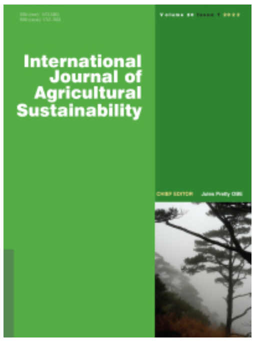

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Amping up soil carbon: soil carbon stocks in California rangelands under adaptive multi-paddock and conventional grazing management

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ABSTRACT

Adaptive multi-paddock (AMP) grazing is gaining attention for its potential to increase soil organic carbon (SOC), yet its efficacy on arid and semi-arid rangelands remains debated. Given the adaptive nature of AMP, on-ranch studies are essential for measuring its applied outcomes. To assess AMP's impact on Mediterranean California rangelands, we collected 1,440 soil samples from four paired AMP and conventional (CONV) grazing sites across northern California. Three AMP ranches had significantly greater SOC stocks in surface soils (17% greater SOC at 0–10 cm), and two had greater SOC stocks to 100 cm (32% greater), compared to CONV ranches. The largest SOC differences occurred in the mineral-associated organic matter fraction, suggesting longer-term SOC storage. While plant community composition did not differ significantly, AMP ranches, on average, had slightly less bare ground, greater live plant cover, and two sites had 82% greater perennial grass cover. These factors may have contributed to SOC differences. Further research is needed to understand site-specific constraints, underlying mechanisms, and SOC changes over time under AMP grazing.

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KEYWORDS
Adaptive multi-paddock grazing; California rangelands; soil carbon sequestration; soil organic matter fractions; plant community composition; grazing management

1. Introduction

Improved grazing management to sequester soil organic carbon (SOC) on grasslands and rangelands as a 'natural climate solution' has sparked persistent debate (Garnett et al., 2017). Proponents cite improved grazing management as a promising strategy to restore the ~75 Pg of SOC lost from millions of acres of native grazing lands (i.e. lands historically grazed, not lands converted from other uses such as forests) in the last two centuries (Sanderman et al., 2017), which could simultaneously improve productivity and aid in climate change mitigation (Conant et al., 2017). Nearly 40% of grazing lands are characterized as semi-arid rangelands, which are non-equilibrium environments often limited by moisture (Rangelands ATLAS, 2021). It is not well understood if grazing management is a viable SOC sequestration strategy on semi-arid rangelands given constraints to SOC accumulation in these systems, including large spatial–temporal variability and limited annual plant growth (Booker et al., 2013). Even less is known about the impact of grazing management on SOC on semi-arid Mediterranean rangelands like those found in California (Kottek et al., 2006), where forage production is further limited by seasonal drought and precipitation (George, 2020). Core to this debate are extremely sparse and conflicting study results on the impact of grazing management on SOC in rangelands (Stanley, Wilson, et al., 2024), and the inappropriate extrapolation of SOC responses from less arid grasslands.

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Rangelands are particularly prevalent in California, USA, where they make up 62% of the total land area (Saitone, 2003). California rangelands are also subject to its Mediterranean climate, only receiving precipitation during a 'wet' seasonal window, creating unique challenges. Like rangelands globally, California rangelands have lost a large quantity of SOC: some estimate SOC losses of 40 Mg C/ha in the top 50 cm of rangeland soils, driven mainly by invasion of exotic annual grasses that replaced deeper-rooted perennial grasses and forbs (Burcham, 1957; Koteen et al., 2011). Settler-colonial practices of dividing and fencing large tracts of rangelands into smaller privately owned ranches, replacing native ungulates with domesticated cattle, overgrazing, as well as climate change and increasingly extreme droughts have also contributed to SOC losses on California rangelands (Bailey, 2008; Stromberg et al., 2007).

Many studies and climate assessments rank grazing management highly as an opportunity to restore lost SOC on grazing lands generally (*Global assessment of soil carbon in grasslands*, 2023; Herrero et al., 2016). However, many believe that grazing management is ineffective or unreliable for SOC sequestration on non-equilibrium rangelands (Briske et al., 2013), despite a lack of comprehensive on-the-ground research spanning the spectrum of grazing management strategies (Stanley, Wilson, et al., 2024). On one extreme, continuous grazing is a simplified one-pasture system characterized by set animal stocking rates and no or low rotations among pastures (Briske, Sayre, et al., 2011). 'Rotational' grazing is an umbrella term encompassing a range of rotational intensities where animals are moved between pastures and has historically been considered an improved form of grazing management over continuous grazing. In many cases however, including California, it is conventional (CONV) practice to extensively rotate animals among few pastures. At the other end of the grazing management spectrum, adaptive multi-paddock (AMP) grazing is among the most intensive forms of rotational grazing, where animals are moved frequently in moderate-high stock densities across lands often divided into temporary paddocks. Each paddock is then rested for plant regrowth before being regrazed. AMP grazers adapt stocking densities, rotation frequencies, and paddock recovery periods according to seasonality, forage quantity and quality, exogenous shocks and stressors (such as droughts), in response to observational monitoring outcomes, as well as to meet social and market needs (Stanley, Sayre, et al., 2024). Compared to low-rotational and continuous grazing management, AMP grazing management is often targeted to soil health improvement and is meant to prevent overgrazing and maintain soil cover. Promisingly, farmers and ranchers report observing benefits from AMP grazing, such as increased forage productivity, improved forage quality, and perennialization (Oates et al., 2011; Roche et al., 2015; Sayre, 2001; Teague et al., 2004; TomKat Ranch, 2019). These benefits are often linked to increased SOC, which has been observed in studies of AMP grazing on temperate and subtropical grasslands, where rates of SOC sequestration reportedly vary widely, ranging from 0.4 to >8.0 Mg C/ha/yr (Conant et al., 2003; Machmuller et al., 2015; Mosier et al., 2021; Stanley et al., 2018; Teague et al., 2011). However, to our knowledge, there has been only one study of AMP grazing on more arid rangeland systems in the US, which did not measure soil outcomes, but showed no improvement in forage quality or quantity compared to continuous grazing (Augustine et al., 2020). To resolve this debate, the efficacy of AMP grazing to sequester SOC and improve ecosystem health needs to be explored on more arid rangelands (Byrnes et al., 2017; Hawkins et al., 2017), especially in light of some non-peer-reviewed and experiential evidence suggesting increased perennialization in California under AMP grazing (Henneman et al., 2014; Strohm & Watt, 2019) and higher drought tolerance arising from similar grazing management principles (Woodmansee et al., 2021).

While climate variables such as temperature and precipitation are master drivers and mediators of SOC stocks on rangelands, one mechanism by which AMP grazing is thought to influence SOC change is via shifting plant community composition. As one example, AMP ranchers report managing their herds adaptively to target perennial grass establishment and growth (i.e. constructing paddocks around areas of high perennial growth and deferring grazing until after perennial grasses have set seed; Stanley, Sayre, et al., 2024), which could increase SOC inputs – especially belowground via deeper roots. This could be especially pertinent in California, where loss of perennial grasses has contributed to degradation of rangeland soils (Koteen et al., 2011). It is generally accepted that this has been exacerbated by heavy continuous grazing (Burcham, 1957; Dlamini et al., 2016). However, management strategies to reestablish perennial grass dominance on California rangelands remain notoriously elusive, and studies have shown promising but highly variable perennial response following improved grazing (Bartolome et al., 2004; Carey, Gravuer, et al., 2020; Davy et al., 2017; Heady, 1961; Henneman et al., 2014; Stahlheber & D'Antonio, 2013). Simultaneously measuring SOC and plant community response to AMP grazing management in California rangelands would therefore greatly improve our scientific understanding.

AMP grazing presents experimental challenges that have stymied research efforts to study its effects on rangeland landscapes. For example, the adaptive nature of AMP grazing is untenable for tightly controlled and replicated experiments, and researchers are not subject to the same drivers, constraints, and decision-making processes that drive ranchers' AMP grazing management, making experimental application of this type of grazing management less meaningful (Briske, Sayre, et al., 2011; Roche et al., 2015). Together, these challenges highlight the importance of on-ranch research to understand the impacts of AMP grazing management on SOC in working rangelands (Chaney, 2017). This type of on-ranch research is an important, yet also challenging and under-utilized, complement to controlled experimental research. On-ranch research broadens the scope of inference by including different ecological contexts and management approaches, helping to determine where and when outcomes from controlled research on AMP grazing match real-world outcomes.

Also driving these research demands is the increasingly urgent need to understand semi-arid grazing lands' potential to sequester SOC as a climate change mitigation strategy. However, different pools of SOC have varying mechanisms of formation and degrees of persistence (Cotrufo & Lavallee, 2022) – which ultimately confers climate change mitigation potential – and thus can be differently impacted by grazing management (Naidu et al., 2022). Soil organic matter (SOM) fractionation methods separate SOM in bulk soils into functionally distinct pools, allowing for the separate analysis of soil organic carbon (SOC) within each pool. Fractionations can provide 'more information about the mechanisms driving SOC accrual, its persistence, and vulnerability to disturbance and management practices' (Mosier et al., 2021). For example, SOC protected by bonding to mineral surfaces, i.e. mineral associated organic matter (MAOM), is on average more persistent in soils than particulate organic matter (POM) (Heckman et al., 2023; Kleber et al., 2007) for which occlusion in soil aggregates is the only moderate form of stabilization (Del Galdo et al., 2003; Haddix et al., 2020). In addition to different mechanisms of protection, POM and MAOM also differ in formation pathways: POM forms from partially decomposed plant and microbial structural components, while MAOM forms from the sorption of dissolved organic matter (DOM) and microbial necromass (Kleber et al., 2015). Because of their different formation and stabilization mechanisms, changes in these SOC fractions can also allude to how management interventions are impacting plant inputs, their microbial transformation, and N dynamics. For example, changes in MAOM are likely impacted by plant inputs, efficiency of microbial transformation, and N availability, while changes in POM are more likely to be driven by limitations on microbial decomposition of structural plant inputs (Cotrufo et al., 2021). Measuring only bulk SOC can mask changes in these important SOC fractions. Additionally, separating and quantifying SOC stocks in each fraction can help to increase the power of detecting SOC changes due to grazing management and provide richer mechanistic understanding (Mosier et al., 2021). This is especially important in rangeland systems where SOC can be extremely heterogeneous, which makes it difficult to detect small SOC changes (Stanley et al., 2023). Fractionating SOC into these functionally distinct pools can therefore improve change detection and provide a more useful and thorough understanding of the impact of grazing management on SOC (Stanley, Wilson, et al., 2024).

