

Review Paper

How soil biota regulate C cycling and soil C pools in diversified crop rotations

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ABSTRACT

Agricultural intensification has substantially reduced soil biodiversity as well as agroecosystem functions and services. Sustainable agroecosystems that increase crop diversity through rotation may promote soil biodiversity and above-belowground interactions. Studying ecological networks, soil communities, and abiotic impacts simultaneously increases our understanding of complex C cycling encompassing all components of a given system. Higher rotational diversity enhances primary productivity by increasing the photosynthetic intensity of crops in rotation relative to systems where a given crop is grown continuously. In addition, greater temporal crop diversity stimulates above-belowground interactions, which affects carbon allocation, rhizodeposition, and the growth of rhizobiomes. Stronger above-belowground interactions will intensify ecological connections between microbial and faunal networks among roots, rhizosphere, and bulk soil. This further strengthens soil functions and interactions between networks of biotic elements (plant inputs and soil food web functioning) and abiotic factors (soil matrix and microenvironments), providing positive feedback loops on soil organic C accrual. This review describes how interactions between rotational and biological diversity drive biodiversity-function relationships. By increasing the quantity, quality, and chemical diversity of C inputs, crop rotations with higher functional diversity foster soil communities and enhance biotic-abiotic interactions, with positive impacts on the formation and storage of soil organic matter.

1. Introduction

Soil C pools, one of the critical components of global C cycling, store around 2500 billion tonnes of soil organic C (SOC), at least three times more than C found in the atmosphere or living biomass (Lal, 2004; Schmidt et al., 2011). SOC contributes roughly 60% of the mass of soil organic matter (SOM), a mixture of heterogeneous materials including exudates and fresh to progressively decaying debris of plants, microorganisms, and soil fauna (Pribyl, 2010). However, to meet the growing demands for food, feed, and fiber, current agricultural systems often rely on intensive management practices (e.g., tillage, excessive fertilization, and pesticides application) that threaten SOM stabilization and formation through soil erosion, salinization, nutrient depletion/imbalance, and deterioration of soil structure and aggregation (Lal, 2011). For example, intensive cultivation accelerates SOM decomposition and leads to SOC losses of 25–75% in agricultural soils at the global scale (Lal, 2011), with an estimated cumulative release of 1500 Gt CO₂ to the

atmosphere between 1751 and 2017 (Sanderman et al., 2017; Friedlingstein et al., 2019). Implementing enhanced system and crop management, such as crop rotations and cover crops, has the potential to reverse this trend and promote soil C sequestration (Table 1; Lal, 2011; Lal et al., 2015).

Crop rotation, the sequential planting of crops over time, is used worldwide. Compared to continuous cropping, rotations containing multiple crops increase the temporal diversity in plants and functional traits, generating a legacy effect within the soil. This legacy effect is caused by historical cropping management that alters soil environments physically or through plant residues remaining after harvest (Crotty et al., 2016), and it is critical in shaping soil biodiversity and agroecosystem functions (Lange et al., 2015; Tiemann et al., 2015; Faucon et al., 2017). For example, adding cover crops, such as Juan triticale (*Triticosecale Wittm.*), Merced rye (*Secale cereale* L.), common vetch (*Vicia sativa* L.), pea (*Pisum sativum* L.), faba bean (*Vicia faba* L.), radish (*Raphanus sativus*), and phacelia (*Phacelia tanacetifoli*) in a tomato-cotton rotation increases the community diversity of symbiotic fungi

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Abbreviations

C	carbon
N	nitrogen
P	phosphorus
SOC	soil organic C
SOM	soil organic matter
DOC	dissolved organic C
CUE	C use efficiency
PGPM	plant growth-promoting microorganisms
AMF	arbuscular mycorrhizal fungi

(mycorrhizal fungi) during the cash crop growing season, improving nutrient uptake and increasing plant tolerance to biotic and abiotic stress (Snapp et al., 2005; Schmidt et al., 2019). Integrating perennial grass (e.g., bahiagrass; *Paspalum notatum*) into a peanut-cotton rotation promotes strong and vigorous root systems that can penetrate through the natural zone of soil compaction and ultimately increase soil aeration, water infiltration, and soil structure (Katsvairo et al., 2007b). Consequently, crop rotations provide important and valuable ecological and economic benefits (Garcia et al., 2013; Tiemann et al., 2015; Lechenet et al., 2017; D'Acunto et al., 2018; Hu et al., 2018a). Increasing SOM is a key benefit of crop rotations given the critical impact of SOM on various properties and processes of productive soils. As soil functions are tightly connected to agroecosystem productivity and sustainability, optimizing the quality and content of SOM will benefit agroecosystems by enhancing soil structure, improving macro-porosity and water infiltration, increasing biotic biomass, activity, and diversity, in addition to acting as a pool of potential plant-available nutrients (Lal, 2011).

The amount of C stored in soils supporting rainfed agriculture is determined by the balance between C inputs – mainly from plant biomass decomposition (Fig. 1c) and rhizodeposition (Fig. 1d) – and losses or outputs – mainly from oxidation/mineralization in addition to erosion and leaching (Fig. 1i; Lal et al., 2015; Ahkami et al., 2017). Larger C pools have been observed in diversified crop rotation systems, especially those containing crops with diverse functional traits, which are referred to as functional crops (Table 1; McDaniel et al., 2014a; King and Blesh, 2018). Examples of functional crops include perennial crops with high root exudation rates or cover crops (non-harvested species) producing larger C litter inputs, both of which have distinct functional traits that would favor a beneficial microbial community relative to annual crops (Faucon et al., 2017; Pausch and Kuzyakov, 2018). Overall, crop rotations containing functional crops can increase primary production, change chemical traits of crop residues (e.g., N and P concentration; Fageria et al., 2005; Maltais-Landry et al., 2014), and alter root traits (e.g., nitrogen-fixing bacteria and mycorrhizal fungi; Möller et al., 2008; Turrini et al., 2016). These differences in functional traits can exert a considerable influence on agroecosystem functions (e.g., C sequestration and nutrient regulation), and in turn enhance the quality, quantity, and chemical diversity of C inputs while reducing leaching and erosion (Fig. 1; Tiemann et al., 2015; Grabau and Chen, 2016; Li et al., 2018). More abundant and chemically-diverse C inputs increase the activity, abundance, and diversity of biotic communities (Venter et al., 2016). For example, the meta-analysis of McDaniel et al. (2014a) reported that crop rotations, especially those with cover crops, increased soil C and microbial biomass C by 8.5% and 20.7% on average compared to monocultures, respectively, highlighting the importance of belowground communities and activities in increasing SOC. This is consistent with an emerging paradigm centered on the biotic regulation of C cycling, where SOM dynamics are strongly linked to the organisms that are active in the rhizosphere and bulk soil (Schmidt et al., 2011; Dungait et al., 2012; Bender et al., 2015; Lehmann and Kleber, 2015; Crowther et al., 2019). Besides, changes in the sequence of crops in rotation

impact C deposition, the timing of rhizodeposition, nutrient availability, and stress tolerance, which modulates the soil community diversity and structure and further affects the formation and storage of SOC (Taheri et al., 2016; Bakhshandeh et al., 2017; Pausch and Kuzyakov, 2018). King and Blesh (2018) reported that crop rotations including perennial and cover crops increased SOC by 12.5% and 6.3% on average relative to grain-only rotations, respectively, while legume-cereal grain rotations decreased SOC by 5.3%.

Soil biota, one of the largest reservoirs of biodiversity in terrestrial ecosystems, comprise a substantial number of organisms, including microorganisms (e.g., bacteria, fungi, and archaea), soil fauna (e.g., nematodes, arthropods, and earthworms), and plants living all or part of their lives in or on the soil (Orgiazzi et al., 2016). Here, we define all C processes involved with soil biota as soil biotic-driven C cycling. Recently, there has been increasing attention devoted to the linkages between the diversity of above and belowground C inputs and the stimulation of soil biological communities and soil biotic-driven processes by increasing functional traits in crop rotations, which results in positive carryover effects on crop production and long-term soil functions (Fig. 1; Tiemann et al., 2015; Finney and Kaye, 2017; King and Blesh, 2018). This paradigm mainly emerges from previous theories that focused on how the quality and quantity of plant inputs affected SOM and its stabilization, including the impacts of specific practices, e.g., stubble retention or straw addition (Rahman et al., 2007; Sommer et al., 2011). Abiotic factors, e.g., soil microenvironments (i.e., conditions in a given location of the soil that differ from the surrounding area, such as the rhizosphere) and the soil matrix, also play a key role in belowground C cycling (Cotrufo et al., 2013; Briones et al., 2014; Kallenbach et al., 2018), and we refer to these processes as abiotic-driven C cycling.

Past research has highlighted that belowground C cycling occurring in plant ecosystems is context-specific, with substantial differences in biotic factors, including the stoichiometry of deposited C (e.g., from living roots and litter) and the associated belowground communities and activities, and abiotic elements (e.g., microenvironments and the soil matrix) among systems. However, knowledge gaps remain in terms of how rotational diversity affects

- 1) the mechanisms that soil biota utilize to regulate C cycling, including C allocation, rhizodeposition and associated rhizosphere microbial activities, and the interactions among crops and different trophic levels of soil biota;
- 2) the interactions among biotic- and abiotic factors in promoting C stabilization;
- 3) the mechanisms that could offset the C cycling benefits of diversified crop rotation.

We address these knowledge gaps in detail in this review by discussing 1) how functionally diverse crop rotations affect above and belowground C movements (mainly C allocation and rhizodeposition), 2) how these movements affect soil microbial and faunal communities and resulting agroecosystem processes (biotic- and abiotic-driven C cycling) and services, and 3) potential mechanisms that could restrict and disrupt C formation and stability in diversified crop rotations (Figs. 1 and 2).

2. Potential mechanisms of soil biotic-driven C cycling under crop rotations

Many studies have demonstrated that soil biota are the primary drivers of soil C cycling through several processes (Dungait et al., 2012; Zhang et al., 2013b; Trivedi et al., 2016), including translocation of fixed C and rhizodeposition, decomposition, anabolism, sequestration, and respiration (Fig. 1b, c, d, e, g, and h). These processes are key factors in regulating and stabilizing above-belowground C fluxes and nutrient cycling, contributing significantly to soil food webs, crop growth, and ultimately SOM formation (Fig. 3; Wardle, 2013). Most importantly,

these processes are stimulated by diversified crop rotations. For example, crop rotations increase the abundance and diversity of soil fauna (e.g., earthworms) and saprotrophs that break down and biochemically transform organic materials into available forms (e.g., DOC, $\text{NH}_4^+\text{-N}$, and $\text{NO}_3^-\text{-N}$), making them accessible for the entire soil food webs (Fig. 1) and plant uptake (Fig. 3; Venter et al., 2016; Ashworth et al., 2017; Fujii and Takeda, 2017). Many plant-associated

microorganisms living in the rhizosphere (e.g., plant symbionts) are promoted by diversified crop rotations and they can interact with free-living saprotrophs and consequently affect C use efficiency (CUE) (Fig. S1; Bedini et al., 2013). Diversified crop rotations also regulate communities of higher trophic levels (e.g., predatory nematodes and earthworms), which affects the decomposition rate of litter and plant debris, as the activity of higher trophic levels manipulates lower trophic

Table 1

SOC concentration of shallow soil (0–20 cm and shallower) under diversified crop rotations. These data are mainly from representative studies published after 2014. A more extensive comparison can be found in the meta-analysis of McDaniel et al. (2014a).

