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Potential of crop-livestock integration to enhance carbon sequestration and agroecosystem functioning in semi-arid croplands

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ABSTRACT

While characteristics of semi-arid climates place limitations on soil organic carbon (SOC) storage, there is opportunity and urgency for increasing the quality and long-term persistence of cropland SOC content within these agroecosystems. Livestock re-integration into cropland shows potential to improve semi-arid agroecosystem functioning through shifts in biogeochemical processes and the facilitation of multiple ecosystem services involved in carbon and nutrient cycling and use-efficiency. Here we review the characteristics of grazing-based Integrated Crop-Livestock (ICL) systems and how various associated management practices may interplay with semi-arid agroecological and biogeochemical dynamics to influence soil microbial ecology and SOC accumulation and stabilization. We argue that livestock re-integration holds notable potential to increase cropland SOC through controls on landscape net primary productivity, allocation of biomass belowground, efficient recycling of residual crop nutrients, and soil biological activity related to a suite of soil ecosystem services. Achieving the full SOC accumulation potential of ICL management will require site-specific consideration of feedbacks between herbivory, soil microbial ecology, soil disturbance, and forage species interactions. Future research should focus on optimizing plant-soil-grazer feedbacks and understanding of mechanistic drivers of ICL system outcomes to optimize the design and management of semi-arid regional ICL systems for enhanced SOC quality and persistence.

1. Introduction

Livestock reintegration into cropland has been proposed as a strategy to ecologically intensify food, fiber, and fuel production systems and reduce the greenhouse gas footprint of industrial agriculture (Garrett et al., 2017; Rota and Sperandini, 2009). Integrated crop-livestock (ICL) systems are characterized by the utilization of on-site animal services as a resource for crop production and/or the use of cropland to support livestock production. These ICL systems are in fact foundational components to agriculture for over two-thirds of global farmers, contributing to about half of the world's food production (Herrero et al., 2010). However, market forces have led to the decoupling of crop and livestock production systems in industrialized agroecosystems, resulting in poor nutrient cycling within and between agricultural operations and an underutilization of ecosystem services provided by such integrated systems (Entz et al., 2005; Lemaire et al., 2014).

ICL practices employ diverse management tools and can be implemented across various scales of cropping systems (Table 1). These grazing-based practices provide economic and biological diversification of agricultural operations and use on-site animal-derived services to offset external inputs (Bell et al., 2014; Garrett et al., 2017) and minimize detrimental impacts of agricultural intensification on soil properties critical to climate change adaptation (Lemaire et al., 2014; Russelle et al., 2007). Growing interest in utilizing cropland to sequester carbon may provide new opportunities to recouple crop and animal production and help achieve the ambitious climate mitigation targets set at the COP21 (UNFCCC, 2015). This is of particular importance in semi-arid regions, which contribute substantially to global crop and livestock production despite their high vulnerability to the impacts of global climate change (Guan et al., 2009). While semi-arid climatic and soil characteristics largely determine soil organic carbon (SOC) storage and turnover, grazing on cropland nevertheless impacts diverse agroecosystem dynamics such as landscape productivity, biodiversity, the adoption of on-farm conservation practices, and trophic interactions that are essential considerations for managing SOC (Salton et al., 2014; Sanderson et al., 2013).

This article explores how and to what extent grazing-based ICL practices, along with variable co-management components, may i)

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Table 1
Characterization of predominant integrated crop-livestock systems.

Key Production Services	Land-based/within farm integration	Examples of ICL system
• Source of animal feed • Labor reduction • Nutrient provision and cycling • Soil carbon deposition • Weed management • Resource conservation • Erosion control • Fire suppression	Grazing of crop residues	• Cotton stubble with sheep or cattle • Soy and grain stubble with sheep or cattle
	Grazing dual-purpose forage crop	• Early-season grazing of alfalfa crop with sheep or cattle
	Grazing of cover crops within cash-crop rotation	• Mixed legume-cereal cover crop grazing with small and large livestock
	Pasture rotation (phase farming)	• Cereal crop and forage rotation with sheep or cattle • Sod intercropping in corn-soy rotation with sheep or cattle
	Grazing of understory vegetation in perennial cropping systems	• Vineyards with sheep • Fruit and nut orchards with small and large livestock

stimulate soil biological activity, ii) improve essential soil ecosystem processes, iii) accumulate additional SOC, and iv) provide co-benefits for climate change adaptation within semi-arid production systems. Globally, ICL systems remain understudied and, to the best of our knowledge, the underlying agroecosystem and soil biological mechanisms have not yet been shown. The body of ICL research is notably limited, and system design and agroecological components vary widely (Table 1). Thus, the lack of system-level ICL research included in this review is acknowledged. Nevertheless, we draw upon research from annual and perennial ICL systems – predominately represented by grazing of medium or large ruminants on pasture-phase rotations, cover crops, and crop residues – as well as rangeland and permanent pature systems to develop working hypotheses and better understand how edaphic, agroecological, and climatic factors may affect the regional potential of semi-arid ICL systems to store SOC and support essential soil ecosystem services. The emphasis of this review is less to predict specific ICL system outcomes and more to further develop mechanistic understanding of how various ICL management components could be utilized to maximize SOC persistence in semi-arid cropland. We specifically focus on ICL management practices that are instrumental to stimulating biological processes and long-term soil carbon sequestration, in order to inform the design of ICL systems that effectively support ecological intensification and agricultural production goals.

2. Semi-arid cropland: an underutilized sink for soil carbon

Semi-arid ecoregions cover ~15% of global land surface (Safriel et al., 2005) and climate change projections anticipate both substantial expansion of semi-arid global land area and increased dryland ecosystem degradation throughout the century (Huang et al., 2016). Semi-arid regions are ecological intermediates between desert and humid regions, with seasonal and highly variable mean annual precipitation that is usually below the regional evapotranspiration potential (Bailey, 1979). While gaps remain in understanding the primary drivers of SOC dynamics in semi-arid production systems, there is a large relative influence of environmental variables such as precipitation, temperature, geological parent material, and their compound impact on soil morphology and physicochemical characteristics such as soil pH and texture (Hoyle et al., 2016; Rabbi et al., 2014).