This study addresses several of these research gaps related to the viability of AMP grazing to sequester SOC on Mediterranean rangelands. We conducted an on-ranch study at four paired sites across northern California to ask three main questions: (1) Does AMP grazing increase SOC storage relative to conventional (CONV), low-rotational grazing on semi-arid California working rangelands?; (2) How do differences in four SOM fractions (dissolved (DOM), free (fPOM) and aggregate occluded (oPOM) particulate, and mineral associated (MAOM) organic matter) help explain changes in SOC persistence under AMP grazing?; and (3) How do plant communities differ in response to AMP grazing, and do these shifts help explain SOC changes? This study is a first step towards answering these questions and improving our understanding of the impact of AMP grazing on semi-arid rangelands.

2. Methods

2.1. Study sites

Paired, adjacent AMP/CONV ranches were selected via an iterative snowball networking and screening process from 2018 to 2020. Networking was initiated with contacts to a key Holistic Management[1] training center in Northern California. Fifteen ranchers who had completed holistic management (or similar, e.g. Ranching for Profit) training and claimed to practice AMP grazing responded to an email solicitation, and initial phone interviews were completed with 12 of those ranchers. We narrowed the qualifying criteria for AMP grazing by focusing on specific management aspects, which were developed in combination with two AMP ranchers outside of the study population. Ultimately five AMP/CONV ranch pairs were chosen based on adherence to the control and management criteria listed in Table 1. Rancher quotes obtained from semi-structured interviews conducted as part of a companion study (Stanley, Sayre, et al., 2024) are included to illustrate the adaptive nature of AMP grazing.

Thus, to define AMP grazing, we focused on ranchers' self-reported, intentional use of animal movement, pasture rest, seasonal use of high stock densities, and adaptability to reach their management goals. We compared management variables considered particularly important for influencing ecological responses to grazing, including stocking rate (Briske, Derner, et al., 2011; Fuhlendorf et al. 2001; Venter et al., 2019). While in this on-ranch study we could not choose AMP and CONV ranches with equivalent stocking rates because they are influenced by the producers' available acres and herd size, stocking rates were similar at the ranch-scale between AMP and CONV in three out of four final pairs (Table 2). We also chose not to set limits or thresholds on stocking density because the application of AMP grazing is highly variable and changes seasonally on California rangelands. Eight AMP ranches met the finalized criteria, but three were excluded because willing CONV neighbors could not be identified within close enough vicinity (within <1mi). We consulted local Cooperative Extension agents/advisors, natural resource advisors, experienced rangeland ecologists and existing grazing management literature in California (Bush & Ptak, 2006) to inform our understanding of CONV grazing management. Ultimately, we defined CONV grazing broadly as the suite of traditional grazing practices common to California, primarily low-rotational systems (i.e. rotation among 5 or fewer pastures) (Huntsinger et al., 2007; Roche et al., 2015). We chose to prioritize proximity of AMP/CONV neighbors (and adherence to strict ecological criteria, see *2.2 Soil Sampling*) rather than increase the number of pairs to maximize the likelihood that differences in outcomes could be reasonably associated with differences in management and not differences in other inherent soil properties. Our goal was not to suggest that any particular grazing strategy is negative, but rather to assess whether the management characteristics outlined in Table 1 brings any measurable benefits to AMP-grazed ranches.

Five AMP/CONV ranch pairs were chosen based on these criteria. We were unable to collect enough soil samples at one site due to extremely high rock content (Site 5, not reported or pictured). Sampling was conducted April–July 2020 on the four remaining paired sites in three distinct ecoregions of Northern California: Central Coast Rangeland, Northern Coast Rangeland and Sierra Nevada Foothills (Figure 1, SI Table 1).

2.2. Soil sampling

Sampling locations on each ranch were determined by initial pasture walks with ranchers, where we could identify adjacent pastures in each ranch pair with the same soil type (based on USDA NRCS soil survey data; Soil Survey Staff, 2022), slope aspect, ecological site descriptions, low tree cover, and that met our other control and management criteria. We determined sample sizes based on a preliminary power analysis using spatial heterogeneity information from prior samples collected on a nearby coastal rangeland site (Stanley et al., 2023). Samples were collected using a stratified transect design with three 50 m transects constructed along each adjacent ranch pair, stratified by slope position: summit/shoulder, backslope, and footslope/toeslope (3 transects per ranch * 2 ranch/pair * 4 pairs = 24 total transects) (Figure 1). Soils were sampled down to 1 m and divided into 4 depth ranges (a: 0–10 cm, b: 10–30 cm, c: 30–50 cm, d: 50–100 cm). Based on our power analysis, we attempted 25 samples along each transect for the 0–10 and 10–30 cm depths, and 5 per transect down to 100 cm. In all, we attempted to collect 1200 topsoil samples (a and b depths) and 240 deep soil samples (c and d depths) for a total of 1440 individual soil samples. Cores were collected down to 100 cm *or* to the point of refusal (either due to bedrock or rock obstruction). Ultimately, we

Table 1. Control and management criteria developed for screening ranchers for study selection.

Control Criteria
1. Grazes beef cattle on rangelands in California and has managed consistently for 3+ years
2. Manages a portion of ranch acreage with grazing only and no other management interventions (no irrigation, compost, other soil amendments, seeding, haying, etc.) and maintained this condition for the entirety of their ownership or management
3. Shares an adjacent fence line with a neighboring 'conventionally' (CONV) grazed ranch (defined below), whose manager/owner was a willing participant

AMP Management Criteria	**Illustrative AMP rancher quote**
1. Rancher claimed to make grazing rotation decisions adaptively rather than according to a set regime (e.g. every 5 days). This helped to distinguish AMP grazing from other high-intensity but non-adaptive forms of grazing management (e.g. mob grazing)	a. 'They're moving, depends on the time of year, when the grass is growing faster, I move them daily, sometimes multiple times a day.' (AMP Rancher, Site 2) b. 'And then, yeah, we basically move them by timing it with the growth of the grasses.' (AMP Rancher, Site 4)
2. Has completed AMP, Holistic Planned Grazing, or similar grazing management training	a. 'So that was my introduction to most of this stuff for me was that week long Ranching for Profit class and then that same year, I started the Holistic Management series. I think I started with the planned grazing part, but then I did the holistic, like the business part of it too. So then I went through all those.' (AMP Rancher, Site 5)
3. Uses a grazing plan (e.g. PastureMap, Gaia, or a grazing chart)	a. 'I knew we weren't utilizing lots of pieces that we could, and so 2017 is when I took the classes. 2018 – that spring is when we started, like holistically managing and that was only, I can look at my PastureMap but I think it was only like five or 600 acres that I would like say that we managed those areas holistically, like plugged them into PastureMap and made sure we didn't go back too early. All that. And then this year, we got up to probably 2600 acres.' (AMP Rancher, Site 2) b. 'We sat here and did our grazing plan and he got overwhelmed and he was just like, what if this? And what if that? What if … ? And I'm like, "You can't do all the what ifs." Like, that's why we're doing it in pencil. We're gonna put something together so we have a guideline. And then all of it will shift because like, something will happen, they'll bust out and we'll have to move. But like we have to start.' (AMP Rancher, Site 2)
4. Subdivides land into smaller paddocks throughout the grazing season or uses range riding to herd and rotate animals	a. 'So if we have interior fences, that's how we set up our paddock. So I thought about interior fences, and thought, now you have to build for the grass. And we started building our paddocks for what feed was available versus going, "Well, there's a field there." It's more work. So we move our animals, in general, once a day during the growing season.' (AMP Rancher, Stanley, Sayre, et al., 2024) b. 'I don't know how to tell you how many like, subdivided paddocks, but I can tell you that in the fast growing season, which is March through Fourth of July, basically, we start off at 75 animals [cattle] per acre. Okay, because it's fast growing season, so you literally can't eat it fast enough. And the finishing herd gets moved every day. We call it leapfrogging them. So we'll build a pasture and then we'll off of that pasture we'll build another one and another one and then another one. So we do it that way, because we're kind of chasing the water, the natural water out there, the creeks and the ponds and stuff because we don't have a lot of water troughs past a certain area on the property.' (AMP Rancher, Site 2)
5. Incorporates targeted pasture rest throughout the year	a. 'And every field is a little bit different so like the field to the north, I have some stands of purple needle grass that have been coming in or that it's increasing. So that's kind of like I guess I've been paying more attention to trying to manage what I want trying to graze that time of the year, that field probably gets more rest than any of the other fields, but then there's patches of foxtail in there that I'll go in and try and hit pretty hard.' (AMP Rancher, Site 5) a. 'So, the cons are that, you know, you make a lot of mistakes cause you're trying a lot of new things. But you get better at, you

(*Continued*)

Table 1. Continued.

Control Criteria	
6. Uses monitoring (quantitative or qualitative methods) of outcomes – such as forage recovery, vegetation cover, residual dry matter, SOC – to adapt management practices	know, the mistakes you're making are generally small. If you're monitoring, so you can correct them really, pretty quickly. And there's, you know, it's kind of a little blip on the screen.' (AMP Rancher, Site 3)
7. Has been using AMP management for 3 or more grazing seasons	NA (this was determined via a simple numerical question)

Note: Illustrative quotes were selected from semi-structured interviews conducted during participant screening (Stanley, Sayre, et al., 2024).

analyzed 1424 individual soil samples: 6 samples could not be collected due to rocks, and 10 were either damaged or lost.

Samples were collected with hand-augers of known volume and separated by depth. All samples were transported back to the Berkeley Agroecology Lab at the University of California, Berkeley, air dried to a consistent weight, and stored in air-tight bags until processing. Samples for bulk SOC were then sieved to <2 mm, finely ground on ball-mill (Retsch, Newtown, PA), and stored for analysis.

2.3. Bulk density and equivalent soil mass

We collected bulk-density data at our first sampling site (Site 1) using a modified core method. We collected three topsoil bulk density (BD) samples at each transect: two 0–30 cm samples at each end (at the 0 and 50 m marks) and one 100 cm sample at the 25 m transect center. We drove a manufactured steel cylinder into the soil at each location with a 30 lb sledgehammer and extracted the cylinder with a Hi-jack lift. Partial pits were dug to allow us to extract the cylinder at deeper depths. Due to the high clay content of these samples, we were unable to reach below 80 cm. We assumed our measured BD at 50–80 cm was consistent from 80 to 100 cm.

At each of the three other sites, we used the equivalent soil mass method (von Haden et al., 2020; Wendt & Hauser, 2013), rather than traditional bulk density estimates, to compare SOC stocks on the basis of equivalent soil mass (ESM). This shift was made because it greatly increases the total number of 'relative' BD estimates, reduces error associated with BD calculations, and was also logistically easier given the challenging soil sampling conditions at these sites (e.g. rocks, high clay content).

