are analogous to their peak in the Late Pleistocene, an admittedly sobering thought (Malhi et al., 2016; Manzano et al., 2023; Zimov et al., 1995). If these re-appraisals are correct, they would support the contention that
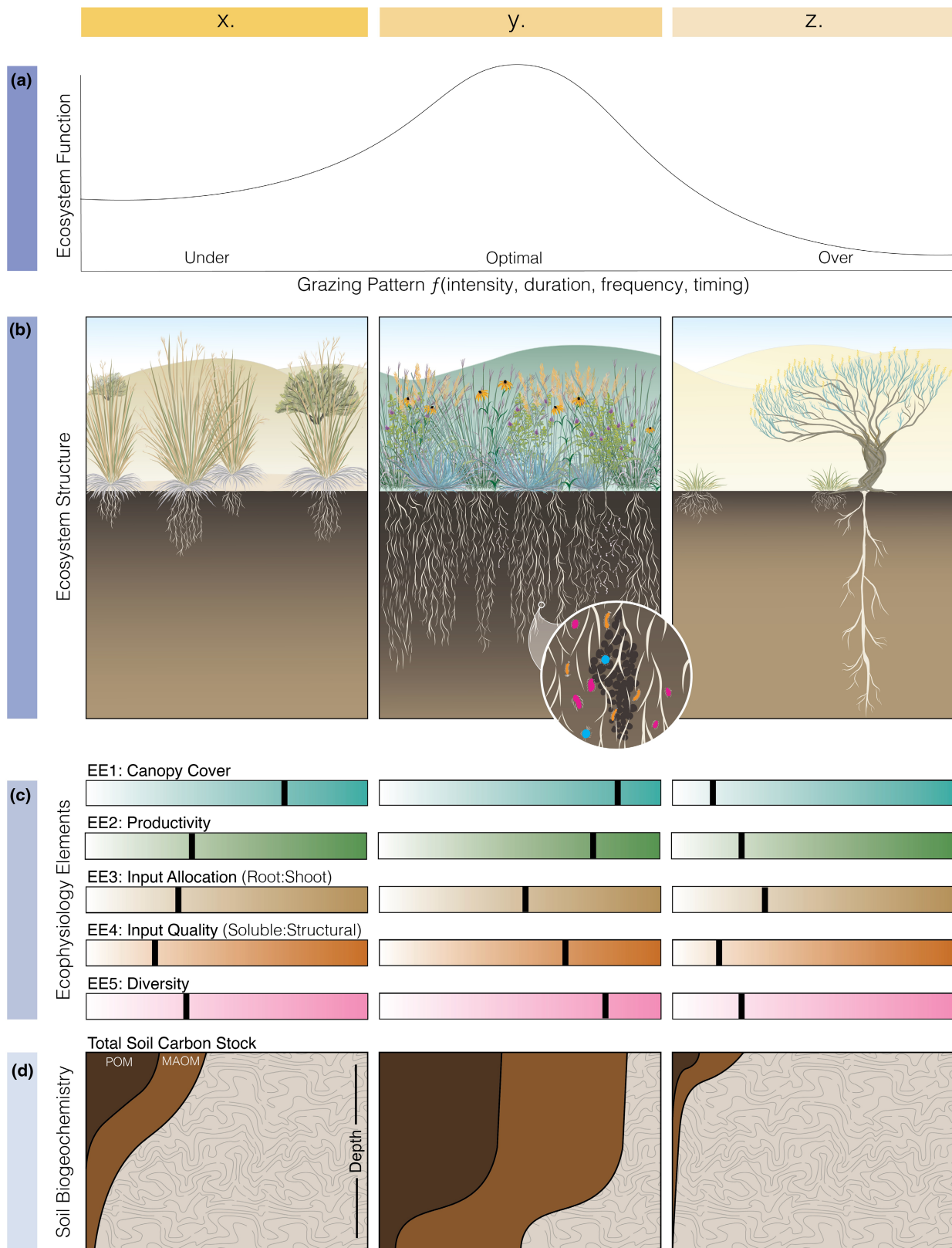
FIGURE 1 Conceptual illustration of how grazing patterns (x, y, z) affect ecosystem function (a) and structure (b) by modulating plant ecophysiological elements [EE; (c)], which together give rise to soil biogeochemical outcomes (d) in terms of total soil organic carbon stock and distribution into particulate (POM) and mineral associated organic matter (MAOM). Each of the three grazing patterns—(x) undergrazing, (y) optimal grazing, and (z) overgrazing—is expected to result in different ecosystem, ecophysiological, and soil biogeochemical outcomes. EEs (c) are expressed either as continuous gradients or as ratios of two components, where the color gradient from left to right represents low–high or left:right, respectively, and the placement of black markers represent the expected outcome from each grazing pattern.

ecosystem degradation (loss of biodiversity, soil erosion, and SOC loss) has more to do with a broken *pattern* of grazing activity (timing, intensity, duration, and frequency) than a simple quantitative excess of grazers.

Our overarching goal was to reenvisage the impacts of grazing on SOC by developing a mechanistic, conceptual framework informed by grazing ecology, plant ecophysiology, and soil biogeochemistry. In this review, we identify important ecophysiological elements (EEs), which mediate SOC response from grazing over both short and long timescales, including canopy and ground cover, productivity, input allocation, input quality, and biodiversity. Grazing-induced changes in each EE then has downstream effects on soil biogeochemistry, influencing pathways of SOC formation and distribution into POM and MAOM (Figure 1). These changes are the result of overall grazing pattern, which is the culmination of timing, intensity, duration, and frequency levers (Figure 2). Grazing management approaches that proactively plan and strategically adapt implementation of these levers according to ecophysiological responses can therefore be used to optimize pathways of SOC formation and stabilization across many climate contexts. Our framework, along with inclusion of producers and methodological improvements, can help inform more reliable research, useful management recommendations, and development of empirical models to generate scalable predictions of SOC changes from grazing.

2 | A HOLISTIC FRAMEWORK FOR ASSESSING GRAZING IMPACTS ON PATHWAYS OF SOC CHANGE

The impact of large herbivore grazing on SOC is largely indirect and ultimately mediated by both top-down and bottom-up processes. Therefore, it requires a holistic approach that considers the interplay of plant and ecosystem physiology and soil biogeochemistry governing SOC outcomes. We illustrate this conceptual approach (Figure 1), review the impacts of grazing on different hierarchical levels of grazing ecosystems, and synthesize how different grazing patterns drive SOC outcomes through mechanistic pathways.

2.1 | Effects of grazing pattern on ecosystem function

In our framework, we define grazing pattern as a function of intensity, duration, frequency, and timing. The resulting grazing pattern has cumulative effects on ecosystem function over time (Holechek et al., 1998). We consider 'undergrazing' as the ecological and SOC conditions that result from under-leveraging the possible benefits of grazing animals—including scenarios of too few animals (poor utilization), too infrequently (over-rest), or both. When grazing animals are optimally leveraged—in the right numbers, at the right time, and in the right place—an 'optimal grazing' scenario is one in which ecosystem structural benefits emerge (Figure 1b) from plant ecophysiological responses (Figure 1c) that can maximize SOC outcomes (Figure 1d). On the most intensive end of the spectrum, 'overgrazing,' in which grazing in excess (i.e., too many animals, grazing too frequently, or both) can lead to negative ecological outcomes and SOC loss.

2.2 | Temporal impacts of grazing at different scales

The impacts of grazing pattern can be differentiated temporally into short-term individual plant responses and long-term ecosystem structure (Figure 1b), which is characterized by EEs (Figure 1c).

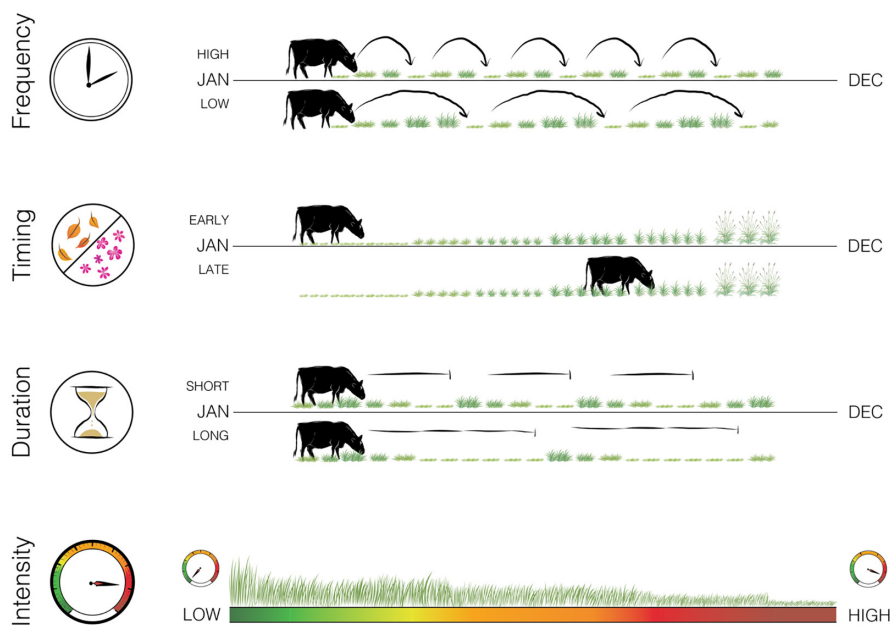**FIGURE 2** Illustrative representations of the four metrics contributing to overall grazing pattern: frequency, timing, duration, and intensity. Frequency, timing, and duration are shown along a calendar year timeline with comparative examples of how they differ under "high" and "low" scenarios. We represent intensity as the amount of biomass utilized from grazing over a given time, which is influenced by the former three factors.

2.2.1 | Short-term individual plant response to defoliation

Defoliation of plant material by grazers has immediate impacts on a plant's photosynthetic capacity and C and nutrient allocation priorities. The extent to which these plant processes are impacted is dependent upon defoliation severity, which is the combined outcome of amount of leaf-area removed, a plant's grazing tolerance (species, functional type, and grazing history), and phenology (capacity to mobilize energy reserves; Briske & Richards, 1994, 1995). Severe defoliation occurs when a grazer removes too much of a plant's photosynthetic tissue, which significantly reduces plant photosynthesis and can halt root growth and respiration (Balogianni et al., 2014; Briske & Richards, 1995). In this scenario, plant regrowth and survival require mobilizing energy reserves typically stored in the crown (and to a lesser extent, roots) of the plants, until sufficient leaf area has been re-established along with a positive C balance to serve as sources of assimilates to sustain growth rates. These mobilized reserves are preferentially partitioned into new shoot and leaf growth at the expense of allocation belowground into roots and rhizomes (Briske & Richards, 1995; Richards & Caldwell, 1985; Ryle & Powell, 1975). If a young plant without sufficient energy reserves is severely defoliated by grazing, it will be unable to regrow photosynthetic tissue and will ultimately die. Similarly, re-grazing a severely defoliated plant before positive carbohydrate balance has been restored can cause substantial stress and has been shown to lead to stand weakening and mortality (Briske & Richards, 1995; Gastal & Lemaire, 2015). By contrast, defoliating less than 40%–50% of leaf area may not lead to any interruption in root growth and respiration and may only modestly and briefly depress canopy C assimilation rates (Richards, 1984; Volesky et al., 2011). Overall, the short-term outcomes of defoliation from grazing are removal of aboveground biomass, leading to reduced photosynthetic surface area, temporary mobilization of energy and nutrients from the crown and other storage depots to support leaf re-growth, and possibly reduced rates of root growth. Somewhat paradoxically, some evidence suggests that rates of rhizodeposition may temporarily increase following grazing (Hamilton et al., 2008), possibly leading to enhanced rates of nutrient mineralization (i.e., "priming" Dijkstra et al., 2013). On the other hand, quantifying fine root exudation in situ is notoriously difficult, relying on labor-intensive stable isotope pulse-labeling methods (e.g., Wilson et al., 2018) or root-level cuvette sampling (e.g., Phillips et al., 2008) so that available studies and sample sizes are extremely limited.

2.2.2 | Long-term ecosystem structure reflects impacts of grazing on EEs

Over longer timescales, the impact of grazing herbivory on individual plants culminates in shifts in whole ecosystem structure, that is, plant community and composition dynamics (Figure 1b), which constrain and shape the significance of the short-term physiological responses outlined above. The resulting plant community ecophysiology creates ecosystem processes and feedbacks with complex, dynamic controls on SOC. Grazinglands with higher SOC stocks are generally associated with greater overall plant density and productivity (Conant et al., 2017), root system biomass and belowground allocation (Wilson et al., 2018), functional diversity [e.g., complementarity among C4 grasses and legumes (Fornara & Tilman, 2008)], and, to an extent, diversity/species-richness (Sanderson et al., 2004; Tilman et al., 2001, 2012). We therefore posit that predicting long-term grazing impacts on SOC devolves into mechanistically understanding how grazing influences the following five EEs that regulate SOC (Figure 1c):

EE1: Ground and canopy cover (i.e., % cover).
EE2: Productivity (i.e., Mg/ha of NPP).
EE3: Input allocation (i.e., root:shoot ratio).
EE4: Input quality (i.e., C:N, soluble:structural component ratios).
EE5: Diversity (i.e., functional group or species richness).

In our framework, grazing impacts on SOC filter through these five EEs in one or more of the following pathways (Ps):

P1: Increasing overall C fixation in plant biomass and soil C inputs.
P2: Reducing SOC losses, via slower decomposition or erosion prevention.
P3: Increasing the efficiency of below ground transformations.