Cropping system	Soil	Tillage ^b	Soil depth	SOC (mg C g ⁻¹)	Main effect of systems on SOC	Reference
Spring wheat-spring wheat-canola- spring wheat-spring wheat-flax	Elstow clay loam	NT	0–15 cm	77.1	Negative effect of fallow	McConkey (2003)
Fallow-flax-spring wheat-fallow-canola-spring wheat				67.8		
Pea-spring wheat-flax-winter wheat	Indian Head clay			56.1		
Spring wheat-spring wheat-flax-winter wheat				56.4		
Fallow-spring wheat-spring wheat-winter wheat				53.0		
Winter wheat-vetch	Loam (Vertic Luvisol)	NT	0–10 cm	13.2	Negative effect of tillage	Hernanz et al. (2009)
		MT	8.5			
		CT	7.2			
Continuous barley	Silty clay (Humic Gleysol)	CT	0–10 cm	33.3	Positive effect of perennials	Maillard et al. (2016)
Barley-red clover/orchard grass				36.9		
Wheat-fallow	NA ^a	NT	0–10 cm	11.4	Positive effect of more diverse rotation	Rosenzweig et al. (2018)
Wheat-corn/sorghum/proso millet/peas/sunflower-fallow				12.3		
Wheat-corn/sorghum/proso millet/peas/sunflower				13.3		
Wheat-flax-alfalfa-alfalfa	Heavy clay (Humic Vertisol)	CT	0–15 cm	29.5	Positive effect of more diverse rotation	Bell et al. (2012)
Oat-soybean/faba bean-wheat-flax				32.9		
Oat-alfalfa-alfalfa-flax	Sandy loam (Orthic Black Chernozem)	NT		14.8		
Oat-canola-wheat-flax				14.3		
Continuous corn	Clay loam	CT	0–20 cm	70.2	Positive effect of more diverse rotation	Congreves et al. (2017)
Corn-soybean				80.0		
Corn-soybean-winter wheat				91.1		
Pearl millet-wheat	Mixed loamy sand (Hyperthermic Typic Haplustepts)	NT	0–15 cm	5.1	Positive effect of more diverse rotation	Singh et al. (2018)
Pearl millet-chickpea				5.3		
Pearl millet-mustard				5.2		
Continuous corn	sandy loam mesic Typic Hapludalfs	CT	0–10 cm	16.2	Positive effect of more diverse rotation	Tiemann et al. (2015)
Soybean-corn				17.0		
Corn-red clover				17.5		
Soybean-wheat-corn				17.1		
Soybean-wheat-corn-red clover	Sandy loam (mesic Typic Hapludalfs)			24.2		
Soybean-wheat-corn-red clover-rye				21.3		
Continuous corn	Silt loam (Typic Hapludalfs)	CT	0–20 cm	54.1	Positive effect of more diverse rotation	Jarecki et al. (2018)
Corn-corn-soybean-soybean				53.5		
Corn-corn-soybean-winter wheat				58.6		
Corn-corn-soybean-winter wheat-red clover				58.4		
Corn-corn-alfalfa-alfalfa				58.3		
Continuous corn	Clay loam (mesic Typic Argiaquolls)			52.0		
Corn-oat-alfalfa-alfalfa		63.0				
Soybean-fallow	Sandy loam (Andosol)	CT	0–15 cm	39.4	Positive effect of cover crop	Higashi et al. (2014)
Soybean-hairy vetch				44.4		
Soybean-rye				43.1		
Wheat-flax-wheat-beet-wheat	Calcisol	CT	0–10 cm	8.1	Positive effect of more diverse rotation	Aschi et al. (2017)
Wheat-beet-faba bean-rape-wheat				12.1		
Maize-wheat-mungbean	Sandy loam (Typic Haplustept)	NT	0–15 cm	6.9	Negative effect of tillage and positive effect of more diverse rotation	Parihar et al. (2016)
Maize-chickpea-sesbania				7.2		
Maize-mustard-mungbean				6.4		
Maize-maize-sesbania				5.6		
Maize-wheat-mungbean		CT		4.9		
Maize-chickpea-sesbania				5.4		
Maize-mustard-mungbean				4.5		
Maize-maize-sesbania				4.6		
Maize-soybean	Fine silty (mesic Udic Haplustolls)	NT	0–15 cm	23.1	Negative effect of tillage and positive effect of more diverse rotation	Alhameid et al. (2017)
Maize-soybean-wheat				23.8		
Maize-soybean-wheat-oat				26.9		
Maize-soybean		CT		22.8		
Maize-soybean-wheat				23.4		
Maize-soybean-wheat-oat				25.2		

^a NA: no data available in the original paper.

^b CT: conventional tillage; MT: minimum tillage; NT: no tillage.

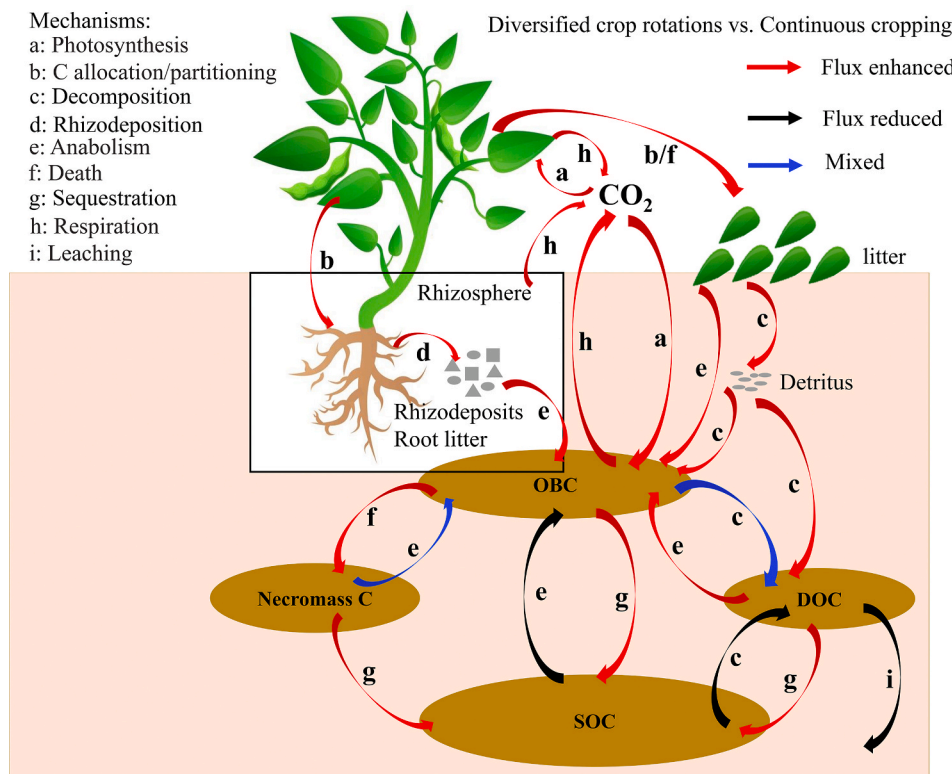


Fig. 1. Schematic model of changes in below-ground C dynamics under diversified crop rotations compared with continuous cropping of a single crop. Soil C is comprised of a complex mixture originating from the decomposition of aboveground biomass, root or root rhizodeposits and the biomass of organisms (mainly soil microbes and fauna; Ahkami et al., 2017). Dissolved organic C (DOC) is generated by organisms and extracellular enzymes that catalyze the conversion of macromolecular constituents to DOC after the breakdown of litter by saprotrophic fungi and fauna. Organismal biomass C (OBC) consists of C from plant, animal or microbial origin used for metabolism and C assimilation in organismal biomass. Necromass C is dead biota. Soil organic C (SOC) is the sequestration of soil biotic-driven C, including OBC, DOC, and necromass C. Soil C pools also undergo C losses via organism respiration (the major source of CO₂ from terrestrial ecosystems) and leaching (Lal et al., 2015; Ahkami et al., 2017). Gray squares, triangles, and circles represent resource-rich rhizodeposits and root litter.

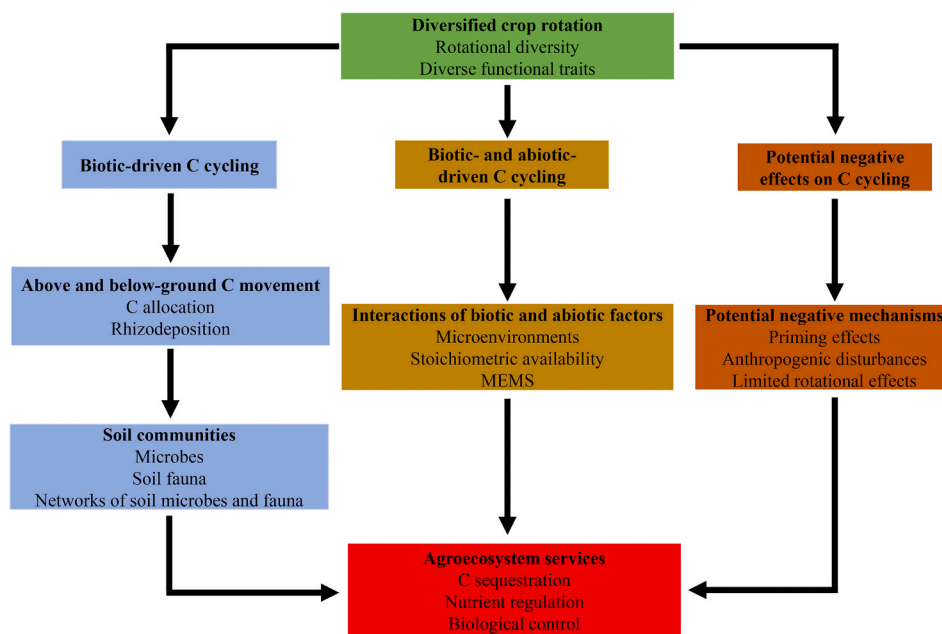


Fig. 2. Summarized overview of interactive effects driven by diversified crop rotations on agroecosystem functions and services. MEMS: Microbial Efficiency-Matrix Stabilization. Different colors refer to knowledge gaps discussed in this review and related to biotic-driven cycling (blue, section 2), interactions between biotic- and abiotic-driven cycling (yellow, section 3), and potentially negative effects on C cycling (orange, section 4). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

groups (e.g., microorganisms and their predators; Geisen et al., 2016; Grabau and Chen, 2016; Fujii and Takeda, 2017; Thakur and Geisen, 2019). For example, bacterial-feeding nematodes reduce microbial abundance and density through grazing, and they can also stimulate the activity of specific microbial groups (e.g., oligotrophs) by releasing nutrients from consumed microbial biomass, which subsequently increases the mineralization rate of organic matter; this effect is known as the microbial loop (Bonkowski, 2004). Additionally, some faunal groups may exert a dual effect on C cycling. With the enrichment of organic litter in diversified crop rotations, earthworms are capable of creating

“resource islands” that promote C cycling by increasing the abundance and activity of microbivorous faunal groups (e.g., protozoa and nematodes; Savin et al., 2004). Simultaneously, the greater activity of large fauna (e.g., earthworms) can physically protect organic C from decomposers in diversified crop rotations through the occlusion of organic matter within aggregates (Angst et al., 2017; Katsvairo et al., 2007a; McCarthy et al., 2008).

Overall, biotic-driven processes play a vital role in the stabilization and formation of SOC under diversified crop rotations, as compared to physical transformations of plant residues and root rhizodeposits that

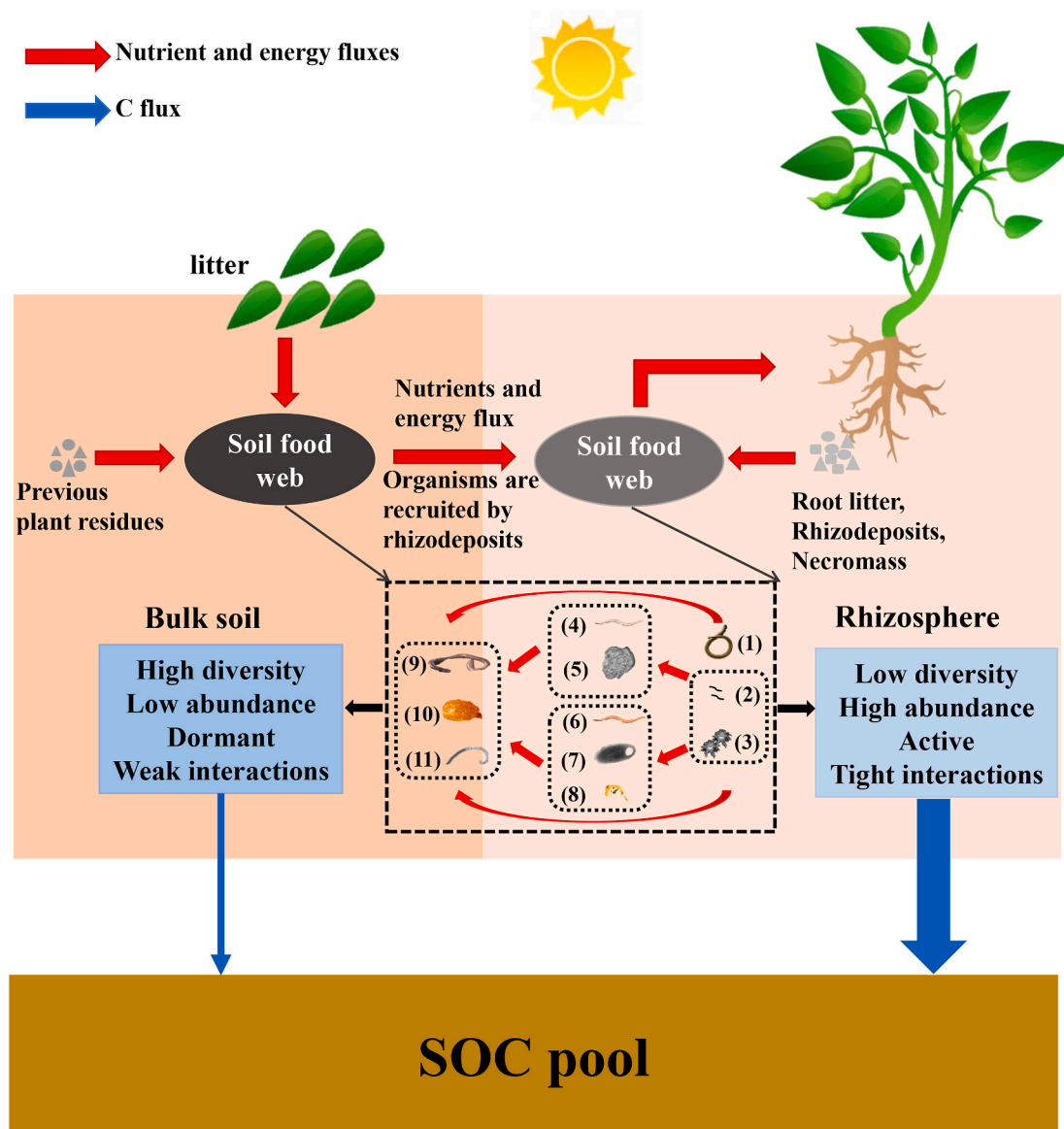


Fig. 3. Spatiotemporal views of nutrient and energy fluxes driven by soil biota under diversified crop rotations. (1) root-parasitic nematodes (2) bacteria; (3) fungi, (4) bacterivorous nematodes, (5) bacterivorous protists, (6) fungivorous nematodes, (7) fungivorous protists, (8) collembola; (9) earthworms; (10) mites; (11) predatory nematodes. Despite the great complexity of soil food webs, they can be simplified as primary consumers (bacteria and fungi), secondary consumers (bacterivores and fungivores) and higher-level consumers (predatory nematodes and mites) based on predatory interactions (Kardol and De Long, 2018). The width of blue arrows is proportional to the magnitude of the C flux. Gray squares, triangles, and circles represent resource-rich rhizodeposits and root litter. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

transfer C to soils and lead to its incorporation into SOC, which makes a small contribution to SOC (Fig. 1; Schmidt et al., 2011; Dungait et al., 2012; Cotrufo et al., 2015; Liang et al., 2017; Kallenbach et al., 2018). This is because diversified crop rotations promote the growth and activity of soil biota (McDaniel et al., 2014a; Venter et al., 2016; King and Blesh, 2018), which may increase biomass production, biologically-derived products (e.g., enzymes, hormones, and metabolites), and organismal necromass (dominantly microbial necromass). As such, higher microbial biomass should stimulate microbial functions, such as soil aggregation and nutrient cycling, which contribute significantly to SOC (Lützow et al., 2006; Kallenbach and Grandy, 2011). Liang et al. (2019) also demonstrated that microbial necromass contributed more than half of SOC. Consequently, diversified crop rotations may lead to a greater deposition of these biotic-driven products, especially microbially-driven C, into the SOM reservoir (McDaniel et al., 2014a; King and Blesh, 2018). Below, we analyze the major routes of C

movements (mainly C allocation and rhizodeposition), the effects of these deposited C sources on soil microbial and faunal communities and their interactions, and the main biological mechanisms that regulate C fluxes and deposition under diversified crop rotations.