Briefly, rather than collecting separate samples for TC% and BD, we collected each sample with a bucket auger of known volume. The total soil collected at each depth increment within a single soil core (0–10, 10–30, 30–50, and 50–100 cm) was weighed in-field. Then a subsample was collected from each depth increment and weighed field-wet. Subsamples were transported back to the lab, air-dried, and then reweighed. Soil water content was calculated based on the difference between wet and dry weight of the subsamples, which was then used to extrapolate the dry weight of the whole depth increment. 'Apparent' BD was calculated for each sample using the dry soil mass and volume and used as input for ESM calculations.

2.4. Plant community composition

To measure the impact of AMP vs CONV grazing on plant community composition, we collected line-point intercept data following the (Herrick et al., 2017) method. Briefly, we made a 'controlled drop' of a pin flag in 0.5 m intervals along each 50 m transect (Figure 1). We recorded the first species intercepting the top of the pin flag (i.e. 'top-hit'). If the pin did not intercept a live plant, we recorded the hit of the pin flag at the soil surface (i.e. either bare ground or plant litter). In total, we recorded 300 vegetation intercepts per ranch (100 intercepts along each of three transects per ranch, six transects per site) and 2,400 overall (along 24 total transects). All vegetation data were collected prior to soil sampling to minimize disturbance.

We attempted to identify the species at every intercept, although some plants were too immature to identify to species level. We opted to categorize our line-point intercept data into common functional groups of interest in California rangelands: perennial grasses, annual grasses, perennial legumes, annual legumes, perennial non-legume forbs, annual non-legume forbs, litter, and bare soil.

We calculated the percentage cover of each functional group as:

$$\text{Percent cover, functional group A} = \left(\frac{\#\ \text{hits functional group A}}{\text{total}\ \#\ \text{of points}}\right) \times 100 \qquad (1)$$

Table 2. Grazing management characteristics of ranches across the four study sites.

site	mgmt category	acres managed	# animals + enterprise	years	# permanent pastures + size ranges	# temporary paddocks	annual avg stocking rate (AU/acre/yr)	max stocking density (AU/acre + length)	rotation schedule (days)	rest duration (days)
Site 1	AMP	>10,000	>2000 cow-calf + yearlings	30	30 permanent pastures 11–106 acres each	>100	0.15–0.18	NR	Spring: 1–1.5 Dry: < 10	Spring: 45 Dry: 90
	CONV	100–300	<50 cow-calf	25	2 permanent pastures 100–150 acres each	NA	0.11–0.15	NR	NA	NA
Site 2	AMP	1000–5000	300–1000 birth-finish	3	29 permanent pastures <10–1000 acres	>100	0.14	75 AU/ac for <1 d	Spring: 1–2 Dry: varies	Spring: 30–40 Dry: 60–70
	CONV	1000–5000	300–1000 cow-calf	>20	<5 permanent pastures 1000–2900 acres each	NA	0.14	NR	NA	NA
Site 3	AMP	1000–5000	300–1000 cow-calf + yearlings	10	40 permanent pastures 30–50 acres each	>100	0.33–0.5	100 AU/ac for <1 day	Spring: < 1–1 Dry: < 30	Spring: 25 Dry: 180
	CONV	100–300	50–100 cow-calf	25	5 permanent pastures 10–100 acres	NA	0.28	NR	NA	NA
Site 4	AMP	5000–10,000	1000–2000 birth-finish	12	25 permanent pastures 30–>1000 acres each	NA range rides	0.05–0.10	10 AU/ac for 2 days	Spring: 2–5 Dry: < 21	Spring: 30 Dry: 90
	CONV	100–300	<50 cow-calf	>20	1 permanent pasture 100–300 acres	NA	0.11	NR	NA	NA

Notes: Quantitative characteristics were reported as ranges to protect confidentiality where appropriate. Average stocking rate is calculated as the number of animal units (AU) per acre for the entire ranch on a given year. Max stocking density is reported for ranchers who were able to estimate their maximum grazing intensity during the growing season, and is reported as the number of animal units (AU) per acre over a short, discrete length of time. Rotation schedule and rest duration are averages for each season reported by the ranchers. NR = not reported, NA = not applicable.
*CONV ranchers did not report using adaptive stocking densities as a tool to reach their management goals. For these ranches, stocking rate (AUs/acre/year) and stocking density (AUs/acre/time) are generally equivalent annually.

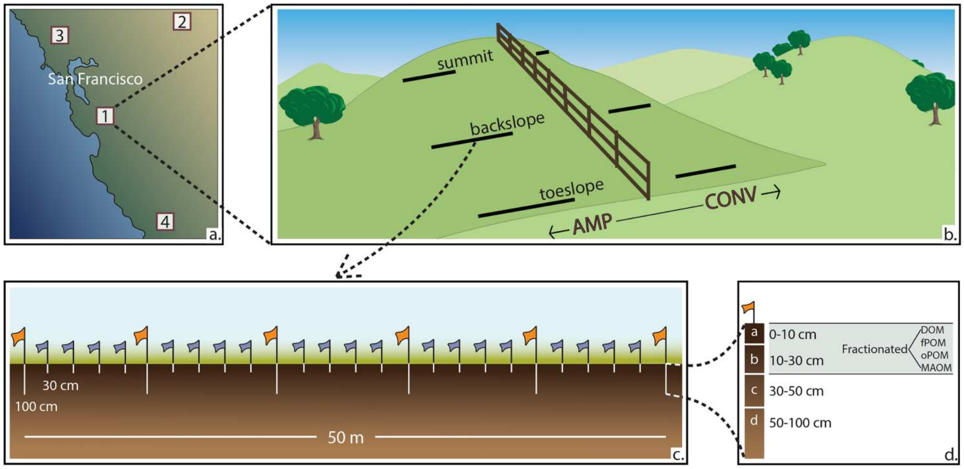

Figure 1. Sampling design schematic. (a) Approximate site locations for four enrolled adaptive multi-paddock (AMP) and conventionally (CONV) grazed ranch pairs located in Northern Coast Rangeland (sites 1 and 3), Sierra Nevada Foothills (2), and Central Coast Rangeland (4); (b) Illustration of sampling design at each site. Adjacent sampling zones were located on each AMP and CONV grazed ranch pair according to our ecological site criteria. Sampling was stratified on each ranch into three slope positions: summit/shoulder, backslope, and footslope/toeslope; (c) Along each transect, we collected five, 1 m deep cores (at 10 m intervals; 6th flag shown to indicate end of the transect) and 25 30 cm cores (at 2 m intervals). We also collected plant community point intercept data along each transect at 1 m intervals; (d) Each core was split into four depth increments (0–10 cm, 10–30 cm, 30–50 cm, and 50–100 cm). Topsoils along each transect were combined into five composite samples per depth (0–10 and 10–30 cm) for fractionations into four fractions (dissolved [DOM], free [fPOM] and occluded [oPOM] particulate, and mineral-associated [MAOM] organic matter).

2.5. Lab analyses

2.5.1. Bulk SOC%

We analyzed samples for TOC% and N% on an Elementar soliTOC cube (Elementar, Ronkonkoma, NY), which improves SOC measurement precision over traditional elemental analyzers (Stanley et al., 2023) by combusting higher sample masses (up to 3 g of soil vs <50 mg) and separating total organic C (TOC), residual organic C (ROC), and total inorganic C (TIC) via a temperature ramping method, DIN19539 (Natali et al., 2020). This negated the need to extract inorganic C prior to combustion. Unfortunately, this instrument was unable to provide reliable TN%.

2.5.2. Soil organic matter fractions

Topsoils (0–10 and 10–30 cm depths) were composited by depth in groups of five along each transect for SOM fractionation analysis (i.e. cores 1–5, 6–10, etc. were composited by depth). This resulted in a total of 240 composite samples for fractionation (5 samples per transect * 2 depths * 24 transects). Soils were fractionated by size and density into four functionally distinct pools: dissolved organic matter (DOM), free particulate organic matter (fPOM), occluded particulate organic matter (oPOM; this fraction also includes sand-sized particles), and mineral-associated organic matter (MAOM), which were then analyzed for SOC in each fraction.

We fractionated following the Haddix et al. (2020) protocol (see **SI 1.3**). This method separates POM before and after aggregate dispersion into ‘free’ and ‘occluded’ POM. We chose this method because it provides information on how grazing management may be forming or disrupting soil aggregates, which may offer short-term OM protection. All fractions were mass recovered to within ±5% of the original soil mass. Samples over or under-recovered were refractionated until within this threshold.

The fPOM, oPOM and MAOM fractions were oven-dried at 60°C, ground, and analyzed on an Elementar varioEL for TC/TN% (Elementar, Ronkonkoma, NY). TC % on all composited samples was recovered to an average of 102% of original bulk TC%. There was no significant inorganic C detected in our bulk soil samples on the soliTOC. Because varioEL only reports TC% for our fractionated soils, we report fraction and bulk soils on the basis of TC%, which is equivalent to TOC for the purposes of SOC stock calculations.

2.5.3. Texture

Surface soils (0–10 and 10–30 cm) were analyzed for texture following a rapid pipette method (Soil

Survey Laboratory Methods Manual, 1992). Briefly, 5 g of soil was shaken overnight on a reciprocal shaker with 40 mL of 0.5% sodium hexametaphosphate. Sand and clay fractions were pipetted at time intervals determined by the temperature and particle sizes. Each fraction was oven dried at 105°C and weighed. Percent sand and clay were determined based on Stoke's Law, which was used to quantify soil texture.

2.6. Soil data analysis

We calculated ESM-based SOC stocks following von Haden et al. (2020). In addition to 'apparent' BD, ESM calculations require four steps/data layers to ultimately determine cumulative SOC stock on the basis of equivalent mineral soil mass: (1) a choice of reference soil, (2) depth increments, (3) SOC%, and (4) SOM%. The CONV grazed ranch within each ranch pair was chosen as the reference soil mass because all AMP ranches were historically CONV grazed (Table 2). To compare SOC stocks on the basis of soil mineral mass, we subtracted the weight of organic matter. We estimated SOM retroactively using Van Bemmelen's factor of 0.58 g SOC/g SOM (McBratney & Minasny, 2010) and the measured TOC% for each sample. Using the von Haden et al. (2020) example R-code, we used a cubic-spline interpolation function to calculate cumulative SOC stocks (g C/cm^2) on the basis of equivalent, cumulative mineral soil mass for each soil core at each site. We calculated the SOC stocks in each of the four fractions using ESM-adjusted BD output for the 0–10 and 10–30 cm depths. Because composite samples were fractionated but ESM-BD was calculated for the original individual samples, the ESM-BDs associated with each of the five samples of the composite fractionated sample were averaged.