Canopy cover and productivity

Grazing removes plant biomass and reduces canopy cover in the short-term, and thereby should have seemingly negative short-term impacts on SOC. However, we have known for decades that aboveground biomass removal by grazing does not consistently translate into reduced belowground biomass (Milchunas & Lauenroth, 1993), and positive SOC outcomes have also been documented in a variety of cases (Piñeiro et al., 2010). How can we rectify these positive long-term SOC outcomes with canopy cover reduction and overall biomass removal in the short term? NPP in plant communities can be understood as a function of the interception of photosynthetically active radiation (PAR) and the conversion of absorbed PAR into new plant tissues, minus respiration. This net conversion of light into biomass is referred to as the "radiation use efficiency" (RUE):

$$NPP = PAR \times fPAR \times RUE$$

where fPAR is the fraction of PAR that is absorbed by the canopy, largely a function of plant canopy characteristics, especially leaf area index (LAI) and leaf angle and orientation, and RUE is the radiation-use efficiency (Sinclair & Muchow, 1999; Sinclaire & Weiss, 2010). Note the product PAR×fPAR is the absorbed PAR or APAR. The most productive ecosystems tend to sustain very high LAI, with a canopy architecture that distributes light relatively evenly, and are characterized by high levels of RUE owing to optimized resource supply (e.g., tissue N) and C4 photosynthetic pathways (e.g., sugarcane). While grazing involves defoliation and hence loss of LAI (leading to

lower fPAR), the NPP response is not uniformly negative, due to a variety of ecological and physiological dynamics which can compensate. In fact, well-managed grazing can optimize canopy structure and hence the absorption and distribution of light to green leaf area, and increase the proportion of younger leaf tissue with higher photosynthetic capacity, both factors acting to enhance RUE. Given the nonlinear saturating relationship of LAI to light interception, even substantial loss of LAI due to grazing could therefore be compensated by improved RUE.

In the long term, there are several mechanisms through which grazing can increase SOC through improved canopy cover (*EE1*) and productivity (*EE2*). If too much LAI is defoliated and not enough energy reserves are available for regrowth, canopy cover will ultimately be reduced, exposing bare soil. Bare soil can perpetuate SOC loss via erosion and exposure to temperature extremes, which creates inhospitable growth conditions for some plants and microbes (Thomson et al., 2010). At the other extreme, very little or no defoliation may ultimately reduce the potential for maximizing NPP by shading out new plant growth. Periodic defoliation by grazing can therefore increase SOC by improving APAR and increasing whole community canopy cover, which minimizes SOC loss from bare soil (*grazing → EE1 → P2*). In turn, increased canopy cover and fPAR increases NPP, creating overall more plant C input opportunities for SOC formation (*grazing → EE1 → EE2 → P1*).

There is a long and somewhat controversial literature addressing an additional possible phenomena through which grazing can lead to positive SOC outcomes from greater overall plant community productivity: "compensatory regrowth" (Balogianni et al., 2014; McNaughton, 1983, 1984; McNaughton et al., 1997; Wilson et al., 2021; Zhao et al., 2008), which corresponds to our scenarios where increased RUE outweighs short-term reductions in APAR. Periodic removal of leaf area in grazinglands leads to plant stands with a younger average leaf age, thus greater tissue N content and maximum photosynthetic rates, both of which correlate to higher RUE (Soltani et al., 2020). Thus, where soil resources are adequate to support rapid re-growth of high-quality tissue in grazing-adapted species, greater RUE and subsequent productivity may be one mechanism supporting "compensatory re-growth" (*grazing → EE2 → P1*). Another mechanism is through the removal of senescent tissue by periodic grazing, which may reduce self-shading, thus increasing the fraction of APAR by green photosynthetically active laminar surfaces and reducing its absorption by brown, senesced tissue. In practice, this would also increase the apparent RUE (*grazing → EE1 → EE4 → P1*) and reduce SOC loss by encouraging denser plant growth (*grazing → EE1 → P2*). Moreover, this mechanism unites with the benefits of grazing for maintenance of plant diversity by limiting plant competition for light (Collins et al., 1998), in effect reducing self-competition for light (*grazing → EE1 → EE5 → P1*). Mechanisms of compensatory re-growth (reduced leaf age, higher N, less self-shading) have implications for P3 as well. If grazing animals are consuming denser, higher-quality forage, they will be recycling higher quality inputs through manure as well as encouraging deposition of higher quality plant litter on the soil surface. Therefore, while a higher fraction of aboveground NPP may go through grazing animals rather than accumulate as litter, the greater quality of inputs may well foster enhanced SOC (*grazing → EE2 → P3*). To sum up, we posit that *when and where the pattern of grazing allows for expression of compensatory re-growth mechanisms sufficient to outweigh short-term reductions in APAR*, grazing may be compatible with increases in SOC by all three pathways.

Input allocation

Grazing can also influence the allocation of a plant community's resources to above versus belowground growth (*EE3*) with implications for SOC outcomes. While total NPP and greater C inputs in general correspond to higher SOC, root-C is preferentially retained and is a significantly greater contributor to SOC than C from aboveground plant litter inputs (Rasse et al., 2005). This is because (a) roots contribute to rhizodeposition and produce high quality exudates which result in efficient MAOM formation (Sokol, Kuebbing, et al., 2019; Sokol, Sanderman, et al., 2019; Villarino et al., 2021); (b) roots turnover in direct contact with the soil matrix, favoring MAOM formation (Fulton-Smith & Cotrufo, 2019; Leichty et al., 2020; Mitchell et al., 2018) and (c) by contributing residues deeper in the soil profile where microbial decomposition is slower, grass roots can result in efficient POM accumulation (van der Pol et al., 2022). There are several root-mediated mechanisms by which grazing can increase SOC despite short-term aboveground C reduction from defoliation, including directly by increasing root:shoot allocation, root exudation and other rhizodeposits, and indirectly by increasing overall plant cover (i.e., total root biomass) or driving plant community shifts toward species with greater root:shoot allocation (e.g., C4 plants, perennials). These mechanisms are supported by research reporting increased SOC from greater root allocation and exudation resulting from grazing compared with grazing exclusion (Wilson et al., 2018). While grazing generally corresponds with positive root outcomes (Piñeiro et al., 2010), and sustained, severe defoliation generally compromises plant root allocation (Chen et al., 2015; Schuster, 1964), there is significant variability across studies on both direction and magnitude of grazing-induced root response and the consequent impact on SOC formation. We posit that the extent to which grazing has positive impacts on root-SOC pathways (*grazing → EE3 + EE4 → P2 + P3*) seemingly depends on plant functional type, prior conditioning to and tolerance to grazing, and the frequency and severity of defoliation (Chen et al., 2015; Dawson et al., 2000; McSherry & Ritchie, 2013; Reeder & Schuman, 2002; Wu & Wang, 2008). For example, even heavy defoliation has been shown to increase root allocation and exudation among C4 plants (*grazing → EE3 → P2*; Ma et al., 2021) whereas it decreases root biomass production among C3 plants (Holland & Detling, 1990; Klumpp et al., 2009; McSherry & Ritchie, 2013). Plant characteristics and tolerance to grazing also interact with defoliation frequency. An increase in root exudation and rhizodeposition has been found immediately following even moderate-to-heavy grazing defoliation

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(Bardgett et al., 1998; Dawson et al., 2000). However, greater rhizodeposition can be maintained in the long-term when defoliation is followed by rest from grazing, even among C3 species with prior conditioning to grazing (Sun et al., 2017). Root exudates are comprised of high quality, low molecular weight compounds (e.g., simple sugars, organic acids), which can prime SOC mineralization (Kuzyakov, 2002), and MAOM destabilization (Jilling et al., 2018), but overall result in high SOC formation (Prescott, 2022) by stimulating microbial growth and turnover or direct sorption on minerals. Thus, grazing-induced rhizodeposition drives belowground microbial transformations of organic material and can increase SOC ($grazing \rightarrow EE3 \rightarrow EE4 \rightarrow P1 + P3$; Gavrichkova et al., 2008; Hamilton et al., 2008). However, as noted above, studies of rhizodeposition under field conditions are currently quite limited for logistical reasons, highlighting the importance of greater investment and methodological innovation in studying how these processes vary with composition, management, soil, and climate factors.

Input quality

Grazing affects the quality of aboveground inputs that mediate the efficiency of SOC formation. Plants undergo stoichiometric changes as they reallocate resources from vegetative growth (i.e., leaves and roots) to reproductive growth (i.e., seed). As plants mature and approach senescence, their C:N ratios increase and their biomass contains proportionally more structural (i.e., lignin) than soluble (i.e., simple sugars) components. Organic soil inputs with higher C:N and structural components reduce microbial carbon use efficiency (CUE), which often limits microbial growth and turnover and ultimately reduces the proportion of C retained in the soil versus C lost via respiration (Cotrufo et al., 2013; Kallenbach et al., 2016; Tao et al., 2023). We hypothesize three general ways in which grazing positively influences input quality, microbial CUE, and subsequent SOC formation. First, defoliation of mature plant tissue encourages growth of newer leaves with greater N content, reducing C:N and improving plant litter quality by an average of 25% (Wang et al., 2016). In turn, higher quality litter enhances decomposition rates and increases microbial CUE ($grazing \rightarrow EE4 \rightarrow P3$; Li et al., 2022; Su et al., 2022; Sun et al., 2018). Second, grazers transform defoliated plant material into manure, returning a significantly higher quality organic input with C:N much closer to that of soil ($grazing \rightarrow EE4 \rightarrow P3$; Soussana & Lemaire, 2014). Third, defoliation and subsequent regrowth of plants during the vegetative phase can defer senescence, thereby increasing higher quality plant inputs to the soil for longer periods of time ($grazing \rightarrow EE4 \rightarrow P1 + P3$; Bremer et al., 2001; Nowak & Caldwell, 1984; Shen et al., 2022). Taken together, if and when grazing improves ecosystem N cycling by upcycling plant materials into higher quality inputs, it can drive more efficient belowground SOC accumulation despite the aboveground biomass C consumed during defoliation. Of course, this impact would need to outweigh any grazing-associated accelerations of N-loss (e.g., ammonia volatilization from urine deposition) which could stoichiometrically constrain ecosystem C accumulation in the long term.

Diversity

Diverse plant communities can support more robust ecosystem functionality by filling a variety of ecological niches, including different rooting depths, phenologies, seasonalities, and nutrient acquisition strategies (Tilman et al., 2014). Increasing plant diversity can drive SOC formation via the same mechanisms outlined above. Generally, more diverse plant communities which improve productivity, N cycling (e.g., especially increased cover of legumes), root allocation (e.g., addition of perennial and C4 plants; Gould et al., 2016), and improve the quality of community plant litter inputs (e.g., forbs, C3 plants, and legumes) lead to improved SOC outcomes compared with less functionally diverse plant communities (Fornara & Tilman, 2009; Furey & Tilman, 2021). While increasing plant functional diversity has clear mechanistic connections to improved SOC, there is some evidence to suggest that improving diversity per se and creating functional redundancy may also have SOC benefits (Lehmann et al., 2020), though the mechanisms are more theoretical and not yet empirically proven (Yang et al., 2019). One hypothesis is the "insurance value" of increased species abundance, as it creates ecosystem stability and resiliency, which minimizes SOC loss from disturbances such as climate change ($grazing \rightarrow EE5 \rightarrow P2$; Tilman et al., 2006). Diverse plants also create diverse litter inputs, which increase microbial community diversity, activity, and turnover, likely resulting in more efficient SOC transformations ($grazing \rightarrow EE5 \rightarrow P3$; Lange et al., 2015; Prommer et al., 2020).

There is a long history of research studying the impacts of grazing on plant community compositional shifts, but these shifts in plant diversity are rarely documented with SOC outcomes. Divergent theories of grazingland vegetation dynamics (e.g., successional vs state-and-transition models) and how accurately they predict ecophysiological responses to defoliation is beyond the scope of this paper, though they contain important contextual background (see Bestelmeyer et al., 2017; Briske et al., 2005; Milchunas et al., 1988). There is majority consensus that in temperate ecosystems, grazing is more reliably and consistently associated with improved plant diversity. However, in more arid ecosystems, the impacts of grazing on plant diversity are nonlinear and complex, where precipitation variability and evolutionary grazing history are known mediating factors (Cingolani et al., 2005; Porensky et al., 2017). In both cases, selectivity of defoliation—driven by both species and grazing management—can directly influence plant diversity by altering competitive advantages within the plant community (Liang et al., 2021; Soder et al., 2007). Large herbivores have been successfully used to maintain diversity and prevent invasive species encroachment through intensive, selective defoliation of invasive species (Molnár et al., 2020). Considering climate and historical constraints, grazing clearly influences plant community composition and diversity, with possible positive SOC outcomes via all three pathways ($grazing \rightarrow EE5 \rightarrow P1 + P2 + P3$).

2.3 | Soil biogeochemistry: Impacts of grazing on SOC accumulation and distribution between POM and MAOM

In concert with soil edaphic factors, these EEs and pathways of SOC accumulation govern final SOC distribution into different soil organic matter fractions: POM and MAOM (Figure 1d). In grazinglands, SOC is distributed on average 70%–72% to MAOM and 28%–30% to POM (Lugato et al., 2021; Sokol et al., 2022). However, the proportion of SOC in MAOM may vary from 25% to 75% (Rocci et al., 2022), and extremely coarsely textured soils may have only 10%–25% SOC in MAOM (Silveira et al., 2014).

Particulate organic matter primarily forms from the structural components of plant and microbial inputs and turns over on an annual to decadal time frame (Lavallee et al., 2020), unless it is protected by occlusion in microaggregates (Angst et al., 2017; Witzgall et al., 2021). At a global scale, POM-C accumulation is not controlled by organic input rates, but rather by factors affecting microbial decomposition activity, such as pH and temperature, with higher POM-C associated with lower temperatures and pH (Hansen et al., 2024). Further, since the chemical recalcitrance of organic inputs is not related to their long-term persistence (Kleber, 2010; Kleber & Johnson, 2010), POM-C storage is not expected to be highly modified by input quality (Huys et al., 2022), though the majority of research shows short-term POM accumulation with higher input rates of lignified tissue. The large contribution of structural inputs (e.g., lignin or suberin rich tissues) to POM-C gives rise to a higher POM C:N stoichiometry than MAOM (Cotrufo et al., 2019): globally, the POM C:N in grazinglands averages 16.7 ± 0.8 (Rocci et al., 2022). These characteristics of POM suggest that when grazing management results in increased structural plant and manure inputs (Mayer & Silver, 2022), especially at depth where decay rates are inherently low, increased soil aggregation and reduced microbial activity would likely lead to greater POM-C stocks.