Temperature and soil moisture are the most significant factors regulating SOC dynamics in semi-arid agroecosystems (Wiesmeier et al., 2013), with annual precipitation rates very highly correlated to SOC storage potentials in non-irrigated landscapes (Liu et al., 2011; Rabbi et al., 2014). Both temperature and soil moisture partially shape broad ecological features that govern the quantity and quality of organic residue inputs, as well as a suite of microbial community processes related to litter decomposition and SOC transformation, stabilization, and mineralization (Conant et al., 2011; Thiessen et al., 2013). For example, soil moisture and temperature-driven decoupling of C, N, and P cycles with increasing aridity (Delgado-Baquerizo et al., 2013) place stoichiometric limitations on SOC formation and stabilization (Cleveland and Liptzin, 2007; Schmidt et al., 2011), especially in coarse-textured soils (Dlamini et al., 2016; Mcsherry and Ritchie, 2013). A sustained decline in soil moisture has been shown to reduce both labile and older, recalcitrant SOC fractions (X. Chen et al., 2015).

Climatic variables influence soil microbial communities and their regulation of ecosystem carbon storage and turnover in diverse and dynamic ways. For example, prolonged periods of both low and high soil water status may restrict microbial mineralization and SOC formation, due to poor carbon substrate and O_2 diffusion rates, respectively (Devêvre and Horwáth, 2000; Zheng et al., 2019). High mean annual temperatures are characteristic of many semi-arid ecoregions and are associated with expedited rates of enzymatic depolymerization and SOC turnover (Bond-Lamberty and Thomson, 2010; Giardina et al., 2014; Qi et al., 2016). While higher temperatures may increase microbial carbon use-efficiency (CUE) under specific soil microbial community and water status interactions, an increase in temperature is more often associated with declines in CUE (Conant et al., 2011; Devêvre and Horwáth, 2000; Manzoni et al., 2012; Zheng et al., 2019). Whereas high microbial CUE promotes microbial growth and SOC stabilization, lower CUE increases soil carbon losses with higher respiration and decreased investment in microbial biomass production (Manzoni et al., 2012).

The soil carbon sequestration potential of a given semi-arid cropland will ultimately be regulated by the most limiting accumulation factor for SOC formation (Hoyle et al., 2016). When precipitation limits biomass production, irrigation technologies are implemented to mitigate negative impacts on plant productivity and crop yield. While this may also provide SOC storage benefits (Wiesmeier et al., 2013), prolonged use of irrigation is often associated with increased salt deposition onto soil surfaces. According to UNEP (2014) estimates, nearly 50% of semi-arid irrigated landscapes are experiencing significant impacts of soil salinity. In addition to adverse impacts on plant productivity (Munns and Termaat, 1986) and subsequent residue deposition, salt-affected soils also tend to have lower microbial CUE (Rietz and Haynes, 2003) and enhanced aggregate dispersion (Wong et al., 2010) which can increase SOC accessibility to mineralization processes and further exacerbate the potential for SOC losses (Setia et al., 2013).

Land use and associated management practices are large regulators of SOC within semi-arid systems (Conant et al., 2017) and designing agroecosystems that maximize carbon inputs and minimize management induced losses could thus enhance SOC storage (Tautges et al., 2019). While some semi-arid ICL systems integrate biodiverse perennial or high-residue annual forage rotations into cropland, others utilize grazing more simply as a termination methodology for crop residues and weeds (Garrett et al., 2017). These approaches can result in widely different system-level outcomes. The adoption of diversified systems with prolonged soil cover, high residue inputs, tightly-coupled C and N cycling, and low soil disturbance have been shown to improve soil carbon sequestration and the provision of ecosystem services within semi-arid irrigated cropland (Bowles et al., 2015; Garcia-Franco et al., 2018; Plaza-Bonilla et al., 2015; Schmidt et al., 2011). While implementation varies across agroecosystems, many ICL studies consider these components essential elements of successful integrated systems (Entz et al., 2005; Herrero et al., 2010; Lemaire et al., 2014; Russelle et al., 2007).

Although semi-arid ecoregions frequently approach climatic threshold limits for SOC storage capacity (Hoyle et al., 2013; Huang et al., 2016), SOC fluxes out of dry semi-arid soils are often small and residence time can be long-lasting when not exacerbated by management-induced losses (Booker et al., 2013). Given the extent of semi-arid agroecosystems across the globe (Safriel et al., 2005) and their significant historical SOC losses, these systems are likely far from soil carbon saturation (Ahlström et al., 2015) and provide a large opportunity for global atmospheric carbon mitigation through optimizing the SOC storage conditions in managed landscapes. While the rate at which SOC sequestration in these regions occurs is generally slow, ICL systems offer varying management approaches that may be a highly effective avenue for largescale carbon storage. This is particularly worthwhile when considering residence time and the potential ecosystem services and production co-benefits resulting from soil quality improvements in semi-arid regions.

3. Pathways for soil organic carbon accumulation in crop-livestock systems

Grazing alters numerous fundamental landscape dynamics and ecological relationships that regulate SOC storage potential. Variation in edaphic properties, co-management and their interactions with grazing means that SOC can increase, decrease, or remain unchanged under diverse grazing practices (Bardgett and Wardle, 2003; Lal, 2002; Orgill et al., 2017; Pineiro et al., 2010). However, most studies implementing grazing best management practices, across various climates and agroecosystems, have reported SOC accumulation in ICL systems relative to non-integrated, less diverse cropping systems (Acosta-Martínez et al., 2004; Assmann et al., 2014; Boeni et al., 2014; Carvalho et al., 2010; Da Silva et al., 2014; Fernández et al., 2011; Fultz et al., 2013b, 2013a; Muniz et al., 2011; Souza et al., 2010; Tian et al., 2010; Tracy and Zhang, 2008). Some ICL publications have attributed potential SOC accumulation to improved rotational complexity, biodiversity, and synergistic feedbacks among ICL production components (de Faccio Carvalho et al., 2010; Entz et al., 2005; Lemaire et al., 2014; Salton et al., 2014).

However, the specific mechanisms influencing SOC stabilization and persistence under ICL management remain unclear. This is especially true in semi-arid ICL systems, resulting from a lack of grazing-specific studies within cropland and large variation in co-management practices and site-specific agroecological processes. Literature from both systems-level studies and management-specific approaches, using examples from within and outside of semi-arid regions, offer insight into potential ICL agroecological and biogeochemical pathways underlying SOC control mechanisms. Pineiro et al. (2010) proposed several mechanistic pathways that could govern the grazing influence on SOC storage, including shifts in i) forage net primary productivity and carbon deposition; ii) N stocks and cycling; and iii) decomposition rates. Furthermore, grazing is proposed here to induce alterations in SOC through additional shifts in agroecosystem and biogeochemical mechanisms of iv) plant community composition and biodiversity; v) forage photosynthate allocation and input stoichiometry; and vi) soil physical structure (Fig. 1a).

