CHAPTER ONE

Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration

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Contents

Abstract

Soil organic matter (SOM) provides vital services to humanity. Its preservation and further accrual are key to sustain food production and avoid an irreversible climate crisis. Here we present the processes and drivers of SOM formation and persistence within a coherent state-of-the-art framework. We posit that SOM forms via two distinct pathways depending on whether inputs are water soluble and/or easily solubilized entering the soil as dissolved organic matter (DOM), or they are structural. These distinct inputs form mineral-associated organic matter (MAOM), and particulate organic matter (POM), respectively. Both these SOM fractions have plant and microbial components but in

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different proportions, with MAOM being more highly microbial. SOM persistence will depend on microbial activity inhibition, the degree of its limitation and carbon use efficiency, and microbial access constraints, primarily due to association to minerals and occlusions in fine aggregates. Climate is the overarching control of SOM persistence, also by affecting ecosystem traits, when persistence is driven by microbial activity inhibition or limitation, largely responsible for POM storage. Soil geochemical traits are the overarching control of SOM persistence driven by microbial access constraints, particularly in the subsoil, specifically controlling MAOM storage. SOM affects soil properties (aggregation, porosity, and cation exchange capacity) which in turn determine the soil's capacity for functioning and ability to provide desired outcomes including erosion and flood prevention, plant productivity, and climate mitigation. The specific properties of SOM which influence its contributions to these functions are discussed, with implications for SOM conservation and regeneration to promote desired outcomes.

1. Introduction

Soil organic matter (SOM) is an incredibly important renewable natural resource which supports many vital ecosystem services, from the provision of food and fiber, to regulating climate and water cycles, regenerating fertility, and supporting the immense biodiversity of soils (Smith et al., 2015). By converting land for agricultural use over recent millennia, but especially over the past 200 years, humanity has consumed large amounts of SOM by accelerating its rates of mineralization and erosion over those of organic matter inputs into the soil and soil formation, resulting in a global estimated loss of 133 Pg carbon (C) from the top 2 m of soils (Sanderman et al., 2017). However, this massive loss of SOM now presents the opportunity for regenerating SOM, accruing the lost C back into the soil. Large-scale soil C sequestration efforts are urgently needed, but they require concerted action to adopt sets of measures adapted to local soil capacities for regeneration and relevant land management opportunities (Amelung et al., 2020). These actions must be grounded in science and use our current understanding of SOM formation, persistence, and functioning.

The scientific understanding of SOM has advanced tremendously in the past decade, with many new conceptual frameworks (e.g., Cotrufo et al., 2013, 2015; Daly et al., 2021; Lehmann and Kleber, 2015; Lehmann et al., 2020; Liang et al., 2017; Schmidt et al., 2011), an increased availability of large datasets on soils at continental to global scales (e.g., Harden et al., 2017; Lawrence et al., 2020), and the development of a new generation of soil biogeochemical models (e.g., Kyker-Snowman et al., 2020; Sulman et al., 2017; Yu et al., 2020; Zhang et al., 2021). These new advancements must be tied together to achieve the desired transformative outcomes and inform meaningful and effective SOM regeneration strategies (Blankinship et al., 2018). In this chapter we synthesize the current understanding of the processes and drivers regulating SOM formation and persistence in a comprehensive framework. We use this understanding to describe SOM properties and link them to SOM functions. We close by proposing how this wealth of understanding and data can be applied to inform practices to preserve existing SOM stocks in natural soils and build new SOM in managed soils.

Managed soils are the focus of most SOM studies and soil C sequestration efforts. However, besides food and fiber production, all the vital ecosystem services that SOM provides, such as climate regulation, water recycling, and supporting soil biodiversity, are offered by both natural and managed soils. Agricultural management usually leads to significant alterations to SOM in terms of its stocks (Ogle et al., 2005), properties, and dynamics, thus agricultural soils are not necessarily an optimal model to determine over-arching SOM properties and drivers of SOM dynamics. We believe that extending principles learned from studying SOM biogeochemistry in natural systems helps to identify the best principles for SOM regeneration in agricultural soils. Hence, we discuss SOM processes and drivers in general terms, independent of specific ecosystems, aiming to provide a general understanding of SOM, and a framework to guide future studies as well as to inform sustainable management solutions.

SOM formation and stabilization processes take place at very small scales, i.e., 1–1000 μm (Kravchenko and Guber, 2017), yet their aggregated outcomes manifest at larger scales which are the typical scale of observation. It is imperative to understand these mechanisms on the scale in which they take place, but also understand how they affect SOM processes and dynamics at a scale which is relevant for monitoring and modeling, to enable accurate forecasting of SOM changes (O'rourke et al., 2015; Paul, 2014). Our aim here is to use current understanding of these small-scale processes to explain emergent ecosystem-scale patterns.