On the other hand, MAOM forms from the chemical binding of microbial necromass and dissolved, low-molecular-weight organic matter to silt and clay sized soil minerals (Kleber et al., 2015). The growth and turnover of microbes is an especially important factor influencing MAOM formation in grazinglands, where >60% of total SOC is derived from microbial necromass (Liang et al., 2019). Because MAOM involves sorption to soil mineral surfaces, a large portion is inaccessible to microbes and considered "protected," which confers long-term stabilization, while a smaller portion is "exchangeable" with soil DOM (Kleber et al., 2021). Given these properties, MAOM is generally controlled by input rates and quality (i.e., NPP [*EE2*] and C:N stoichiometry [*EE4*]; Cotrufo et al., 2013; Hansen et al., 2024), availability and type of active soil mineral surfaces (i.e., texture and mineralogy; King et al., 2023), and efficiency of microbial transformations (Kallenbach et al., 2015, 2016). Because of the large contribution of microbially transformed and N-rich organic matter to MAOM, its C:N stoichiometry is consistently lower than POM, averaging C:N of 12.1 ± 0.6 across grazinglands globally—which also suggests that N availability may constrain MAOM formation (Rocci et al., 2022). Therefore, all else equal, we expect that grazing management that leads to greater total inputs (NPP), higher plant litter quality (lower C:N, greater soluble inputs and leguminous species), and increased availability of other N-rich inputs (e.g., manure, enhanced root exudation) for microbial use will enhance MAOM formation. Manure deposition by herbivores also enhances MAOM formation by direct DOM sorption (Brewer et al., 2023). Notably, MAOM will only accumulate in soils with unsaturated mineral capacity, though the majority of grazinglands globally are far below their saturation capacity (Georgiou et al., 2022).

In many cases, grazing-induced shifts in the five EEs likely influence POM and MAOM simultaneously. For example, enhanced fine root biomass will primarily drive MAOM formation (Sokol et al., 2022). However, greater root inputs at lower depths in the soil profile, where microbial activity is typically much lower than in topsoil (Rumpel & Kögel-Knabner, 2011), may result in meaningful POM accrual (van der Pol et al., 2022). Similarly, strategies that enhance MAOM via root exudation (Sokol, Sanderman, et al., 2019) also increase arbuscular mycorrhizal colonization of grass roots, which play an important role in soil aggregate formation and stability (Baumert et al., 2018; Li et al., 2015). Occlusion of POM inside of soil aggregates results in slowed turnover and overall increased POM accumulation (Yamashita et al., 2006).

2.4 | Toward a mechanistic understanding of grazing-induced SOC change

Combining understanding of plant ecophysiology and soil biogeochemistry creates a unified lens through which we can explain and predict SOC outcomes from grazing in a variety of scenarios (Figure 1).

Many grazingland ecosystems coevolved with large herbivores and benefit from some level of defoliation and disturbance (Anderson, 2006; Macfadden, 1997; Strömberg, 2011). Undergrazing can occur when grazers are excluded from these systems, or they are grazed by too few animals or too infrequently. As a result, ecosystems exemplified by Figure 1x arise, in which senesced aboveground biomass accumulates in the absence of defoliation. In temperate and humid grazinglands, lack of defoliation also leads to canopy closure, shading out growth of new plants, and encroachment of woody biomass. Further, a plethora of literature indicates that grazing exclosure and undergrazing can lead to biodiversity loss and homogenization of plant communities across a range of climates, including arid and semi-arid grazinglands (Blakesley & Buckley, 2016; Fuhlendorf & Engle, 2001; Stroh et al., 2017; Waters et al., 2017; Yayneshet et al., 2009). Therefore, undergrazed ecosystems accumulate more biomass in the short term, but can ultimately result in less productivity, root biomass, diversity, and lower quality soil inputs. These ecophysiological conditions limit all three pathways of SOC accumulation and likely favor distribution into POM (Steffens et al., 2011).

In contrast, an optimal grazing pattern can enhance all or some EEs, which facilitate pathways of SOC sequestration (Figure 1y). Improved functioning of these EEs can maximize total SOC sequestration and increase distribution into more persistent MAOM pools (Dong, Martinsen, et al., 2020; Dong, Zhang, et al., 2020), while maintaining high POM stocks through the inputs of structural perennial root residues to depth. As wildfires and other climate-change induced stressors worsen, optimal grazing by livestock has also emerged as a tool to transform at-risk pools of aboveground plant-C into more stable soil pools less susceptible to loss (Kristensen et al., 2021; Ratcliff et al., 2023).

On the extreme end of the grazing pattern function, grazinglands that have been subject to overgrazing have lost significant SOC stocks (Conant & Paustian, 2002; Sanderman et al., 2017). Studies have been unable to directly quantify the proportion of grazingland SOC loss attributable to overgrazing compared to other contributors (e.g., land use change, increasing aridity, etc.), though SOC loss on grazinglands generally correlate with increasing grazing intensity in many cases (Hilker et al., 2014). Subject to chronic defoliation, all five EEs are arrested, resulting in increased bare ground and decreased productivity, belowground input allocation, input quality, and diversity (Figure 1z). Overgrazing not only limits SOC accumulation by all three pathways, but also increases vulnerability of existing SOC stocks to further loss. For example, plant mortality increases with chronic, repeated defoliation, eventually exposing bare soil. Compared to soil covered by plant canopy, bare soil loses SOC via erosion, reduced aggregate stability (Zheng et al., 2021), exposure to increased temperature extremes (Lefèvre et al., 2014), and shifts in microbial communities and activities that increase decomposition of native SOC (Breidenbach et al., 2022). While overgrazing clearly reduces overall SOC stocks, few studies have investigated how overgrazing influences POM:MAOM. We suspect that overgrazing reduces POM relative to MAOM by enhancing decomposition pathways (increased soil temperature, disruption of aggregate protection, microbial shifts), to which MAOM is less susceptible (Dong, Martinsen, et al., 2020; Dong, Zhang, et al., 2020; Oliveira Filho et al., 2019). While the SOC deficit created by historical overgrazing creates current opportunities for SOC sequestration, restoring SOC stocks is not always a simple linear function of reduced grazing intensity or exclusion (Derner et al., 2018; Dlamini et al., 2016). This is because in arid and semi-arid grazinglands, which are more sensitive to disturbance (Dlamini et al., 2016; Liu et al., 2022), even short-term overgrazing can create alternative stable ecosystem "states" where ecophysiological processes are severely altered (Kachergis et al., 2014), limiting opportunities for SOC sequestration (Bestelmeyer et al., 2017; Schuman et al., 2002). Therefore, overgrazing also has cascading impacts on potential SOC accumulation from restoration efforts.

3 | UNPACKING STOCKING RATE AS AN INCOMPLETE METRIC FOR STUDYING GRAZING AND SOC

Grazing intensity is by far the most used grazing management metric in the SOC literature. Grazing intensity theoretically refers to the level of defoliation, or the percentage of aboveground net primary production (ANPP) consumed by grazers over some period of time compared to residual ANPP (Holechek et al., 1998, 2000). The majority of studies aiming to investigate the effects of grazing intensity on SOC define intensity on the basis of stocking rate (total AUs/total grazed area), commonly grouped into "high," "moderate," and "low," where more AUs are presumed to confer greater grazing intensities (Lu et al., 2017). Thus, response variables (e.g., biodiversity, SOC) are presumed to be direct outcomes of the number of AUs. Sometimes, numerical stocking rate is not explicitly reported and only defined qualitatively (e.g., "high", "low"). This problem is particularly prominent among meta-analyses, which attempt to summarize effects of grazing intensity on SOC without a consistent definition or quantitative metric (Byrnes et al., 2018; Zhou et al., 2017). This is illustrated by a recent global meta-analysis on the impact of grazing intensity on SOC in which, due to a lack of reporting and consistency across the literature (Abdalla et al., 2018) were forced to retroactively define "intensity" qualitatively with modeled and estimated NPP and carrying capacity (an ambiguous and controversial estimate of how many animals a given land base can support; Ungar, 2019), and assumptions about the relationship between number of animals (i.e., stocking rate) and the amount of biomass removed. This lack of consistency in defining grazing intensity (generally and with respect to stocking rate) makes interpreting SOC results from these studies in the context of grazing management nearly impossible. Nevertheless, despite the complications in measurement, we support the notion that grazing intensity should be defined with respect to the amount of ANPP utilized by grazing over a given time period (e.g., % ANPP utilization averaged over a year or grazing season), which is a useful indicator that could be used to better predict the impacts of grazing on SOC. Consistently defining grazing intensity in terms of % utilization averaged per year or season would also create alignment with literature showing improved EE outcomes from grazing following residual dry matter indicators, which are inversely related to % utilization (Da Silva et al., 2014; Huntsinger et al., 2007).

An additional, potentially more problematic challenge is that in nearly all cases, stocking rate is the standalone metric relied upon to determine grazing intensity without consideration of other factors—timing, frequency, and duration—known to mediate overall grazing pattern, which drives grazing intensity and subsequent SOC response (Derner & Schuman, 2007). *Timing* of grazing can govern plant vulnerability to defoliation during different seasons and phenological growth stages (Browning et al., 2019). *Frequency* is the length of time that passes, or the amount of rest that pastures receive, between grazing events, which impacts plant nutrient allocation and recovery. *Duration* is the length of time animals spend grazing in a given pasture, which influences both selectivity and utilization. These three factors influence *intensity*, or the amount of total aboveground biomass removed during a grazing window. Together, all four factors culminate in grazing pattern—including amount and arrangement of biomass removal—which are variables of importance

in determining SOC outcomes (Roche et al., 2015). Thus, we posit that grazing pattern (Figure 1a) is a function of each of these levers illustrated (Figure 2).

Without considering duration, frequency, and timing, the majority of studies report negative relationships between grazing intensity and SOC, which can be simplistically interpreted as higher stocking rates = higher grazing intensity = greater defoliation = less SOC. It follows that the most common recommendation to increase grazingland SOC sequestration is to reduce grazing intensity by reducing the total number of AUs (Cui et al., 2015; He et al., 2011; McDonald et al., 2023; Soussana & Lemaire, 2014). While this conclusion may be correct in some cases, we use a simplistic example below to argue how and why this approach could lead to incorrect interpretations and less than optimal SOC outcomes (Table 1).

A *Continuous grazing*: Imagine a simplistic 1000 acre ranch with 100 AUs, resulting in an overall stocking rate of 0.1 AU/acre (or 1 AU/10 acres), characteristic of "low" intensity (Table 1A). Managed continuously and without rotation, animals in this system will preferably and repeatedly defoliate palatable (i.e., high quality) plants and those nearest water sources (Bailey & Provenza, 2008; Hart et al., 1993; O'Connor, 1992). While feeding on the most palatable plants can favor livestock production goals (Augustine et al., 2020), the realized utilization and grazing pattern will be a mosaic of patchy over and undergrazing, with resulting ecophysiology and influence on pathways of SOC similar to those represented in Figure 1x,z. Many studies attribute some degree of SOC loss and grazingland degradation to patchy overgrazing characteristic of continuous grazing systems (Fuls, 1992; Ring et al., 1985; Willms et al., 1988).

B *Low rotational grazing*: The same ranch implements a low-rotational grazing system in which animals are moved across five, 200 acre pastures. Now, 100 AUs occupy only 1/5 of the total ranch land base at any given time. The long-term stocking rate remains the same, but the short-term stocking density of an occupied pasture is 0.5 AU/acre—a temporary 5× increase. After spending 73 days grazing in each pasture, they are rotated to the next, giving each pasture 292 days of rest before being re-grazed (Table 1B). Again, grazing intensity as defined by stocking rate is still "low," though the pattern of grazing and downstream ecophysiological and SOC implications are different. While grazers can still exhibit patchy and selective defoliation in extensive rotational systems, the degree of patchy *overgrazing* is often diminished, but ultimately depends on timing, frequency, and duration of grazing in each pasture (Augustine et al., 2023; Barnes et al., 2008; Teague & Dowhower, 2003).

C *High intensity, short duration grazing*: Finally, the ranch implements a highly intensive rotational grazing system, moving the same 100 AUs across the same 1000 acres which are now subdivided into 100 pastures of 10 acres each. Again, stocking rate remains unchanged, though stocking density is now 10 AUs/acre—a temporary 100× increase from the continuous grazing scenario. In this case, animals only graze in each pasture for ~4 days before being moved to the next, so that each pasture receives 361 days of rest between grazing events (Table 1C). Despite being defined by an equivalent stocking rate and "low" grazing intensity, the short-term stocking density, duration, and frequency are vastly different in this grazing system compared to both others. In this case, the high stocking density will distribute grazing utilization more evenly (Augustine et al., 2023; Bailey et al., 1996; Barnes et al., 2008), which can more readily result in "optimal" grazing pattern for ecophysiological and SOC outcomes if managed adaptively.

That grazing intensity is defined as "low" in all three cases illustrated above despite a 100× increase in stocking density, a range of 0–361 days of rest, and a range of grazing duration from 365 to 4 days, illustrates its shortcomings as a standalone metric. Grazing intensity is simply too coarse to capture realistic utilization and grazing pattern dynamics that arise from changes to grazing management.

4 | ENVIRONMENTAL MEDIATORS OF SOC RESPONSE FROM GRAZING

There are several other factors that influence the direction and magnitude of SOC response and distribution into POM and MAOM from grazing that are not explicitly represented in our conceptual framework (Figure 1). These include climate, ecosystem fire history, native large herbivore grazing history, dominant plant communities (including susceptivity to invasives), and soil texture and mineralogy.

TABLE 1 An example of how overall grazing pattern metrics change under different grazing systems, while overall stocking rate can stay constant.