We analyzed the overall effect of AMP grazing on bulk cumulative SOC stocks, SOM fraction C stocks, N stocks, and C:N ratios using linear mixed-effect models (with the 'lme4' and 'lmeTest' packages in R version 4.2.2), and accounted for sampling design by using nested random effects for 'site' and 'transect'.

Considering the differences among sites, we were also interested in differential effects between grazing management pairs at each site. To ensure results were conservative and to avoid overgeneralizations by only estimating global effects of AMP grazing, we also paired results from our linear mixed-effect models with individual, sitewise linear models (using the 'lm' function in R version 4.2.2) to assess the impact of AMP grazing on each of our response variables separately by site. For these site-level models, we adjusted *p*-values for multiple comparisons (i.e. four sites) using Bonferroni corrections.

2.7. Vegetation data analysis

To visualize differences in plant community composition by treatment and site, we conducted non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity using the 'metamds' function in the 'vegan' package in R. We dropped rare species (with <3 occurrences) from our analysis. To test these differences, we performed a permutational multivariate analysis of variance (PERMANOVA) using the 'adonis' function in the 'vegan' package in R. We used 'pairwise.adonis2' to further examine the effect of grazing management on plant community composition individually by site.

3. Results

3.1. Texture and site characteristics

Site characteristics, including time under management, acreage, and management characteristics are reported in Table 2. Results from our texture analysis largely parallel SSURGO soil maps at each site. Ranches within pairs all categorized as the same textural class: soils at three ranch pairs were within 3% clay of their ranch neighbors, and Site 1 ranch pair soils were within 9%. Soils were categorized as clay, loam, loam/sandy loam, and loam/sandy loam/silt loam at Sites 1, 2, 3 and 4, respectively (SI Table 2). This established that soils were similarly textured within each ranch pair and that any differences in SOC were unlikely to be due to textural differences.

3.2. Bulk SOC stocks, TOC%, and BD

Bulk SOC stocks varied across sites, ranging from a low of 71.6 Mg C/ha at Site 2 to a high of 199.2 at Site 3 (SI Table 3, Figure 2). Average whole-profile SOC stock (0–100 cm) across all sites was 121.7 Mg C/ha.

Considered together, AMP grazed ranches contained significantly greater SOC stocks in the top 0–10 cm of soil compared to CONV grazed ranches ($p = 0.017$; SI Table 5). AMP ranches also tended to contain greater cumulative SOC in 10–30 cm soil ($p = 0.14$, SI Table 5). On average, this totalled 8.6% greater cumulative SOC stocks down to 30 cm on AMP ranches, though differences were more pronounced in the 0–10 cm depth (SI Table 3). There was no clear difference in SOC stock between grazing management types below 30 cm (SI Table 5).

Considered individually, there was a statistically clear difference in whole-profile SOC stocks on AMP vs CONV grazed ranches at two of the four sites. At sites 2 and 4, the AMP grazed ranch in each pair had 25% (20.9 Mg C/ha; 0–100 cm, $p < 0.01$) and 38% (37.9 Mg C/ha; 0–100 cm, $p < 0.01$) greater cumulative SOC down to 100 cm, respectively, compared to their CONV neighbors (Figure 2, SI Table 8). SOC differences were more variable and less clear at sites 1 and 3.

Though ESM adjusts BD for any potential compaction, ESM BD was not significantly different between any ranch pair (SI Table 3, SI Table 6, SI Table 9), suggesting that greater SOC stocks at some AMP sites were due to greater TOC%. For example, compared to their CONV neighbors, AMP grazed ranches at sites 2, 3, and 4 had significantly greater TOC% in the 0–10 cm depth, and AMP ranches at sites 2 and 4 contained greater TOC% in the 10–30 cm depth, respectively (SI Table 3, SI Table 10). This resulted in a significantly greater global TOC% on AMP ranches in the topsoil ($p = 0.018$; SI Table 7). Like SOC stock results, the differences in TOC% between AMP and CONV grazed ranches were inconsistent at sites 1 and 3.

3.3. Soil organic matter fraction C stocks, N stocks, and C:N ratios

The MAOM fraction accounted for the majority of topsoil SOC and N at all sites, containing an average of 77% and 76% of total SOC and N stocks (0–30 cm), respectively. The oPOM and fPOM fractions contained an average of 15% and 7.5% of total SOC stocks, and 12% and 13%, of total N stocks, respectively. The DOM fraction contained very little SOC and N, averaging only <0.01% of SOC and N stocks across sites (SI Table 4, Figure 3, SI Figure 1).

AMP tended to have a positive global effect on MAOM-C stocks overall in both the 0–10 cm ($p = 0.17$) and 10–30 cm ($p = 0.11$) depths (SI Table 11). Individually, the effect was only statistically clear at sites 2 and 4 (SI Table 12). AMP grazed ranches at both sites

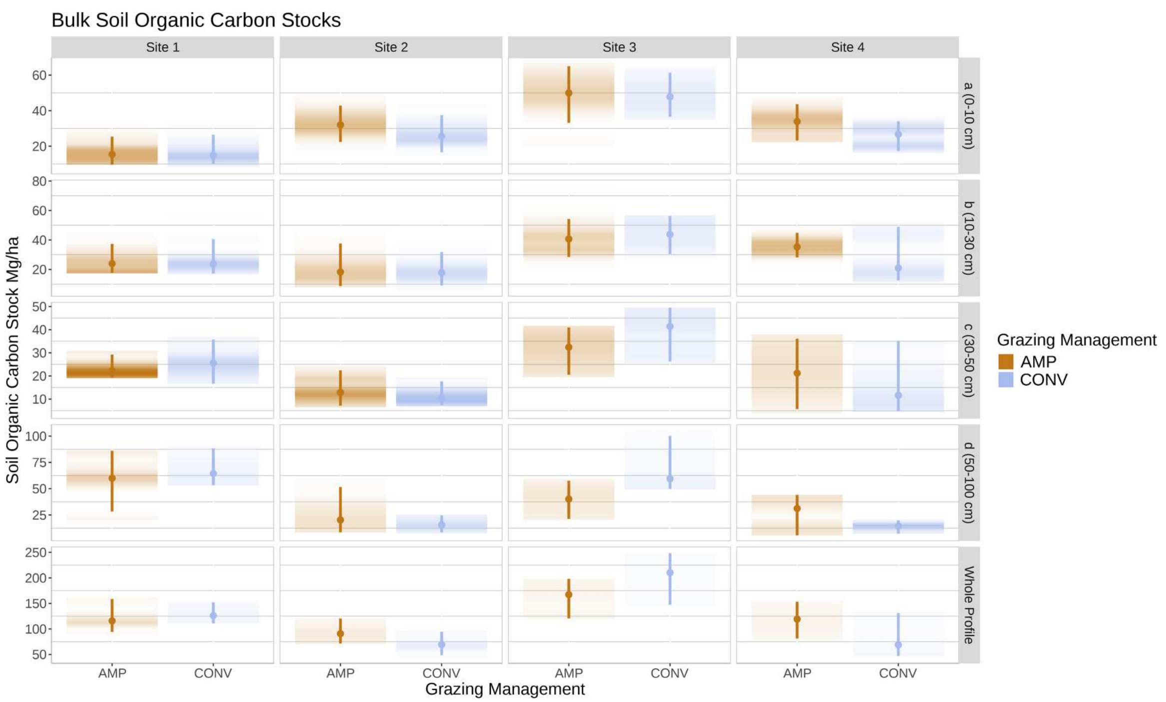

Figure 2. Bulk soil organic carbon stock (Mg C/ha) by site and depth. These are SOC stocks separated by depth for visual purposes, but statistical comparisons were made on the basis of cumulative SOC stocks at each depth. Colour gradients correspond to sample density.

had significantly greater MAOM-C stocks in the 0–10 (site 2, $p < 0.01$; site 4, $p = 0.028$) and 10–30 cm (site 2, $p < 0.01$, site 4, $p < 0.01$) depths (SI Table 12). There were no clear differences in MAOM-C stocks between AMP and CONV grazed ranches at sites 1 and 3.

Overall, MAOM-N stocks largely followed the same trends as MAOM-C, though the effect was not statistically clear at any depth (SI Table 13). Individually, only the AMP grazed ranch at site 2 contained significantly greater MAOM-N stock than the neighboring CONV ranch in both 0–10 cm ($p < 0.01$) and 10–30 cm depths ($p < 0.01$). There were no clear differences in MAOM-N stock between AMP and CONV grazing at any other site (SI Table 14).

The differences in oPOM, fPOM, and DOM-C stocks between grazing management pairs were more variable across sites and depths. In the global models, there were no clear effects of AMP grazing on oPOM, fPOM, or DOM C or N stocks at any depth (though AMP ranches tended to contain greater oPOM-C, $p = 0.14$; SI Tables 15 and 17). However, these results were not consistent across all ranch pairs individually. The AMP grazed ranch at site 2 contained significantly greater oPOM-C at 0–10 cm ($p = 0.012$; SI Table 16), and the AMP ranch at site 4 contained significantly greater fPOM-C at both 0–10 cm ($p < 0.01$) and 10–30 cm ($p = 0.004$; SI Table 18) depths. However, the CONV ranch at site 1 contained significantly greater oPOM-C in the 10–30 cm depth ($p < 0.01$; SI Table 16). Differences in oPOM, fPOM, and DOM N-stocks were not consistent by grazing management, site, or depth (see SI 2.6).