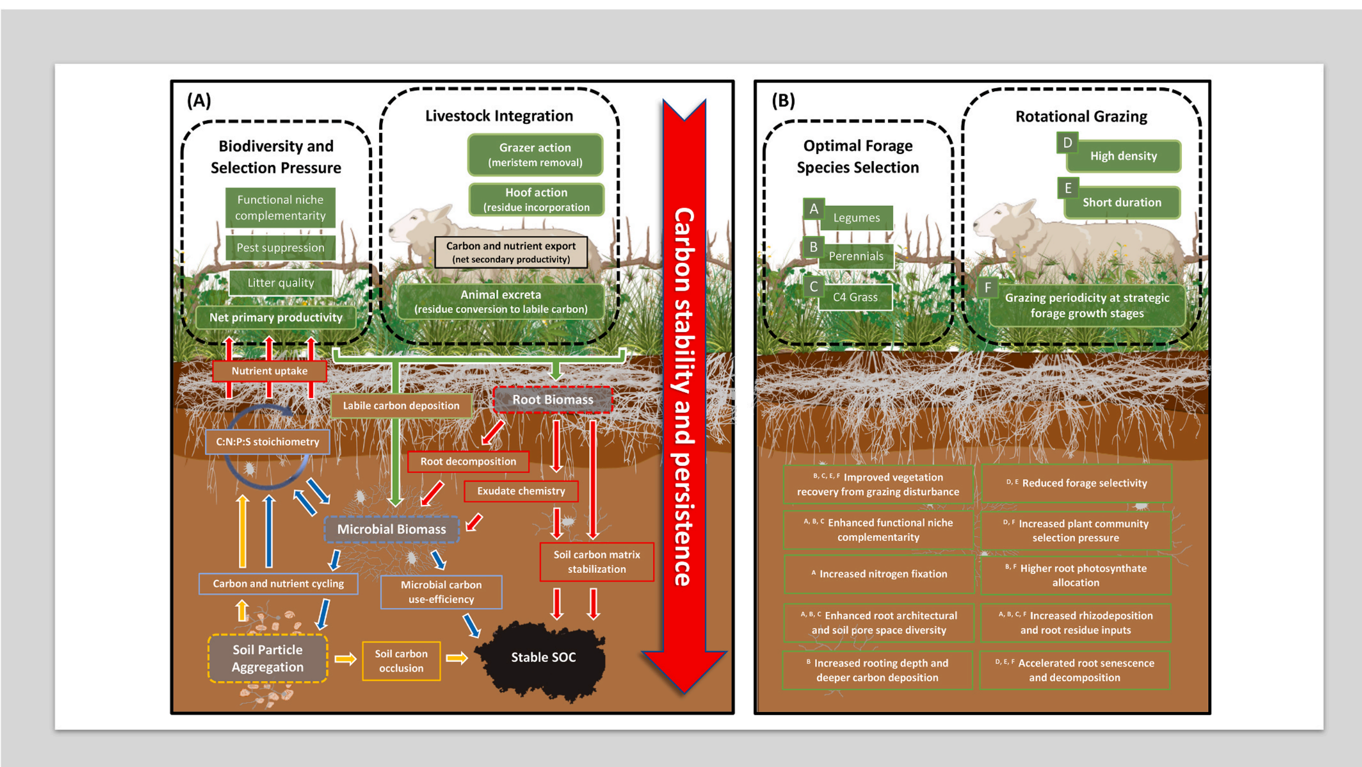

Fig. 1. Potential agroecological outcomes of ICLS adoption and the underlying soil biogeochemical mechanisms.
(A) Potential changes in functional ecological and biogeochemical relationships with ICL adoption. Grazing directly influences plant community dynamics and organic carbon inputs (green) and indirectly alters root photosynthate allocation and decomposition (red), microbial community functioning (blue), and soil particle aggregation and physical structure (yellow) with feedbacks to soil organic carbon (SOC) formation and stabilization. SOC persistence is increased as residues and animal excreta are processed through microbial transformations and stabilized through the soil mineral matrix or within soil aggregates. Where grazing may decouple carbon from essential nutrients, increasing bioavailability and reactivity, alterations in plant and microbial productivity will influence recoupling of C and N. In tandem, these counteracting forces will determine ICL agroecosystem carbon and nutrient use-efficiency. (B) Schematic representation of the agroecological implications of livestock integration under best management. Ideal forage species mixtures are biodiverse and include legumes and high-residue C4 perennial grasses. Best grazing management utilizes high density, short duration rotational grazing practices at strategic and site-specific forage growth periods. When managed properly and in tandem, these practices provide a suite of aboveground agroecological and belowground productivity and SOC accumulation benefits. Letters on belowground text boxes reference to influential practices (aboveground). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.1. Net primary productivity and carbon deposition

The accumulation of SOC is a function of the balance between carbon deposition – from plant residues, animal excreta, root exudates, and external inputs – and microbial decomposition and SOC stabilization (Jastrow et al., 2007). Increases in landscape net primary productivity (NPP) deposit more organic carbon into the agroecosystem and are positively correlated with SOC accruement in semi-arid rangelands and croplands (Briske et al., 2011; Hoyle et al., 2013). Increases in soil carbon deposition stimulate belowground trophic networks (Hoyle et al., 2013; Peterson and Lajtha, 2013) and microbially-regulated mineralization processes that can enhance soil C-, N-, P-, and S-cycling rates and nutrient availability (Leff et al., 2012). In turn, these processes increase plant nutrient uptake (Baligar and Fageria, 2015) and positive plant-soil feedbacks on system productivity and SOC accumulation (Flavel and Murphy, 2006; Lal, 2002; Ryals and Silver, 2013; Ryals et al., 2015).