Grazing system example	Stocking rate (AU/acre)	Pasture quantity and size (# | acres)	Stocking density (AU/acre)	Duration (days/year)	Frequency (days/year)
A: Continuous	0.1	1 | 1000	0.1	365	0
B: Low rotational	0.1	5 | 200	0.5	73	292
C: High intensity, short duration	0.1	100 | 10	10	4	361

Note: Long-term stocking rate refers to the total animal units (AUs) divided by the whole land base acres (or hectares), stocking density is AUs divided by the acres of the temporary pasture, duration is the number of days spent grazing per pasture per year, and frequency refers to how often a pasture is regrazed, which is equal to the number of days of rest per year between grazing events.

Climate is a main controlling factor of SOC storage (Wiesemeier et al., 2019) and of its distribution in POM and MAOM (Hansen et al., 2024) and its thus expected to interact with grazing management in determining echophysiological and SOC outcomes. Warming temperatures and elevated CO_2 conditions associated with climate change may also alter expected SOC responses from improved grazing management globally (Izaurralde et al., 2011; Wang et al., 2012), though literature suggests that grazing currently dominates (Zhou et al., 2019). Landscapes that evolved with periodic disturbances of fire and/or large herbivore grazing tend to have more positive SOC responses to current grazing generally (Davies et al., 2009; Harrison et al., 2003; Knapp et al., 1998; Vermeire et al., 2018). Though much less common, currently grazed ecosystems that did not evolve under these disturbance pressures are typically more sensitive to SOC loss from any overgrazing (Rice & Owensby, 2000). Characteristics of the dominant plant community, especially representation of C3 or C4 photosynthetic pathways, can also drive variable SOC responses to grazing (McSherry & Ritchie, 2013). Lastly, soil texture and mineralogy are significant mediators of SOC accrual and stabilization on all agricultural lands (King et al., 2023; Rasmussen et al., 2018). Finely textured soils with active clay mineral surfaces typically have greater SOC stocks and a greater capacity for stabilizing accumulated SOC as MAOM (Georgiou et al., 2022). In sandy soils, SOC accrual and persistence is more challenging due to lack of soil structure, aggregation, and mineral surfaces (Haddix et al., 2020). The effects of soil texture also apparently interact with precipitation to mediate the direction and magnitude of SOC response to grazing: increases in precipitation can reduce the efficacy of grazing to increase SOC in finely textured soils, but enhance efficacy in sandy soils (McSherry & Ritchie, 2013).

5 | OPTIMIZING GRAZING MANAGEMENT FOR SOC

Our framework (Figure 1) can be used to inform adaptive implementation of the four grazing management levers (Figure 2) which contribute to overall grazing pattern in ways that are appropriate, given context-specific grazing conditions, including climates (e.g., arid, humid), grazingland types (e.g., pasture, rangeland), dominant plant communities (e.g., sagebrush steppe, perennial tallgrass prairie, invasive annuals), and soil characteristics (e.g., texture, mineralogy). We believe this approach will enable overcoming the two main challenges preventing generalizations of mechanistic pathways of SOC change from grazing—(1) lack of scientific representation of metrics contributing to grazing pattern, and (2) variable environmental conditions mediating SOC response in grazing systems.

Inherent variability and increasing climate change driven uncertainty on grazinglands necessitate adaptive approaches to meet SOC goals. Appropriate timing, frequency, duration, and intensity of grazing changes both inter- and intra-seasonally due to variability in temperature and precipitation (droughts and floods) and as the result of shocks such as fire. Prescriptive use of even the recommended

best grazing management levers will always fail in some scenario under these changing conditions. For example, producers may be grazing rotationally and incorporating rest—two commonly recommended practices (Byrnes et al., 2018). However, if used prescriptively, rest and rotations based on arbitrary schedules (e.g., rotate every 30 days) may overgraze plants, regraze plants before they have adequately recovered, or harm sensitive species or plants in vulnerable phenological stages—all leading to negative SOC outcomes (Anderson, 1988; Barnes et al., 2008; Jacobo et al., 2006; McCosker, 1994). Further, not carefully planning and adapting the timing of grazing can cause soil compaction under wet conditions, limiting productivity and affecting SOC outcomes (Drewry et al., 2008; Greenwood & McKenzie, 2001).

Rather, grazing management decisions made adaptively with plant phenology, seasonality, recovery, vulnerability, and growing conditions in mind are required to optimize SOC sequestration and possible stabilization (Derner et al., 2022; Steffens et al., 2013). For example, optimizing timing and duration of grazing can mitigate soil compaction, an issue that can be difficult to manage with larger herd sizes and sporadic precipitation events (Laycock & Conrad, 1967). Social science work highlights that success in adaptive grazing systems is attributable to closed decision-making feedback loops characterized by proactive planning, monitoring and observation of ecophysiological outcomes, adaptation of grazing management levers, and the capacity to be flexible (Darnhofer et al., 2010; Gosnell et al., 2020; Kothmann et al., 2009; Mann & Sherren, 2018; Roche, 2016; Stanley et al., 2024). This suggests that socio-economic aspects are of primary importance in both the adoption and success of adaptive grazing management for optimal SOC outcomes.

Physical science studies examining adaptive grazing, however, have remained elusive for numerous reasons. Most common agronomic approaches to grazing research employ simplistic grazing treatments on small, highly controlled and replicated plots in order to discern cause and effect, despite mounting evidence suggesting that these small-scale experimental conditions consistently produce different results than farm and ranch scale studies (Barnes et al., 2008; Roche et al., 2015). Additionally, adaptive management is very difficult to represent and replicate in experimental settings because researchers are not subject to the same decision-making processes as producers (Briske et al., 2008; Teague et al., 2013). In tandem with the lack of mechanistic approach to understanding grazing-SOC outcomes, this discrepancy between research and reality of adaptive grazing has hindered tangible, science-informed management recommendations. We invite new research following application of our framework (Figure 2), which scales mechanistic insights across large, heterogeneous landscapes that producers manage.

Adaptive multi-paddock (AMP) grazing is an example of a short-duration, high intensity grazing approach (Table 1C) in which proactive planning, adaptive management of grazing levers, observation of EEs, and systems thinking (Mann et al., 2019; Stanley et al., 2024) have been successfully combined by producers with documented SOC sequestration outcomes (Chaplot et al., 2016; Machmuller et al., 2015; Mosier

et al., 2021; Stanley et al., 2018; Teague et al., 2011). Interestingly, measured SOC sequestration rates from AMP have often exceeded expectations based on historical grazing improvements, and with proportionally greater distribution into the more persistent MAOM fraction. We posit that its SOC successes, when and where they exist, are likely attributable to the fact that AMP grazing puts to practice the grazing levers listed above, which, tailored to ecophysiological cues, optimize $EE \rightarrow P$ pathways leading to SOC formation and stabilization. AMP grazers employ more frequent rotations, longer rest periods, and greater stocking densities compared to other rotational grazing strategies (Bork et al., 2021; Roche et al., 2015; Sherren et al., 2022). This creates more opportunities for experimentation and observation of ecophysiological responses following grazing, allows greater spatial and temporal control to adapt grazing timing, duration, frequency, and intensity in response (Mann & Sherren, 2018; McDonald et al., 2019; Sherren et al., 2012; Teague et al., 2013), and ultimately creates functional decision-making feedback loops more capable of consistently achieving "optimal" grazing patterns (Figure 1).

Together, the AMP grazers' ability to observe and adapt management to EEs within shorter timeframes, combined with knowledge how these influence pathways of SOC formation (our framework of $EE \rightarrow Ps$), could make this management approach conducive to sequestering SOC. There is preliminary evidentiary support on the benefits of AMP grazing on increased ground and canopy cover, productivity, and biodiversity (*EE1*, *EE2*, *EE5*; Wang et al., 2021), and input allocation (*EE3*; Teutscherová et al., 2021). We are not aware of any studies directly measuring the impact of AMP grazing on input quality (*EE4*), though the use of higher stock densities and improved landscape utilization could improve the distribution of manure, itself a high quality input. By "grassbanking" rested pastures and grazing only a portion of the total available land at a time, AMP grazing also creates indirect SOC benefits by improving drought resiliency and flexibility, reducing risk of SOC loss (Raynor et al., 2022). In sum, these observed ecophysiological improvements linking greater overall C fixation (*P1*; Apfelbaum et al., 2022), and improved belowground transformation and retention (*P3*, *P2*; White et al., 2023), help mechanistically explain measured SOC accrual and distribution into MAOM from AMP grazing (Mosier et al., 2021).

However, adoption of AMP grazing principles is low among producers (Roche et al., 2015). Our hope is that our framework can help facilitate increased adoption of these principles with measurable SOC benefits. Producers can combine their own experiential and deeply local knowledge with our conceptual framework to more explicitly link "visible" aboveground EEs with pathways of "invisible" SOC accrual, helping to inform use of adaptive grazing levers with effective SOC outcomes.

6 | TOWARD A NEW FRONTIER OF GRAZING-SOC RESEARCH

Although much more research is needed, the mechanistic framework developed here can be used to begin conversations with producers seeking science-informed guidance on managing for SOC sequestration. On the other hand, researchers should explicitly incorporate producers throughout the research process to ensure that future work avoids the pitfalls of our priors and generates more equitable, representative, and applicable data moving forward. Communicating with producers, who hold valuable knowledge, provides critical context that researchers may otherwise not consider, leading to more realistic studies with applied relevance to working grazing landscapes. For example, building relationships with producers can provide opportunities for on-ranch research at "real-life," representative scales. Further, making efforts to conduct producer interviews, collaborate with social scientists, integrate ecological with socio-economic research, and solicit input from producer advisors could go a long way toward improving understanding of producer decision-making contexts and management details that influence measured SOC outcomes. In the context of adaptive grazing management, accurately interpreting SOC outcomes often requires detailed management records and explanations of decision-making processes (e.g., proactive grazing plans and how they changed in response to EEs or other cues), which is only possible through close researcher–producer relationships. These conversations also provide other rich context including financial and technical barriers, logistical challenges, and insights into if and when livestock production goals misalign with SOC outcomes. Taking a "producer forward" approach to grazing-SOC research in this way can help color in our understanding of these complex systems and, in turn, contribute to improved incentive structures with scalable SOC benefits.

There are also methodological considerations that would greatly improve reliability of soil science conducted on grazinglands. These are heterogeneous landscapes with SOC coefficients of variation often double that of croplands (Stanley et al., 2023), and where low and often slow rates of SOC sequestration are expected from grazing management interventions. To be accurate and reliable, SOC sequestration studies require adequate sample density and sampling design, informed by spatial heterogeneity a priori power analyses (Stanley et al., 2023). Analytical advancements including mid infrared spectroscopy may soon reduce the substantial costs and improve throughput of SOC measurements (Ramírez et al., 2022), though improvements of current methods are required nonetheless.

Improved decision support tools are also needed (Hudson et al., 2021) to facilitate producers' ability to operationalize the conceptual $EE \rightarrow P$ mechanisms developed here Tools able to assess patterns of EE responses from grazing management decisions over larger spatial and temporal scales could provide a more robust picture of ecosystem-level responses to grazing alongside producer observations on-the-ground. This is especially important given that SOC change is not reliably visible, but the supporting EE responses are—lending themselves to more accurate representation by technologies like remote sensing. Providing these data-driven tools to producers in ways that are accessible and visual (e.g., rangelands. app), can thus also aid in managing for SOC outcomes.

We invite a new frontier of grazing-SOC research in line with these recommendations and informed by our conceptual mechanisms to

yield more reliable primary data for a chain of downstream uses. These data would create the foundation for reliable large-scale syntheses on the impacts of grazing management on SOC and its controlling factors. These improved data would then support more accurate model development to better represent, generalize, and predict SOC response from grazing at scale, which is necessary to predict the SOC sequestration potential of these systems as a natural climate solution and to inform appropriate incentive structures and climate policies.

7 | CONCLUSION

Issues related to poorly defined grazing metrics, uncoupled understanding of SOC-ecophysiology, soil sampling design and lack of producer inclusion have plagued grazing-SOC research for decades. The resulting variability of measured SOC responses and inapplicability to realistic grazingland conditions have generated confusion rather than consensus. In an effort to unify understanding, drive improved research to generate more reliable data, and make consensus possible, we present a conceptual, mechanistic framework of grazing and pathways of SOC response. Our framework explicitly incorporates both plant and soil processes, and a more robust ecosystem function of grazing pattern. We propose mechanisms by which grazing impacts EEs and pathways of SOC formation and stabilization which are generalizable across the range of climates and ecotypes characteristic of grazinglands globally. We posit that management strategies which adaptively leverage grazing frequency, duration, timing, and intensity will more consistently and reliably create "optimal" grazing patterns necessary for optimizing pathways of SOC sequestration. This work has important utility for those engaged in SOC on grazinglands at all levels, including researchers, producers, agencies, and policy makers.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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REFERENCES

Abdalla, M., Hastings, A., Chadwick, D. R., Jones, D. L., Evans, C. D., Jones, M. B., Rees, R. M., & Smith, P. (2018). Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. *Agriculture, Ecosystems & Environment*, *253*, 62–81. https://doi.org/10.1016/j.agee.2017.10.023

Allred, B. W., Fuhlendorf, S. D., & Hamilton, R. G. (2011). The role of herbivores in Great Plains conservation: Comparative ecology of bison and cattle. *Ecosphere (Washington, D.C)*, *2*(3), 26. https://doi.org/10.1890/ES10-00152.1

Anderson, D. M. (1988). Seasonal stocking of tobosa managed under continuous and rotation grazing. *Journal of Range Management*, *41*(1), 78. https://doi.org/10.2307/3898796

Anderson, R. (2006). Evolution and origin of the Central Grassland of North America: Climate, fire, and mammalian grazers. *The Journal of the Torrey Botanical Society*, *133*(4), 626–647. https://doi.org/10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2

Angst, G., Mueller, K. E., Kögel-Knabner, I., Freeman, K. H., & Mueller, C. W. (2017). Aggregation controls the stability of lignin and lipids in clay-sized particulate and mineral associated organic matter. *Biogeochemistry*, *132*(3), 307–324. https://doi.org/10.1007/s10533-017-0304-2