Fraction C:N ratios are reported in SI Table 19, visualized in SI Figure 2. C:N ratios were lowest in the DOM

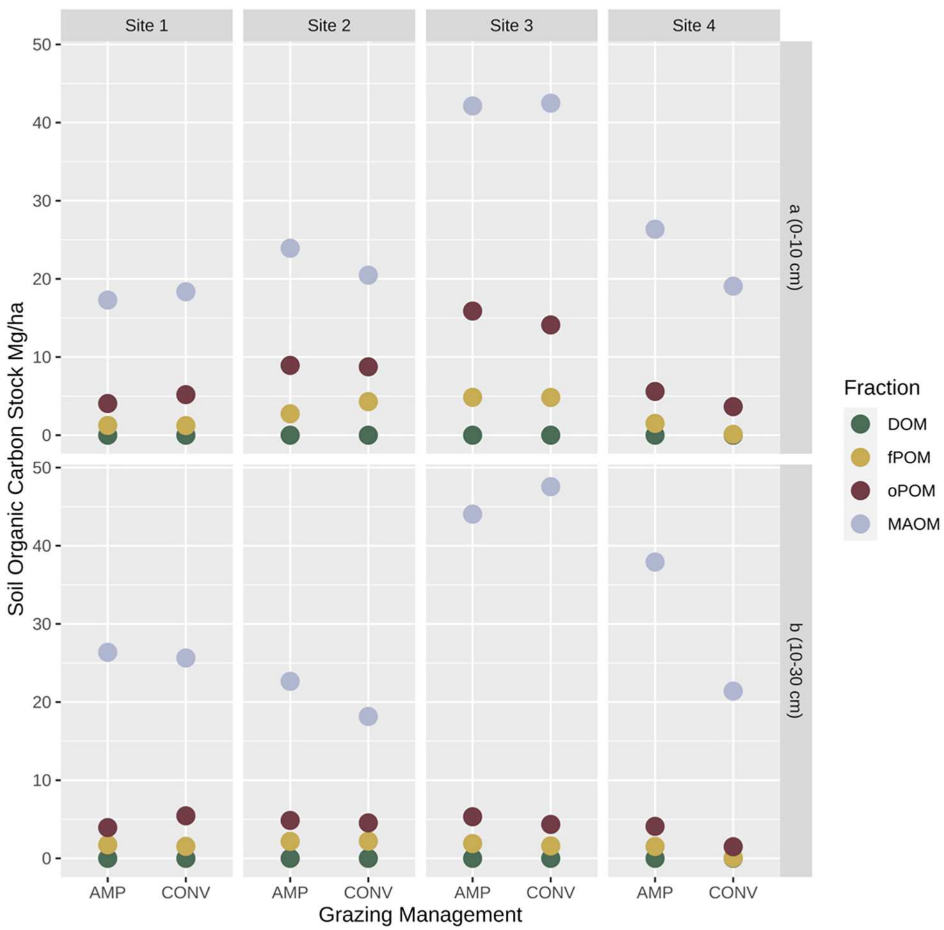

Figure 3. Mean soil organic carbon fraction stocks (Mg C/ha) by site (sites 1–4), depth (a:0–10 cm; b:10–30 cm), and grazing management (adaptive multi-paddock (AMP) and conventional (CONV)) in each fraction: mineral associated organic matter (MAOM), occluded particulate organic matter (oPOM), free particulate organic matter (fPOM), and dissolved organic matter (DOM).

fraction, followed by MAOM, oPOM, and fPOM. AMP ranches had overall statistically lower DOM C:N ratios in 0–10 cm soils ($p = 0.022$; SI Table 20). Differences in C:N ratios of other fractions between grazing management types were inconsistent and differed by site. For example, at site 2, the AMP grazed ranch had significantly lower oPOM C:N than the CONV grazed neighbor in both 0–10 ($p = 0.02$) and 10–30 cm ($p = 0.02$; SI Table 21) depths. There were no significant differences in fPOM C:N between grazing management pairs at any site.

3.4. Plant community composition

Plant communities differed significantly by site ($p = 0.03$). Plant communities at sites 1 and 3 (both coastal ranch sites) were primarily driven by perennial grasses, while plant communities at sites 2 and 4 (foothill and coastal sites, respectively) were driven by annual grasses and perennial and annual forbs (Figure 4, SI Figure 3). Across all sites, bare ground was rare. However, AMP ranches generally contained less bare ground and greater living plant cover compared to CONV-grazed ranches. Across all sites, AMP ranches had 4% greater living plant cover, 4% less litter, and 0.5% less bare ground than CONV ranches (SI Table 23).

Apart from perennial forbs and bare ground, all other plant functional groups were significant drivers of plant community composition. Percent cover by functional group for each site and ranch are reported in SI Table 23, and all identified plant species and their assigned functional groups are reported in SI Table 24.

There was a significant interaction of site and grazing management ($p = 0.02$), and plant community composition tended to differ between AMP and CONV grazed pairs, but not significantly ($p = 0.12$) (SI Table 22). Examined individually, there was no statistically clear difference in plant community composition between AMP and CONV grazing management ranches at any site, though there were some apparent differences at site 3 ($p = 0.1$).

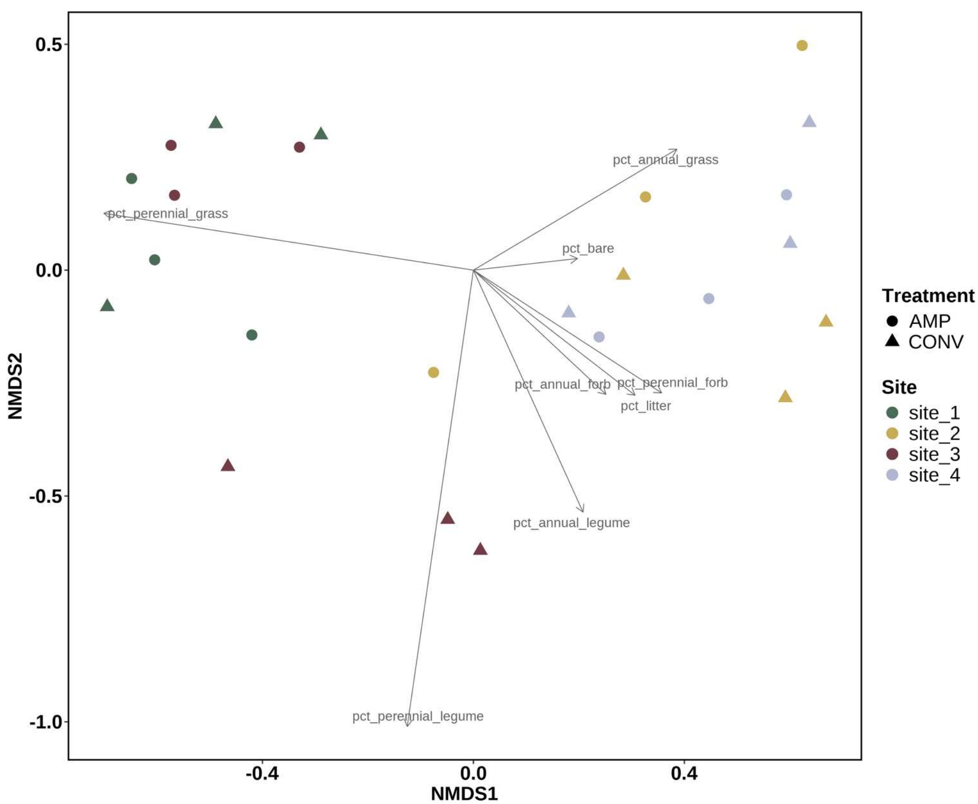

Figure 4. Non-metric multidimensional scaling of plant communities on adaptive multi-paddock (AMP) and conventionally (CONV) grazed ranches. Sites are differentiated by colour and grazing management type is differentiated by shape. Individual points are transects. Vectors indicate strength of plant community composition explained by functional group.

4. Discussion

We intensively sampled eight working ranches in northern California, collecting 1440 soil samples and 2,400 vegetation point intercepts, to evaluate ecological outcomes of AMP and CONV grazing systems in northern California. To our knowledge, this is the largest and most comprehensive single assessment of SOC on California rangelands to-date. We incorporated many current methodological gold-standards, including using improved ESM methods to more reliably calculate SOC stocks compared to traditional BD methods, fractionating SOC into functionally distinct pools to assess SOC persistence, and incorporating deep soil sampling to more accurately capture SOC response to grazing at-depth.

4.1. Soil carbon and vegetation characteristics of California rangelands

Our data reveal several characteristics of California rangelands. The three coastal rangeland sites had greater SOC stocks (average cumulative 0–100cm: 134.9 Mg C/ha) than the foothill site (average cumulative 0–100cm: 82.05 Mg C/ha) likely due to differences in precipitation – which aligns with other studies in California rangelands (Carey, Weverka, et al., 2020; Silver et al., 2010). Coastal rangelands generally have a higher composition of perennial grasses than inland foothill rangelands in California (Barry et al., 2020; Bartolome, 1987). We observed this trend at coastal rangeland sites 1 and 3, which contained 60% and 46% perennial grass, respectively, compared to only 11% perennial grass cover at our foothill site (site 2). Coastal site 4, however, had lower perennial grass cover (9%) compared to our other coastal sites, but higher perennial forb cover (19%) than any other site (SI Figure 3, SI Table 23).

The body of literature on rangeland SOC is scant and contains varying fractionation methods and depths, complicating cross-study comparisons. Across all our sites, MAOM contained 58% of total SOC on average in the 0–10 cm depth, while other studies report ~60–70% in European grasslands (Cotrufo et al., 2019; Lugato et al., 2021), ~57% in Southeastern US grasslands (Mosier et al., 2021), and 45–67% in similar California grasslands (Ryals et al., 2014). Compared to Ryals et al. (2014), soils in our study contained less SOC in oPOM (18% vs ~28%), though fractionation methods were slightly different.

4.2. Site-wise comparisons of bulk SOC on AMP vs CONV ranches

Compared to CONV-grazed ranches, some, but not all, paired AMP-grazed ranches contained greater bulk SOC stocks, indicating that potential impacts of AMP grazing on SOC may be site specific on California rangelands. Given the nuances of each pair of AMP and CONV ranches (e.g. coastal vs foothill, land use history, etc), we consider each pair to be a case study in possible impacts of AMP grazing on representative sites of common working California rangeland systems.

At sites 2 and 4, AMP grazed ranches contained 25% (20.9 Mg C/ha) and 38% (37.9 Mg C/ha) greater whole-profile SOC stocks, respectively, suggesting that effect sizes are similar at responsive sites despite soil type and geographical differences. Site 2 is a foothill site with loamy soils, while site 4 is a coastal site with sandy and silt loam soils. Site 2 also generally has hotter average summer and cooler average winter temperatures compared to site 4, which has a coastal climate that is slightly more seasonally constrained, on average. At site 2, ranch sizes and stocking rates were nearly equivalent, though the AMP grazed ranch utilizes a greater number of smaller permanent pastures which are seasonally subdivided into paddocks of varying sizes. This allows the AMP rancher to temporarily graze at significantly greater stocking densities to meet their management goals. Alternatively, characteristics of the paired ranches at site 4 were more dissimilar. The AMP grazed ranch at site 4 is a significantly larger operation than the neighboring CONV ranch and contains 25 permanent pastures of varying sizes. This AMP rancher does not subdivide pastures into temporary paddocks, but rather utilizes seasonal range riding (i.e. movement of animals from horseback) to achieve greater stocking densities to meet management goals. Alternatively, the CONV ranch at site 4 is a small enterprise which grazes a small number of animals in one pasture continuously. Despite these diverging characteristics, both ranches at site 4 have comparable stocking rates in most years, though the stocking rate of the AMP ranch at this site is more variable from year-to-year based on sales, projected forage quantity, and weather extremes. The similar stocking rates among ranch pairs at these sites suggest that applied management differences could have contributed to our measured soil outcomes.