In this chapter, we adopt the simple conceptualization of SOM being primarily in the forms of particulate (POM), mineral-associated (MAOM), and—as a much smaller proportion, i.e., 1–2%—dissolved organic matter (DOM). These SOM forms are defined on the bases of their physical properties, with MAOM being heavier (>1.6–$1.85\,\mathrm{g\,cm^{-3}}$) and/or finer ($<50$–$60\,\mu\mathrm{m}$) than POM, and DOM being water-soluble/extractable (Lavallee et al., 2020). Aggregates are composite hierarchical and dynamic structures (Tisdall and Oades, 1982) containing both POM and MAOM (Christensen, 2001). Thus, they are to be considered as a "state" in which

POM and MAOM can be found (Lavallee et al., 2020), and not as primary fractions themselves. However, MAOM can also be considered as very fine aggregates of organic matter and minerals, though for organo-mineral complexes <60 μm, the physical protection offered to very fine POM by occlusion may be as strong as that offered by organo-mineral chemical binding (Angst et al., 2017). We acknowledge that SOM is very complex and heterogeneous both chemically and physically, and that research will need to continue exploring its complexity. However, we adopt here this simplified conceptualization based on a few procedurally defined physical fractions (Fig. 1), since those fractions have been shown to form differently

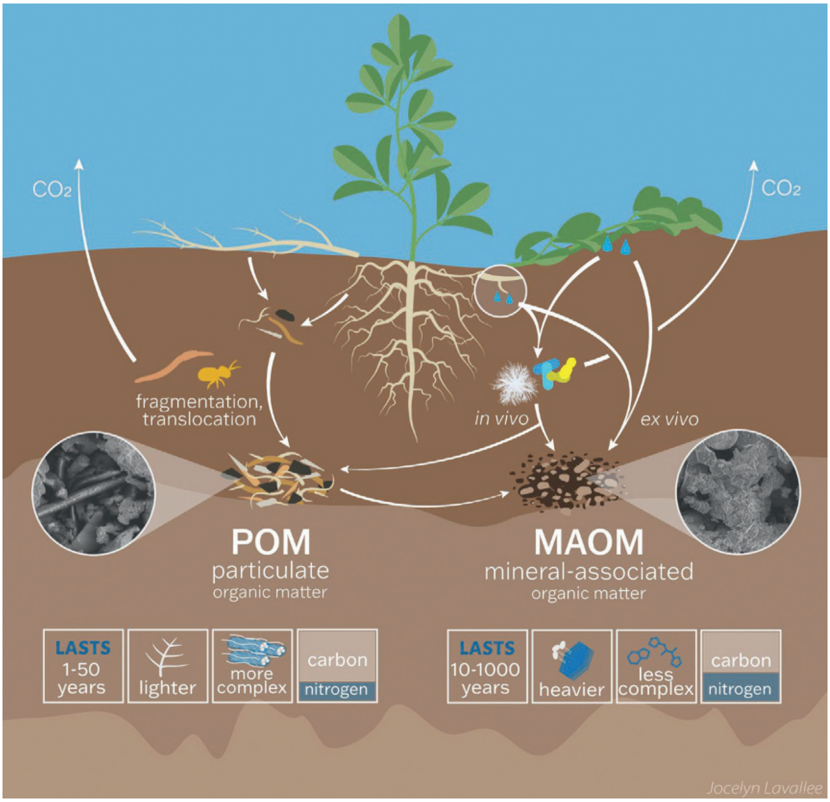

Fig. 1 Overview of key differences between particulate (POM) and mineral-associated organic matter (MAOM), including dominant formation pathways. Fragmentation and translocation of structural litter residues primarily form POM, while direct association (*ex vivo*) or microbe-mediated transformation and deposition (*in vivo*) of soluble and low molecular weight litter or exudate compounds primarily form MAOM. Compared to POM, MAOM tends to last longer in soil, has a higher density (when including the minerals it is associated with), contains less chemically complex compounds on average, and has a lower carbon-to-nitrogen (C:N) ratio.

(Cotrufo et al., 2015; Haddix et al., 2016), respond differently to land use, management, and climate changes (Jilling et al., 2020; Lugato et al., 2021; Rocci et al., 2021; Viscarra Rossel et al., 2019), and have different potentials for accrual (Cotrufo et al., 2019).