Apfelbaum, S. I., Thompson, R., Wang, F., Mosier, S., Teague, R., & Byck, P. (2022). Vegetation, water infiltration, and soil carbon response to adaptive multi-paddock and conventional grazing in southeastern USA ranches. *Journal of Environmental Management*, *308*, 114576. https://doi.org/10.1016/j.jenvman.2022.114576

Augustine, D. J., Derner, J. D., Fernández-Giménez, M. E., Porensky, L. M., Wilmer, H., & Briske, D. D. (2020). Adaptive, multipaddock rotational grazing management: A ranch-scale assessment of effects on vegetation and livestock performance in semiarid rangeland. *Rangeland Ecology & Management*, *73*, 796–810. https://doi.org/10.1016/j.rama.2020.07.005

Augustine, D. J., Kearney, S. P., Raynor, E. J., Porensky, L. M., & Derner, J. D. (2023). Adaptive, multi-paddock, rotational grazing management alters foraging behavior and spatial grazing distribution of free-ranging cattle. *Agriculture, Ecosystems & Environment*, *352*, 108521. https://doi.org/10.1016/j.agee.2023.108521

Bai, Y., & Cotrufo, M. F. (2022). Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science*, *377*(6606), 603–608. https://doi.org/10.1126/science.abo2380

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386. https://doi.org/10.2307/4002919

Bailey, D. W., & Provenza, F. D. (2008). Mechanisms determining large-herbivore distribution. In H. H. T. Prins & F. van Langevelde (Eds.), *Resource ecology* (pp. 7–28). Springer. https://doi.org/10.1007/978-1-4020-6850-8_2

Balogianni, V. G., Wilson, S. D., Vaness, B. M., MacDougall, A. S., & Pinno, B. D. (2014). Different root and shoot responses to mowing and fertility in native and invaded grassland. *Rangeland Ecology & Management*, 67(1), 39–45. https://doi.org/10.2111/REM-D-13-00080.1

Bardgett, R. D., Wardle, D. A., & Yeates, G. W. (1998). Linking above-ground and below-ground interactions: How plant responses to fo-liar herbivory influence soil organisms. *Soil Biology and Biochemistry*, 30(14), 1867–1878. https://doi.org/10.1016/S0038-0717(98)00069-8

Barnes, M. K., Norton, B. E., Maeno, M., & Malechek, J. C. (2008). Paddock size and stocking density affect spatial heterogeneity of grazing. *Rangeland Ecology & Management*, 61(4), 380–388. https://doi.org/10.2111/06-155.1

Barnosky, A. D. (2008). Colloquium paper: Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 105(Suppl 1), 11543–11548. https://doi.org/10.1073/pnas.0801918105

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*, 115(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Baumert, V. L., Vasilyeva, N. A., Vladimirov, A. A., Meier, I. C., Kögel-Knabner, I., & Mueller, C. W. (2018). Root exudates induce soil macroaggregation facilitated by fungi in subsoil. *Frontiers in Environmental Science*, 6, 140. https://doi.org/10.3389/fenvs.2018.00140

Bestelmeyer, B. T., Ash, A., Brown, J. R., Densambuu, B., Fernández-Giménez, M., Johanson, J., Levi, M., Lopez, D., Peinetti, R., Rumpff, L., & Shaver, P. (2017). State and transition models: Theory, appli-cations, and challenges. In D. D. Briske (Ed.), *Rangeland systems* (pp. 303–345). Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_9

Blakesley, D., & Buckley, P. (2016). *Grassland restoration and management* (Illustrated ed.). Pelagic Publishing Ltd.

Bork, E. W., Döbert, T. F., Grenke, J. S. J., Carlyle, C. N., Cahill, J. F., & Boyce, M. S. (2021). Comparative pasture management on cana-dian cattle ranches with and without adaptive multipaddock graz-ing. *Rangeland Ecology & Management*, 78, 5–14. https://doi.org/10.1016/j.rama.2021.04.010

Bråthen, K. A., Pugnaire, F. I., & Bardgett, R. D. (2021). The paradox of forbs in grasslands and the legacy of the mammoth steppe. *Frontiers in Ecology and the Environment*, 19, 584–592. https://doi.org/10.1002/fee.2405

Breidenbach, A., Schleuss, P.-M., Liu, S., Schneider, D., Dippold, M. A., de la Haye, T., Miehe, G., Heitkamp, F., Seeber, E., Mason-Jones, K., Xu, X., Huanming, Y., Xu, J., Dorji, T., Gube, M., Norf, H., Meier, J., Guggenberger, G., Kuzyakov, Y., & Spielvogel, S. (2022). Microbial functional changes mark irreversible course of Tibetan grassland degradation. *Nature Communications*, 13(1), 2681. https://doi.org/10.1038/s41467-022-30047-7

Bremer, D. J., Auen, L. M., Ham, J. M., & Owensby, C. E. (2001). Evapotranspiration in a prairie ecosystem. *Agronomy Journal*, 93(2), 338–348. https://doi.org/10.2134/agronj2001.932338x

Brewer, K. M., Muñoz-Araya, M., Martinez, I., Marshall, K. N., & Gaudin, A. C. (2023). Long-term integrated crop-livestock grazing stimu-lates soil ecosystem carbon flux, increasing subsoil carbon storage in California perennial agroecosystems. *Geoderma*, 438, 116598. https://doi.org/10.1016/j.geoderma.2023.116598

Briske, D., & Richards, J. (1994). Physiological responses of individual plants to grazing: Current status and ecological significance. In M. Vavra, W. A. Laycock, & R. D. Pieper (Eds.), *Ecological implications of livestock herbivory in the west* (pp. 147–176). Society for Range Management.

Briske, D. D., Derner, J. D., Brown, J. R., Fuhlendorf, S. D., Teague, W. R., Havstad, K. M., Gillen, R. L., Ash, A. J., & Willms, W. D. (2008). Rotational grazing on rangelands: Reconciliation of perception and experimental evidence. *Rangeland Ecology & Management*, 61(1), 3–17.

Briske, D. D., Fuhlendorf, S. D., & Smeins, F. E. (2005). State-and-transition models, thresholds, and rangeland health: A synthesis of ecological con-cepts and perspectives. *Rangeland Ecology & Management*, 58(1), 1–10. https://doi.org/10.2111/1551-5028(2005)58<1:SMTARH>2.0.CO;2

Briske, D. D., & Richards, J. H. (1995). Plant responses to defoliation: A physiological, morphological and demographic evaluation. In D. J. Bedunah & R. E. Sosebee (Eds.), *Wildland plants: Physiological ecol-ogy and developmental morphology* (pp. 635–710). Society for Range Management.

Browning, D. M., Snyder, K. A., & Herrick, J. E. (2019). Plant phenology: Taking the pulse of rangelands. *Rangelands*, 41(3), 129–134. https://doi.org/10.1016/j.rala.2019.02.001

Byrnes, R. C., Eastburn, D. J., Tate, K. W., & Roche, L. M. (2018). A global meta-analysis of grazing impacts on soil health indicators. *Journal of Environmental Quality*, 47(4), 758–765. https://doi.org/10.2134/jeq2017.08.0313

Chaplot, V., Dlamini, P., & Chivenge, P. (2016). Potential of grassland re-habilitation through high density-short duration grazing to seques-ter atmospheric carbon. *Geoderma*, 271, 10–17. https://doi.org/10.1016/j.geoderma.2016.02.010

Chen, W., Huang, D., Liu, N., Zhang, Y., Badgery, W. B., Wang, X., & Shen, Y. (2015). Improved grazing management may increase soil carbon sequestration in temperate steppe. *Scientific Reports*, 5, 10892. https://doi.org/10.1038/srep10892

Cingolani, A. M., Noy-Meir, I., & Díaz, S. (2005). Grazing effects on range-land diversity: A synthesis of contemporary models. *Ecological Applications*, 15(2), 757–773. https://doi.org/10.1890/03-5272

Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., & Steinauer, E. M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280(5364), 745–747.

Conant, R. T., Cerri, C. E. P., Osborne, B. B., & Paustian, K. (2017). Grassland management impacts on soil carbon stocks: A new syn-thesis. *Ecological Applications*, 27(2), 662–668. https://doi.org/10.1002/eap.1473

Conant, R. T., & Paustian, K. (2002). Potential soil carbon sequestration in overgrazed grassland ecosystems. *Global Biogeochemical Cycles*, 16(4), 90-1–90-9. https://doi.org/10.1029/2001GB001661

Cotrufo, M. F., & Lavallee, J. M. (2022). Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration. In D. L. Sparks (Ed.), *Advances in agronomy* (Vol. 172, pp. 1–66). Elsevier. https://doi.org/10.1016/bs.agron.2021.11.002

Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J., & Lugato, E. (2019). Soil carbon storage informed by particulate and mineral-associated organic matter. *Nature Geoscience*, 12, 989–994. https://doi.org/10.1038/s41561-019-0484-6

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, 19(4), 988–995. https://doi.org/10.1111/gcb.12113

Cui, J., Askari, M. S., & Holden, N. M. (2015). Grassland soil carbon and nitrogen stocks under temperate livestock grazing. *Soil Research*, 53(5), 485. https://doi.org/10.1071/SR14252

Da Silva, F. D., Amado, T. J. C., Ferreira, A. O., Assmann, J. M., Anghinoni, I., & Carvalho, P. C. D. F. (2014). Soil carbon indices as affected by 10 years of integrated crop–livestock production with different pasture grazing intensities in Southern Brazil. *Agriculture, Ecosystems & Environment*, 190, 60–69. https://doi.org/10.1016/j.agee.2013.12.005

Darnhofer, I., Bellon, S., Dedieu, B., & Milestad, R. (2010). Adaptiveness to enhance the sustainability of farming systems. A review. *Agronomy for Sustainable Development*, 30(3), 545–555. https://doi.org/10.1051/agro/2009053

Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165–173. https://doi.org/10.1038/nature04514

Davies, K. W., Svejcar, T. J., & Bates, J. D. (2009). Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications*, 19(6), 1536–1545. https://doi.org/10.1890/09-0111.1

Dawson, L. A., Grayston, S. J., & Paterson, E. (2000). Effects of grazing on the roots and rhizosphere of grasses. In G. Lemaire, J. Hodgson, A. de Moraes, C. Nabinger, & P. C. D. F. Carvalho (Eds.), *Grassland ecophysiology and grazing ecology* (pp. 61–84). CABI Publishing. https://doi.org/10.1079/9780851994529.0061

Deng, L., Shangguan, Z., Bell, S. M., Soromotin, A. V., Peng, C., An, S., Wu, X., Xu, X., Wang, K., Li, J., Tang, Z., Yan, W., Zhang, F., Li, J., Wu, J., & Kuzyakov, Y. (2023). Carbon in Chinese grasslands: Meta-analysis and theory of grazing effects. *Carbon Research*, 2(1), 19. https://doi.org/10.1007/s44246-023-00051-7

Derner, J. D., Augustine, D. J., & Frank, D. A. (2018). Does grazing matter for soil organic carbon sequestration in the Western North American Great Plains? *Ecosystems*, 22, 1088–1094. https://doi.org/10.1007/s10021-018-0324-3

Derner, J. D., Budd, B., Grissom, G., Kachergis, E. J., Augustine, D. J., Wilmer, H., Scasta, J. D., & Ritten, J. P. (2022). Adaptive grazing management in semiarid rangelands: An outcome-driven focus. *Rangelands*, 44(1), 111–118. https://doi.org/10.1016/j.rala.2021.02.004

Derner, J. D., & Schuman, G. E. (2007). Carbon sequestration and rangelands: A synthesis of land management and precipitation effects. *Journal of Soil and Water Conservation*, 62(2), 77–85.

Dijkstra, F. A., Carrillo, Y., Pendall, E., & Morgan, J. A. (2013). Rhizosphere priming: A nutrient perspective. *Frontiers in Microbiology*, 4, 216. https://doi.org/10.3389/fmicb.2013.00216

Dlamini, P., Chivenge, P., & Chaplot, V. (2016). Overgrazing decreases soil organic carbon stocks the most under dry climates and low soil pH: A meta-analysis shows. *Agriculture, Ecosystems & Environment*, 221, 258–269. https://doi.org/10.1016/j.agee.2016.01.026

Dondini, M., Martin, M., De Camillis, C., Uwizeye, A., Soussana, J. F., Robinson, T., & Steinfeld, H. (2023). *Global assessment of soil carbon in grasslands. From current stock estimates to sequestration potential* (FAO Animal Production and Health Paper 187). FAO.