2.1. C allocation

As mentioned above, soil biota are the key driver of soil C cycling, and the magnitude of SOC stabilization driven by biotic processes critically depends on the C allocated from crop residues and rhizodeposits (Lal et al., 2015). In this section, we describe how diversified crop rotations affect C allocation. Recent studies suggest that belowground C inputs contribute more to SOC than aboveground inputs across plant systems, implying that allocating more of the photosynthetically fixed C by crops to belowground structures would stimulate SOC formation (Pausch and Kuzyakov, 2018; Sokol and Bradford, 2019). Belowground

C inputs mainly consist of root litter and rhizodeposits (Fig. 1b and d), and the net amount of C translocated belowground largely depends on plant species (Kaiser et al., 2015; Pausch and Kuzyakov, 2018). Compared to monoculture systems, diversified crop rotations increase species richness with higher belowground C inputs. For example, crop rotations including cover crops and perennial crops notably increase SOC, which is tightly linked to total and root C inputs (King and Blesh, 2018). Perennial grasses translocate 33% of their C to belowground structures and exudates (Pausch and Kuzyakov, 2018), due to their heavy dependence on C stored in belowground structures for regrowth in spring or after grazing or mowing (Pausch et al., 2013). In contrast, annual crops only transfer about 21% of fixed C to belowground structures because the majority of assimilated C is allocated to grains and removed during harvest (Pausch and Kuzyakov, 2018). In addition, including a perennial grass in annual systems (e.g., adding bahiagrass in a peanut-cotton rotation) has the potential to increase photosynthesis of crops grown in rotation, mostly by increasing N availability, which would stimulate above and belowground C exchange (Fig. 1; Zhao et al., 2010). Similarly, cover-cropped grain-only rotations have greater shoot and root C inputs to the soil compared to rotations without cover crops, due to the extended period when photosynthetically-active vegetation is present, which increases the total biomass that is ultimately returned to the soil (King and Blesh, 2018).

2.2. Rhizodeposition and associated specific rhizosphere microbial communities

As one of the main sources of stabilized SOM along with root litter (Kuzyakov and Domanski, 2000; Pausch and Kuzyakov, 2018), rhizodeposits account for about 11% of fixed C or 27% - 50% of C allocated belowground (Nguyen, 2009; Jones et al., 2009a). Rhizodeposits include a variety of substances that are released from damaged or intact cells, and they consist of sloughed off root cells, tissues, mucilage, volatiles, and soluble lysates and exudates. Recent studies have demonstrated that the amount and type of rhizodeposits are highly context-specific, suggesting that greater plant diversity found in diversified crop rotations would increase the chemical diversity of rhizodeposits, including carbohydrates, organic and amino acids, phenolics, fatty acids, sterols, enzymes, vitamins, hormones, and nucleosides (Jones et al., 2009b; Steinauer et al., 2016; Dignac et al., 2017). Some studies found a tight relationship between root rhizodeposition (i.e., the quantity and

diversity of rhizodeposits) and the diversity and structure of the rhizosphere microbial community (Steinauer et al., 2016; Eisenhauer et al., 2017; Sasse et al., 2018). For example, a high chemical diversity of rhizodeposits, encompassing a large number of antibiotic agents, antimicrobial compounds, or plant hormones, not only reduces pressure from microbial pathogens and antagonistic microorganisms (Lange et al., 2015; Taheri et al., 2016; Bakhshandeh et al., 2017; Zhou et al., 2017), but also promotes the growth of beneficial rhizobiomes (Sasse et al., 2018; Canarini et al., 2019). In return, beneficial rhizobiomes may play a pivotal role in promoting root rhizodeposition by stimulating nutrient supply to the host crop, providing a channel for C transfer, and enhancing passive diffusion between rhizosphere and root through the large concentration gradient generated by microbial uptake (Table 2; Jones et al., 2009; Canarini et al., 2019).

Specific groups of beneficial microorganisms associated with diversified crop rotations include plant growth-promoting microorganisms (PGPM), fungal endophytes, and rhizosphere saprophytes (Fig. S1; Zhou et al., 2017; Zhalmna et al., 2018; Hontoria et al., 2019; Rillig et al., 2019). The activity of PGPM is expected to promote plant growth by stimulating the acquisition of essential nutrients (e.g., N, P, and Fe), modulating the level of hormones, and decreasing infection by phytopathogens (Hossain et al., 2017; Hassan et al., 2019; Verma et al., 2019). The response of PGPM, especially arbuscular mycorrhizal fungi (AMF), to stress and defense leads to variations in plant metabolites, as well as higher diversity and quantity of exudates (Souza et al., 2015; Pérez-de-Luque et al., 2017; Zhu et al., 2020). In particular, AMF form mutualistic associations with host crops to provide them with N and P required for growth and proliferation in exchange for photosynthetically fixed C (Hoysted et al., 2018). Such symbiotic relationships serve as the main channel for C transfer between root and rhizosphere through several pathways (Fig. 1d; Jones et al., 2009): 1) direct allocation of C (exudates) through intra- and extraradical mycelium structures; 2) production of C-rich fungal structures; and 3) metabolism in AMF cells. Diversified crop rotations have the potential to strengthen these pathways. For example, crop rotations, especially those including AMF-associated crops (e.g., rye and oat), promote diversity and activity of the AMF community, which subsequently increases total external mycelium length, the number of spores of AMF, and AMF colonization (Schmidt et al., 2019; Moitinho et al., 2020b; Murrell et al., 2020). Ultimately, these traits facilitate the formation of melanized hyphae that improve the formation and stabilization of soil aggregates by

Table 2

Major soil biotic-driven mechanisms involved in above- and belowground C cycling and the expected effects of diversified crop rotations.

Mechanisms	Chemical reactions (or pathways)	Key enzymes involved	Potential organisms	Predicted effect of rotation on C cycling	References
Photosynthesis	Calvin-Benson-Bassham cycle (CBB)	Ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO)	cbbl-carrying Bacteria, Cyanobacteria	Increase	(Tahir et al., 2015; Wu et al., 2015)
Belowground allocation	Translocation	NA ^a	NA	Increase	Pausch & Kuzyakov (2018)
Rhizodeposition	Sloughing of root border cells, secretion of mucilage by roots, root exudation, senescence of root epidermis	Amylase, invertase, peroxidase, phenolase, acid/alkaline phosphatase, polygalacturonase, protease	Mycorrhizal fungi, Endophytes, PGPM, Root herbivores	Mixed	(Nguyen, 2009; Kaiser et al., 2015)
Litter decomposition	Catabolism, Depolymerisation	β -glucosidase, Cellulase complex, Xylanases, mannanase, galactanase, pectinases, lignocellulolytic enzymes	Annelida, Microarthropods, Earthworms, Termites, Saprotrophs	Increase	(Fujii and Takeda, 2017; Zhou et al., 2017; Ai et al., 2018)
Respiration	Catabolism	Soil enzymes	Microbes, Soil fauna	Increase	(D'Acunto et al., 2018; Zhang et al., 2018)
Biomass formation	Anabolism	NA	Microbes, Soil fauna	Increase	(McDaniel et al., 2014a; D'Acunto et al., 2018; Zhang et al., 2018)
Sequestration	DOC-microbes pathways	NA	Microbes, Soil fauna	Increase	(Gougoulas et al., 2014; Cotrufo et al., 2015)

^a NA: no data available at this stage.

stimulating the production of microbial metabolites, which stabilizes SOM in the long term (Kahiluoto et al., 2009; Wu et al., 2014). Diversified crop rotations also promote glycoprotein and glomalin production by AMF (Bedini et al., 2013; Moitinho et al., 2020a), contributing not only to approximately 5% of soil C directly (Bakhshandeh et al., 2017), but also to aggregate stability and formation, which help sequester substantial amounts of C (Lal et al., 2015; Singh et al., 2017).

Crop rotations also substantially affect the activity and abundance of endophytes, especially fungal endophytes (Taheri et al., 2016; Xia et al., 2019). Root endophytic fungi (non-mycorrhizal fungi) have the potential to regulate the allocation of rhizosphere C due to their ubiquitous presence and dual lifestyle, which comprises both endophytic and saprotrophic activity (Fesel and Zuccaro, 2016). The saprotrophic lifestyle of fungal endophytes may alter rhizodeposition by increasing fungal biomass C (Table 2). They also produce extracellular enzymes that catalyze soil C and N degradation: for example, some fungal endophytes (e.g., *Metarhizium robertsii*) can provide insect-derived N to plants by infecting soil-borne insects and exchanging this N with photosynthate from host plants via fungal hyphae or endophytic associations (Behie et al., 2017). Finally, they produce alkaloids that affect litter decomposition (Guo et al., 2016), although the effect of alkaloids on decomposition and their subsequent fate in soils remains elusive. Overall, the link between the endophytic lifestyle of fungal endophytes and above-belowground C movement remains largely unknown, due to the lack of functional studies on fungal endophyte-plant interactions. Given that only a few studies provided evidence on how crop rotations affect rhizodeposition and C cycling driven by these specific rhizobiomes (Table 2), the potential feedbacks of these rhizobiomes in response to crop rotations should be investigated more thoroughly.

2.3. Interactions between crops and soil microbiomes and their involvement in belowground C cycling

Rotational diversity increases the quality, quantity, and chemical diversity of C inputs that not only feed rhizosphere microbes, but also affect the majority of soil microbial communities (Zhou et al., 2017; Ai et al., 2018). As a result, diversified crop rotations directly manipulate the community structure and composition of microbiomes, because microbiomes with different traits preferentially utilize different types of C sources (Sauvadet et al., 2016; Vries et al., 2017). Specifically, fast-growing bacteria in the Beta- and Gamma-subgroups of Proteobacteria and Bacteroidetes are considered as copiotrophic/r-selected bacteria that utilize soluble constituents and higher quality litter (e.g., relatively high N concentrations, low C/N ratios, and low phenol/lignin concentrations) and can thereby lead to high CUE (Cotrufo et al., 2013). This is due to nutrient-rich litter making the whole decomposer community C-limited, which facilitates C assimilation into new biomass of r-selected communities (Manzoni et al., 2012). In contrast, oligotrophic/k-selected bacteria (e.g., Actinobacteria and Firmicutes) and most of the fungal phyla (Ascomycota, Basidiomycota, and Zygomycota) are more competitive in systems dominated by complex molecules or low-quality litter characterized by low N concentrations, high C/N ratios, and high phenol/lignin concentrations, which typically result in low CUE (Cotrufo et al., 2013; Souza et al., 2013; Castellano et al., 2015; Dignac et al., 2017). For example, cereal residues mainly consist of cellulose and hemicellulose with lower N and P concentrations and induce a slower mineralization rate of residues, while legume residues are rich in sugars and proteins that have higher N and P concentrations, which stimulates soil nutrient recycling and increases CUE (Damon et al., 2014; Yu et al., 2016; Pan et al., 2019). Consequently, this greater C quality of legume residues could lead to the efficient stabilization of a greater proportion of residue C in the soil, potentially mitigating the effect of lower residue quantity in legumes relative to cereals (Johnson et al., 2007). However, rotations including both legumes and cereals have slightly lower amounts of SOC than cereal-only cropping systems (King and Blesh, 2018), suggesting a rapid decomposition of C

originating from legume residues. Increasing functional traits in crop rotations, e.g., by integrating cover crops or perennial crops in legume-cereal grain rotations, might be more effective at increasing SOC compared to grain-only rotations (Wright et al., 2004; Katsvairo et al., 2007a; King and Blesh, 2018). These results suggest that the use of functional plants with higher quality and quantity of C inputs can counteract the negative effects of lower residue quantity in legume grains on SOC storage. In addition, functionally diverse crop rotations can increase nutrient availability (e.g., N and P), which may strengthen microbial interactions and microbiome-crop interactions, as the stoichiometry of available resources steers nutrient- and community-dependent metabolic shifts that underpin microbial community functions and interactions (Manzoni et al., 2012; Hartman et al., 2017). This maintains the stability and adaptability of agroecosystem functions, with a positive impact on SOC formation and accumulation (Hartman et al., 2017; Luo et al., 2020), and highlights that crop rotations with a higher functional diversity contribute largely to SOC accrual.