2. Soil organic matter formation

2.1 Organic matter inputs

Soils receive organic matter primarily from plants, through the continued release of exudates from plant roots, root tissue turnover, and deposition of aboveground plant residues, in amounts that vary greatly in space and time and depend on the ecosystem type (Table 1). Plants also transfer organic C to their mycorrhizal symbionts, which in turn are among the highest contributors of organic C to soil (Godbold et al., 2006). In managed ecosystems, organic matter inputs to soil are highly controlled by humans through crop selection, biomass harvesting, and organic amendments, the latter of which can contribute significant amounts of C to cropland soils (Table 1).

Fire, which is a natural disturbance and is also used as a management practice, reduces the amount of C and nitrogen (N) returning to the soil since a large fraction is combusted and lost in gaseous and particulate forms to the atmosphere. Fire also modifies the physicochemical structure of plant inputs to highly condensed polyaromatic organic matter, defined as pyrogenic organic matter (PyOM), thus reducing SOM decomposability (Bird et al., 2015; Knicker, 2011; Pellegrini et al., 2020). All of these different inputs are composed of a broad array of chemical structures (Kögel-Knabner, 2002). Depending on their water solubility, energetic return on investment to microbial breakdown, and soil environmental properties, inputs will have different fates in the soil, affecting the resulting SOM formation, turnover, and persistence (Cotrufo et al., 2015; Lehmann et al., 2020; Schmidt et al., 2011; Waring et al., 2020).

Since the definition of SOM is vague and often refers simply to the organic molecules within the soil (Paul, 2014), the *formation* of SOM can be considered as starting from all of these inputs, which are defined as SOM from the moment they are found in soil. However, after entering the soil, organic matter inputs undergo a series of chemical and physical transformations, with or without the contribution of faunal and microbial processing, that together contribute to the formation and persistence of SOM. During these transformations, most of the C input into the soil is

Table 1 Synthesis of published values for most common types of organic carbon inputs to soils both from above- and below-ground for croplands, grasslands, and forest systems.

		Input ranges ($g\,C\,m^{-2}\,year^{-1}$)						References
	Input type	Croplands		Grasslands		Forests		
		Low	High	Low	High	Low	High	
Above-ground	Leaves and stems	20.60	500	9.90	151.14	90.0	860.0	1–19
	Wood residues	N/A		N/A		19.8	176.2	16, 20–22
	Farmyard Manure (managed)	50	300	N/A		N/A		2, 9, 17, 23, 24
	Green Manure	176	800	N/A		N/A		2, 24
	Compost	185	862	N/A		N/A		25, 26
Below-ground	Root exudates	16.6	61.3	0.003	60	42.4	120.4	8, 14, 18, 27–33
	Root turnover	55.4	92.0	3.00	400	80.0	839	8, 11, 13, 14, 17–19, 27, 34–36
	Mycorrhizae/hyphae	2426.6		124.5	5187.9	1228.0	6889.8	34, 37, 38
	Microbial biomass	114.3	938.0	18.0	2065.8	70	2508.0	11, 12, 18, 37, 39–42

When a range of input values was available, the lowest and highest values reported by the listed references for each land use are presented. N/A not applicable.

Reference numbers refer to: 1.Berhongaray et al. (2019); 2.Bhardwaj et al. (2019); 3.Bowden et al. (2014); 4.Clemmensen et al. (2013); 5.Díaz-Pinés et al. (2011); 6. Henry et al. (2008); 7.Jha et al. (2014); 8.Johnson et al. (2006); 9.Kimura et al. (2011); 10. Koga and Tsuji (2009); 11.Leff et al. (2012); 12.Liu et al. (2021); 13.Morais et al. (2013); 14.Shen et al. (2020); 15.Smyth et al. (2013); 16. Villanova et al. (2019); 17. Wang et al. (2015); 18. Wilson et al. (2018); 19.Zatta et al. (2014); 20. Aryal et al. (2014); 21.Gough et al. (2007); 22.Magalhães (2017); 23.García-Palacios et al. (2018); 24. Kätterer et al. (2011); 25.Jaiarree et al. (2014); 26.Maris et al. (2021); 27.Gougherty et al. (2018); 28. Pausch and Kuzyakov (2018); 29. Pausch and Kuzyakov (2018); 30. Moscôso et al. (2018); 31. Aoki et al. (2012); 32. Jones et al. (2009); 33. Sun et al. (2017); 34.Godbold et al. (2006); 35. Ventura et al. (2019); 36. Neumann et al. (2020); 37. Liang et al. (2019); 38. Soudzilovskaia et al. (2015); 39. Fisk et al. (2015); 40.Fontaine et al. (2004); 41. Laudicina et al. (2011); 42.Xiao et al. (2007).

mineralized to CO_2 with a SOM formation efficiency that we define as the amount of input-derived C retrieved in the soil vs the amount of C lost during the decomposition of such input (Lavallee et al., 2018), typically ranging between 3% and 33% (Castellano et al., 2015).