Dong, L., Martinsen, V., Wu, Y., Zheng, Y., Liang, C., Liu, Z., & Mulder, J. (2020). Effect of grazing exclusion and rotational grazing on labile soil organic carbon in north China. *European Journal of Soil Science*, 72, 372–384. https://doi.org/10.1111/ejss.12952

Dong, S., Zhang, J., Li, Y., Liu, S., Dong, Q., Zhou, H., Yeomans, J., Li, Y., Li, S., & Gao, X. (2020). Effect of grassland degradation on aggregate-associated soil organic carbon of alpine grassland ecosystems in the Qinghai-Tibetan Plateau. *European Journal of Soil Science*, 71(1), 69–79. https://doi.org/10.1111/ejss.12835

Drewry, J. J., Cameron, K. C., & Buchan, G. D. (2008). Pasture yield and soil physical property responses to soil compaction from treading and grazing—A review. *Soil Research*, 46(3), 237. https://doi.org/10.1071/SR07125

Fornara, D. A., & Tilman, D. (2008). Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology*, 96(2), 314–322. https://doi.org/10.1111/j.1365-2745.2007.01345.x

Fornara, D. A., & Tilman, D. (2009). Ecological mechanisms associated with the positive diversity-productivity relationship in an N-limited grassland. *Ecology*, 90(2), 408–418. https://doi.org/10.1890/08-0325.1

Franzluebbers, A. J., Paine, L. K., Winsten, J. R., Krome, M., Sanderson, M. A., Ogles, K., & Thompson, D. (2012). Well-managed grazing systems: A forgotten hero of conservation. *Journal of Soil and Water Conservation*, 67(4), 100A–104A. https://doi.org/10.2489/jswc.67.4.100A

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *Bioscience*, 51(8), 625. https://doi.org/10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2

Fuls, E. R. (1992). Ecosystem modification created by patch-overgrazing in semi-arid grassland. *Journal of Arid Environments*, 23(1), 59–69. https://doi.org/10.1016/S0140-1963(18)30541-X

Fulton-Smith, S., & Cotrufo, M. F. (2019). Pathways of soil organic matter formation from above and belowground inputs in a *Sorghum bicolor* bioenergy crop. *GCB Bioenergy*, 11(8), 971–987. https://doi.org/10.1111/gcbb.12598

Furey, G. N., & Tilman, D. (2021). Plant biodiversity and the regeneration of soil fertility. *Proceedings of the National Academy of Sciences of the United States of America*, 118(49), 1118. https://doi.org/10.1073/pnas.2111321118

Gastal, F., & Lemaire, G. (2015). Defoliation, shoot plasticity, sward structure and herbage utilization in pasture: Review of the underlying ecophysiological processes. *Agriculture*, 5(4), 1146–1171. https://doi.org/10.3390/agriculture5041146

Gavrichkova, O., Moscatelli, M. C., Grego, S., & Valentini, R. (2008). Soil carbon mineralization in a Mediterranean pasture: Effect of grazing and mowing management practices. *Agrochimica*, 52(5), 285–296.

Georgiou, K., Jackson, R. B., Vindušková, O., Abramoff, R. Z., Ahlström, A., Feng, W., Harden, J. W., Pellegrini, A. F. A., Polley, H. W., Soong, J. L., Riley, W. J., & Torn, M. S. (2022). Global stocks and capacity of mineral-associated soil organic carbon. *Nature Communications*, 13(1), 3797. https://doi.org/10.1038/s41467-022-31540-9

Gosnell, H., Grimm, K., & Goldstein, B. E. (2020). A half century of holistic management: What does the evidence reveal? *Agriculture and Human Values*, 37, 849–867. https://doi.org/10.1007/s10460-020-10016-w

Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., & Bardgett, R. D. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, 19(9), 1140–1149. https://doi.org/10.1111/ele.12652

Greenwood, K. L., & McKenzie, B. M. (2001). Grazing effects on soil physical properties and the consequences for pastures: A review. *Australian Journal of Experimental Agriculture*, 41(8), 1231. https://doi.org/10.1071/EA00102

Haddix, M. L., Gregorich, E. G., Helgason, B. L., Janzen, H., Ellert, B. H., & Francesca Cotrufo, M. (2020). Climate, carbon content, and soil texture control the independent formation and persistence of particulate and mineral-associated organic matter in soil. *Geoderma*, 363, 114160. https://doi.org/10.1016/j.geoderma.2019.114160

Hamilton, E. W., Frank, D. A., Hinchey, P. M., & Murray, T. R. (2008). Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biology and Biochemistry*, 40(11), 2865–2873. https://doi.org/10.1016/j.soilbio.2008.08.007

Hansen, P., King, A., Lavallee, J., Schipanski, M., & Cotrufo, M. F. (2024). Distinct, direct and climate-mediated environmental controls on global particulate and mineral-associated organic carbon storage. *Global Change Biology*, 30(1), e17080.

Harrison, S., Inouye, B. D., & Safford, H. D. (2003). Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology*, 17(3), 837–845. https://doi.org/10.1046/j.1523-1739.2003.01633.x

Hart, R. H., Bissio, J., Samuel, M. J., & Waggoner, J. W. (1993). Grazing systems, pasture size, and cattle grazing behavior, distribution and gains. *Journal of Range Management*, 46(1), 81. https://doi.org/10.2307/4002452

He, N. P., Zhang, Y. H., Yu, Q., Chen, Q. S., Pan, Q. M., Zhang, G. M., & Han, X. G. (2011). Grazing intensity impacts soil carbon and nitrogen storage of continental steppe. *Ecosphere*, 2(1), art8. https://doi.org/10.1890/ES10-00017.1

Hilker, T., Natsagdorj, E., Waring, R. H., Lyapustin, A., & Wang, Y. (2014). Satellite observed widespread decline in Mongolian grasslands largely due to overgrazing. *Global Change Biology*, 20(2), 418–428. https://doi.org/10.1111/gcb.12365

Holecheck, J. L., Galt, D., & Society for Range Management. (2000). Grazing intensity guidelines. *Rangelands*, 22(3), 11–14. https://doi.org/10.2458/azu_rangelands_v22i3_holecheck

Holechek, J. L., Gomes, H. D., Molinar, F., & Galt, D. (1998). Grazing intensity: Critique and approach. *Rangelands Archives*, 20(5), 15–18.

Holland, E. A., & Detling, J. K. (1990). Plant response to herbivory and belowground nitrogen cycling. *Ecology*, 71(3), 1040–1049. https://doi.org/10.2307/1937372

Hudson, T. D., Reeves, M. C., Hall, S. A., Yorgey, G. G., & Neibergs, J. S. (2021). Big landscapes meet big data: Informing grazing management in a variable and changing world. *Rangelands*, 43(1), 17–28. https://doi.org/10.1016/j.rala.2020.10.006

Huntsinger, L., Bartolome, J. W., & D'antonio, C. M. (2007). Grazing management on California's mediterranean grasslands. In M. R. Stromberg, J. D. Corbin, & C. M. D'Antonio (Eds.), *California grasslandsecology and management* (pp. 232–253). University of California Press. https://doi.org/10.1525/california/9780520252202.003.0020

Huys, R., Poirier, V., Bourget, M. Y., Roumet, C., Hättenschwiler, S., Fromin, N., Munson, A. D., & Freschet, G. T. (2022). Plant litter chemistry controls coarse-textured soil carbon dynamics. *Journal of Ecology*, 110, 2911–2928. https://doi.org/10.1111/1365-2745.13997

Izaurralde, R. C., Thomson, A. M., Morgan, J. A., Fay, P. A., Polley, H. W., & Hatfield, J. L. (2011). Climate impacts on agriculture: Implications for forage and rangeland production. *Agronomy Journal*, 103(2), 371–381. https://doi.org/10.2134/agronj2010.0304

Jacobo, E. J., Rodríguez, A. M., Bartoloni, N., & Deregibus, V. A. (2006). Rotational grazing effects on rangeland vegetation at a farm scale. *Rangeland Ecology & Management*, 59(3), 249–257. https://doi.org/10.2111/05-129R1.1

Jilling, A., Keiluweit, M., Contosta, A. R., Frey, S., Schimel, J., Schnecker, J., Smith, R. G., Tiemann, L., & Grandy, A. S. (2018). Minerals in the rhizosphere: Overlooked mediators of soil nitrogen availability to plants and microbes. *Biogeochemistry*, 139(2), 103–122. https://doi.org/10.1007/s10533-018-0459-5

Kachergis, E., Rocca, M. E., & Fernández-Giménez, M. E. (2014). Long-term vegetation change provides evidence for alternate states in Silver sagebrush. *Rangeland Ecology & Management*, 67(2), 183–194. https://doi.org/10.2111/REM-D-12-00066.1

Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications*, 7, 13630. https://doi.org/10.1038/ncomms13630

Kallenbach, C. M., Grandy, A. S., Frey, S. D., & Diefendorf, A. F. (2015). Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biology and Biochemistry*, 91, 279–290. https://doi.org/10.1016/j.soilbio.2015.09.005

King, A. E., Amsili, J. P., Córdova, S. C., Culman, S., Fonte, S. J., Kotcon, J., Liebig, M., Masters, M. D., McVay, K., Olk, D. C., Schipanski, M., Schneider, S. K., Stewart, C. E., & Cotrufo, M. F. (2023). A soil matrix capacity index to predict mineral-associated but not particulate organic carbon across a range of climate and soil pH. *Biogeochemistry*, 165, 1–14. https://doi.org/10.1007/s10533-023-01066-3

Kleber, M. (2010). What is recalcitrant soil organic matter? *Environmental Chemistry*, 7(4), 320. https://doi.org/10.1071/EN10006

Kleber, M., Bourg, I. C., Coward, E. K., Hansel, C. M., Myneni, S. C. B., & Nunan, N. (2021). Dynamic interactions at the mineral–organic matter interface. *Nature Reviews Earth and Environment*, 2, 402–421. https://doi.org/10.1038/s43017-021-00162-y

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., & Nico, P. S. (2015). Mineral–organic associations: Formation, properties, and relevance in soil environments. In D. L. Sparks (Ed.), *Advances in agronomy* (Vol. 130, pp. 1–140). Elsevier. https://doi.org/10.1016/bs.agron.2014.10.005

Kleber, M., & Johnson, M. G. (2010). Advances in understanding the molecular structure of soil organic matter. In D. L. Sparks (Ed.), *Advances in agronomy* (Vol. 106, pp. 77–142). Elsevier. https://doi.org/10.1016/S0065-2113(10)06003-7

Klumpp, K., Fontaine, S., Attard, E., Le Roux, X., Gleixner, G., & Soussana, J.-F. (2009). Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. *Journal of Ecology*, 97(5), 876–885. https://doi.org/10.1111/j.1365-2745.2009.01549.x

Knapp, A. K., Conard, S. L., & Blair, J. M. (1998). Determinants of soil CO_2 flux from a sub-humid grassland: Effect of fire and fire history. *Ecological Applications*, 8(3), 760–770.

Kothmann, M., Teague, R., Díaz-Solís, H., & Grant, W. (2009). Viewpoint: New approaches and protocols for grazing management research. *Rangelands*, 31(5), 31–36. https://doi.org/10.2111/1551-501X-31.5.31

Kristensen, J. A., Svenning, J.-C., Georgiou, K., & Malhi, Y. (2021). Can large herbivores enhance ecosystem carbon persistence? *Trends in Ecology & Evolution*, 37, 117–128. https://doi.org/10.1016/j.tree.2021.09.006

Kuzyakov, Y. (2002). Review: Factors affecting rhizosphere priming effects. *Journal of Plant Nutrition and Soil Science*, 165(4), 382–396. https://doi.org/10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-%23

Laca, E. A. (2009). New approaches and tools for grazing management. *Rangeland Ecology & Management*, 62(5), 407–417. https://doi.org/10.2111/08-104.1

Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., Mellado-Vázquez, P. G., Malik, A. A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B. C., Trumbore, S. E., & Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, 6, 6707. https://doi.org/10.1038/ncomms7707

Lavallee, J. M., Soong, J. L., & Cotrufo, M. F. (2020). Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology*, 26(1), 261–273. https://doi.org/10.1111/gcb.14859

Laycock, W. A., & Conrad, P. W. (1967). Effect of grazing on soil compaction as measured by bulk density on a high elevation cattle range. *Rangeland Ecology & Management/Journal of Range Management Archives*, 20(3), 136–140.

Lefèvre, R., Barré, P., Moyano, F. E., Christensen, B. T., Bardoux, G., Eglin, T., Girardin, C., Houot, S., Kätterer, T., van Oort, F., & Chenu, C. (2014). Higher temperature sensitivity for stable than for labile soil organic carbon – evidence from incubations of long-term bare fallow soils. *Global Change Biology*, 20(2), 633–640. https://doi.org/10.1111/gcb.12402

Lehmann, J., Hansel, C. M., Kaiser, C., Kleber, M., Maher, K., Manzoni, S., Nunan, N., Reichstein, M., Schimel, J. P., Torn, M. S., Wieder, W. R., & Kögel-Knabner, I. (2020). Persistence of soil organic carbon caused by functional complexity. *Nature Geoscience*, 13, 529–534. https://doi.org/10.1038/s41561-020-0612-3

Leichty, S., Cotrufo, M. F., & Stewart, C. E. (2020). Less efficient residue-derived soil organic carbon formation under no-till irrigated corn. *Soil Science Society of America Journal*, 84(6), 1928–1942. https://doi.org/10.1002/saj2.20136

Li, X., Zhang, J., Gai, J., Cai, X., Christie, P., & Li, X. (2015). Contribution of arbuscular mycorrhizal fungi of sedges to soil aggregation along an altitudinal alpine grassland gradient on the Tibetan plateau. *Environmental Microbiology*, *17*(8), 2841–2857. https://doi.org/10.1111/1462-2920.12792

Li, Y., Gong, J., Zhang, Z., Shi, J., Zhang, W., & Song, L. (2022). Grazing directly or indirectly affect shoot and root litter decomposition in different decomposition stage by changing soil properties. *Catena*, *209*, 105803. https://doi.org/10.1016/j.catena.2021.105803

Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology*, *25*(11), 3578–3590. https://doi.org/10.1111/gcb.14781

Liang, M., Smith, N. G., Chen, J., Wu, Y., Guo, Z., Gornish, E. S., & Liang, C. (2021). Shifts in plant composition mediate grazing effects on carbon cycling in grasslands. *Journal of Applied Ecology*, *58*(3), 518–527. https://doi.org/10.1111/1365-2664.13824

Liu, J., Isbell, F., Ma, Q., Chen, Y., Xing, F., Sun, W., Wang, L., Li, J., Wang, Y., Hou, F., Xin, X., Nan, Z., Eisenhauer, N., & Wang, D. (2022). Overgrazing, not haying, decreases grassland topsoil organic carbon by decreasing plant species richness along an aridity gradient in Northern China. *Agriculture, Ecosystems & Environment*, *332*, 107935. https://doi.org/10.1016/j.agee.2022.107935

Lu, X., Kelsey, K. C., Yan, Y., Sun, J., Wang, X., Cheng, G., & Neff, J. C. (2017). Effects of grazing on ecosystem structure and function of alpine grasslands in Qinghai-Tibetan Plateau: A synthesis. *Ecosphere*, *8*(1), e01656. https://doi.org/10.1002/ecs2.1656

Lugato, E., Lavallee, J. M., Haddix, M. L., Panagos, P., & Cotrufo, M. F. (2021). Different climate sensitivity of particulate and mineral-associated soil organic matter. *Nature Geoscience*, *14*(5), 295–300. https://doi.org/10.1038/s41561-021-00744-x

Ma, Z., Bork, E. W., Li, J., Chen, G., & Chang, S. X. (2021). Photosynthetic carbon allocation to live roots increases the year following high intensity defoliation across two ecosites in a temperate mixed grassland. *Agriculture, Ecosystems & Environment*, *316*, 107450. https://doi.org/10.1016/j.agee.2021.107450

Macfadden, B. J. (1997). Origin and evolution of the grazing guild in new world terrestrial mammals. *Trends in Ecology & Evolution*, *12*(5), 182–187. https://doi.org/10.1016/s0169-5347(97)01049-5

Machmuller, M. B., Kramer, M. G., Cyle, T. K., Hill, N., Hancock, D., & Thompson, A. (2015). Emerging land use practices rapidly increase soil organic matter. *Nature Communications*, *6*, 6995. https://doi.org/10.1038/ncomms7995

Malhi, Y., Doughty, C. E., Galetti, M., Smith, F. A., Svenning, J.-C., & Terborgh, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(4), 838–846. https://doi.org/10.1073/pnas.1502540113

Mann, C., Parkins, J. R., Isaac, M. E., & Sherren, K. (2019). Do practitioners of holistic management exhibit systems thinking?. *Ecology and Society*, *24*(3).