Though no study to our knowledge has directly measured the effect of grazing management on SOC on California rangelands (Byrnes et al., 2017), effects of this magnitude were unexpected, given results from other studies and factors moderating SOC accumulation on California rangelands. For example, a similar management-based study in the US Southeast showed an average of 13% greater SOC stocks on AMP vs continuously grazed farms (Mosier et al., 2021), and a study of compost application on nearby California rangelands showed 18% and 9% increases in SOC stocks at valley and coastal sites, respectively (Ryals et al., 2014). Compared to these results, we expected SOC gains from AMP grazing management to be smaller, especially considering California's Mediterranean climate (e.g. limited rainfall), and dominance of non-native annual grasses, which have very short growing seasons compared to grasslands in other ecoregions (Booker et al., 2013).

Given these constraints to SOC accumulation on California rangelands, it is unlikely that changes of this magnitude are wholly attributable to AMP grazing. Given a maximum of 2–5 Mg C/ha/yr aboveground NPP in northern California and ~10% of NPP-C incorporation into soils (Li et al., 2012), we estimate that five years of AMP grazing could potentially sequester ~2.5 Mg C/ha in surface soils. Accounting for belowground NPP could increase this estimate. However, factors other than grazing management likely partially contributed to the large differences in SOC measured at these sites. Though AMP grazing cannot account for the total difference in SOC stocks at these sites, a portion of the observed differences is likely due to AMP grazing, especially in surface soils that change more rapidly. We expected to observe any SOC stock differences primarily in surface soils (0–30 cm) because California rangelands are dominated by annual grasses with rooting depths concentrated in this zone (Gordon & Rice, 1992).

We observed early signs of SOC surface accumulation at site 3, a coastal ranch site, where the AMP grazed ranch had 4% (2.1 Mg C/ha) greater SOC only in the 0–10 cm depth compared to the CONV grazed neighboring ranch, though this result was not statistically clear. Despite our preliminary interviews, criteria development, and stratification efforts to limit sampling to areas with no other management interventions reported by ranchers, we learned after the conclusion of our sampling that the AMP ranch at site 3 had been tilled 12 years prior. Though this tillage event likely caused SOC loss (see 30–100 cm in Figure 2), the 0–10 cm surface soils show evidence of SOC accumulation under AMP grazing post-tillage. However, the CONV ranch contained significantly greater cumulative SOC at-depth (SI Table 8).

Site 1 was the only ranch pair with no clear differences in SOC stocks between AMP and CONV grazing at any depth. Though generally SOC and clay are positively correlated, we suspect that the extremely high clay content (>65% clay) of the Vertisol soils (in the Diablo soil series, which covers 276,034 acres in California) at this site may constrain SOC accumulation from grazing management. Despite the high clay content, 0–30 cm SOC stocks at this site were among the lowest of all sites in this study. Prior studies have documented SOC response on Vertisol soils to intensive management changes (e.g. tillage), but not to more extensive changes like grazing management or changes in plant residue management (Jha et al., 2020; Muñoz-Romero et al., 2017; Waters et al., 2017). In addition to the possible soil textural constraints to increasing SOC inputs, it is possible that the grazing intensity differences between AMP and CONV were not stark enough to create measurable differences in SOC at this site (Table 2).

4.3. MAOM drives greater SOC on AMP grazed ranches

We expected that fractionating and quantifying SOC from functionally distinct SOC pools could increase the power to detect SOC changes from grazing management that may be masked by analyzing bulk soils (Six et al., 2002). While we only detected consistent differences in SOC fractions at the sites where bulk SOC was greater in AMP versus CONV ranches (sites 2 and 4), fractionations did provide information about which SOC fractions were most different between AMP and CONV ranches.

Along with other recent work (Mosier et al., 2021), our data suggest that AMP grazed ranches may consistently contain greater MAOM than CONV grazed farms and ranches compared to other, more labile fractions. In this study, AMP grazed ranches had greater MAOM-C stocks by 26% (25.8 Mg C/ha) and 43% (42.9 Mg C/ha) in 0–30 cm at sites 2 and 4, respectively. Differences in MAOM-C stocks were detected after less than five years of AMP grazing at site 2 and 12 years at site 4, indicating SOC changes in this fraction may happen quickly and potentially continue for more than a decade in response to AMP grazing in California rangelands. This also indicates long-term persistence of SOC on AMP-grazed ranches.

Particulate organic matter (POM) fractions, especially fPOM, are thought to be the youngest forms of SOC and most sensitive to management changes (Gregorich et al., 2006; Poeplau et al., 2018), but we did not find consistent differences in fPOM and oPOM in our study. Compared to MAOM, patterns of oPOM and fPOM-C stock differences between AMP and CONV grazing were inconsistent and generally small in magnitude, even when statistically significant. For example, the AMP grazed ranch at site 2 had statistically greater oPOM-C stock than the CONV grazed neighbor ranch, but the absolute difference was only 1.73 Mg C/ha. Despite their small magnitudes, the fact that AMP grazed ranches contained greater oPOM and fPOM-C stocks at different sites (versus universally greater MAOM-C stocks at responsive sites) suggests site-dependent SOC accumulation mechanisms. Another likely possibility is that POM and DOM fractions are in fact sensitive to management changes, but turnover rapidly and were not detected at our point-in-time sampling.

4.4. Plants possibly mediate SOC differences from grazing management

Increases in NPP – either from increasing soil cover or changing plant communities – could partially drive greater SOC on AMP vs CONV ranches at sites 2, 3, and 4. At all three sites, the AMP grazed ranches contained greater living plant cover and less bare ground than the CONV grazed neighboring ranches (SI Table 23). The slight reduction in bare soil (by both living plants and litter) and increased living plant cover observed at AMP ranches could drive SOC sequestration through reducing C losses and increasing both above and belowground NPP inputs to soil.

Vegetation is an important explanatory driver of SOC stocks on California rangelands (Carey, Weverka, et al., 2020), and grazing management that shifts plant communities towards greater perennial cover is another potential mechanism of SOC accumulation under AMP grazing. AMP grazed ranches in this study tended to have differing plant communities than their CONV neighbors ($p = 0.12$; SI Table 22), and though these differences varied by site ($p = 0.02$; SI Table 22), potential shifts in plant communities under AMP grazing could also partially drive greater SOC at these sites. For example, AMP ranches at sites 2 and 3 had greater perennial grass cover compared to their CONV neighbors. Perennial grasses and forbs, relative to annuals, allocate more of their biomass to below-ground roots (Brown et al., 1998; Walker et al., 2017). Root litter inputs and exudates are highly effective contributors to SOC sequestration via MAOM formation compared to above-ground plant litter inputs because they have lower C:N ratios and are in close spatial proximity to soil microbes and mineral surfaces (Austin et al., 2017; Bird et al., 2008; Sokol, Kuebbing, et al., 2019). Our data provide some support for this as a potential strategy: at site 2, the AMP grazed ranch had greater perennial grass coverage (0.16% vs 0.06%, a 91% relative difference), greater MAOM-C and MAOM-N stocks, and lower C:N ratios than the neighboring CONV grazed ranch. Bulk SOC stocks were also greater throughout the whole 0–100 cm soil profile. We speculate that one possible explanation is deeper penetrating perennial grass roots. However, when AMP grazing does impact SOC, further studies are needed to determine whether this effect is driven by shifts in plant community composition.

There was a clear division of plant communities and bulk SOC stocks by site which closely aligns with measured differences in SOC stocks under AMP grazing management (Figure 4). At the two sites with the highest cover of perennial grasses and greatest bulk SOC stocks (sites 1 and 3), we did not observe clear differences in SOC stocks between AMP and CONV grazing ranch pairs. At sites 2 and 4, which were covered by a greater percentage of annual grasses and forbs and contained lower bulk SOC stocks, AMP grazed ranches contained significantly greater SOC. This suggests that sites with less perennial grass cover, and with lower SOC stocks, could be in a greater SOC deficit and possibly more responsive to AMP grazing management. However, this hypothesis requires testing in future mechanistic research.

Lastly, our plant community data combined with AMP ranches' greater MAOM-C and SOM fraction N stocks, and lower DOM C:N ratios suggest that AMP's impact on N in these rangeland systems could drive SOC changes. While we did not find consistent, significant differences in whole plant communities between grazing management pairs, AMP grazing could be influencing plant-soil N dynamics by changing the quality of plant inputs to soils (e.g. changing root biomass allocation, exudation, and plant litter chemistry (Derner et al., 2006; Gao et al., 2008; Johnson & Matchett, 2001; McNaughton et al., 1998; Pucheta et al., 2004; Stanley, Wilson, et al., 2024; Wilson et al., 2018). For example, the careful timing and intensity of grazing reported by AMP ranchers could reduce C:N ratios of plant inputs or shift shoot/root allocation, thereby more effectively forming MAOM, which is heavily N reliant. MAOM is thought to form along two pathways: (1) an in vivo microbial turnover pathway, where high carbon use efficiency (CUE, i.e. low C:N ratio) soil inputs are preferentially and rapidly assimilated by microbes and sorbed to mineral surfaces, or, (2) a DOM-leachate direct sorption pathway, where C is leached from plant materials as DOM and directly sorbed to mineral surfaces, or a combination of both mechanisms (Cotrufo et al., 2015; Cotrufo & Lavallee, 2022; Lavallee et al., 2020; Robertson et al., 2019; Sokol, Sanderman, et al., 2019). Our results show two supporting lines of evidence for this: (1) AMP ranches at sites 2 and 4 contained greater fraction-N stocks, and (2) surface soils from AMP ranches had significantly lower DOM C:N ratios (SI Table 20). Lastly, denser distribution of manure, an important N source in grazing systems, on AMP vs CONV ranches could also partially explain this N mechanism of SOC differences. While our study alludes to shifting N dynamics as a possible pathway of increased MAOM formation, more research is needed to explore this causal relationship.

4.5. Study limitations & future research

Without ongoing long-term experiments, the only option to investigate the potential for AMP grazing to affect SOC in Mediterranean/semi-arid rangelands was an on-ranch, space-for-time study approach. Benefits of this approach include gaining understanding of outcomes from applied management, faster study results relative to over-time sampling, and utility for informing future research. However, because this technique extrapolates ecological trends (i.e. SOC change from AMP grazing) from sites with contrasting histories of management (i.e. AMP ranches that were previously CONV grazed vs CONV grazed neighbors), it requires cautious inference about the impact of management practices (Damgaard, 2019; Pickett, 1989). SOC is heavily influenced by past land management, soil texture, vegetative cover (e.g. the presence of trees), and other factors. We attempted to minimize the influence of these factors on spatial differences at our sites by establishing strict control criteria (i.e. no soil amendments or other management interventions), choosing sites that had all been historically CONV grazed prior to AMP grazing establishment, and shared the same soil type, ecological site description, and land use histories. However, despite our best efforts, it remains possible that other drivers not considered here (e.g. diverging ranch characteristics listed in Table 2) could have attributed to SOC differences in ranch pairs.