2.2 The SOM formation process

The SOM formation process was traditionally seen as beginning when necromass, in the form of polymeric compounds in structural residues, entered the soil. According to this view, the slower the residue decomposition and the more residue remaining throughout the decomposition process (Fig. 2), the more SOM is formed (Berg and Mcclaugherty, 2008). Higher lignin content and lower nutrient availability typically slow the residue mass loss rate and increase the amount of residue mass remaining partially undecomposed (i.e., the asymptotic value of litter mass loss) within the time frame of typical decomposition experiments (e.g., <10 years; Adair et al., 2008). Because of this finding, it was thought that the more chemically recalcitrant (i.e., higher lignin and C:nutrient ratios) the organic matter inputs, the higher the asymptotic value of litter mass loss and the more SOM would be formed (Aber et al., 1990; Berg et al., 1984).

However, detailed chemical characterization of litter residues during longer-term decomposition did not support the idea of selective preservation of lignin in the remaining residues (Preston et al., 2009). Additionally, lignin moieties extracted from soils did not prove to be more resistant to degradation than other soil compounds (Dungait et al., 2008), indicating that the abundance of chemically recalcitrant structures in organic matter inputs to soil is not a main driver for long-term SOM persistence, as we will discuss below. However, these residue structures contribute to the formation of light POM in soils (Haddix et al., 2016), with light POM typically being enriched in lignin compared to other SOM fractions (Cambardella and Elliott, 1992; Christensen, 2001).

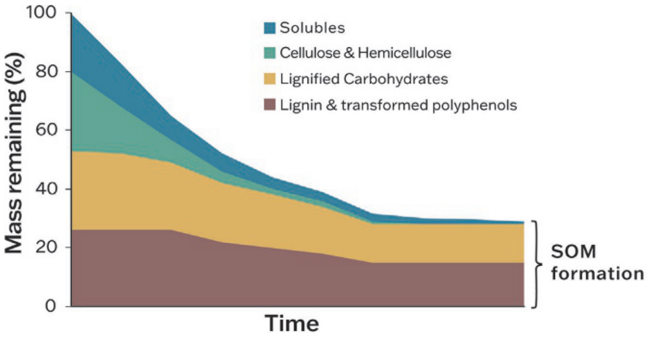

Fig. 2 Representation of the former view of plant residue contribution to soil organic matter (SOM) formation. According to this view the higher the initial residue content of lignin and lignin encrusted celluloses (i.e., lignified carbohydrates) the more mass remaining and thus the more residue contribution to SOM formation.

This view of structural residue of plant input decomposition as the dominant input to SOM leads to the conception of the SOM formation process as initiating from the POM fraction (Grandy and Neff, 2008; Lehmann and Kleber, 2015), and neglects the large portion of organic matter inputs entering the soil in water-soluble forms (Kaiser and Guggenberger, 2000) through exudation from living plants and leaching from decomposition residues on the soil surface and rhizosphere. Exudation may represent 20–40% of plant assimilated C (Canarini et al., 2019; Prescott et al., 2020), and we estimated that 2–16% of initial aboveground plant residue C is lost as DOM within the first year of decomposition, depending on the initial residue chemistry (Fig. 3; Soong et al., 2015), while root residues were observed to release about 2.4% of their C as DOM within the first 50 days of decomposition (Uselman et al., 2007). Additionally, rain deposits small amounts of DOM on the soil, estimated to be on average 1.5–3.0 g organic $\mathrm{C\,m^{-2}\,year^{-1}}$ (Willey et al., 2000). Soluble inputs are typically considered readily available substrates for microbes; they are characterized by fast turnover, and may even accelerate the loss of native SOM by increasing microbial activity, thus priming SOM mineralization (Kuzyakov, 2010), or by liberating organic matter bonded to minerals (Jilling et al., 2018; Keiluweit et al., 2015). However, a systematic review of the effects of fresh organic matter inputs on SOM showed higher replenishment of SOM than its loss by priming or organo-mineral destabilization, with an average new SOM formation corresponding to 32% of the added C (Liang et al., 2018).

Multiple studies in contrasting ecosystems are confirming that low molecular weight C inputs as DOM are efficient precursors of SOM (e.g., Lynch et al., 2018; Strickland et al., 2012). In particular, DOM derived from above ground residues is expected to contribute to the formation of SOM in the topsoil, while DOM derived from exudates and root litter decomposition would contribute to SOM formation at depths (Gmach et al., 2020). However, DOM inputs are usually not accounted for during decomposition studies, which typically use the mass remaining in litter bags as a measure of residue contribution to SOM formation, significantly biasing the study of SOM formation (Cotrufo et al., 2009). We thus stress the need to better quantify the fluxes of DOM into the soil during residue decomposition and root exudation, and their net contributions to SOM formation.