Crop rotations may also strengthen ecological connections of microbial networks among roots, rhizosphere, and bulk soil (Figs. 1 and 3; Vries et al., 2017). By increasing the chemical diversity and amount of rhizodeposits, a greater diversity of microbes is recruited from the bulk soil to the rhizosphere and facilitates rhizobiome-rhizobiome and plant-rhizobiome connections, with the concomitant release of greater root-derived energy (i.e., photosynthate excreted from roots and energy released from the decomposition of rhizodeposits and root litter) back to rhizosphere organisms (Fig. 3b; Pausch et al., 2016; Vries et al., 2017). This greater release of root-derived energy will benefit fungal saprotrophs found in the rhizosphere that serve as the primary consumers of root-derived C, as enhanced enzymatic activity will allow for the effective assimilation of root exudates (Hugoni et al., 2018; Vivel and Bhatnagar, 2019). In addition, the hyphae of fungal saprotrophs will become potential energy resources for other rhizobiomes (Kong et al., 2011), as some rhizobiomes have the ability to colonize and feed on these hyphae, which accelerates the production and turnover of microbial biomass (Rudnick et al., 2015; Ballhausen and de Boer, 2016). For example, mycophagous soil bacteria that are commonly found in agroecosystems, such as those belonging to the *Collimonas* genus, can exploit living fungal hyphae to obtain energy and nutrients for growth (Leveau and Preston, 2008; Ballhausen et al., 2015). Ultimately, rhizosphere microbial C uptake is positively linked to the level of root exudation, as reported by Prommer et al. (2020) who found that microbial growth (indicated by microbial biomass C) increased by twofold but respiration (indicated by CO₂) only increased by 1.5-fold when comparing systems with high plant diversity to monocultures.

Diversified crop rotations that are beneficial to the growth and activity of saprotrophs promote higher rates of biomass production as a result of ongoing loops of microbial proliferation, growth, and death, ultimately increasing the contribution of microbially-derived C to SOC storage (Ellouze et al., 2014; Schmidt et al., 2019). Some fungal saprotrophs species, such as *Trichoderma harzianum*, can penetrate into roots to access plant metabolites before they are secreted into the rhizosphere, and the external phase of hypha, in return, takes up organic nutrients from the rhizosphere and supplies them to the plant through the hypha section located inside the plant root (Harman, 2006; Rudnick et al., 2015). This suggests that these saprotrophs act as the primary consumer of root exudates by competing with other rhizobiomes, especially the rhizobacterial community, which has the potential to accelerate the turnover rate of saprotrophs and thereby promotes their necromass formation (Six et al., 2006). Some rhizobiome-plant interactions can also stimulate the release of specific compounds (e.g., cyclopropyl fatty acids) in addition to the supply of C sources from symbiotrophs (e.g., glomalin) linked to plant hosts, accelerating fermentation by saprotrophic fungi (Herman et al., 2012; Hugoni et al., 2018). For example, compared to a wheat-fallow rotation, a wheat-corn-proso millet rotation increased glomalin production by AMF (Wright and Anderson, 2000),

which could promote the activity and growth of saprotrophs in the rhizosphere. Simultaneously, some rhizosphere microbial groups, such as symbiotrophs, can compete for nutrients with saprotrophs that would otherwise mineralize organic matter in crop rotations, as reported by a two-year tomato and cotton rotation including cover crops Juan triticale, Merced rye, and common vetch that led to a more diverse and symbiotroph-enriched community (Jastrow et al., 2007; Schmidt et al., 2019). These suggest that crop rotations could lead to tighter interactions between saprotrophs and other rhizobiomes living in the rhizosphere, ultimately altering microbial mediation of C decomposition and C sequestration.

Compared to the rhizosphere microbiomes, the microbial community living in the bulk soil (free-living microbes) presents a lower abundance but higher diversity, with higher relative abundances of oligotrophic bacterial taxa (e.g., Acidobacteria, Chloroflexi, and Firmicutes; Liu et al., 2017; Oberholster et al., 2018). This is likely due to the lower quantity but higher diversity of litter inputs supplied to the bulk soil (aboveground C inputs of current and previous crops) relative to root litter and root exudates excreted in the rhizosphere (Lugtenberg and Dekkers, 1999; García-Salamanca et al., 2013; Liu et al., 2017). As a result, free-living microbial communities in the bulk soil benefit less from diversified crop rotations, with C cycling regulated by free-living microbes making a relatively smaller contribution to SOC than C cycling driven by rhizosphere microbes (Oberholster et al., 2018; Zhou et al., 2017, Fig. 3a). This would be consistent with the study of McDaniel et al. (2014b) where soil microbial properties (e.g., basal respiration and extracellular enzyme activities) affected by 11 years of corn-soybean and corn-soybean-wheat rotations had little effect on soil total C in the bulk soil. However, similar to the rhizosphere, the greater quantity and quality of aboveground biomass inputs owing to rotational effects (i.e., a direct effect from current crop and a carryover effect from previous crops) can still increase the abundance and activity of free-living microbes in the bulk soil relative to continuous cropping systems, especially copiotrophic taxa (e.g., Betaproteobacteria, Actinobacteria, and Bacteroidetes; Liu et al., 2017; Lupwayi et al., 2017) that can enhance DOC-associated pathways (Figs. 1 and 3a; Cotrufo et al., 2015; Preissel et al., 2015).

2.4. Soil faunal activity regulating belowground C cycling

Soil faunal activity is another key contributor to C cycling through interactions between top-down and bottom-up effects, with critical impacts on the decomposition and turnover rates of C sources (Fig. 3; Bender et al., 2015; Zhang et al., 2015; Sauvadet et al., 2016). While soil microbial communities and their impact on C cycling are mainly affected by the crop species and cropping sequences of the rotation (Liu et al., 2017; Ai et al., 2018), soil faunal communities are likely sensitive to the microbial community and nutrient concentration that result from bottom-up control (Hobbie and Villéger, 2015; Thakur and Geisen, 2019). Changes in the faunal community composition and abundance directly affect faunal feeding activity, which provides feedback loops and further mediates microbial activity through top-down control (Hobbie and Villéger, 2015; Thakur and Geisen, 2019). Accordingly, rotational diversity can affect the interdependence of microbial and faunal communities through changes in the quantity and quality of organic matter inputs (Osler and Sommerkorn, 2007; Schmitz, 2010; Maron et al., 2018), which subsequently and overwhelmingly affects belowground C cycling (Hobbie and Villéger, 2015).

With a higher quantity, quality, and chemical diversity of C inputs, diversified crop rotations can facilitate population dynamics in the soil food webs and C-related life history parameters, including C assimilation (e.g., the amount of C resources for growth, physiological maintenance, and excretion), production efficiency (e.g., the amount of C assimilated into biomass), and the C:N ratio of soil biota (Osler and Sommerkorn, 2007; Bender et al., 2015; Hobbie and Villéger, 2015). Given the disparity of energy and nutrient demands for bacterial and fungal-based

soil food webs, these parameters will vary both within and among species (Vanni et al., 2002). For example, as bacterial-based soil food webs largely consume C and N, this could stimulate the loss of most of the consumed C as CO₂ through respiration and lead to a small proportion of the C and N consumed being excreted back to the soil, which ultimately will contribute less to SOC compared to fungal-based soil food webs (Six et al., 2006; Osler and Sommerkorn, 2007; Malik et al., 2016). This is because fungal-based soil food webs have higher C:N ratios than bacterial-based soil food webs (e.g., 3–5 for bacteria relative to 5–15 for fungi), resulting in more C contained per unit of N in fungal-based soil food webs. Consequently, fungal-based soil food webs retain a large amount of ingested materials with a high C:N ratio and mineralize a small proportion of the C they ingest (Stirling et al., 2002; Grabau and Chen, 2016), increasing soil biotic-driven products and ultimately making a large contribution to soil C pools. Overall, by leading to diverse soil communities associated with more complex population dynamics in soil food webs, especially fungal-based soil food webs, diversified crop rotations promote the formation and stability of SOC (Bender et al., 2016; Grabau and Chen, 2016; Santos et al., 2020; Yin et al., 2020).

In addition to directly grazing on microorganisms, some organisms (e.g., earthworms, isopods, millipedes, and enchytraeids) indirectly consume microorganisms through the ingestion of soil, litter, and SOM (Thakur and Geisen, 2019). Among them, earthworms are the most dominant consumer group in agroecosystems (Curry and Schmidt, 2007; Jackson et al., 2017), and the abundance and richness of earthworms increase with rotation complexity (Ashworth et al., 2017; Rodríguez et al., 2020). It is well known that the activity of earthworms regulates C dynamics (Ernst et al., 2009; Zheng et al., 2018). In particular, their activity can increase SOM decomposability and nutrient availability by selecting specific soil microbes, altering microbial stoichiometry, and increasing microbial colonization of SOM through direct contact between organic materials and microbes (Nielsen et al., 2011; Medina-Sauza et al., 2019). Simultaneously, earthworms develop symbiotic relationships with microbiomes within their gut (Ekschmitt et al., 2005), where earthworms build biogenic structures (e.g., castings, galleries, and fungi wheels) that form organic-mineral associations. These structures have a great impact on soil aggregation and soil structure, increasing the mean residence time of SOM by protecting it from decomposition (Hobbie, 2015). Moreover, the feeding process of earthworms can stabilize labile organic compounds and/or incorporate organic residues into aggregates that ultimately increase SOC storage (Lavelle et al., 2006; Don et al., 2008; Dignac et al., 2017). Greater earthworm activity may increase both C mineralization and C stability under diversified crop rotations, with a larger increase in C stability relative to C mineralization (Zhang et al., 2013a). This is highlighted by a long-term bahiagrass-bahiagrass-peanut-cotton rotation that increased both earthworm population density and SOC (Katsvairo et al., 2006, 2007b).

Herbivores also have a profound effect on C cycling (Bardgett and Wardle, 2003; Hobbie and Villéger, 2015; Gan and Wickings, 2020). The waste products herbivores excrete and their necromass are enriched in nutrients relative to the primary producers they consume, supplying decomposers with nutrient-rich sources and energy that ultimately increases CUE (Hunter, 2001; Bardgett and Wardle, 2003). On the other hand, herbivores may affect C cycling by altering plant allocation of C, e.g., plant-parasitic nematodes that may stimulate the release of root exudates due to root damage (Bardgett and Wardle, 2003; Gebremikael et al., 2016). However, the growth of herbivores, especially root herbivores, exerts tremendous damage to plants, which leads to substantial losses of crop productivity and ultimately decreases C inputs to the soil (Blackshaw and Kerry, 2008; Zvereva and Kozlov, 2012). Therefore, diversified crop rotations can regulate C cycling by controlling the population of herbivores, and they do so through several mechanisms. Firstly, the growth of herbivores can trigger the release of phytohormones that act as a chemical defense (e.g., gibberellins, brassinosteroids, auxins, and cytokinins), and diversified crop rotations can increase the

magnitude of this defense, such as a mung bean – wheat rotation compared to continuous wheat (Nguyen et al., 2016; Hu et al., 2018b; Ilyas et al., 2018; Peralta et al., 2018). Secondly, crop rotations may promote the growth of PGPM that have biocontrol effects against herbivores (Schouteden et al., 2015; Mhatre et al., 2019). For example, a tomato-celery-cucumber-Chinese cabbage rotation was significantly enriched in *Flavobacterium* spp. and *Pseudomonas* spp. compared to a cucumber monoculture system (Zhou et al., 2017). Thirdly, crop rotations that include perennial grasses can suppress the growth of herbivores, as they decrease the frequency at which herbivore-susceptible annual crops are grown (Katsvairo et al., 2007a). Lastly, the higher biodiversity in soil food webs associated with rotational diversity can exert top-down control over herbivore populations (Srivastava et al., 2009; Bender et al., 2015). These rotational effects on herbivores profoundly affect the decomposition rate of organic materials (Gan and Wickings, 2020). Consequently, given the benefits and disadvantages of herbivory on soil C cycling, it is difficult to estimate the quantitative contribution of herbivores to SOC under diversified crop rotations due to rotational effects on the growth and activity of herbivores.

Overall, greater rotational diversity increases the diversity and complexity of soil fauna communities, affecting the functioning of soil food webs, with positive feedbacks on nutrient recycling and SOM formation and stability. This is especially true when using functional crops that not only increase litter input, which ensures adequate C supply for each trophic group in soil food webs, but also increase environmental heterogeneity, niche diversity and biotope space, all of which promote plant productivity and CUE (Vukicevich et al., 2016; Leslie et al., 2017; Seabloom et al., 2017).