We contextualize our work in several other ways. First, we sampled intensively at four sites concentrated in Northern California, which is not representative of all rangelands generally or in California. More work is needed on rangelands in other regions of California and semi-arid rangelands broadly. Lastly, we also attempted but were unable to identify grazing exclosures at each site, which would have improved our understanding of baseline SOC stocks on rangelands and how they change with varying grazing management approaches.

This work highlights the need for further research and science-management collaborations to better document and understand the impact of AMP grazing on SOC over time, across broader geographic rangeland areas, and pathways of MAOM formation under AMP grazing.

5. Conclusions and implications

This study provides a unique comparison of SOC stocks among ranches using different grazing systems in Mediterranean rangelands of California. Based on our intensive sampling, our results suggest that AMP grazing systems may increase soil carbon stocks in certain contexts, especially in MAOM fractions that persist in soil for longer than other forms of SOC; however, it is clear that other management and ecological factors play a large role in determining SOC given that differences were not consistent. Since both CONV and AMP ranches contain substantial stocks of SOC, research is needed to improve our understanding of how grazing impacts SOC over time and across systems, including across different ecological conditions. This work and continued research will help inform current conservation practice programs and creation of new policies, including those aimed at helping California meet its goals for carbon neutrality through agricultural SOC sequestration (e.g. Healthy Soils Program Incentives Program). Given the scalability of grazing management compared to other practices like rangeland compost application, research investments into grazing systems and

SOC will be critical for determining how to guide policy incentives in California and other Mediterranean rangelands.

Note

1. Holistic Management refers to a broader decision-making framework attributed to Allan Savory that integrates goal setting, decision making, and financial planning into grazing management. Holistic planned grazing, which we refer to here as adaptive multi-paddock grazing, is the on-the-ground grazing management practice associated with, but distinct from, Holistic Management.

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Disclosure statement

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References

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*(6), 796–810. https://doi.org/10.1016/j.rama.2020.07.005

Austin, E. E., Wickings, K., McDaniel, M. D., Robertson, G. P., & Grandy, A. S. (2017). Cover crop root contributions to soil carbon in a no-till corn bioenergy cropping system. *GCB Bioenergy*, *9*(7), 1252–1263. https://doi.org/10.1111/gcbb.12428

Bailey, D. (2008). 2A. Mechanisms determining large-herbivore distribution. In H. H. T. Prins & F. van Langevelde (Eds.), & P. Frederick (Trans.), *Resource ecology: Spatial and temporal dynamics of foraging* (illustrated ed., pp. 7–29). Springer Science & Business Media.

Barry, S., Larson, S., & George, M. (2020). California native grasslands: A historical perspective a guide for developing realistic restoration objectives. *California Native Grasslands Association*, *91*(12), 2404–2423.

Bartolome, J. W. (1987). California annual grassland and oak savannah. *Rangelands Archives*, *9*(3), 122–125.

Bartolome, J. W., Fehmi, J. S., Jackson, R. D., & Allen-Diaz, B. (2004). Response of a native perennial grass stand to disturbance in California's coast range grassland. *Restoration Ecology*, *12*(2), 279–289. https://doi.org/10.1111/j.1061-2971.2004.00355.x

Bird, J. A., Kleber, M., & Torn, M. S. (2008). 13C and 15N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Organic Geochemistry*, *39*(4), 465–477. https://doi.org/10.1016/j.orggeochem.2007.12.003

Booker, K., Huntsinger, L., Bartolome, J. W., Sayre, N. F., & Stewart, W. (2013). What can ecological science tell us about opportunities for carbon sequestration on arid rangelands in the United States? *Global Environmental Change*, *23*(1), 240–251. https://doi.org/10.1016/j.gloenvcha.2012.10.001

Briske, D. D., Bestelmeyer, B. T., Brown, J. R., Fuhlendorf, S. D., & Wayne Polley, H. (2013). The savory method can not green deserts or reverse climate change. *Rangelands*, *35*(5), 72–74. https://doi.org/10.2111/RANGELANDS-D-13-00044.1

Briske, D. D., Derner, J. D., Milchunas, D. G., & Tate, K. W. (2011). An evidence-based assessment of prescribed grazing practices. In D. D. Briske (Ed.), *Conservation benefits of rangeland practices: Assessment, recommendations, and knowledge gaps* (pp. 21–74). USDA-NRCS.

Briske, D. D., Sayre, N. F., Huntsinger, L., Fernandez-Gimenez, M., Budd, B., & Derner, J. D. (2011). Origin, persistence, and resolution of the rotational grazing debate: Integrating human dimensions into rangeland research. *Rangeland Ecology & Management*, *64*(4), 325–334. https://doi.org/10.2111/REM-D-10-00084.1

Brown, C. S., Rice, K. J., & Claassen, V. P. (1998). *Competitive growth characteristics of native and exotic grasses*. California Department of Transportation.

Burcham, L. T. (1957). *California range land: An historico-ecological study of the range resource of California*. Division of Forestry Department of Natural Resources.

Bush, L., & Ptak, E. (2006). *Grazing handbook: A guide for resource managers in coastal California*. Sotoyome Resource Conservation District.

Byrnes, R., Eviner, V., Kebreab, E., Horwath, W. R., Jackson, L., Jenkins, B. M., Kaffka, S., Kerr, A., Lewis, J., Mitloehner, F. M., Mitchell, J. P., Scow, K. M., Steenwerth, K. L., & Wheeler, S. (2017). Review of research to inform California's climate scoping plan: Agriculture and working lands. *California Agriculture*, *71*(3), 160–168. https://doi.org/10.3733/ca.2017a0031

Carey, C. J., Gravuer, K., Gennet, S., Osleger, D., & Wood, S. A. (2020). Supporting evidence varies for rangeland management practices that seek to improve soil properties and forage production in California. *California Agriculture*, *74*(2), 101–111. https://doi.org/10.3733/ca.2020a0015

Carey, C. J., Weverka, J., DiGaudio, R., Gardali, T., & Porzig, E. L. (2020). Exploring variability in rangeland soil organic carbon stocks across California (USA) using a voluntary monitoring network. *Geoderma Regional*, *22*, e00304. https://doi.org/10.1016/j.geodrs.2020.e00304

Chaney, D. (2017). *What is on-farm research? How to conduct research on your farm or ranch* (2nd ed., Ag Innovations Series). USDA Sustainable Agriculture Research and Education.

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

Conant, R. T., Six, J., & Paustian, K. (2003). Land use effects on soil carbon fractions in the southeastern United States. I. Management-intensive versus extensive grazing. *Biology and Fertility of Soils*, *38*(6), 386–392. https://doi.org/10.1007/s00374-003-0652-z

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. *Advances in Agronomy*, *172*, 1–66. https://doi.org/10.1016/bs.agron.2021.11.002

Cotrufo, M. F., Lavallee, J. M., Zhang, Y., Hansen, P. M., Paustian, K. H., Schipanski, M., & Wallenstein, M. D. (2021). In-N-out: A hierarchical framework to understand and predict soil carbon storage and nitrogen recycling. *Global Change Biology*, *27*(19), 4465–4468. https://doi.org/10.1111/gcb.15782

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*(12), 989–994. https://doi.org/10.1038/s41561-019-0484-6

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. https://doi.org/10.1038/ngeo2520

Damgaard, C. (2019). A critique of the space-for-time substitution practice in community ecology. *Trends in Ecology & Evolution*, *34*(5), 416–421. https://doi.org/10.1016/j.tree.2019.01.013

Davy, J. S., Dykier, K., Turri, T., & Gornish, E. (2017). Forage seeding in rangelands increases production and prevents weed invasion. *California Agriculture*, *71*(4), 1–10. https://doi.org/10.3733/ca.2017a0025

Del Galdo, I., Six, J., Peressotti, A., & Francesca Cotrufo, M. (2003). Assessing the impact of land-use change on soil C sequestration in agricultural soils by means of organic matter fractionation and stable C isotopes. *Global Change Biology*, *9*(8), 1204–1213. https://doi.org/10.1046/j.1365-2486.2003.00657.x

Derner, J. D., Boutton, T. W., & Briske, D. D. (2006). Grazing and ecosystem carbon storage in the North American great plains. *Plant and Soil*, *280*(1–2), 77–90. https://doi.org/10.1007/s11104-005-2554-3

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

Fuhlendorf, S. D., Briske, D. D., & Smeins, F. E. (2001). Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability. *Applied Vegetation Science*, *4*, 177–188. https://doi.org/10.1111/j.1654-109X.2001.tb00486.x

Gao, Y. Z., Giese, M., Lin, S., Sattelmacher, B., Zhao, Y., & Brueck, H. (2008). Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. *Plant and Soil*, *307*(1–2), 41–50. https://doi.org/10.1007/s11104-008-9579-3

Garnett, T., Godde, C., Muller, A., Röös, E., Smith, P., de Boer, I., zu Ermgassen, E., Herrero, M., van Middelaar, C., Schader, C., & van Zanten, H. (2017). *Grazed and confused? Ruminating on cattle, grazing systems, methane, nitrous oxide, the soil carbon sequestration question – and what it all means for greenhouse gas emissions*. FCRN.

George, M. (2020). *Ecology and management of annual rangelands series, part 1: Mediterranean climate* (Ecology and Management of Annual Rangelands Series). University of California Agriculture and Natural Resources.

Global assessment of soil carbon in grasslands. (2023). FAO. https://doi.org/10.4060/cc3981en

Gordon, D. R., & Rice, K. J. (1992). Partitioning of space and water between two California annual grassland species. *American Journal of Botany*, *79*(9), 967–976. https://doi.org/10.1002/j.1537-2197.1992.tb13685.x

Gregorich, E. G., Beare, M. H., McKim, U. F., & Skjemstad, J. O. (2006). Chemical and biological characteristics of physically uncomplexed organic matter. *Soil Science Society of America Journal*, *70*(3), 975–985. https://doi.org/10.2136/sssaj2005.0116

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*, Article 114160. https://doi.org/10.1016/j.geoderma.2019.114160

Hawkins, H.-J., Short, A., & Kirkman, K. P. (2017). Does holistic planned grazing™ work on native rangelands? *African Journal of Range & Forage Science*, *34*(2), 59–63. https://doi.org/10.2989/10220119.2017.1367328

Heady, H. F. (1961). Continuous vs. specialized grazing systems: A review and application to the California annual type.