The two-pathway model of SOM formation (Cotrufo et al., 2015) reconciles the differing views regarding the role of litter chemistry for SOM

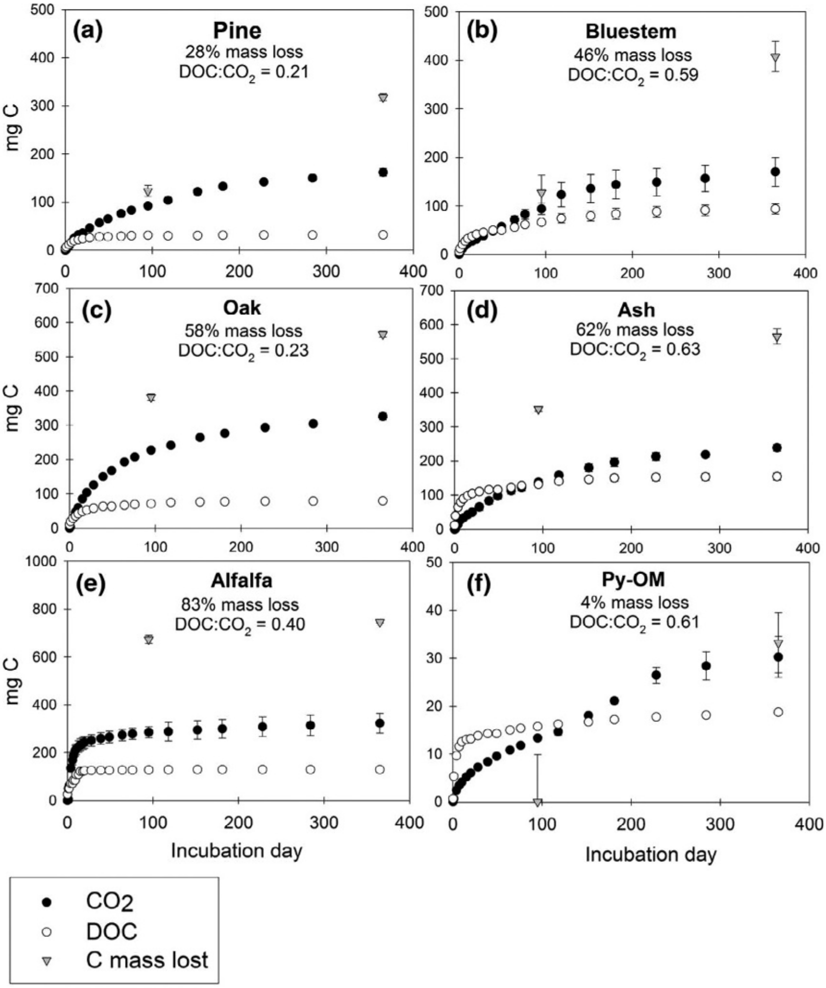

Fig. 3 Residue-derived carbon loss as carbon dioxide (CO_2), dissolved organic carbon (DOC), and residue mass loss during decomposition of above ground residues from different plant species and pyrogenic organic matter (PyOM), during a one-year laboratory incubation. Carbon lost as DOC represented 21–63% of carbon losses as CO_2. *Figure is reused with permission from Soong, J.L., Parton, W.J., Calderon, F.J., Campbell, N. & Cotrufo, M.F., 2015. A new conceptual model on the fate and controls of fresh and pyrolized plant litter decomposition. Biogeochemistry.*

formation by suggesting that low molecular weight, soluble inputs and polymeric, structural inputs each contribute primarily to the formation of different SOM components (Fig. 4). In particular, DOM from water-soluble inputs is a primary precursor of MAOM formation, while POM is formed