Mann, C., & Sherren, K. (2018). Holistic management and adaptive grazing: A trainers' view. *Sustainability*, *10*(6), 1848. https://doi.org/10.3390/su10061848

Manzano, P., Pardo, G., Itani, M. A., & del Prado, A. (2023). Underrated past herbivore densities could lead to misoriented sustainability policies. *npj Biodiversity*, *2*(1), 2. https://doi.org/10.1038/s44185-022-00005-z

Mayer, A., & Silver, W. L. (2022). The climate change mitigation potential of annual grasslands under future climates. *Ecological Applications*, *32*, e2705. https://doi.org/10.1002/eap.2705

McCosker, T. (1994). The dichotomy between research results and practical experience with time control grazing. *Australian Rural Science Annual*, *1994*, 26–31.

McDonald, S. E., Badgery, W., Clarendon, S., Orgill, S., Sinclair, K., Meyer, R., Butchart, D. B., Eckard, R., Rowlings, D., Grace, P., Doran-Browne, N., Harden, S., Macdonald, A., Wellington, M., Pachas, A. N. A., Eisner, R., Amidy, M., & Harrison, M. T. (2023). Grazing management for soil carbon in Australia: A review. *Journal of Environmental Management*, *347*, 119146. https://doi.org/10.1016/j.jenvman.2023.119146

McDonald, S. E., Lawrence, R., Kendall, L., & Rader, R. (2019). Ecological, biophysical and production effects of incorporating rest into grazing regimes: A global meta-analysis. *Journal of Applied Ecology*, *56*(12), 2723–2731. https://doi.org/10.1111/1365-2664.13496

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos*, *40*(3), 329. https://doi.org/10.2307/3544305

McNaughton, S. J. (1984). Grazing lawns: Animals in herds, plant form, and coevolution. *The American Naturalist*, *124*(6), 863–886. https://doi.org/10.1086/284321

McNaughton, S. J., Banyikwa, F. F., & McNaughton, M. M. (1997). Promotion of the cycling of diet-enhancing nutrients by african grazers. *Science*, *278*(5344), 1798–1800. https://doi.org/10.1126/science.278.5344.1798

McSherry, M. E., & Ritchie, M. E. (2013). Effects of grazing on grassland soil carbon: A global review. *Global Change Biology*, *19*(5), 1347–1357. https://doi.org/10.1111/gcb.12144

Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, *63*(4), 327–366. https://doi.org/10.2307/2937150

Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, *132*(1), 87–106. https://doi.org/10.1086/284839

Mitchell, E., Scheer, C., Rowlings, D., Conant, R. T., Cotrufo, M. F., & Grace, P. (2018). Amount and incorporation of plant residue inputs modify residue stabilisation dynamics in soil organic matter fractions. *Agriculture, Ecosystems & Environment*, *256*, 82–91. https://doi.org/10.1016/j.agee.2017.12.006

Molnár, Z., Kelemen, A., Kun, R., Máté, J., Sáfián, L., Provenza, F., Díaz, S., Barani, H., Biró, M., Máté, A., & Vadász, C. (2020). Knowledge co-production with traditional herders on cattle grazing behaviour for better management of species-rich grasslands. *Journal of Applied Ecology*, *57*(9), 1677–1687. https://doi.org/10.1111/1365-2664.13664

Mosier, S., Apfelbaum, S., Byck, P., Calderon, F., Teague, R., Thompson, R., & Cotrufo, M. F. (2021). Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern U.S. grazing lands. *Journal of Environmental Management*, *288*, 112409. https://doi.org/10.1016/j.jenvman.2021.112409

Nowak, R. S., & Caldwell, M. M. (1984). A test of compensatory photosynthesis in the field: Implications for herbivory tolerance. *Oecologia*, *61*(3), 311–318. https://doi.org/10.1007/BF00379627

O'Connor, T. G. (1992). Patterns of plant selection by grazing cattle in two savanna grasslands: A plant's eye view. *Journal of the Grassland Society of Southern Africa*, *9*(3), 97–104. https://doi.org/10.1080/02566702.1992.9648307

Oliveira Filho, J., De, S., Vieira, J. N., Ribeiro Da Silva, E. M., Beserra De Oliveira, J. G., Pereira, M. G., & Brasileiro, F. G. (2019). Assessing the effects of 17 years of grazing exclusion in degraded semi-arid soils: Evaluation of soil fertility, nutrients pools and stoichiometry. *Journal of Arid Environments*, *166*, 1–10. https://doi.org/10.1016/j.jaridenv.2019.03.006

Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-smart soils. *Nature*, *532*(7597), 49–57. https://doi.org/10.1038/nature17174

Phillips, R. P., Erlitz, Y., Bier, R., & Bernhardt, E. S. (2008). New approach for capturing soluble root exudates in forest soils. *Functional Ecology*, *22*(6), 990–999. https://doi.org/10.1111/j.1365-2435.2008.01495.x

Piñeiro, G., Paruelo, J. M., Jobbágy, E. G., Jackson, R. B., & Oesterheld, M. (2009). Grazing effects on belowground C and N stocks along a network of cattle exclosures in temperate and subtropical grasslands of South America. *Global Biogeochemical Cycles*, 23(2), 3168. https://doi.org/10.1029/2007GB003168

Piñeiro, G., Paruelo, J. M., Oesterheld, M., & Jobbágy, E. G. (2010). Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology & Management*, 63(1), 109–119. https://doi.org/10.2111/08-255.1

Porensky, L. M., Derner, J. D., Augustine, D. J., & Milchunas, D. G. (2017). Plant community composition after 75 yr of sustained grazing intensity treatments in shortgrass steppe. *Rangeland Ecology & Management*, 70(4), 456–464. https://doi.org/10.1016/j.rama.2016.12.001

Prescott, C. E. (2022). Sinks for plant surplus carbon explain several ecological phenomena. *Plant and Soil*, 476(1–2), 689–698. https://doi.org/10.1007/s11104-022-05390-9

Prommer, J., Walker, T. W. N., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., & Richter, A. (2020). Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. *Global Change Biology*, 26(2), 669–681. https://doi.org/10.1111/gcb.14777

Ramírez, P. B., Mosier, S., Calderón, F., & Cotrufo, M. F. (2022). Using mid-infrared spectroscopy to optimize throughput and costs of soil organic carbon and nitrogen estimates: An assessment in grassland soils. *Environments*, 9(12), 149. https://doi.org/10.3390/environments9120149

Rangelands ATLAS. (2021). *Distribution of rangeland types globally*. https://www.rangelandsdata.org/atlas/maps/distribution-rangeland-types-globally

Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C., Crow, S. E., Druhan, J. L., Hicks Pries, C. E., Marin-Spiotta, E., Plante, A. F., Schädel, C., Schimel, J. P., Sierra, C. A., Thompson, A., & Wagai, R. (2018). Beyond clay: Towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry*, 137(3), 297–306. https://doi.org/10.1007/s10533-018-0424-3

Rasse, D. P., Rumpel, C., & Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269(1–2), 341–356. https://doi.org/10.1007/s11104-004-0907-y

Ratcliff, F., Barry, S., Rao, D., Peterson, R., Becchetti, T., Kebreab, E., Motamed, K., Jung, M., & Mitloehner, F. (2023). Cattle grazing moderates greenhouse gas and particulate matter emissions from California grassland wildfires. *Sustainability*, 15(18), 13539. https://doi.org/10.3390/su151813539

Raynor, E. J., Derner, J. D., Augustine, D. J., Jablonski, K. E., Porensky, L. M., Ritten, J., Hoover, D. L., & Elliott, J. (2022). Balancing ecosystem service outcomes at the ranch-scale in shortgrass steppe: The role of grazing management. *Rangelands*, 44(6), 391–397. https://doi.org/10.1016/j.rala.2022.05.003

Reeder, J. D., & Schuman, G. E. (2002). Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. *Environmental Pollution*, 116(3), 457–463. https://doi.org/10.1016/S0269-7491(01)00223-8

Rice, C., & Owensby, C. (2000). The effects of fire and grazing on soil carbon in rangelands. In J. Kimble, R. Lal, & R. Follett (Eds.), *The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect* (pp. 323–342). CRC Press. https://doi.org/10.1201/9781420032468.ch13

Richards, J. H. (1984). Root growth response to defoliation in two *Agropyron* bunchgrasses: Field observations with an improved root periscope. *Oecologia*, 64(1), 21–25. https://doi.org/10.1007/BF00377538

Richards, J. H., & Caldwell, M. M. (1985). Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *The Journal of Applied Ecology*, 22(3), 907. https://doi.org/10.2307/2403239

Ring, C. B., Nicholson, R. A., & Launchbaugh, J. L. (1985). Vegetational traits of patch-grazed rangeland in West-Central Kansas. *Journal of Range Management*, 38(1), 51. https://doi.org/10.2307/3899333

Rocci, K. S., Barker, K. S., Seabloom, E. W., Borer, E. T., Hobbie, S. E., Bakker, J. D., MacDougall, A. S., McCulley, R. L., Moore, J. L., Raynaud, X., Stevens, C. J., & Cotrufo, M. F. (2022). Impacts of nutrient addition on soil carbon and nitrogen stoichiometry and stability in globally-distributed grasslands. *Biogeochemistry*, 159(3), 353–370. https://doi.org/10.1007/s10533-022-00932-w

Roche, L. (2016). Adaptive rangeland decision-making and coping with drought. *Sustainability*, 8(12), 1334. https://doi.org/10.3390/su8121334

Roche, L. M., Cutts, B. B., Derner, J. D., Lubell, M. N., & Tate, K. W. (2015). On-ranch grazing strategies: Context for the rotational grazing dilemma. *Rangeland Ecology & Management*, 68(3), 248–256. https://doi.org/10.1016/j.rama.2015.03.011

Rumpel, C., & Kögel-Knabner, I. (2011). Deep soil organic matter—A key but poorly understood component of terrestrial C cycle. *Plant and Soil*, 338(1–2), 143–158. https://doi.org/10.1007/s11104-010-0391-5

Ryle, G. J. A., & Powell, C. E. (1975). Defoliation and regrowth in the graminaceous plant: The role of current assimilate. *Annals of Botany*, 39(2), 297–310. https://doi.org/10.1093/oxfordjournals.aob.a084943

Sanderman, J., Hengl, T., & Fiske, G. J. (2017). Soil carbon debt of 12,000 years of human land use. *Proceedings of the National Academy of Sciences of the United States of America*, 114(36), 9575–9580. https://doi.org/10.1073/pnas.1706103114

Sanderson, M. A., Skinner, R. H., Barker, D. J., Edwards, G. R., Tracy, B. F., & Wedin, D. A. (2004). Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Science*, 44(4), 1132–1144. https://doi.org/10.2135/cropsci2004.1132

Schuman, G. E., Janzen, H. H., & Herrick, J. E. (2002). Soil carbon dynamics and potential carbon sequestration by rangelands. *Environmental Pollution*, 116(3), 391–396. https://doi.org/10.1016/S0269-7491(01)00215-9

Schuster, J. L. (1964). Root development of native plants under three grazing intensities. *Ecology*, 45(1), 63–70. https://doi.org/10.2307/1937107

Shen, M., Wang, S., Jiang, N., Sun, J., Cao, R., Ling, X., Fang, B., Zhang, L., Zhang, L., Xu, X., Lv, W., Li, B., Sun, Q., Meng, F., Jiang, Y., Dorji, T., Fu, Y., Iler, A., Vitasse, Y., ... Fu, B. (2022). Plant phenology changes and drivers on the Qinghai–Tibetan Plateau. *Nature Reviews Earth and Environment*, 3(10), 633–651. https://doi.org/10.1038/s43017-022-00317-5

Sherren, K., Fischer, J., & Fazey, I. (2012). Managing the grazing landscape: Insights for agricultural adaptation from a mid-drought photo-elicitation study in the Australian sheep-wheat belt. *Agricultural Systems*, 106(1), 72–83. https://doi.org/10.1016/j.agsy.2011.11.001

Sherren, K., Hodbod, J., MathisonSlee, M., Chappell, E., & King, M. (2022). Adaptive multi-paddock grazing and wellbeing: Uptake, management practices and mindset among Canadian beef producers. *Agroecology and Sustainable Food Systems*, 46(9), 1304–1329. https://doi.org/10.1080/21683565.2022.2107597

Silveira, M. L., Xu, S., Adewopo, J., Franzluebbers, A. J., & Buonadio, G. (2014). Grazing land intensification effects on soil C dynamics in aggregate size fractions of a spodosol. *Geoderma*, 230–231, 185–193. https://doi.org/10.1016/j.geoderma.2014.04.012