3. Interactive effects of biotic and abiotic factors on promoting C stabilization

Crop rotations can also affect SOC stabilization by improving soil physical properties (e.g., soil aggregation, water infiltration, and soil structure) that further alter microenvironments (Madari et al., 2005; Katsvairo et al., 2007b; Singh et al., 2018). In addition to soil aggregate formation, one of the most important soil physical properties for SOC stabilization (Lal et al., 2015), diversified crop rotations also promote SOC stabilization through the improvement of soil structure and water infiltration as well as the reduction of bulk density and soil compaction (Katsvairo et al., 2006; Calegari et al., 2013; Zuber et al., 2015). These improved physical attributes favor the growth and activity of diverse soil biota (Young et al., 1998), such as N_2 -fixing bacteria that can release polysaccharides, which positively affects soil aggregate formation (Martins and Angers, 2015). Besides, higher biological activity detected in diversified crop rotations can release a large amount of biologically-derived products (e.g., enzymes, amino acids, and fatty acids) and extracellular polymeric substances (Acosta-Martínez and Burow, 2010; Sun et al., 2016; D'Acuneto et al., 2018). These substances are the main contributors to the formation of organic-mineral associations and SOM stabilization by promoting aggregation and strong chemical bonding to the mineral soil matrix (Cotrufo et al., 2013), which increases aggregate formation and stability and improves the resistance of soils to leaching and erosion (Lal, 2011). On the other hand, the rapid turnover of living organisms under crop rotations can produce substantial amounts of necromass from dead biota over time (Fig. 1f), which are vital to SOC stabilization (Castellano et al., 2015; Kallenbach et al., 2015; Liang et al., 2019). Compared with biomass production that has a fast turnover, necromass is regarded to be relatively stable, due to its main constituents that include particulate organic matter from cell envelope fragments, some colloidal former cytosolic matter, and small biopolymers (Liang et al., 2019). Soil aggregate stability further increases the capacity of soils to store C, as SOM formed in aggregates or sorbed by organic-mineral interfaces is physically protected due to its physical inaccessibility to extracellular enzymes and/or microclimatic conditions, referred to as an “entombing effect” (Fig. 3; Gougoulis

et al., 2014; Cotrufo et al., 2015; Liang et al., 2017).

These physical properties improved by diversified crop rotations are related to physical stability, enabling nutrients to be transported along the soil surface with runoff or downward in the soil profile with infiltrating water (Rabot et al., 2018). For example, greater soil structure and lower bulk density in a bahiagrass-bahiagrass-peanut-cotton rotation help the root to efficiently get access to available water and nutrients, leading to greater root biomass and crop productivity (Katsvairo et al., 2007b). In turn, greater root litter inputs impart many positive attributes to these physical properties and ultimately contribute largely to SOM (Lal, 2011; Veen et al., 2019). In sum, diversified crop rotations can optimize microenvironments that enhance the interactions between soil biota and physical properties, with positive effects on C sequestration and stability.

4. Potential mechanisms that could offset C cycling benefits of crop rotation

Although diversified crop rotations increase new C inputs, priming effects and anthropogenic disturbances (i.e., tillage, fertilization, and pest management) can limit the accumulation of SOC and accelerate its turnover (Fig. 4A). Priming effects refer to an increase in the degradation of old SOM when the activity of soil decomposers is stimulated by fresh C inputs (e.g., root exudates, secretions or excretions, and labile litter). This could be driven by four potential, non-mutually exclusive mechanisms (Dignac et al., 2017; Chao et al., 2019): 1) an increase in the activity of r-strategists (via the exponential growth of short-lived microbial groups) and thus soil enzymatic activity that degrades old SOM; 2) the adaptation of k-strategists (long-lived microbes under stable environmental conditions) to the decomposition of recalcitrant substrates, increasing their decomposition; 3) greater root exudation (e.g., oxalic acid) disrupting organic-mineral associations and increasing accessibility to stabilized SOC; 4) a change in the stoichiometry of C inputs that modulates the magnitude and direction of priming effects. As priming effects accelerate SOM decomposition, they can also potentially increase N and P availability (Faucon et al., 2017). Overall, there is little information available on the effects of diversified crop rotations on the magnitude and direction of priming effects, in addition to their biological drivers.

Crop rotations, especially those including functional plants (e.g., cover and perennial crops), can have relatively closed nutrient cycles, where above- and below-ground organic inputs are decomposed or mineralized into available forms that are taken up by plants, potentially reducing the reliance on external inputs compared with continuous cropping systems. However, these benefits may not be immediate, and growers may still implement intensive tillage, fertilization, and pest management to ensure short-term profitability. These anthropogenic disturbances not only change the soil biota community structure and soil food web functioning, they also disrupt the connection between bulk and rhizosphere soil networks (Vries et al., 2017; Yang et al., 2018; Banerjee et al., 2019). For example, tillage can disrupt soil structure and aggregates, resulting in drastic effects on soil microenvironments (e.g., temperature, moisture, and oxygen), biological activity, and SOC stabilization (Sá et al., 2014). Tillage can also disrupt the network of mycorrhizal fungi and AMF communities, and affect faunal communities (e.g., nematodes and earthworms) through killing or injuring them directly or exposing them to the risk of predation. Such disturbances stimulate SOM mineralization and deplete SOC by increasing microbial turnover rates and metabolic quotients (Table 1; Roger-Estrade et al., 2010; Kabiri et al., 2016; Pelosi et al., 2017).

Large inputs of synthetic fertilizers also reduce network complexity and the abundance of key taxa in the root microbiome as well as fungal biomass and diversity (Bakhshandeh et al., 2017; Banerjee et al., 2019), potentially reducing the contribution of organisms to soil ecosystem functions (Bender et al., 2016). High N availability from water-soluble fertilizers may reduce belowground C allocation and rhizodeposition,

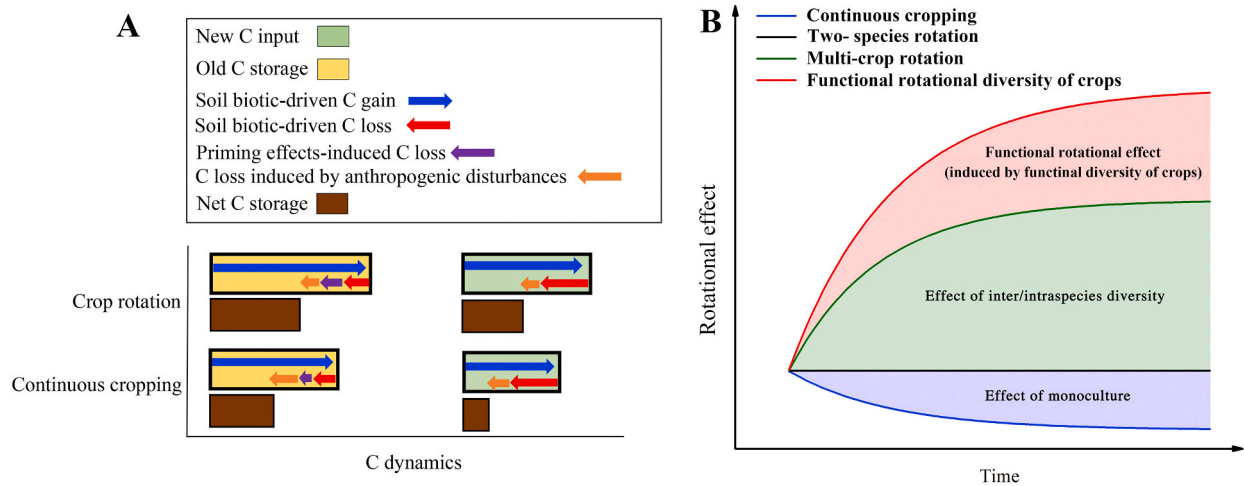


Fig. 4. Conceptual view of the C dynamics triggered by soil communities and management practices under crop rotation and continuous cropping of a single crop (A). Boxes represent old C storage (yellow) and new C inputs (green). Arrows indicate C cycling triggered by direct biological pathways (C gain in blue and C loss in red), priming effects (in purple), and anthropogenic disturbances (in orange). Crop rotation leads to both positive (soil biotic-driven C storage: C reservoir derived from biomass production, biologically-derived products, and necromass) and negative (biotic-driven C loss, priming effects and C loss induced by anthropogenic disturbances) feedbacks on C cycling, although net C storage (brown boxes) ultimately increases compared to continuous cropping of a single crop. (B) Compared to a two-species rotation (black line), continuous cropping with a single species (blue curve) decreases the biodiversity and functionality of soil, which in turn reduces crop productivity (blue area). In contrast, rotations with multiple crops enhance the biodiversity and functionality of soil (green curves), although benefits may be limited as biodiversity reaches a saturation point within agroecosystems. Biodiversity and functionality of soils under functional rotational diversity of crops include those induced by intra/interspecies diversity *per se* (green area) and further increases induced by functional diversity of crops, known as the functional rotational effect (pink area). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

as above- and belowground allocation is strongly related to soil nutrient availability (Liu et al., 2017; Pausch and Kuzyakov, 2018). Moreover, high N inputs significantly accelerate the decomposition of native SOM through priming effects (Qiu et al., 2016). However, using the optimal rate of synthetic fertilizers or combining synthetic and organic fertilizers can decrease SOM decomposition and facilitate the efficiency of C sequestration (Li et al., 2017). This raises the question of how N fixed by legumes affects the dynamics of native and new C sources, which remains unanswered to our knowledge.

There is an ongoing debate on whether rotational effects induced by crop rotational diversity are functionally limited, because of functional redundancy in biotic communities (McDaniel et al., 2014a; Tiemann et al., 2015). Nielsen et al. (2011) synthesized studies in natural systems that focused on the relationship between soil biodiversity and C cycling and found that species richness improved C cycling at low levels of soil biodiversity but did so less frequently at higher levels of soil biodiversity. In managed agroecosystems, the effects of rotational diversity on soil biodiversity may be tied to the low level of soil biodiversity typically observed in these systems, resulting in a low saturation point. More specifically, intra/interspecies diversity in crop rotations can result in only minor differences in the diversity of plant functional traits. This results in substantial functional redundancy in soil communities and agroecosystem functions compared with diversified crop rotation that include functional trait diversity, as represented by the pink and green areas in Fig. 4B (Bender et al., 2016; Raffard et al., 2019). The meta-analysis of McDaniel et al. (2014a) highlighted this, by determining that changes in microbial biomass C were not correlated with the number of crops in the rotation and that total C accretion only occurred up to three crops in the rotation. Hence, to enhance plant-mediated long-term effects that affect biotic interactions and their roles in C recycling and accumulation, plant functional trait diversity should be considered when managing crop sequences rather than focusing solely on intra/interspecies diversity (Wurst and Ohgushi, 2015).

5. Concluding remarks and future perspectives

Our review describes the potential mechanisms that regulate C

cycling within diversified crop rotations (Fig. 2). High rotational diversity coupled with diversified functional traits positively correlates to soil C allocation and rhizodeposition. This will affect interactions among groups of soil biota and between soil biota and plant species through synergistic (e.g., nutritional networks, symbiotic association) or antagonistic associations (e.g., competition, pathogenetic or predatory associations), ultimately determining the fate of C dynamics (Figs. 1 and 3; Bardgett and Wardle, 2010). Further uncovering the mechanistic connections among plant inputs, soil communities, and abiotic factors may shed additional light on our understanding of C cycling and ecological functions under agroecosystems. This would provide insights into the benefits that diversified crop rotations offer to improve CUE and resistance to pathogens or to reduce the reliance on agrochemicals. Given these benefits, high rotational diversity may mitigate the susceptibility of agroecosystem functions and services (e.g., C sequestrations and soil biodiversity) to agricultural intensification (Fig. 4A).

Finally, we should give more consideration to functional trait diversity rather than intra/interspecies diversity alone when managing crop sequences in rotation (Fig. 4B). However, considerable uncertainty remains on how functional traits may interact within or among plant species and affect C and nutrient dynamics through time. This is due to interactive effects that are most likely context-dependent, and divergence in factors affecting these interactions among biomes (Manzoni et al., 2012; Hartman et al., 2017; Crowther et al., 2019; Thakur and Geisen, 2019). Accordingly, future studies exploring species-specific mechanisms of organism-soil-crop interactions under functionally diverse crop rotations and their roles in governing C and nutrient cycling would be especially useful.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2021.108219>.