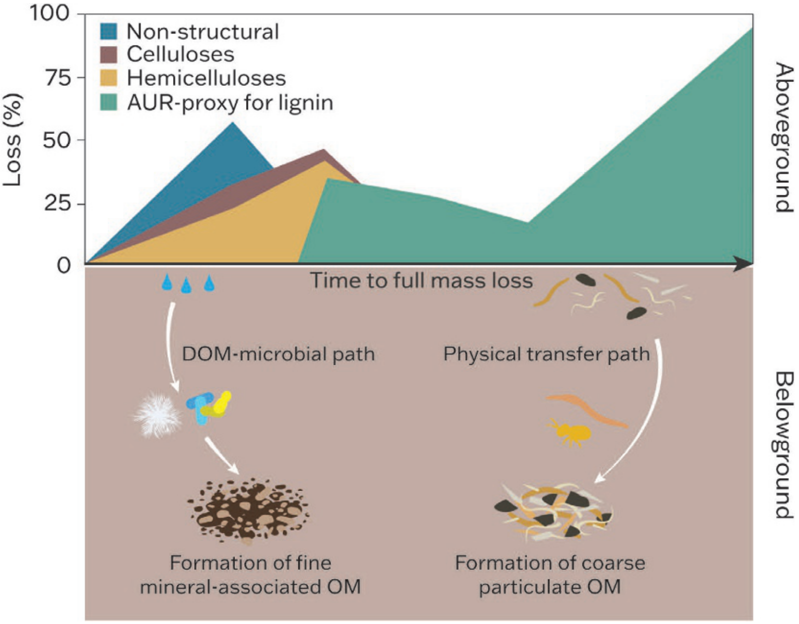

Fig. 4 Conceptual representation of the *two-pathway model* of SOM formation from above ground plant residue decomposition (Cotrufo et al., 2015). Top panel: As decomposition proceeds, water soluble are lost first in higher proportion, then free celluloses and hemicellulose are depolymerized, while at a later decomposition stage the acid unhydrolyzable (AUR) fraction, considered a proxy for lignin and lignin encrusted celluloses, is lost. This time sequence is proportional to the time it takes a residue to reach full mass loss (i.e., months to years). Bottom panel: The loss of water-solubles and free celluloses and hemicelluloses is expected to produce dissolved organic matter (DOM) and result in the formation of MAOM, via direct adsorption or after microbial assimilation, and necromass association to minerals. The remaining fibrous residue is expected to enter the soil via physical transfer, and to result in the formation of particulate organic matter (POM). *Redrawn after Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.H., Wall, D.L., Parton, W.J. 2015. Soil organic matter formation from biochemical and physical pathways of litter mass loss. Nat. Geosci.*

primarily from the polymeric structural residues of plant, animal, and microbial residues, in differing proportions depending on the ecosystem. Both fractions have been shown to contain plant and microbial-derived compounds. However POM is believed to be dominated by plant-derived compounds, while MAOM by microbial-derived compounds based on differences in their chemical structures, stoichiometries, and isotopic enrichments (Grandy and Neff, 2008). While the relative contribution of plant- and microbial-derived compounds in POM and MAOM is still hard to quantify, more recently it has been proposed that MAOM may have roughly equal contributions from plant and microbial compounds (Angst et al., 2021). In support of this, Almeida et al. (2018) traced the fate of the acid unhydrolyzable fraction of plant residues (often used as a proxy for lignin) in soils, and observed that it made a significant contribution both to light POM (37%), and MAOM (31%). This contrasts with the findings of Haddix et al. (2016), who also used isotope tracing to show that only the water-soluble metabolic components of plant material contributed to MAOM formation. More studies characterizing the chemical structure of POM and MAOM and tracing their sources to compounds of plant or microbial origin are required to better understand the specific mechanisms of formation and microbial vs plant contribution of these two main SOM components.

We suggest studies on POM and MAOM formation consider organic matter inputs entering the soil as both structural and DOM. The relative proportion of structural and DOM inputs into the soil will depend on—besides root exudation—the relative contributions of residue inputs to the soil through fragmentation vs leaching, which in turn depend on the chemical composition of the residues, the physical environment where residue decomposition occurs, and the decomposer community structure and activity (Swift et al., 1979). The movement of DOM into the soil is controlled by vertical water flow and interactions with minerals and microbes (Kaiser and Kalbitz, 2012). DOM contributes to the formation of MAOM via different pathways; it can associate directly to mineral surfaces, or it can be assimilated by microbes and converted to microbial extracellular and necromass compounds which then associate with mineral surfaces (Kleber et al., 2015). Liang et al. (2017), respectively, defined these as the *ex-vivo* and *in-vivo* pathways of MAOM formation. On the other hand, the processes that control POM incorporation into the mineral soil, from root turnover to vertical transport of above ground residues mostly via bioturbation, are still poorly defined (Johnson et al., 2014), often hindering the accuracy of models representing them (Zhang et al., 2021). The processes of residue fragmentation, and the incorporation and vertical transfer of POM as well as their biotic and abiotic drivers should be studied across different soil and ecosystem types.

2.3 Controls of SOM formation

While the conceptualization of SOM into POM and MAOM is becoming common (e.g., Chen et al., 2020; Daly et al., 2021; Jilling et al., 2020), our understanding of the factors that control their specific formation is limited.

Organic matter input chemistry and N levels have been proposed as major controls on the formation of these SOM fractions. Inputs richer in water-soluble compounds and with low C/N ratios would promote the formation of MAOM both through direct sorption of water-soluble compounds and efficient microbial transformation of the inputs (Fig. 5; Cotrufo et al., 2013; Kallenbach et al., 2016; Liang et al., 2017). Similarly, N additions would stimulate efficient microbial processing of organic matter including POM, leading to MAOM accrual, unless it generates acidification, limiting microbial activity and causing the accumulation of undecomposed POM (Averill and Waring, 2018).