Grazing of cash crop residues, cover crops, and understory biomass provide an opportunity to enhance NPP by maintaining longer vegetation cover and managing for forage quality and composition, especially by promoting the use of forage legumes (Garrett et al., 2017; Lemaire et al., 2014; Reddy and Reddy, 2016; Rota and Sperandini, 2009). Additionally, grazing has been shown to impact NPP (Bardgett and Wardle, 2003; Briske and Noy-Meir, 1998) through i) shifting photosynthate allocation toward roots (Assmann et al., 2014; W. Chen et al., 2015; Pineiro et al., 2010); ii) defoliation, removal of senescent tissues and greater light availability for actively photosynthesizing vegetation (Klumpp et al., 2009; Reeder et al., 2001; Rumpel et al., 2015); iii) changes in litter C-to-N ratios (Pineiro et al., 2010) and residue transformation rates (Breland and Eltun, 1999; W. Chen et al., 2015; Shariff et al., 1994); and iv) shifts in plant and soil microbial community structure and biomass (Bardgett and Wardle, 2003; Hanke et al., 2014). While livestock integration into cropland will export a small percentage of C and nutrients, in the form of livestock gains and respiration (Sulc and Franzluebbers, 2014), precision management may increase nutrient turnover rates and bioavailability (de Faccio Carvalho et al., 2010) to the extent that subsequent crop yields have been shown to be maintained or increased (Bell et al., 2014; Peterson et al., 2020).

Whereas increases in NPP are essential for improving SOC, there is a diminishing soil carbon sequestration benefit of increasing NPP beyond a site-specific threshold. A 20-year trial that artificially doubled plant residue inputs within unmanaged systems found that bulk SOC storage did not significantly increase, especially in more protected and stable SOC pools with slower turnover periods (Lajtha et al., 2014). This may partially be explained by a priming effect, where the decomposition of older SOC is stimulated by low concentrations of microbially-accessible N, or excessive N mineralization from recently deposited low C-to-N litter causing increased microbial competition for substrate (Kuzyakov, 2002; Qiao et al., 2016; Zatta et al., 2014). The introduction of grazing may increase priming, as defoliation triggers root senescence and quick bursts of belowground N-rich residue deposition (Bardgett and Wardle, 2003). Adversely, where best grazing practices promote the proliferation of living roots, exudates and other rhizodeposits may contribute more to long-term SOC storage through preferential and efficient utilization by soil microbes (Sokol et al., 2019). While the stimulation of NPP and maintenance of residue inputs within semi-arid ICL systems are important for SOC regulation, further increases in SOC storage will further depend on short- and long-term variability in aboveground and belowground diversity, residue quality and input stoichiometry, and spatial distribution (Peterson and Lajtha, 2013; Qiao et al., 2016).

3.2. Forage composition and biodiversity

A growing body of literature has observed a positive relationship between plant composition richness and soil carbon sequestration (Cong et al., 2014; De Deyn et al., 2008; Fornara and Tilman, 2008; Lambers et al., 2004; Lange et al., 2015; Steinbeiss et al., 2008). This benefit is associated with improvements in NPP, exudate release rate and diversity, and microbial functioning (Cardinale et al., 2012; Dijkstra et al., 2006; Lange et al., 2015; Steinbeiss et al., 2008), which result from shifts in trophic interactions and resource use and allocation among multiple species (Fornara and Tilman, 2008; Hooper et al., 2005). For instance, increased plant species richness has been shown to increase root architectural diversity and belowground biomass production, altering the spatial and temporal deposition of belowground carbon inputs (Cong et al., 2014; DuPont et al., 2014; Lange et al., 2015) and promoting the formation of soil micropores that may partially determine the storage capacity of C inputs (Kravchenko et al., 2019). More diverse plant assemblies have also been shown to enhance soil pathogen suppression, which may partially drive diversity-productivity relationships (Maron et al., 2011).

The introduction of grazing alters forage biodiversity and quality through ecological selection pressures, with resulting shifts in plant functional niche relationships and biogeochemical cycling (Hanke et al., 2014; Rumpel et al., 2015; Rutherford and Powrie, 2013; Stahlheber and D'Antonio, 2013). Heavily stocked and continuously grazed systems tend to reduce plant species richness (Pavlů et al., 2006; Rutherford and Powrie, 2013) and might shift vegetation compositions toward annual and exotic forbs and grasses (Díaz et al., 2007; Stahlheber and D'Antonio, 2013; Waters et al., 2017). However, this does not necessarily translate to reductions in vegetation cover or biomass accumulation (Stahlheber and D'Antonio, 2013). Precision grazing practices, such as rotational grazing with managed exclusion periods, are common under ICL (de Faccio Carvalho et al., 2010) and have been shown to conserve or improve plant diversity within semi-arid landscapes (Bakoglu et al., 2009; Pineiro et al., 2010), especially under conditions of low precipitation (Abdalla et al., 2018).

Variation in grazing intensity and periodicity also exert unique selective pressures over specific plant functional groups (Hart, 2001; Reeder et al., 2001; Reeder et al., 2004). The plant species composition and biodiversity of grazed lands may be controlled with proper grazing management (Sanderson et al., 2005; Stahlheber and D'Antonio, 2013). For example, persistence of annual species may be lowered by late season heavy grazing through direct hindrance of seed production (Briske and Noy-Meir, 1998), whereas perennial species tend to decrease in continuously grazed systems, as maturing buds are removed and tiller replacement is constrained (Briske and Noy-Meir, 1998; Gutman et al., 2002). Once established, perennial and C4-dominated grasslands appear more resilient to grazer-induced disturbances than annual and C3-dominated grasslands, in terms of maintaining biodiversity (Hanke et al., 2014;Reeder et al., 2001), annual biomass production (Gutman et al., 2002; Zatta et al., 2014; Zheng et al., 2011), and SOC accumulation (Abdalla et al., 2018; Beniston et al., 2014).

3.3. Decomposition, nutrient cycling and stoichiometry

Reports throughout different pedoclimatic conditions outline the significance of the nitrogen cycle in regulating SOC formation and turnover processes (Oren et al., 2001; J. Six et al., 2002; Van Groenigen et al., 2006). The stability of these SOC pools, and resulting soil carbon storage potential, not only depends on the cycling of nutrients during formation and turnover processes, but the consistency and narrow range of C, N, P, and S ratios as well (Cleveland and Liptzin, 2007; Hessen et al., 2004; Kirkby et al., 2013, 2011; Schmidt et al., 2011). Consumption of plant biomass by grazers significantly alters stoichiometric relationships in agroecosystems (Elser and Urabe, 1999; Metcalfe et al., 2014), profoundly impacting N and P cycling mechanisms by i) removal, transformation, return, and redistribution of N and P through urine and dung deposition (Parsons et al., 2013; Pineiro et al., 2010; Rumpel et al., 2015); ii) decoupling of C with N and P through animal metabolic processes (Parsons et al., 2013; Soussana and Lemaire, 2014); iii) modification of NPP, forage root activity, and C input quality (Gao et al., 2008; Hamilton et al., 2008; Hamilton and Frank, 2001; Klumpp et al., 2009; Rumpel et al., 2015); and iv) changes in compaction and aeration of top soil from hoof action (Beukes and Cowling, 2003) that differentially alter denitrification and soil respiration rates (Sexstone et al., 1985). Understanding the impacts of livestock integration on agroecosystem nutrient dynamics is therefore necessary to manage ICL systems for greater SOC accumulation.