Journal of Range Management, *14*(4), 182. https://doi.org/10.2307/3895147

Heckman, K. A., Possinger, A. R., Badgley, B. D., Bowman, M. M., Gallo, A. C., Hatten, J. A., Nave, L. E., SanClements, M. D., Swanston, C. W., Weiglein, T. L., Wieder, W. R., & Strahm, B. D. (2023). Moisture-driven divergence in mineral-associated soil carbon persistence. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(7), e2210044120. https://doi.org/10.1073/pnas.2210044120

Henneman, C., Seavy, N. E., & Gardali, T. (2014). Restoring native perennial grasses by changing grazing practices in central coastal California. *Ecological Restoration*, *32*(4), 352–354. https://doi.org/10.3368/er.32.4.352

Herrero, M., Henderson, B., Havlík, P., Thornton, P. K., Conant, R. T., Smith, P., Wirsenius, S., Hristov, A. N., Gerber, P., Gill, M., Butterbach-Bahl, K., Valin, H., Garnett, T., & Stehfest, E. (2016). Greenhouse gas mitigation potentials in the livestock sector. *Nature Climate Change*, *6*(5), 452–461. https://doi.org/10.1038/nclimate2925

Herrick, J. E., Van Zee, J. W., McCord, S. E., Courtright, E. M., Karl, J. W., & Burkett, L. M. (2017). *Monitoring manual for grassland, shrubland, and savanna ecosystems, Volume 1: Core methods*. USDA–ARS Jornada Experimental Range.

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

Jha, P., Hati, K. M., Dalal, R. C., Dang, Y. P., Kopittke, P. M., & Menzies, N. W. (2020). Soil carbon and nitrogen dynamics in a Vertisol following 50 years of no-tillage, crop stubble retention and nitrogen fertilization. *Geoderma*, *358*, Article 113996. https://doi.org/10.1016/j.geoderma.2019.113996

Johnson, L. C., & Matchett, J. R. (2001). Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology*, *82*(12), 3377–3389. https://doi.org/10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2

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

Kleber, M., Sollins, P., & Sutton, R. (2007). A conceptual model of organo-mineral interactions in soils: Self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochemistry*, *85*(1), 9–24. https://doi.org/10.1007/s10533-007-9103-5

Koteen, L. E., Baldocchi, D. D., & Harte, J. (2011). Invasion of non-native grasses causes a drop in soil carbon storage in California grasslands. *Environmental Research Letters*, *6*(4), 044001. https://doi.org/10.1088/1748-9326/6/4/044001

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263. https://doi.org/10.1127/0941-2948/2006/0130

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

Li, S., Potter, C., & Hiatt, C. (2012). Monitoring of net primary production in California rangelands using landsat and MODIS satellite remote sensing. *Natural Resources*, *3*(2), 56–65. https://doi.org/10.4236/nr.2012.32009

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

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*(1), 6995. https://doi.org/10.1038/ncomms7995

McBratney, A. B., & Minasny, B. (2010). Comment on "Determining soil carbon stock changes: Simple bulk density corrections fail" [Agric. Ecosyst. Environ. 134 (2009) 251–256]. *Agriculture, Ecosystems & Environment*, *136*(1–2), 185–186. https://doi.org/10.1016/j.agee.2009.12.010

McNaughton, S. J., Banyikwa, F. F., & McNaughton, M. M. (1998). Root biomass and productivity in a grazing ecosystem: The serengeti. *Ecology*, *79*(2), 587–592. https://doi.org/10.2307/176955

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*, Article 112409. https://doi.org/10.1016/j.jenvman.2021.112409

Muñoz-Romero, V., Lopez-Bellido, R. J., Fernandez-Garcia, P., Redondo, R., Murillo, S., & Lopez-Bellido, L. (2017). Effects of tillage, crop rotation and N application rate on labile and recalcitrant soil carbon in a Mediterranean Vertisol. *Soil and Tillage Research*, *169*, 118–123. https://doi.org/10.1016/j.still.2017.02.004

Naidu, D. G. T., Roy, S., & Bagchi, S. (2022). Loss of grazing by large mammalian herbivores can destabilize the soil carbon pool. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(43), e2211317119. https://doi.org/10.1073/pnas.2211317119

Natali, C., Bianchini, G., & Carlino, P. (2020). Thermal stability of soil carbon pools: Inferences on soil nature and evolution. *Thermochimica Acta*, *683*, Article 178478. https://doi.org/10.1016/j.tca.2019.178478

Oates, L. G., Undersander, D. J., Gratton, C., Bell, M. M., & Jackson, R. D. (2011). Management-intensive rotational grazing enhances forage production and quality of subhumid cool-season pastures. *Crop Science*, *51*(2), 892. https://doi.org/10.2135/cropsci2010.04.0216

Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In G. E. Likens (Ed.), *Long-term studies in ecology* (pp. 110–135). Springer. https://doi.org/10.1007/978-1-4615-7358-6_5

Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M. F., Derrien, D., Gioacchini, P., Grand, S., Gregorich, E., Griepentrog, M., Gunina, A., Haddix, M., Kuzyakov, Y., Kühnel, A., Macdonald, L. M., Soong, J., Trigalet, S., … Nieder, R. (2018). Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – a comprehensive method comparison. *Soil Biology and Biochemistry*, *125*, 10–26. https://doi.org/10.1016/j.soilbio.2018.06.025

Pucheta, E., Bonamici, I., Cabido, M., & Díaz, S. (2004). Belowground biomass and productivity of a grazed site and a neighboring ungrazed exclosure in a grassland in central Argentina. *Austral Ecology*, *29*(2), 201–208. https://doi.org/10.1111/j.1442-9993.2004.01337.x

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

Robertson, A. D., Paustian, K., Ogle, S., Wallenstein, M. D., Lugato, E., & Cotrufo, M. F. (2019). Unifying soil organic matter formation and persistence frameworks: The MEMS model. *Biogeosciences*, *16*(6), 1225–1248. https://doi.org/10.5194/bg-16-1225-2019

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

Ryals, R., Kaiser, M., Torn, M. S., Berhe, A. A., & Silver, W. L. (2014). Impacts of organic matter amendments on carbon and nitrogen dynamics in grassland soils. *Soil Biology and Biochemistry*, *68*, 52–61. https://doi.org/10.1016/j.soilbio.2013.09.011

Saitone, T. (2003). Chapter 9. Livestock and rangeland in California. In J. Siebert (Ed.), *California agriculture: Dimensions and issues* (2nd ed., pp. 207–224). UC Berkeley: Giannini Foundation of Agricultural Economics.

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

Sayre, N. F. (2001). *The new ranch handbook: A guide to restoring western rangelands (quivira collection)* (p. 120). Quivira Coalition.

Silver, W. L., Ryals, R., & Eviner, V. (2010). Soil carbon pools in California's annual grassland ecosystems. *Rangeland Ecology & Management*, *63*(1), 128–136. https://doi.org/10.2111/REM-D-09-00106.1

Six, J., Callewaert, P., Lenders, S., De Gryze, S., Morris, S. J., Gregorich, E. G., Paul, E. A., & Paustian, K. (2002). Measuring and understanding carbon storage in afforested soils by physical fractionation. *Soil Science Society of America Journal*, *66*(6), 1981–1987. https://doi.org/10.2136/sssaj2002.1981

Soil Survey Laboratory Methods Manual. (1992). *Soil survey investigations* (Report No. 42).

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. (2022). Soil survey geographic (SSURGO) database for [California]. Retrieved January 3, 2020, from https://websoilsurvey.nrcs.usda.gov/

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

Stahlheber, K. A., & D'Antonio, C. M. (2013). Using livestock to manage plant composition: A meta-analysis of grazing in California Mediterranean grasslands. *Biological Conservation*, *157*, 300–308. https://doi.org/10.1016/j.biocon.2012.09.008

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

Stanley, P., Sayre, N., & Huntsinger, L. (2024). Holistic management shifts ranchers' mental models for successful adaptive grazing. *Rangeland Ecology & Management*, *93*, 33–48. https://doi.org/10.1016/j.rama.2023.11.004

Stanley, P., Spertus, J., Chiartas, J., Stark, P., & Bowles, T. (2023). Valid inferences about soil carbon in heterogeneous landscapes. *Geoderma*, *430*, Article 116323. https://doi.org/10.1016/j.geoderma.2022.116323

Stanley, P., Wilson, C., Patterson, E., Machmuller, M., & Cotrufo, M. F. (2024). Ruminating on soil carbon: Applying current understanding to inform grazing management. *Global Change Biology*, *30*(3), e17223. https://doi.org/10.1111/gcb.17223

Strohm, H., & Watt, K. A. (2019). *Native perennial grasses continue expanding across TomKat ranch*. Point Blue Conservation Science. https://tomkatranch.org/2019/04/24/native-perennial-grasses-continue-expanding-across-tomkat-ranch/

Stromberg, M. R., Corbin, J. D., & Antonio, C. M. (2007). *California grasslands: Ecology and management*. University of California Press.

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

Teague, W. R., Dowhower, S. L., & Waggoner, J. A. (2004). Drought and grazing patch dynamics under different grazing management. *Journal of Arid Environments*, *58*(1), 97–117. https://doi.org/10.1016/S0140-1963(03)00122-8

TomKat Ranch. (2019). *Lonetree Ranch Riparian management and planned adaptive grazing to improve land value, livestock carrying capacity, and wildlife health* (Profiles in Land and Management: Benefits of Regenerative Ranching).

Venter, Z. S., Hawkins, H.-J., & Cramer, M. D. (2019). Cattle don't care: Animal behaviour is similar regardless of grazing management in grasslands. *Agriculture, Ecosystems & Environment*, *272*, 175–187. https://doi.org/10.1016/j.agee.2018.11.023

von Haden, A. C., Yang, W. H., & DeLucia, E. H. (2020). Soils' dirty little secret: Depth-based comparisons can be inadequate for quantifying changes in soil organic carbon and other mineral soil properties. *Global Change Biology*, *26*(7), 3759–3770. https://doi.org/10.1111/gcb.15124

Walker, J. T., James, J. J., & Drenovsky, R. E. (2017). Competition from *Bromus tectorum* removes differences between perennial grasses in N capture and conservation strategies. *Plant and Soil*, *412*(1–2), 177–188. https://doi.org/10.1007/s11104-016-3053-4

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

Wendt, J. W., & Hauser, S. (2013). An equivalent soil mass procedure for monitoring soil organic carbon in multiple soil layers. *European Journal of Soil Science*, *64*(1), 58–65. https://doi.org/10.1111/ejss.12002

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

Woodmansee, G., Macon, D., Schohr, T., & Roche, L. M. (2021). On-ranch adaptation to California's historic 2012–2016 drought. *Rangelands*, *43*(6), 222–230. https://doi.org/10.1016/j.rala.2021.10.003