Consistent with these hypotheses (Fig. 5), structural residue inputs with high lignin and low N content were shown to promote the formation of SOM in the light POM ($<1.7\,\mathrm{g\,cm^{-3}}$, $>53\,\mu\mathrm{m}$) and coarse MAOM ($>1.7\,\mathrm{g\,cm^{-3}}$, $>53\,\mu\mathrm{m}$), whereas animal manure inputs with low C/N promoted fine MAOM ($<53\,\mu\mathrm{m}$) formation in Canadian agricultural soils (Samson et al., 2020). This study supports the two-pathway model of SOM formation (Cotrufo et al., 2015), but also points to the role of coarse MAOM (sometimes called "heavy POM") as a minor but important fraction for the formation of SOM (Samson et al., 2020), which is an area of SOM research requiring further investigation.

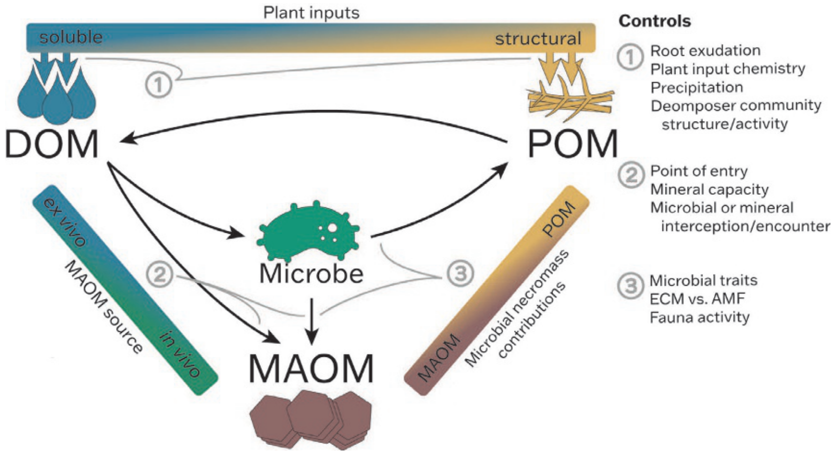

Fig. 5 Conceptual representation of soil organic matter formation processes and their primary controls, including the relative formation of dissolved (DOM) and particulate organic matter (POM) from plant inputs (1), the relative formation of mineral-associated organic matter (MAOM) through *in vivo* and *ex vivo* pathways (2), and the relative formation of MAOM and POM from microbial products (3).

The soil biota also control SOM formation (Coleman et al., 2004). While most soil C and N transformations are generalist functions, different soil organisms vary in their functional roles and impacts on SOM processes (Crowther et al., 2019). Specifically, higher fungal-to-bacterial abundance is associated with higher efficiency of SOM formation from plant residue decomposition (Malik et al., 2016). Since fungal-to-bacterial ratios are modulated by mycorrhizal associations, these are expected to affect the formation of SOM and its relative distribution between POM and MAOM (Fig. 5). Bacteria typically dominate SOM transformation processes in systems characterized by arbuscular mycorrhiza fungal (AMF) associations, while fungal-to-bacterial ratios are higher in systems with ectomycorrhiza fungal (EMF) associations. Ectomycorrhizas were shown to reduce SOM mineralization to CO_2 and promote overall C storage (Averill and Hawkes, 2016; Averill et al., 2014), predominantly in the POM fraction (Craig et al., 2018). On the other hand, systems dominated by AMF favored MAOM formation due to more rapid decomposition and microbial residue production (Craig et al., 2018). Many more studies are required to test these hypotheses at scale. However, they have so far found support in continental scale observations of the distribution of POM and MAOM in European broadleaved forests (Cotrufo et al., 2019). Soil meso- and macrofauna also play several major roles involved in SOM formation, from accelerating residue fragmentation and incorporation of POM into the soil (Soong et al., 2016), as well as its transport to depth (Frouz, 2018), to altering the amount and chemistry of root inputs as well as the biomass, turnover, and diversity of the microbial community (Filser et al., 2016, and references therein). These processes have yet to be quantified across different soils and ecosystems, and this is certainly an area that deserves more quantitative studies at scale.