High intensity grazing in grasslands has been shown to increase soil C-to-N ratios, as N is exported by animal biomass and expedited litter decomposition rates alter soil C and N mineralization (Hassink, 1994; Klumpp et al., 2009; Tracy and Zhang, 2008). This increase in soil C-to-N may decrease microbial CUE (Manzoni et al., 2012), thereby decreasing the relative allocation of soil C toward microbial growth (Kallenbach et al., 2016) and therefore SOC storage. Additionally, spatially heterogeneous build-ups of reactive soil N, from patches of urine and dung deposition (Afzal and Adams, 1992), can accelerate the initial stages of microbial litter decomposition (Berg, 2000; Berg and Meentemeyer, 2002). This build-up of reactive soil N may also increase the potential for N losses through leaching, denitrification, and volatilization of NH_3 (Núñez et al., 2007; Pineiro et al., 2010). Alternatively, there may be significant agroecosystem N removal upon grazing (Parsons et al., 2013) and potential N limitation for SOC stabilization. Where this occurs, N fertility management is likely to mitigate constraints within ICL systems (Janssen, 2006; Zhu and Chen, 2002). Removal of residual inorganic N with the introduction of ICL management may actually help to improve N use-efficiency and environmental outcomes relative to continuous cropping (Janssen, 2006; Snyder et al., 2009). This is achieved when ICL best management practices promote forage root biomass production and greater net ecosystem N uptake (Pineiro et al., 2009).

A majority of consumed biomass is returned to the soil as dung and urine, where carbon and nutrients are stoichiometrically decoupled and present in more labile and bioavailable forms (Eldridge et al., 2017; Rumpel et al., 2015). As stocking rates increase, nutrient decoupling by animals can outpace the C, N, and P coupling gained through greater NPP (Lemaire et al., 2014). However, significant increases in microbial biomass and enzymatic activity under ICL management (Acosta-Martínez et al., 2010, 2004; da Silva et al., 2015; Franzluebbers and Stuedemann, 2008; Muniz et al., 2011; Salton et al., 2014) may facilitate a recoupling and balancing of stoichiometric relationships (Drinkwater and Snapp, 2007; Rumpel et al., 2015). This stoichiometric balancing of C, N, and P is not only important for determining SOC ordination, quality and stability of freshly deposited carbon, but also for the mineralization of older, stable SOC stocks (Schmidt et al., 2011). The stoichiometric relationships of plant-grazer-soil interactions are mediated by species-specific herbivore metabolic processes and body size managed according to plant community composition and productivity. Whereas herbivore metabolic processes might exacerbate stoichiometric decoupling, other characteristics of ICL systems, such as enhanced agroecosystem NPP and microbial activity, can help recouple soil C with N and P and provide new avenues to prevent reactive soil N build-up and losses.

3.4. Soil physical structure and SOC occlusion

Physical protection of SOC, through intra-aggregate occlusion and mineral sorption, promotes stabilization longevity of SOC through reduced access to microbial mineralization and oxidation (Brodowski et al., 2006; Dungait et al., 2012; Kaiser and Guggenberger, 2000; Schmidt et al., 2011; J. Six et al., 2002). The strength of mineral sorption is related to the collective surface area and bonding properties of the mineral phase and the lability and aromaticity of SOC compounds (J. Six et al., 2002). While conventional understanding suggested that recalcitrant, lignin-derived, and aromatic organic C inputs contribute more to mineral-associated organic carbon (MOC), a protected and persistent pool of soil C (Kaiser and Guggenberger, 2000; Lavallee et al., 2020; Smith et al., 1997), recent research emphasizes the contributions of labile and non-structural compounds toward MOC stabilization (Cotrufo et al., 2015; Kallenbach et al., 2016). Ruminant conversion of plant structural components, such as lignin, cellulose, and hemi-cellulose (Jung and Allen, 1995), into more labile carbon compounds (Rumpel et al., 2015) may therefore enhance MOC accumulation (Cotrufo et al., 2015; Kallenbach et al., 2016) under ICL. There may be a positive feedback between MOC stabilization and soil aggregate formation, where physically occluded intra-aggregate SOC is composed predominantly of MOC, and is further protected from microbial degradation (Bongiovanni and Lobartini, 2006; Kallenbach et al., 2016, 2015; Lavallee et al., 2020).

While the existing literature is scarce, multiple ICL studies have shown improvements in aggregate stabilization (Acosta-Martínez et al., 2004; Fultz et al., 2013b; Maughan et al., 2009; Salton et al., 2014) and occluded intra-aggregate SOC (Boeni et al., 2014; Fultz et al., 2013b; Salton et al., 2014) relative to continuous cropping. However, other studies have found no increase in intra-aggregate SOC from ICL adoption (Assmann et al., 2014; Franzluebbers and Stuedemann, 2008). Souza et al. (2010) monitored three grazing intensities under integrated no-tillage soybean/pasture rotations and found that light and moderate grazing intensities substantially improved macroaggregate (4.67–9.52 mm) formation, while having a non-significant impact on microaggregates (<1 mm). They hypothesized that animal integration stimulated pasture root biomass and exudate release, resulting in higher soil particle aggregation and modest increases in total SOC content – corroborating recent findings on the relative contributions of living roots and rhizodeposits to SOC accumulation (Kallenbach et al., 2016; Sokol et al., 2019). Fultz et al. (2013a) observed significant relative increases in recalcitrant, intra-aggregate SOC pools within semi-arid ICL systems, further highlighting the potential soil carbon sequestration benefit with improved aggregate size and stability.