References

- Acosta-Martínez, V., Burow, G., 2010. Soil microbial communities and function in alternative systems to continuous cotton. *Soil Science Society of America Journal* 74, 1181–1192.
- Ahkami, A.H., White, R.A., Handakumbura, P.P., Jansson, C., 2017. Rhizosphere engineering: enhancing sustainable plant ecosystem productivity. *Rhizosphere* 3, 233–243.
- Ai, C., Zhang, S., Zhang, X., Guo, D., Zhou, W., Huang, S., 2018. Distinct responses of soil bacterial and fungal communities to changes in fertilization regime and crop rotation. *Geoderma* 319, 156–166.
- Alhameid, A., Ibrahim, M., Kumar, S., Sexton, P., Schumacher, T.E., 2017. Soil organic carbon changes impacted by crop rotational diversity under no-till farming in South Dakota, USA. *Soil Science Society of America Journal* 81, 868–877. *Soil Science Society of America*.
- Angst, S., Mueller, C.W., Cajthaml, T., Angst, G., Lhotáková, Z., 2017. Stabilization of soil organic matter by earthworms is connected with physical protection rather than with chemical changes of organic matter. *Geoderma* 289, 29–35.
- Aschi, A., Aubert, M., Riah-Anglet, W., Nélieu, S., Dubois, C., Akpa-Vinceslas, M., Trinsoutrot-Gattin, I., 2017. Introduction of Faba bean in crop rotation: impacts on soil chemical and biological characteristics. *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment* 120, 219–228.
- Ashworth, A.J., Allen, F.L., Tyler, D.D., Pote, D.H., Shipitalo, M.J., 2017. Earthworm populations are affected from long-term crop sequences and bio-covers under no-tillage. *Pedobiologia* 60, 27–33.
- Bakhshandeh, S., Corneo, P.E., Mariotte, P., Kertesz, M.A., Dijkstra, F.A., 2017. Effect of crop rotation on mycorrhizal colonization and wheat yield under different fertilizer treatments. *Agriculture, Ecosystems & Environment* 247, 130–136.
- Ballhausen, M.-B., de Boer, W., 2016. The sapro-rhizosphere: carbon flow from saprotrophic fungi into fungus-feeding bacteria. *Soil Biology and Biochemistry* 102, 14–17.
- Ballhausen, M.-B., van Veen, J.A., Hundscheid, M.P.J., de Boer, W., 2015. Methods for baiting and enriching fungus-feeding (mycophagous) rhizosphere bacteria. *Frontiers in Microbiology* 6, 1416.
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R., van der Heijden, M.G.A., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *The ISME Journal* 13, 1722–1736.
- Bardgett, R.D., Wardle, D.A., 2010. *Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*. Oxford University Press.
- Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84, 2258–2268.
- Bedini, S., Avio, L., Sbrana, C., Turriani, A., Migliorini, P., Vazzana, C., Giovannetti, M., 2013. Mycorrhizal activity and diversity in a long-term organic Mediterranean agroecosystem. *Biology and Fertility of Soils* 49, 781–790.
- Behie, S.W., Moreira, C.C., Sementchoukova, I., Barello, L., Zelisko, P.M., Bidochka, M.J., 2017. Carbon translocation from a plant to an insect-pathogenic endophytic fungus. *Nature Communications* 8, 1–5.
- Bell, L.W., Sparling, B., Tenuta, M., Entz, M.H., 2012. Soil profile carbon and nutrient stocks under long-term conventional and organic crop and alfalfa-crop rotations and re-established grassland. *Agriculture, Ecosystems & Environment* 158, 156–163.
- Bender, S.F., Franz Bender, S., van der Heijden, M.G.A., 2015. Soil biota enhance agricultural sustainability by improving crop yield, nutrient uptake and reducing nitrogen leaching losses. *Journal of Applied Ecology* 52, 228–239.
- Bender, S.F., Franz Bender, S., Wagg, C., van der Heijden, M.G.A., 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends in Ecology & Evolution* 31, 440–452.
- Blackshaw, R.P., Kerry, B.R., 2008. *Root Herbivory in Agricultural Ecosystems*. Root Feeders: an Ecosystem Perspective. CAB International, Wallingford, pp. 35–53.
- Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. *New Phytologist* 162, 617–631.
- Briones, M.J.I., McNamara, N.P., Poskitt, J., Crow, S.E., Ostle, N.J., 2014. Interactive biotic and abiotic regulators of soil carbon cycling: evidence from controlled climate experiments on peatland and boreal soils. *Global Change Biology* 20, 2971–2982.
- Calegari, A., Tourdonnet, S., Tessier, D., Rheinheimer, D.S., Ralisch, R., Hargrove, W., Guimarães, M.F., Filho, J.T., 2013. Influence of soil management and crop rotation on physical properties in a long-term experiment in paraná, Brazil. *Communications in Soil Science and Plant Analysis* 44, 2019–2031.
- Canarini, A., Kaiser, C., Merchant, A., Richter, A., Wanek, W., 2019. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Frontiers of Plant Science* 10, 157.
- Castellano, M.J., Mueller, K.E., Olk, D.C., Sawyer, J.E., Six, J., 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Global Change Biology* 21, 3200–3209.
- Chao, L., Liu, Y., Freschet, G.T., Zhang, W., Yu, X., Zheng, W., Guan, X., Yang, Q., Chen, L., Dijkstra, F.A., Wang, S., 2019. Litter carbon and nutrient chemistry control the magnitude of soil priming effect. *Functional Ecology* 33, 876–888.
- Congreves, K.A., Hooker, D.C., Hayes, A., Verhallen, E.A., Van Eerd, L.L., 2017. Interaction of long-term nitrogen fertilizer application, crop rotation, and tillage system on soil carbon and nitrogen dynamics. *Plant and Soil* 410, 113–127.
- Cotrufo, M.F., Francesca Cotrufo, M., 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, 776–779.
- Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Deneff, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology* 19, 988–995.
- Crotty, F.V., Fychan, R., Sanderson, R., Rhymes, J.R., Bourdin, F., Scullion, J., Marley, C. L., 2016. Understanding the legacy effect of previous forage crop and tillage management on soil biology, after conversion to an arable crop rotation. *Soil Biology and Biochemistry* 103, 241–252.
- Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. *Science* 365.
- Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms—a review. *Pedobiologia* 50, 463–477.
- D'Acunto, L., Andrade, J.F., Poggio, S.L., Semmartin, M., 2018. Diversifying crop rotation increased metabolic soil diversity and activity of the microbial community. *Agriculture, Ecosystems & Environment* 257, 159–164.
- Damon, P.M., Bowden, B., Rose, T., Rengel, Z., 2014. Crop residue contributions to phosphorus pools in agricultural soils: a review. *Soil Biology and Biochemistry* 74, 127–137.
- Dignac, M.-F., Derrien, D., Barré, P., Barot, S., Cécillon, L., Chenu, C., Chevallier, T., Freschet, G.T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P.-A., Nunan, N., Roumet, C., Basile-Doelsch, I., 2017. Increasing soil carbon storage: mechanisms, effects of agricultural practices and proxies. A review. *Agronomy for Sustainable Development* 37, 14.
- Don, A., Steinberg, B., Schöning, I., Pritsch, K., Joschko, M., Gleixner, G., Schulze, E.-D., 2008. Organic carbon sequestration in earthworm burrows. *Soil Biology and Biochemistry* 40, 1803–1812.
- Dungait, J.A.J., Hopkins, D.W., Gregory, A.S., Whitmore, A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology* 18, 1781–1796.
- Eisenhauer, N., Lanoue, A., Strecker, T., Scheu, S., Steinauer, K., Thakur, M.P., Mommer, L., 2017. Root biomass and exudates link plant diversity with soil bacterial and fungal biomass. *Scientific Reports* 7, 44641.
- Ekschmitt, K., Liu, M., Vetter, S., Fox, O., Wolters, V., 2005. Strategies used by soil biota to overcome soil organic matter stability—why is dead organic matter left over in the soil? *Geoderma* 128, 167–176.
- Elouze, W., Esmaili Taheri, A., Bainard, L.D., Yang, C., Bazghaleh, N., Navarro-Borrell, A., Hanson, K., Hamel, C., 2014. Soil fungal resources in annual cropping systems and their potential for management. *BioMed Research International* 2014, 531824.
- Ernst, G., Henseler, I., Felten, D., Emmerling, C., 2009. Decomposition and mineralization of energy crop residues governed by earthworms. *Soil Biology and Biochemistry* 41, 1548–1554.
- Fageria, N.K., Baligar, V.C., Bailey, B.A., 2005. Role of cover crops in improving soil and row crop productivity. *Communications in Soil Science and Plant Analysis* 36, 2733–2757.
- Faucon, M.-P., Houben, D., Lambers, H., 2017. Plant functional traits: soil and ecosystem services. *Trends in Plant Science* 22, 385–394.
- Fesel, P.H., Zuccaro, A., 2016. Dissecting endophytic lifestyle along the parasitism/mutualism continuum in *Arabidopsis*. *Current Opinion in Microbiology* 32, 103–112.
- Finney, D.M., Kaye, J.P., 2017. Functional diversity in cover crop polycultures increases multifunctionality of an agricultural system. *Journal of Applied Ecology* 54, 509–517.
- Friedlingstein, P., Jones, M., O'Sullivan, M., Andrew, R., Hauck, J., Peters, G., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Others, 2019. *Global carbon budget 2019*. *Earth System Science Data* 11, 1783–1838.
- Fujii, S., Takeda, H., 2017. Succession of soil microarthropod communities during the aboveground and belowground litter decomposition processes. *Soil Biology and Biochemistry* 110, 95–102.
- Gan, H., Wickings, K., 2020. Root herbivory and soil carbon cycling: shedding “green” light onto a “brown” world. *Soil Biology and Biochemistry* 150, 107972.
- García, R.A., Li, Y., Rosolem, C.A., 2013. Soil organic matter and physical attributes affected by crop rotation under No-till. *Soil Science Society of America Journal* 77, 1724–1731.
- García-Salamanca, A., Molina-Henares, M.A., van Dillewijn, P., Solano, J., Pizarro-Tobías, P., Roca, A., Duque, E., Ramos, J.L., 2013. Bacterial diversity in the rhizosphere of maize and the surrounding carbonate-rich bulk soil. *Microbial Biotechnology* 6, 36–44.