Sinclair, T. R., & Muchow, R. C. (1999). Radiation use efficiency. In A. G. Norman (Ed.), *Advances in agronomy* (Vol. 65, pp. 215–265). Elsevier. https://doi.org/10.1016/S0065-2113(08)60914-1

Sinclaire, T. R., & Weiss, A. (Eds.). (2010). *Principles of ecology in plant production*. CABI. https://doi.org/10.1079/9781845936549.0000

Soder, K. J., Rook, A. J., Sanderson, M. A., & Goslee, S. C. (2007). Interaction of plant species diversity on grazing behavior and performance of livestock grazing temperate region pastures. *Crop Science*, 47(1), 416–425. https://doi.org/10.2135/cropsci2006.01.0061

Sokol, N. W., Kuebbing, S. E., Karlsen-Ayala, E., & Bradford, M. A. (2019). Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *The New Phytologist*, 221(1), 233–246. https://doi.org/10.1111/nph.15361

Sokol, N. W., Sanderman, J., & Bradford, M. A. (2019). Pathways of mineral-associated soil organic matter formation: Integrating the role of plant carbon source, chemistry, and point of entry. *Global Change Biology*, 25(1), 12–24. https://doi.org/10.1111/gcb.14482

Sokol, N. W., Whalen, E. D., Jilling, A., Kallenbach, C., Pett-Ridge, J., & Georgiou, K. (2022). Global distribution, formation and fate of mineral-associated soil organic matter under a changing climate: A trait-based perspective. *Functional Ecology*, 36(6), 1411–1429. https://doi.org/10.1111/1365-2435.14040

Soltani, A., Alimagham, S. M., Nehbandani, A., Torabi, B., Zeinali, E., Dadrasi, A., Zand, E., Ghassemi, S., Pourshirazi, S., Alasti, O., Hosseini, R. S., Zahed, M., Arabameri, R., Mohammadzadeh, Z., Rahban, S., Kamari, H., Fayazi, H., Mohammadi, S., Keramat, S., ... Sinclair, T. R. (2020). SSM-iCrop2: A simple model for diverse crop species over large areas. *Agricultural Systems*, 182, 102855. https://doi.org/10.1016/j.agsy.2020.102855

Soussana, J.-F., & Lemaire, G. (2014). Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. *Agriculture, Ecosystems & Environment*, 190, 9–17. https://doi.org/10.1016/j.agee.2013.10.012

Stanley, P., Sayre, N., & Huntsinger, L. (2024). Holistic management shifts ranchers' mental models for successful adaptive grazing. *Rangeland Ecology & Management*, 93, 33–48.

Stanley, P., Spertus, J., Chiartas, J., Stark, P., & Bowles, T. (2023). Valid inferences about soil carbon in heterogeneous landscapes. *Geoderma*, 430, 116323.

Stanley, P. L., Rowntree, J. E., Beede, D. K., DeLonge, M. S., & Hamm, M. W. (2018). Impacts of soil carbon sequestration on life cycle greenhouse gas emissions in Midwestern USA beef finishing systems. *Agricultural Systems*, 162, 249–258. https://doi.org/10.1016/j.agsy.2018.02.003

Steffens, M., Kölbl, A., Schörk, E., Gschrey, B., & Kögel-Knabner, I. (2011). Distribution of soil organic matter between fractions and aggregate size classes in grazed semiarid steppe soil profiles. *Plant and Soil*, 338(1–2), 63–81. https://doi.org/10.1007/s11104-010-0594-9

Steffens, T., Grissom, G., Barnes, M., Provenza, F., & Roath, R. (2013). Adaptive grazing management for recovery. *Rangelands*, 35(5), 28–34. https://doi.org/10.2111/RANGELANDS-D-13-00018.1

Stroh, P. A., Pescott, O. L., & Mountford, J. O. (2017). Long-term changes in lowland calcareous grassland plots using *Tephroseris integrifolia* subsp. *integrifolia* as an indicator species. *Plant Ecology*, 218(11–12), 1269–1281. https://doi.org/10.1007/s11258-017-0767-1

Strömberg, C. A. E. (2011). Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, 39(1), 517–544. https://doi.org/10.1146/annurev-earth-040809-152402

Su, Y., Dong, K., Wang, C., & Liu, X. (2022). Grazing promoted plant litter decomposition and nutrient release: A meta-analysis. *Agriculture, Ecosystems & Environment*, 337, 108051. https://doi.org/10.1016/j.agee.2022.108051

Sun, G., Zhu-Barker, X., Chen, D., Liu, L., Zhang, N., Shi, C., He, L., & Lei, Y. (2017). Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: An implication for pasture management. *Plant and Soil*, 416(1–2), 515–525. https://doi.org/10.1007/s11104-017-3236-7

Sun, Y., He, X. Z., Hou, F., Wang, Z., & Chang, S. (2018). Grazing increases litter decomposition rate but decreases nitrogen release rate in an alpine meadow. *Biogeosciences*, 15(13), 4233–4243. https://doi.org/10.5194/bg-15-4233-2018

Taboada, M. A., Rubio, G., Chaneton, E. J., Hatfield, J. L., & Sauer, T. J. (2011). Grazing impacts on soil physical, chemical, and ecological properties in forage production systems. In J. L. Hatfield & T. J. Sauer (Eds.), *Soil management: Building a stable base for agriculture*. Soil Science Society of America. 301–320. https://doi.org/10.2136/2011.soilmanagement.c20

Tao, F., Huang, Y., Hungate, B. A., Manzoni, S., Frey, S. D., Schmidt, M. W. I., Reichstein, M., Carvalhais, N., Ciais, P., Jiang, L., Lehmann, J., Wang, Y.-P., Houlton, B. Z., Ahrens, B., Mishra, U., Hugelius, G., Hocking, T. D., Lu, X., Shi, Z., ... Luo, Y. (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, 618(7967), 981–985. https://doi.org/10.1038/s41586-023-06042-3

Teague, R., Provenza, F., Kreuter, U., Steffens, T., & Barnes, M. (2013). Multi-paddock grazing on rangelands: Why the perceptual dichotomy between research results and rancher experience? *Journal of Environmental Management*, 128, 699–717. https://doi.org/10.1016/j.jenvman.2013.05.064

Teague, W. R., & Dowhower, S. L. (2003). Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. *Journal of Arid Environments*, 53(2), 211–229. https://doi.org/10.1006/jare.2002.1036

Teague, W. R., Dowhower, S. L., Baker, S. A., Haile, N., DeLaune, P. B., & Conover, D. M. (2011). Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. *Agriculture, Ecosystems & Environment*, 141(3–4), 310–322. https://doi.org/10.1016/j.agee.2011.03.009

Teutscherová, N., Vázquez, E., Sotelo, M., Villegas, D., Velásquez, N., Baquero, D., Pulleman, M., & Arango, J. (2021). Intensive short-duration rotational grazing is associated with improved soil quality within one year after establishment in Colombia. *Applied Soil Ecology*, 159, 103835. https://doi.org/10.1016/j.apsoil.2020.103835

Thomson, B. C., Ostle, N., McNamara, N., Bailey, M. J., Whiteley, A. S., & Griffiths, R. I. (2010). Vegetation affects the relative abundances of dominant soil bacterial taxa and soil respiration rates in an upland grassland soil. *Microbial Ecology*, 59(2), 335–343. https://doi.org/10.1007/s00248-009-9575-z

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, D., Reich, P. B., & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, 109(26), 10394–10397. https://doi.org/10.1073/pnas.1208240109

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441(7093), 629–632. https://doi.org/10.1038/nature04742

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294(5543), 843–845. https://doi.org/10.1126/science.1060391

Ungar, E. D. (2019). Perspectives on the concept of rangeland carrying capacity, and their exploration by means of Noy-Meir's two-function model. *Agricultural Systems*, 173, 403–413. https://doi.org/10.1016/j.agsy.2019.03.023

van der Pol, L. K., Nester, B., Schlautman, B., Crews, T. E., & Cotrufo, M. F. (2022). Perennial grain Kernza® fields have higher particulate organic carbon at depth than annual grain fields. *Canadian Journal of Soil Science*, 102(4), 1005–1009. https://doi.org/10.1139/cjss-2022-0026

Vermeire, L. T., Strong, D. J., & Waterman, R. C. (2018). Grazing history effects on rangeland biomass, cover and diversity responses to fire and grazing utilization. *Rangeland Ecology & Management*, 71(6), 770–775. https://doi.org/10.1016/j.rama.2018.05.001

Villarino, S. H., Pinto, P., Jackson, R. B., & Piñeiro, G. (2021). Plant rhizo-deposition: A key factor for soil organic matter formation in stable fractions. *Science Advances*, 7(16), eabd3176.

Volesky, J. D., Schacht, W. H., Koehler, A. E., Blankenship, E., & Reece, P. E. (2011). Defoliation effects on herbage production and root growth of wet meadow forage species. *Rangeland Ecology & Management*, 64(5), 506–513. https://doi.org/10.2111/REM-D-10-00010.1

Wang, F., Apfelbaum, S. I., Thompson, R. L., Teague, R., & Byck, P. (2021). Effects of adaptive multiple paddock and continuous grazing on fine-scale spatial patterns of vegetation species and biomass in commercial ranches. *Landscape Ecology*, 36(9), 2725–2741. https://doi.org/10.1007/s10980-021-01273-z

Wang, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., Luo, C., Xu, B., Zhu, X., Chang, X., Cui, X., Niu, H., Zhao, X., & Wang, W. (2012). Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, 93(11), 2365–2376. https://doi.org/10.1890/11-1408.1

Wang, X., McConkey, B. G., VandenBygaart, A. J., Fan, J., Iwaasa, A., & Schellenberg, M. (2016). Grazing improves C and N cycling in the Northern Great Plains: A meta-analysis. *Scientific Reports*, 6, 33190. https://doi.org/10.1038/srep33190

Waters, C. M., Orgill, S. E., Melville, G. J., Toole, I. D., & Smith, W. J. (2017). Management of grazing intensity in the semi-arid rangelands of southern Australia: Effects on soil and biodiversity. *Land Degradation & Development*, 28(4), 1363–1375. https://doi.org/10.1002/ldr.2602

White, L. J., Yeater, K. M., & Lehman, R. M. (2023). Soil microorganisms respond distinctly to adaptive multi-paddock and conventional grazing in the southeastern United States. *Soil Science Society of America Journal*, 87(5), 1096–1108. https://doi.org/10.1002/saj2.20573

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., … Kögel-Knabner, I. (2019). Soil organic carbon storage as a key function of soils-A review of drivers and indicators at various scales. *Geoderma*, 333, 149–162.

Willms, W. D., Dormaar, J. F., & Schaalje, G. B. (1988). Stability of grazed patches on rough fescue grasslands. *Journal of Range Management*, 41(6), 503. https://doi.org/10.2307/3899527

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. https://doi.org/10.1111/gcb.14070

Wilson, C. H., Vendramini, J. M., Sollenberger, L. E., & Flory, S. L. (2021). Root production in a subtropical pasture is mediated by cultivar identity and defoliation severity. *Tropical Grasslands-Forrajes Tropicales*, 9(2), 144–158. https://doi.org/10.17138/tgft(9)144-158

Witzgall, K., Vidal, A., Schubert, D. I., Höschen, C., Schweizer, S. A., Buegger, F., Pouteau, V., Chenu, C., & Mueller, C. W. (2021). Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nature Communications*, 12(1), 4115. https://doi.org/10.1038/s41467-021-24192-8

Wu, Y., & Wang, H. (2008). Impacts of grazing intensity on nitrogen pools and nitrogen cycle in an alpine meadow on the eastern Tibetan Plateau. *Applied Ecology and Environmental Research*, 6(3), 69–79.

Yamashita, T., Flessa, H., John, B., Helfrich, M., & Ludwig, B. (2006). Organic matter in density fractions of water-stable aggregates in silty soils: Effect of land use. *Soil Biology and Biochemistry*, 38(11), 3222–3234. https://doi.org/10.1016/j.soilbio.2006.04.013

Yang, Y., Tilman, D., Furey, G., & Lehman, C. (2019). Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nature Communications*, 10(1), 718. https://doi.org/10.1038/s41467-019-08636-w

Yayneshet, T., Eik, L. O., & Moe, S. R. (2009). The effects of exclosures in restoring degraded semi-arid vegetation in communal grazing lands in northern Ethiopia. *Journal of Arid Environments*, 73(4–5), 542–549. https://doi.org/10.1016/j.jaridenv.2008.12.002

Zhao, W., Chen, S.-P., & Lin, G.-H. (2008). Compensatory growth responses to clipping defoliation in *Leymus chinensis* (Poaceae) under nutrient addition and water deficiency conditions. *Plant Ecology*, 196(1), 85–99. https://doi.org/10.1007/s11258-007-9336-3

Zheng, J. Y., Zhao, J. S., Shi, Z. H., & Wang, L. (2021). Soil aggregates are key factors that regulate erosion-related carbon loss in citrus orchards of southern China: Bare land vs. grass-covered land. *Agriculture, Ecosystems & Environment*, 309, 107254. https://doi.org/10.1016/j.agee.2020.107254

Zhou, G., Luo, Q., Chen, Y., He, M., Zhou, L., Frank, D., He, Y., Fu, Y., Zhang, B., & Zhou, X. (2019). Effects of livestock grazing on grassland carbon storage and release override impacts associated with global climate change. *Global Change Biology*, 25(3), 1119–1132. https://doi.org/10.1111/gcb.14533

Zhou, G., Zhou, X., He, Y., Shao, J., Hu, Z., Liu, R., Zhou, H., & Hosseinibai, S. (2017). Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: A meta-analysis. *Global Change Biology*, 23(3), 1167–1179. https://doi.org/10.1111/gcb.13431

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Chapin, M. C., & Reynolds, J. F. (1995). Effects of mammals on ecosystem change at the Pleistocene-Holocene boundary. In F. S. Chapin & C. Körner (Eds.), *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences* (Vol. 113, pp. 127–135). Springer. https://doi.org/10.1007/978-3-642-78966-3_9