Aggregate formation is enhanced by biological activity, due to the particle binding dynamics of microbially-derived decomposition products (Chotte, 2005; Kallenbach et al., 2015) and the physical effects of roots and fungal hyphae (Rillig and Mummey, 2006; Tisdall et al., 1997). In addition to an increase in total microbial biomass and activity, ICL management may promote a shift toward more fungal dominated populations (Acosta-Martínez et al., 2010; Davinic et al., 2013). Improvements in particle aggregation and SOC physical protection under ICL management are also attributed to increases in organic inputs, reductions in mechanization, and increases in root growth due to forage integration into previously continuously cropped land (Acosta-Martínez et al., 2004; Salton et al., 2014; Souza et al., 2010). The introduction of livestock to cropland does provide concern over soil compaction and associated decreases in water and air conductivity (Hamza and Anderson, 2005). Whereas some field studies (Lobry De Bruyn and Kingston, 1997) and modeling approaches (Kaine and Tozer, 2005) have shown reduced soil porosity and infiltration with increased livestock trampling, other studies have found no effects of increasing stocking rates on soil physical condition (Monaghan et al., 2005). Some studies suggest that higher earthworm abundances – that result from higher stocking densities and subsequent manure deposition – could partially counter the compaction impacts from trampling (Curry et al., 2008; Schon et al., 2008). While compaction has been observed in ICL systems with cattle integration (Tracy and Zhang, 2008), the extent of compaction is drastically reduced when animal traffic occurs during dry and thawed soil conditions, as compared to wet and frozen periods (Bell et al., 2011; Drewry et al., 2004). Additionally, increases in compaction under ICL management are generally isolated to shallow soil depths, may be ameliorated through root growth and conservative tillage (Bell et al., 2011; Tracy and Zhang, 2008), and do not appear to decrease subsequent crop yields (Bell et al., 2011; Rakkar et al., 2017; Tracy and Zhang, 2008). Although it remains unclear to what extent ICL displacement of mechanization, such as tillage, weed cultivation, and mowing, will contribute to improvements in subsurface soil compaction (Soane et al., 1982), the degree to which ICL itself contributes to soil compaction largely depends on grazing management and co-management practices.

4. Managing integrated crop-livestock systems for soil organic carbon sequestration

Based on the fundamental understanding described above, there are various opportunities that exist to optimize ICL systems for enhanced SOC accumulation including management of i) grazer stocking intensity, frequency, and duration; ii) vegetation composition and coverage; and iii) soil disturbance levels (Fig. 1b). While the potential impacts of ICL adoption on SOC storage remain inconclusive, much of the literature underscores the value of controlled grazing management and some of the co-management conservation practices frequently implemented within ICL systems (Da Silva et al., 2014; Ryschawy et al., 2017; Salton et al., 2014).

4.1. Stocking intensity and rotational grazing

Grazing intensity is a function of grazer density and duration and is one of the main management drivers of SOC accumulation or decline within grazed ecosystems (Holechek et al., 1995; Zhou et al., 2017). The response of plant communities and SOC to grazing is highly context specific and dependent on interacting agroecological, edaphic, and climatic conditions (Mcsherry and Ritchie, 2013; Pineiro et al., 2010; Stahlheber and D'Antonio, 2013). However, the magnitude of these impacts will largely be determined by management with respect to the timing (periodicity and frequency) and intensity with which livestock are grazed. ICL systems may utilize either continuous grazing, where livestock graze for extended periods of time with no or infrequent rest periods, or rotational grazing where livestock are rotated frequently amongst smaller sections, allowing for longer vegetation rest periods. When compared to grazing exclusion, some studies have found a positive relationship between stocking density and SOC accumulation under both continuous and rotational grazing regimens (Conant et al., 2003; Derner et al., 2006; Dubeux et al., 2006; Manley et al., 1995; Reeder et al., 2004; Schuman et al., 2002). However, there is a site-specific threshold at which stocking rates become inversely associated with SOC storage (W. Chen et al., 2015; Da Silva et al., 2014; Dlamini et al., 2016; Ernst and Siri-Prieto, 2009; Mcsherry and Ritchie, 2013; Plaza-Bonilla et al., 2015; Teague et al., 2011), especially for labile SOC fractions (Cao et al., 2013; Silveira et al., 2013). For instance, grasslands dominated by C3 and mixed C3–C4 species are more sensitive to SOC losses at higher grazing pressures (Frank et al., 1995; Mcsherry and Ritchie, 2013) than those dominated by C4 grasses.

Under continuous grazing, lower intensity may help maximize the potential SOC accumulation provided by animal integration while minimizing the detrimental impacts of heavier grazing intensities. High intensity, continuous duration grazing practices have been shown to reduce vegetation biodiversity (Teague et al., 2011; Waters et al., 2017) and landscape productivity (W. Chen et al., 2015; Plaza-Bonilla et al., 2015; Schönbach et al., 2011), while light or moderate intensity grazing can maintain or improve biodiversity and aboveground biomass productivity compared to grazing exclusion (Cui et al., 2005). Heavy stocking rates may enhance litter decomposition and turnover rates through (i) shifts in forage population toward fast-growing species with low lignin and high N content (Rumpel et al., 2015); (ii) return of carbon in more labile forms as dung and urine (Rumpel et al., 2015); and (iii) physical breakdown and incorporation of residues with animal traffic (Schuman et al., 2002, 1999). However, belowground productivity and carbon deposition appears to benefit from light to moderate grazing, relative to high intensity or grazing exclusion (W. Chen et al., 2015; Zhou et al., 2017). A meta-analysis by Zhou et al. (2017) found that, while heavy and moderate intensity grazing decreased SOC pools, light intensity grazing significantly increased microbial biomass and total SOC compared to grazing exclusion. The importance of grazing intensity management is even more pronounced in arid and semi-arid ecoregions, where sustained high intensity grazing may result in rapid SOC decline (Dlamini et al., 2016).