- Gebremikael, M.T., Steel, H., Buchan, D., Bert, W., De Neve, S., 2016. Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. *Scientific Reports* 6, 32862.
- Geisen, S., Koller, R., Hünninghaus, M., Dumack, K., Ulrich, T., Bonkowski, M., 2016. The soil food web revisited: diverse and widespread mycophagous soil protists. *Soil Biology and Biochemistry* 94, 10–18.
- Gougoulias, C., Clark, J.M., Shaw, L.J., 2014. The role of soil microbes in the global carbon cycle: tracking the below-ground microbial processing of plant-derived carbon for manipulating carbon dynamics in agricultural systems. *Journal of the Science of Food and Agriculture* 94, 2362–2371.
- Grabau, Z.J., Chen, S., 2016. Influence of long-term corn–soybean crop sequences on soil ecology as indicated by the nematode community. *Applied Soil Ecology* 100, 172–185.
- Guo, J., McCulley, R.L., Phillips, T.D., McNear, D.H., 2016. Fungal endophyte and tall fescue cultivar interact to differentially affect bulk and rhizosphere soil processes governing C and N cycling. *Soil Biology and Biochemistry* 101, 165–174.
- Harman, G.E., 2006. Overview of mechanisms and uses of *Trichoderma* spp. *Phytopathology* 96, 190–194.
- Hartman, W.H., Ye, R., Horwath, W.R., Tringe, S.G., 2017. A genomic perspective on stoichiometric regulation of soil carbon cycling. *The ISME Journal* 11, 2652–2665.
- Hassan, M., McInroy, J., Kloepper, J., 2019. The interactions of rhizodeposits with plant growth-promoting rhizobacteria in the rhizosphere: a review. *Agriculture* 9, 142.
- Herman, D.J., Firestone, M.K., Nuccio, E., Hodge, A., 2012. Interactions between an arbuscular mycorrhizal fungus and a soil microbial community mediating litter decomposition. *FEMS Microbiology Ecology* 80, 236–247.
- Hernanz, J.L., Sanchez-Giron, V., Navarrete, L., 2009. Soil carbon sequestration and stratification in a cereal/leguminous crop rotation with three tillage systems in semiarid conditions. *Agriculture, Ecosystems & Environment* 133, 114–122.
- Higashi, T., Yungui, M., Komatsuzaki, M., Miura, S., Hirata, T., Araki, H., Kaneko, N., Ohta, H., 2014. Tillage and cover crop species affect soil organic carbon in Andosol, Kanto, Japan. *Soil and Tillage Research* 138, 64–72.
- Hobbie, S.E., 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in Ecology & Evolution* 30, 357–363.
- Hobbie, S.E., Villéger, S., 2015. Interactive effects of plants, decomposers, herbivores, and predators on nutrient cycling. *Trophic Interactions: Bottom-up and Top-down Interactions in Aquatic and Terrestrial Ecosystems* 233–259.
- Hontoria, C., García-González, I., Quemada, M., Roldán, A., Alguacil, M.M., 2019. The cover crop determines the AMF community composition in soil and in roots of maize after a ten-year continuous crop rotation. *The Science of the Total Environment* 660, 913–922.
- Hossain, M.M., Sultana, F., Islam, S., 2017. Plant growth-promoting fungi (PGPF): phyto-stimulation and induced systemic resistance. *Plant-Microbe Interactions in Agro-Ecological Perspectives* 135–191.
- Hoysted, G.A., Kowal, J., Jacob, A., Rimington, W.R., Duckett, J.G., Pressel, S., Orchard, S., Ryan, M.H., Field, K.J., Bidartondo, M.I., 2018. A mycorrhizal revolution. *Current Opinion in Plant Biology* 44, 1–6.
- Hugoni, M., Luis, P., Guyonnet, J., Haichar, F.E.Z., 2018. Plant host habitat and root exudates shape fungal diversity. *Mycorrhiza* 28, 451–463.
- Hu, L., Robert, C.A.M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., van der Heijden, M.G.A., Schlaeppli, K., Erb, M., 2018a. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nature Communications* 9, 2738.
- Hunter, M.D., 2001. Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology* 3, 77–84.
- Hu, W., Strom, N., Haarith, D., Chen, S., Bushley, K.E., 2018b. Mycobiome of cysts of the soybean cyst nematode under long term crop rotation. *Frontiers in Microbiology* 9, 386.
- Ilyas, N., Ambreen, F., Batool, N., Arshad, M., 2018. Contribution of nitrogen fixed by mung bean to the following wheat crop. In *Soil Science and Plant Analysis* 49, 148–158.
- Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Piñeiro, G., 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology, Evolution, and Systematics* 48, 419–445.
- Jarecki, M., Grant, B., Smith, W., Deen, B., Drury, C., VanderZaag, A., Qian, B., Yang, J., Wagner-Riddle, C., 2018. Long-term trends in corn yields and soil carbon under diversified crop rotations. *Journal of Environmental Quality* 47, 635–643.
- Jastrow, J.D., Amonette, J.E., Bailey, V.L., 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. *Climatic Change* 80, 5–23.
- Johnson, J.M.F., Barbour, N.W., Weyers, S.L., 2007. Chemical composition of crop biomass impacts its decomposition. *Soil Science Society of America Journal* 71, 155–162.
- Jones, D.L., Nguyen, C., Finlay, R.D., 2009. Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant and Soil* 321, 5–33.
- Kabiri, V., Raiesi, F., Ghazavi, M.A., 2016. Tillage effects on soil microbial biomass, SOM mineralization and enzyme activity in a semi-arid Calcixerepts. *Agriculture, Ecosystems & Environment* 232, 73–84.
- Kahiluoto, H., Ketoja, E., Vestberg, M., 2009. Contribution of arbuscular mycorrhiza to soil quality in contrasting cropping systems. *Agriculture, Ecosystems & Environment* 134, 36–45.
- Kaiser, C., Kilburn, M.R., Clode, P.L., Fuchslueger, L., Koranda, M., Cliff, J.B., Solaiman, Z.M., Murphy, D.V., 2015. Exploring the transfer of recent plant photosynthates to soil microbes: mycorrhizal pathway vs direct root exudation. *New Phytologist* 205, 1537–1551.
- Kallenbach, C., Grandy, A.S., 2011. Controls over soil microbial biomass responses to carbon amendments in agricultural systems: a meta-analysis. *Agriculture, Ecosystems & Environment* 144, 241–252.
- Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2018. Author Correction: direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications* 9, 3929.
- Kallenbach, C.M., Grandy, A.S., Frey, S.D., Diefendorf, A.F., 2015. Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biology and Biochemistry* 91, 279–290.
- Kardol, P., De Long, J.R., 2018. How anthropogenic shifts in plant community composition alter soil food webs. *F1000Research* 7.
- Katsvairo, T.W., Wright, D.L., Marois, J.J., 2006. Sod–livestock integration into the peanut–cotton rotation: a systems farming approach. *Agronomy* 98, 1156–1171.
- Katsvairo, T.W., Wright, D.L., Marois, J.J., Hartzog, D.L., Balkcom, K.B., Wiatrak, P.P., Rich, J.R., 2007a. Cotton roots, earthworms, and infiltration characteristics in sod–peanut–cotton cropping systems. *Agronomy Journal* 92, 390–398.
- Katsvairo, T.W., Wright, D.L., Marois, J.J., Rich, J.R., 2007b. Transition from conventional farming to organic farming using bahiagrass. *Journal of the Science of Food and Agriculture* 87, 2751–2756.
- King, A.E., Blesh, J., 2018. *Crop Rotations for Increased Soil Carbon: Perenniality as a Guiding Principle. Ecological Applications*, vol. 28. A Publication of the Ecological Society of America, pp. 249–261.
- Kong, A.Y.Y., Scow, K.M., Córdova-Kreylos, A.L., Holmes, W.E., Six, J., 2011. Microbial community composition and carbon cycling within soil microenvironments of conventional, low-input, and organic cropping systems. *Soil Biology and Biochemistry* 43, 20–30.
- Kuzyakov, Y., Domanski, G., 2000. Carbon input by plants into the soil. *Review. Journal of Plant Nutrition and Soil Science* 163, 421–431.
- Lal, R., 2011. Sequestering carbon in soils of agro-ecosystems. *Food Policy* 36, S33–S39.
- Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* 304, 1623–1627.
- Lal, R., Negassa, W., Lorenz, K., 2015. Carbon sequestration in soil. *Current Opinion in Environmental Sustainability* 15, 79–86.
- Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* 6, 6707.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J., 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology* 42, S3–S15.
- Lechenet, M., Dessaint, F., Py, G., Makowski, D., Munier-Jolain, N., 2017. Reducing pesticide use while preserving crop productivity and profitability on arable farms. *Nat. Plants* 3, 17008.
- Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. *Nature* 528, 60–68.
- Leslie, A.W., Wang, K.-H., Meyer, S.L.F., Marahatta, S., Hooks, C.R.R., 2017. Influence of cover crops on arthropods, free-living nematodes, and yield in a succeeding no-till soybean crop. *Applied Soil Ecology* 117, 21–31.
- Leveau, J.H.J., Preston, G.M., 2008. Bacterial mycophagy: definition and diagnosis of a unique bacterial–fungal interaction. *New Phytologist* 177, 859–876.
- Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology* 25, 3578–3590.
- Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. *Nat. Microbiol.* 2, 17105.
- Li, J., Liu, K., Zhang, J., Huang, L., Coulter, J.A., Woodburn, T., Li, L., Gan, Y., 2018. Soil-plant indices help explain legume response to crop rotation in a semiarid environment. *Frontiers of Plant Science* 9, 1488.
- Liu, J., Yu, Z., Yao, Q., Hu, X., Zhang, W., Mi, G., Chen, X., Wang, G., 2017. Distinct soil bacterial communities in response to the cropping system in a Mollisol of northeast China. *Applied Soil Ecology* 119, 407–416.
- Li, X.G., Jia, B., Lv, J., Ma, Q., Kuzyakov, Y., Li, F.-M., 2017. Nitrogen fertilization decreases the decomposition of soil organic matter and plant residues in planted soils. *Soil Biology and Biochemistry* 112, 47–55.
- Lugtenberg, B.J., Dekkers, L.C., 1999. What makes *Pseudomonas* bacteria rhizosphere competent? *Environmental Microbiology* 1, 9–13.
- Luo, G., Xue, C., Jiang, Q., Xiao, Y., Zhang, F., Guo, S., Shen, Q., Ling, N., 2020. Soil Carbon, Nitrogen, and Phosphorus Cycling Microbial Populations and Their Resistance to Global Change Depend on Soil C:N:P Stoichiometry mSystems 5.
- Lupwayi, N.Z., Larney, F.J., Blackshaw, R.E., 2017. Pyrosequencing reveals profiles of soil bacterial communities after 12 years of conservation management on irrigated crop rotations. *Applied Soil Ecology* 121, 65–73.
- Lützw, M., Kögel-Knabner, I., Ekschmitt, K., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. *European Journal of Soil Science* 57, 426–445.
- Madari, B., Machado, P.L.O.A., Torres, E., de Andrade, A.G., Valencia, L.I.O., 2005. No tillage and crop rotation effects on soil aggregation and organic carbon in a Rhodic Ferralsol from southern Brazil. *Soil and Tillage Research* 80, 185–200.
- Maillard, É., Angers, D.A., Chantigny, M., Lafond, J., Pageau, D., Rochette, P., Lévesque, G., Leclerc, M.-L., Parent, L.-É., 2016. Greater accumulation of soil organic carbon after liquid dairy manure application under cereal-forage rotation than cereal monoculture. *Agriculture, Ecosystems & Environment* 233, 171–178.
- Malik, A.A., Chowdhury, S., Schlager, V., Oliver, A., Puissant, J., Vazquez, P.G.M., Jehmlich, N., von Bergen, M., Griffiths, R.I., Gleixner, G., 2016. Soil fungal:bacterial ratios are linked to altered carbon cycling. *Frontiers in Microbiology* 7, 1247.

- Maltais-Landry, G., Scow, K., Brennan, E., 2014. Soil phosphorus mobilization in the rhizosphere of cover crops has little effect on phosphorus cycling in California agricultural soils. *Soil Biology and Biochemistry* 78, 255–262.
- Manzoni, S., Taylor, P., Richter, A., Porporato, A., Agren, G.I., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist* 196, 79–91.
- Maron, P.A., Sarr, A., Kaisermann, A., Lévêque, J., Mathieu, O., Guigue, J., Karimi, B., Bernard, L., Dequiedt, S., Terrat, S., Chabbi, A., Ranjard, L., 2018. High microbial diversity promotes soil ecosystem functioning. *Applied and Environmental Microbiology* 84.
- Martins, M., dos, R., Angers, D.A., 2015. Different plant types for different soil ecosystem services. *Geoderma* 237, 266–269.
- McCarthy, J.F., Ilavsky, J., Jastrow, J.D., Mayer, L.M., Perfect, E., Zhuang, J., 2008. Protection of organic carbon in soil microaggregates via restructuring of aggregate porosity and filling of pores with accumulating organic matter. *Geochimica et Cosmochimica Acta* 72, 4725–4744.
- McConkey, B., 2003. Crop rotation and tillage impact on carbon sequestration in Canadian prairie soils. *Soil and Tillage Research* 74, 81–90.
- McDaniel, Grandy, A.S., Tiemann, L.K., Weintraub, M.N., 2014a. Crop rotation complexity regulates the decomposition of high and low quality residues. *Soil Biology and Biochemistry* 78, 243–254.
- McDaniel, M.D., Tiemann, L.K., Grandy, A.S., 2014b. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecological Applications* 24, 560–570.
- Medina-Sauza, R.M., Álvarez-Jiménez, M., Delhal, A., Reverchon, F., Blouin, M., Guerrero-Analco, J.A., Cerdán, C.R., Guevara, R., Villain, L., Barois, I., 2019. Earthworms building up soil microbiota, a review. *Frontiers of Environmental Science* 7, 81.
- Mhatre, P.H., Karthik, C., Kadirvelu, K., Divya, K.L., Venkatasalam, E.P., Srinivasan, S., Ramkumar, G., Saranya, C., Shanmuganathan, R., 2019. Plant growth promoting rhizobacteria (PGPR): a potential alternative tool for nematodes bio-control. *Biocatalysis and Agricultural Biotechnology* 17, 119–128.
- Moitinho, M.R., Fernandes, C., Truber, P.V., Marcelo, A.V., Corá, J.E., da Silva Bicalho, E., 2020. Arbuscular mycorrhizal fungi and soil aggregation in a no-tillage system with crop rotation. *Journal of Plant Nutrition and Soil Science* 183, 482–491.
- Möller, K., Stinner, W., Leithold, G., 2008. Growth, composition, biological N₂ fixation and nutrient uptake of a leguminous cover crop mixture and the effect of their removal on field nitrogen balances and nitrate leaching risk. *Nutrient Cycling in Agroecosystems* 82, 233.
- Murrell, E.G., Ray, S., Lemmon, M.E., Luthe, D.S., Kaye, J.P., 2020. Cover crop species affect mycorrhizae-mediated nutrient uptake and pest resistance in maize. *Renewable Agriculture and Food Systems* 35, 467–474.
- Nguyen, C., 2009. Rhizodeposition of organic C by plants: mechanisms and controls. *Sustainable Agriculture* 97–123.
- Nguyen, D., Rieu, I., Mariani, C., van Dam, N.M., 2016. How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory. *Plant Molecular Biology* 91, 727–740.
- Nielsen, U.N., Ayres, E., Wall, D.H., Bardgett, R.D., 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *European Journal of Soil Science* 62, 105–116.
- Oberholster, T., Vikram, S., Cowan, D., Valverde, A., 2018. Key microbial taxa in the rhizosphere of sorghum and sunflower grown in crop rotation. *The Science of the Total Environment* 624, 530–539.
- Orgiazzi, A., Bardgett, R.D., Barrios, E., 2016. *Global Soil Biodiversity Atlas*. European Commission.
- Osler, G.H.R., Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. *Ecology* 88, 1611–1621.
- Pan, Z., Zhang, R., Zicari, S., 2019. *Integrated Processing Technologies for Food and Agricultural By-Products*. Academic Press.
- Parihar, C.M., Yadav, M.R., Jat, S.L., Singh, A.K., Kumar, B., Pradhan, S., Chakraborty, D., Jat, M.L., Jat, R.K., Saharawat, Y.S., Yadav, O.P., 2016. Long term effect of conservation agriculture in maize rotations on total organic carbon, physical and biological properties of a sandy loam soil in north-western Indo-Gangetic Plains. *Soil and Tillage Research* 161, 116–128.
- Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandler, E., Marhan, S., Riederer, M., Scheu, S., Kuznyakov, Y., Ruess, L., 2016. Small but active-pool size does not matter for carbon incorporation in below-ground food webs. *Functional Ecology* 30, 479–489.
- Pausch, J., Kuznyakov, Y., 2018. Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology* 24, 1–12.
- Pausch, J., Tian, J., Riederer, M., Kuznyakov, Y., 2013. Estimation of rhizodeposition at field scale: upscaling of a ¹⁴C labeling study. *Plant and Soil* 364, 273–285.
- Pelosi, C., Grandeau, G., Capowiez, Y., 2017. Temporal dynamics of earthworm-related macroporosity in tilled and non-tilled cropping systems. *Geoderma* 289, 169–177.
- Peralta, A.L., Sun, Y., McDaniel, M.D., Lennon, J.T., 2018. Crop rotational diversity increases disease suppressive capacity of soil microbiomes. *Ecosphere* 9, e02235.
- Pérez-de-Luque, A., Tille, S., Johnson, I., Pascual-Pardo, D., Ton, J., Cameron, D.D., 2017. The interactive effects of arbuscular mycorrhiza and plant growth-promoting rhizobacteria synergistically enhance host plant defences against pathogens. *Scientific Reports* 7, 16409.
- Preissel, S., Reckling, M., Schläpke, N., Zander, P., 2015. Magnitude and farm-economic value of grain legume pre-crop benefits in Europe: a review. *Field Crops Research* 175, 64–79.
- Pribyl, D.W., 2010. A critical review of the conventional SOC to SOM conversion factor. *Geoderma* 156, 75–83.
- Prommer, J., Walker, T.W.N., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., Richter, A., 2020. Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. *Global Change Biology* 26, 669–681.
- Qiu, Q., Wu, L., Ouyang, Z., Li, B., Xu, Y., Wu, S., Gregorich, E.G., 2016. Priming effect of maize residue and urea N on soil organic matter changes with time. *Applied Soil Ecology* 100, 65–74.
- Rabot, E., Wiesmeier, M., Schlüter, S., Vogel, H.-J., 2018. Soil structure as an indicator of soil functions: a review. *Geoderma* 314, 122–137.
- Raffard, A., Santoul, F., Cucherousset, J., Blanchet, S., 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biological Reviews of the Cambridge Philosophical Society* 94, 648–661.
- Rahman, L., Chan, K.Y., Heenan, D.P., 2007. Impact of tillage, stubble management and crop rotation on nematode populations in a long-term field experiment. *Soil and Tillage Research* 95, 110–119.
- Rillig, M.C., Aguilar-Trigueros, C.A., Camenzind, T., Cavagnaro, T.R., Degrange, F., Hohmann, P., Lammel, D.R., Mansour, I., Roy, J., Heijden, M.G.A., Yang, G., 2019. Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytologist* 222, 1171–1175.
- Rodríguez, M.P., Domínguez, A., Moreira Ferroni, M., Wall, L.G., Bedano, J.C., 2020. The diversification and intensification of crop rotations under No-till promote earthworm abundance and biomass. *Agronomy* 10, 919.
- Roger-Estrade, J., Anger, C., Bertrand, M., Richard, G., 2010. Tillage and soil ecology: partners for sustainable agriculture. *Soil and Tillage Research* 111, 33–40.
- Rosenzweig, S.T., Fonte, S.J., Schipanski, M.E., 2018. Intensifying rotations increases soil carbon, fungi, and aggregation in semi-arid agroecosystems. *Agriculture, Ecosystems & Environment* 258, 14–22.
- Rudnick, M.B., van Veen, J.A., de Boer, W., 2015. Baiting of rhizosphere bacteria with hyphae of common soil fungi reveals a diverse group of potentially mycophagous secondary consumers. *Soil Biology and Biochemistry* 88, 73–82.
- Sá, J.C. de M., de Moraes Sá, J.C., Tivet, F., Lal, R., Briedis, C., Hartman, D.C., dos Santos, J.Z., dos Santos, J.B., 2014. Long-term tillage systems impacts on soil C dynamics, soil resilience and agronomic productivity of a Brazilian Oxisol. *Soil and Tillage Research* 136, 38–50.
- 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, 9575–9580.
- Santos, S.S., Schöler, A., Nielsen, T.K., Hansen, L.H., Schloter, M., Winding, A., 2020. Land use as a driver for protist community structure in soils under agricultural use across Europe. *The Science of the Total Environment* 717, 137228.
- Sasse, J., Martiñoia, E., Northen, T., 2018. Feed your friends: do plant exudates shape the root microbiome? *Trends in Plant Science* 23, 25–41.
- Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.-A., Villenave, C., Bertrand, I., 2016. The dynamics of soil micro-food web structure and functions vary according to litter quality. *Soil Biology and Biochemistry* 95, 262–274.
- Savin, M.C., Görres, J.H., Amador, J.A., 2004. Microbial and microfaunal community dynamics in artificial and lumbricus terrestris (L.) burrows. *Soil Science Society of America Journal*. Soil Science Society of America 68, 116–124.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49–56.
- Schmidt, R., Mitchell, J., Scow, K., 2019. Cover cropping and no-till increase diversity and symbiotroph:saprotroph ratios of soil fungal communities. *Soil Biology and Biochemistry* 129, 99–109.
- Schmitz, O.J., 2010. *Resolving Ecosystem Complexity (MPB-47)*. Princeton University Press.
- Schouteden, N., De Waele, D., Panis, B., Vos, C.M., 2015. Arbuscular mycorrhizal fungi for the biocontrol of plant-parasitic nematodes: a review of the mechanisms involved. *Frontiers in Microbiology* 6, 1280.
- Seabloom, E.W., Kinkel, L., Borer, E.T., Hautier, Y., Montgomery, R.A., Tilman, D., 2017. Food webs obscure the strength of plant diversity effects on primary productivity. *Ecology Letters* 20, 505–512.
- Singh, A.K., Rai, A., Pandey, V., Singh, N., 2017. Contribution of glomalin to dissolve organic carbon under different land uses and seasonality in dry tropics. *Journal of Environmental Management* 192, 142–149.
- Singh, G., Bhattacharyya, R., Das, T.K., Sharma, A.R., Ghosh, A., Das, S., Jha, P., 2018. Crop rotation and residue management effects on soil enzyme activities, glomalin and aggregate stability under zero tillage in the Indo-Gangetic Plains. *Soil and Tillage Research* 184, 291–300.
- Six, J., Frey, S.D., Thiet, R.K., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal* 70, 555–569.
- Snapp, S.S., Swinton, S.M., Labarta, R., Mutch, D., 2005. Evaluating cover crops for benefits, costs and performance within cropping system niches. *Agronomy* 97, 322–332.
- Sokol, N.W., Bradford, M.A., 2019. Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nature Geoscience* 12, 46–53.
- Sommer, R., Ryan, J., Masri, S., Singh, M., Diekmann, J., 2011. Effect of shallow tillage, moldboard plowing, straw management and compost addition on soil organic matter and nitrogen in a dryland barley/wheat-vetch rotation. *Soil and Tillage Research* 115, 39–46.
- Souza, R. de, de Souza, R., Ambrosini, A., Passaglia, L.M.P., 2015. Plant growth-promoting bacteria as inoculants in agricultural soils. *Genetics and Molecular Biology* 38, 401–419.