Depending on the type of ICL system, rotational grazing may be essential to maintain or improve SOC (Fig. 1b). Within semi-arid agroecosystems the adoption of rotational grazing practices, which incorporate periods of rest between short and intensively stocked grazing periods, have been observed to increase SOC (Briske et al., 2011; Conant et al., 2003; Teague et al., 2011; Waters et al., 2017) and maintain topsoil (Mcsherry and Ritchie, 2013; Sanjari et al., 2008; Teague et al., 2015) relative to continuous grazing. Though some experimental results are mixed (Briske et al., 2008). Intensive rotational grazing can result in reduced animal selectivity and more uniform and homogenous grazing (Dumont et al., 2007; Leigh and Holgate, 1978; Teague and Dowhower, 2003). When grazing periodicity best management practices are utilized, this can result in a shift toward more beneficial pasture composition for SOC accumulation (W. Chen et al., 2015; Teague et al., 2011; Waters et al., 2017), with higher perennial grass content (Kemp et al., 2000) and soil coverage (Earl and Jones, 1996; Teague et al., 2011). Longer periods of rest can also enhance vegetation recovery (Sanderman et al., 2015), improve aboveground (Briske et al., 2011; Teague et al., 2011) and belowground productivity (W. Chen et al., 2015), enhance nutrient retention (W. Chen et al., 2015; Conant et al., 2003; Teague et al., 2011; Waters et al., 2017), and reduce soil erosion potential (Kemp et al., 2000; Sanjari et al., 2008).

4.2. Forage species selection

Forage species may be chosen to provide annual or short term-cover, such as through cover cropping, or as part of longer perennial understory or pasture-phase rotations. The adoption of pasture-phase rotations have shown strong evidence to maintain or improve cropland SOC (Conant et al., 2017; Franzluebbers et al., 2014; Glover et al., 2010; Jarecki and Lal, 2003; Salton et al., 2014), especially under conservation tillage management (Da Silva et al., 2014; De Souza et al., 2008; Gamble et al., 2014). Pasture-phase rotations are also more efficient than crop phases at recycling and retaining residual crop nutrients (Lemaire et al., 2014; Rumpel et al., 2015; Russelle et al., 2007), providing direct benefits for subsequent crop yields (Maughan et al., 2009; Tracy and Zhang, 2008). Choice of forage species for pasture or cover cropping is an important consideration when implementing ICL systems (Fig. 1b), as specific plant functional groups have been shown to strongly mediate SOC storage potentials (Lange et al., 2015; Oelmann et al., 2007; Steinbeiss et al., 2008; Temperton et al., 2007; Wu et al., 2017).

Pasture-phase rotations are often dominated by cool or warm-season perennial grasses, sometimes incorporating leguminous N-fixing species (Bell et al., 2014; Bell and Moore, 2012; Russelle et al., 2007). Perennial grasses have more extensive root development and prolonged soil cover compared to annual pastures or cropland (Beniston et al., 2014; Glover et al., 2010; Schipanski and Drinkwater, 2012). Studies have consistently shown that root-deposited C has a longer residence time than aboveground-derived carbon (Mazzilli et al., 2015; Rasse et al., 2005), potentially due to increased physico-chemical protection and sorption interactions during decomposition (Rasse et al., 2005). Additionally, increased biological activity from fine root development and rhizosphere exudation also promote microaggregate formation and subsequent enhancement of SOC physical occlusion within the soil matrix (Jastrow et al., 2007, 1998; Johan Six et al., 2002). Perennial pastures have also been shown to (i) mitigate soil carbon loss from erosion (Robertson et al., 2009; Russelle et al., 2007; Schipanski and Drinkwater, 2012); (ii) improve water holding capacity and use-efficiency (Bell et al., 2014; Tracy and Zhang, 2008); (iii) and increase microbial biomass and activity (Acosta-Martínez et al., 2010, 2004; Beniston et al., 2014; DuPont et al., 2014) relative to annual-dominated pastures and continuous cropland, potentially providing positive feedbacks for SOC accumulation.

While plant community composition strongly affects SOC storage processes, the influence of specific plant functional groups within more complex and diverse communities remains poorly understood. Introducing legumes may partially mediate belowground productivity and turnover as well as a suite of biogeochemical functions that benefit SOC storage. Semi-arid grassland communities containing legumes show increases in plant functional complementarity and facilitation that reduce competition for soil N (Wu et al., 2017), increase leaf N uptake (Temperton et al., 2007), and enhance P bioavailability (Drinkwater and Snapp, 2007). Drinkwater et al. (1998) found that even when leguminous mixtures did not increase aboveground biomass production, these systems still resulted in higher accumulation of new SOC compared to non-leguminous mixtures. However, other studies have found that predominately leguminous plant mixtures negatively affect SOC storage (Lange et al., 2015). This may be due to reduced root biomass production and rhizosphere activity (Bessler et al., 2009; Lange et al., 2015) or decreasing C-to-N ratios accelerating the decomposition of resident SOC (Kuzyakov, 2002; Qiao et al., 2016).

Different forage legumes do not perform equally to grazing disturbances (Kleen et al., 2011; Schwinning and Parsons, 1996) and species selection is therefore an important best management practice consideration. Annual re-planting of red or white clovers may provide an optimal outcome, due to their preferential selection by grazers (Dumont et al., 2007) and positive performance under grazing pressure with respect to total forage productivity (Sanderson et al., 2005) and protein content (Kleen et al., 2011). The pairing of grass species, especially C4 grasses, with legumes appear to maximize ecosystem functional niche complementarity and SOC accumulation benefits, especially compared to monocultures (Fornara and Tilman, 2008). This is likely achieved through increased access and provision of N by legumes and greater N uptake and use-efficiency by C4 grasses, in both high and low diversity plant communities (Fornara and Tilman, 2008). In addition, landscapes dominated by C4 and perennial grasses show greater adaptation to heavier stocking rates. Their higher root-to-shoot ratios and subsequent increases in belowground carbon deposition have been shown to sequester additional SOC with grazing (Dubeux et al., 2006; Mcsherry and Ritchie, 2013; Orgill et al., 2017; Waters et al., 2017).

4.3. Tillage disturbance and residue retention

The interaction of grazing traffic and h and adaptationeavy tillage co-management is likely to reduce the SOC accumulation potential of semi-arid ICL systems (de Faccio Carvalho et al., 2010; Franzluebbers and Stuedemann, 2008; Siri-Prieto et al., 2007; Sulc and Franzluebbers, 2014), especially at shallow soil depths (Acosta-Martínez et al., 2004; Fultz et al., 2013b). However, the use of controlled grazing and the introduction of forage plants can assist in noxious weed suppression and residue management (Schoofs and Entz, 2000; Schuster et al., 2016; Sean Clark and Gage, 1996; Tracy and Davis, 2009), potentially reducing the use of mechanical disturbance and better facilitating a transition to conservation tillage management within semi-arid cropland (Smith et al., 2015).