- Souza, R.C., Cantão, M.E., Vasconcelos, A.T.R., Nogueira, M.A., Hungria, M., 2013. Soil metagenomics reveals differences under conventional and no-tillage with crop rotation or succession. *Applied Soil Ecology* 72, 49–61.
- Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P., 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90, 1073–1083.
- Steinauer, K., Chatzinotas, A., Eisenhauer, N., 2016. Root exudate cocktails: the link between plant diversity and soil microorganisms? *Ecology and Evolution* 6, 7387–7396.
- Stirling, G., Blair, B., Wilson, E., Stirling, M., 2002. Crop Rotation for Managing Nematode Pest and Improving Soil Health in Sugarcane Cropping Systems.
- Sun, B., Jia, S., Zhang, S., McLaughlin, N.B., Liang, A., Chen, X., Liu, S., Zhang, X., 2016. No tillage combined with crop rotation improves soil microbial community composition and metabolic activity. *Environmental Science and Pollution Research International* 23, 6472–6482.
- Taheri, A.E., Hamel, C., Gan, Y., 2016. Cropping practices impact fungal endophytes and pathogens in durum wheat roots. *Applied Soil Ecology* 100, 104–111.
- Tahir, M., Sajjad Mirza, M., Hameed, S., Dimitrov, M.R., Smidt, H., 2015. Cultivation-based and molecular assessment of bacterial diversity in the rhizosphere of wheat under different crop rotations. *PLoS One* 10, e0130030.
- Thakur, M.P., Geisen, S., 2019. Trophic regulations of the soil microbiome. *Trends in Microbiology* 27, 771–781.
- Tiemann, L.K., Grandy, A.S., Atkinson, E.E., Marin-Spiotta, E., McDaniel, M.D., 2015. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecology Letters* 18, 761–771.
- Trivedi, P., Delgado-Baquerizo, M., Trivedi, C., Hu, H., Anderson, I.C., Jeffries, T.C., Zhou, J., Singh, B.K., 2016. Microbial regulation of the soil carbon cycle: evidence from gene–enzyme relationships. *The ISME Journal* 10, 2593–2604.
- Turrini, A., Sbrana, C., Avio, L., Njeru, E.M., Bocci, G., Barberi, P., Giovannetti, M., 2016. Changes in the composition of native root arbuscular mycorrhizal fungal communities during a short-term cover crop-maize succession. *Biology and Fertility of Soils* 52, 643–653.
- Vanni, M.J., Flecker, A.S., Hood, J.M., 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* 5, 285–293.
- Veen, G.F., Fry, E.L., ten Hooven, F.C., Kardol, P., Morriën, E., De Long, J.R., 2019. The role of plant litter in driving plant-soil feedbacks. *Front. Environ. Sci.* 7, 168.
- Venter, Z.S., Jacobs, K., Hawkins, H.-J., 2016. The impact of crop rotation on soil microbial diversity: a meta-analysis. *Pedobiologia* 59, 215–223.
- Verma, M., Mishra, J., Arora, N.K., 2019. Plant growth-promoting rhizobacteria: diversity and applications. *Environmental Biotechnology: For Sustainable Future* 129–173.
- Vivelo, S., Bhatnagar, J.M., 2019. An evolutionary signal to fungal succession during plant litter decay. *FEMS Microbiology Ecology* 95, fiz145.
- Vries, F.T. de, de Vries, F.T., Wallenstein, M.D., 2017. Below-ground connections underlying above-ground food production: a framework for optimising ecological connections in the rhizosphere. *Journal of Ecology* 105, 913–920.
- Vukicevich, E., Lowery, T., Bowen, P., Urbez-Torres, J.R., Hart, M., 2016. Cover crops to increase soil microbial diversity and mitigate decline in perennial agriculture. *A review. Agronomy for Sustainable Development* 36, 48.
- Wardle, D.A., 2013. *Communities and Ecosystems: Linking the Aboveground and Belowground Components (MPB-34)*. Princeton University Press.
- Wright, D., Marois, J., Katsvairo, T., Wiatrak, P., Rich, J., Others, 2004. Value of perennial grasses in conservation cropping systems. In: *Proc. Of the 26th Southern Conservation Tillage Conference for Sustainable Agriculture*. Raleigh, NC 8–9.
- Wright, S.F., Anderson, R.L., 2000. Aggregate stability and glomalin in alternative crop rotations for the central Great Plains. *Biology and Fertility of Soils* 31, 249–253.
- Wu, Q.S., Cao, M.Q., Zou, Y.N., He, X.H., 2014. Direct and indirect effects of glomalin, mycorrhizal hyphae, and roots on aggregate stability in rhizosphere of trifoliolate orange. *Scientific Reports* 4, 5823.
- Wurst, S., Ohgushi, T., 2015. Do plant- and soil-mediated legacy effects impact future biotic interactions? *Functional Ecology* 29, 1373–1382.
- Wu, X., Ge, T., Wang, W., Yuan, H., Wegner, C.E., Zhu, Z., Whiteley, A.S., Wu, J., 2015. Cropping systems modulate the rate and magnitude of soil microbial autotrophic CO₂ fixation in soil. *Frontiers in Microbiology* 6, 379.
- Xia, Y., Sahib, M.R., Amna, A., Opiyo, S.O., Zhao, Z., Gao, Y.G., 2019. Culturable endophytic fungal communities associated with plants in organic and conventional farming systems and their effects on plant growth. *Scientific Reports* 9, 1669.
- Yang, G., Wagg, C., Veresoglou, S.D., Hempel, S., Rillig, M.C., 2018. How soil biota drive ecosystem stability. *Trends in Plant Science* 23, 1057–1067.
- Yin, R., Kardol, P., Thakur, M.P., Gruss, I., Wu, G.L., Eisenhauer, N., Schädler, M., 2020. Soil functional biodiversity and biological quality under threat: intensive land use outweighs climate change. *Soil Biology and Biochemistry*, 107847.
- Young, I.M., Blanchart, E., Chenu, C., 1998. The interaction of soil biota and soil structure under global change. *Global Change Biology* 4, 703–712.
- Yu, X., Yuan, F., Fu, X., Zhu, D., 2016. Profiling and relationship of water-soluble sugar and protein compositions in soybean seeds. *Food Chemistry* 196, 776–782.
- Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., da Rocha, U.N., Shi, S., Cho, H., Karaoz, U., Loqué, D., Bowen, B.P., Firestone, M.K., Northen, T.R., Brodie, E.L., 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480.
- Zhang, S., Li, Q., Lü, Y., Zhang, X., Liang, W., 2013a. Contributions of soil biota to C sequestration varied with aggregate fractions under different tillage systems. *Soil Biology and Biochemistry* 62, 147–156.
- Zhang, W., Hendrix, P.F., Dame, L.E., Burke, R.A., Wu, J., Neher, D.A., Li, J., Shao, Y., Fu, S., 2013b. Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nature Communications* 4, 2576.
- Zhang, Z., Liang, S., Wang, J., Zhang, X., Mahmood, M., Yu, J., Zhang, X., Liang, A., Liang, W., 2018. Tillage and crop succession effects on soil microbial metabolic activity and carbon utilization in a clay loam soil. *European Journal of Soil Biology* 88, 97–104.
- Zhang, Z.Y., Zhang, X.K., Zhao, J.S., Zhang, X.P., Liang, W.J., 2015. Tillage and rotation effects on community composition and metabolic footprints of soil nematodes in a black soil. *European Journal of Soil Biology* 66, 40–48.
- Zhao, D., Wright, D.L., Marois, J.J., Mackowiak, C.L., Brennan, M., 2010. Improved growth and nutrient status of an oat cover crop in sod-based versus conventional peanut-cotton rotations. *Agronomy for Sustainable Development* 30, 497–504.
- Zheng, Y., Wang, S., Bonkowski, M., Chen, X., Griffiths, B., Hu, F., Liu, M., 2018. Litter chemistry influences earthworm effects on soil carbon loss and microbial carbon acquisition. *Soil Biology and Biochemistry* 123, 105–114.
- Zhou, X., Liu, J., Wu, F., 2017. Soil microbial communities in cucumber monoculture and rotation systems and their feedback effects on cucumber seedling growth. *Plant and Soil* 415, 507–520.
- Zhu, X., Li, X., Xing, F., Chen, C., Huang, G., Gao, Y., 2020. Interaction between Root Exudates of the Poisonous Plant *Stellera Chamaejasme* L. and Arbuscular Mycorrhizal Fungi on the Growth of *Leymus Chinensis* (Trin.) Tzvel. *Microorganisms*, vol. 8.
- Zuber, S.M., Behnke, G.D., Nafziger, E.D., Villamil, M.B., 2015. Crop rotation and tillage effects on soil physical and chemical properties in Illinois. *Agronomy Journal* 107, 971–978.
- Zvereva, E.L., Kozlov, M.V., 2012. Sources of variation in plant responses to belowground insect herbivory: a meta-analysis. *Oecologia* 169, 441–452.