A decrease in mechanical cultivation abates the turnover of macro- and microaggregates that facilitate the physical occlusion and protection of SOC, thereby reducing the exposure of older, stable SOC to microbial decomposition (Mikha and Rice, 2004; Six et al., 2000). This is particularly critical for semi-arid ICL systems where increases in occluded intra-aggregate SOC are proposed to be a significant part of the SOC accumulation benefit. In addition to increasing SOC storage potential, conservation tillage practices can increase microbial biomass (Acosta-Martínez et al., 2004; Angers et al., 1993; Franzluebbers et al., 1995) and activity (Acosta-Martínez et al., 2010; Deng and Tabatabai, 1997) and promote the proliferation of soil fungi (Frey et al., 1999) which have shown to be critical for stable SOC formation (Kallenbach et al., 2016; Liang et al., 2019). A 13-year study comparing the relative outcomes of different semi-arid annual cropping systems found 22% more SOC in the 0–15 cm depth fraction under no-till (NT) ICL management than conventional tillage (CT) continuous cropping, with significantly more SOC within occluded intra-aggregate pools (Fultz et al., 2013a). A study by Carvalho et al. (2010) also observed significantly higher SOC accumulation in multiple depth fractions down to 25 cm under NT ICL management relative to both CT ICL and continuous cropping systems. Larger amounts of retained surface residues under NT also help reduce soil surface exposure, thereby improving soil water conservation and soil temperature regulation (Lal and Kimble, 1997; Ramakrishna et al., 2006) and reducing soil erosion potential (Lal and Kimble, 1997; Plaza-Bonilla et al., 2015).

5. Ecosystem services and co-benefits

The overwhelming thrust of agronomic research and technological development over the last half century has focused on improving the productivity and sustainability outcomes of agricultural systems that are increasingly specialized in crop or livestock production. Nevertheless, a growing body of literature suggests that reintegrating livestock at the farm-scale can provide economic and environmental benefits while reducing risks associated with manure nutrients and market and weather variability (Garrett et al., 2017). In the face of increasing resource scarcities, climate change, and societal demands for a broad set of sustainability outcomes, ICL systems offer the potential to advance agriculture toward several key sustainability goals that are essential for climate change resilience, including: (i) improved net landscape carbon sequestration; (ii) increased growth of total agricultural productivity per unit of land; (iii) significant gains in N and P nutrient use-efficiency; (iv) improved erosion control; and (iv) reduced vulnerability to crop and livestock losses associated with environmental stresses. For instance, pasture-phase rotations in annual cropping system and prolonged maintenance of understory vegetation in perennial cropping systems enhance landscape NPP, reduce erosion and surface runoff, and increase nutrient recycling efficiency through deep and fibrous forage rooting that reintroduce leached nutrients back into the crop rooting zone. This further reduces groundwater contamination and external input requirements.

When managed properly, the introduction of forages and grazing have also been shown to suppress weed pressure, mitigating the use of mechanical and chemical pest control methods. Additionally, multiple ICL studies have observed the maintenance or improvement of subsequent crop yields following the introduction of grazing and pasture-phase integration (Maughan et al., 2009; Peterson et al., 2020; Tracy and Zhang, 2008). Improvements in soil structure increase infiltration rates and facilitate groundwater recharge while prolonging the period before initiation of seasonal irrigation requirements, with significant benefit for semi-arid producers. However, more ICL-specific research must be conducted to quantify the co-outcomes – including potential improvements in soil health, decreases in chemical inputs and labor, and potential tradeoffs such as compaction, stoichiometric nutrient decoupling and the build-up of reactive soil N.

6. Conclusion and knowledge gaps

With a diversity of applications and management options, ICL systems have significant global adoption opportunity and climate change mitigation and adaptation potential. Livestock re-integration may impact cropland SOC dynamics through modifying (i) above- and belowground biomass production; (ii) recycling of residual crop nutrients; (iii) biological activity and trophic networks complexity; (iv) soil structure and SOC physical protection; (v) accumulation of labile SOC fractions; and (vi) impacts on noxious weed cycles and subsequent use of mechanical cultivation (Lemaire et al., 2014; Salton et al., 2014; Vilela et al., 2011). The direction and magnitude of these impacts will largely be determined by climate and soils as well as interactions with other agroecosystem management components including plant species composition and cover, crop rotations, fertilization regimens, and soil disturbance.

Maximizing SOC accumulation potential under ICL management will require consideration of the important feedback between herbivory, soil microbial ecology, and forage species interactions (Fig. 1a). While various findings of this overview were drawn from isolated management approaches, and may contradict or be altered over time, the existing body of research strongly supports the use of no-till management to capitalize on other potential SOC accumulation mechanisms of semi-arid ICL systems. Research also supports the utilization of C4 and perennial or high-residue annual forages, legumes, and light to moderate intensity rotational grazing practices for building SOC within semi-arid cropland (Fig. 1b). Managing for enhanced biodiversity and tighter nutrient control will also assist in capitalizing on proposed SOC benefits of ICL.

However, specific knowledge gaps remain in optimizing plant-soil-grazer feedback and co-management practices to improve SOC quality and quantity. While much of the literature highlights potential changes in total SOC stoichiometry and quantity under ICL management, it is still unclear to what extent simply increasing SOC content provides short, medium, and long-term benefits. The accumulation of SOC may be central to realizing the climate change mitigation potential of agriculture, especially in semi-arid ecoregions where SOC storage potentials are rarely achieved (Ahlström et al., 2015) and often limit improvements in soil health and agroecosystem resilience to climate change. However, the utilization of SOC for its nutrients and energy to conduct microbial functions is an essential consideration. In this case, the quality of SOC may be much more important than the total quantity sequestered, and long-term persistence and stabilization of SOC, especially to mineral surfaces, may come as a trade-off for microbial accessibility.

As discussed, the integration of ruminant grazing into cropland may alter many SOC transformation pathways, and further research should focus on better understanding the mechanistic drivers of these outcomes, especially relating to semi-arid SOC quality, turnover, and stabilization dynamics. Additionally, the breadth of ICL research must expand across diverse climatic, edaphic, and agroecological conditions while placing a stronger emphasis on the biogeochemical outcomes of systems-level analyses. The extent to which specific ICL system practices, or combinations of management decisions, provide SOC benefits still remains unclear, and more long-term research is necessary to develop a comprehensive and interdisciplinary understanding of how these specific agroecological systems may benefit producers, the environment, and society at large.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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