Mechanistically, the biotic role in MAOM formation has also been suggested to depend on the *point of entry* of the DOM (Figs. 5 and 6), with DOM leaching from aboveground residues having a lower probability of being assimilated by microbes than DOM entering directly belowground through the rhizosphere (Sokol et al., 2019b), where microbial abundance is 2–20 times higher than in the bulk soil (Kuzyakov and Blagodatskaya, 2015). Thus, MAOM formation from aboveground inputs would be mostly controlled by the availability of mineral surfaces, while MAOM formation from rhizosphere inputs would be predominantly controlled by the efficiency of microbial transformation (Fig. 6; Sokol et al., 2019b). This hypothesis regarding the dependency of biotic vs mineral control on

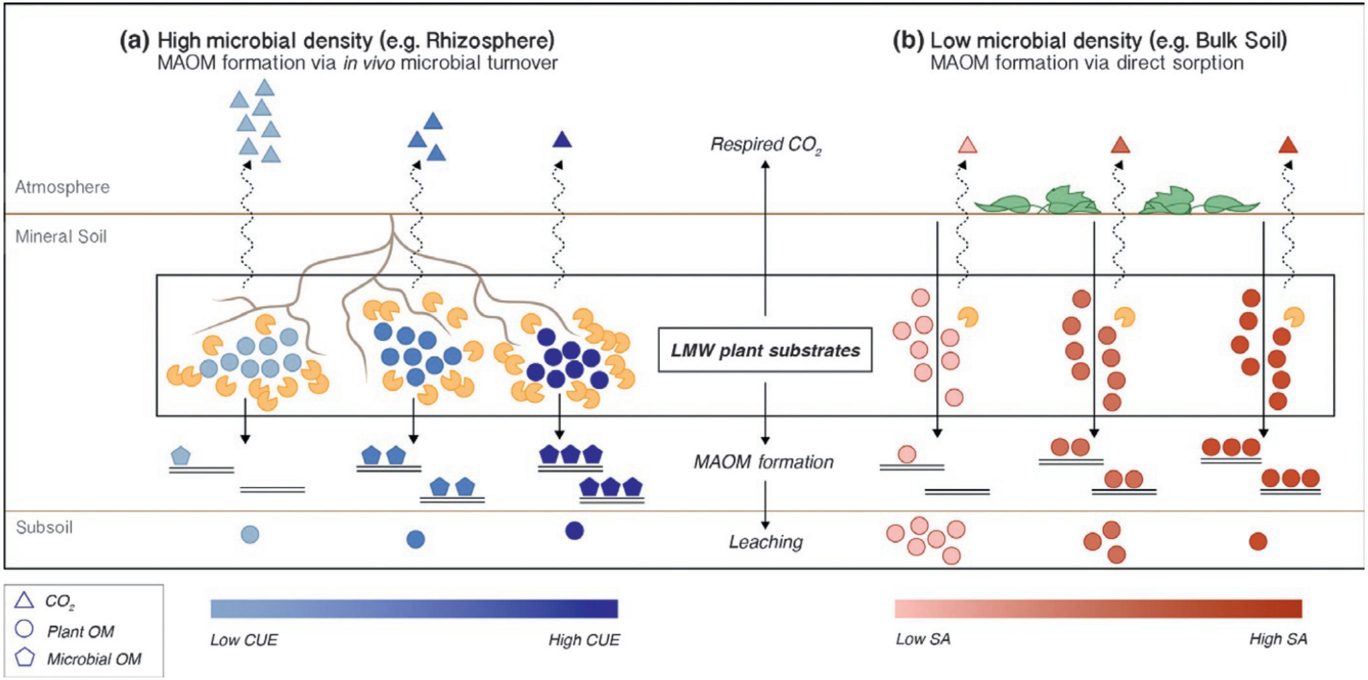

Fig. 6 Conceptual representation of the *point of entry* hypothesis (Sokol et al., 2019b). When low molecular weight (LMW) C inputs enter the soil from the microbial-rich rhizosphere (A), mineral-associated organic matter MAOM is expected to form preferentially via the *in vivo* pathway, because C inputs have a higher probability of being assimilated and transformed by microbes than encountering a mineral surface. Conversely, when LMW C inputs enter the bulk soil (B), MAOM is expected to form preferentially via direct sorption due to the higher relative abundance of mineral surface vs microbial cells in the bulk soil. Also, more C is expected to leach to depth when inputs occur in bulk vs rhizosphere soils. *Reused with permission from Sokol, N.W., Sanderman, J., Bradford, M.A., 2019b. Pathways of mineral-associated soil organic matter formation: integrating the role of plant carbon source, chemistry, and point of entry, Glob. Chang. Biol. 25, 12–24.*

MAOM formation on the point of entry of organic matter inputs to soil has found some empirical support (Sokol and Bradford, 2019), but it requires additional testing in the field. With further support, it can have significant impact in driving management decisions regarding residue placement and prioritizing above vs belowground inputs. For example, field studies looking at the SOM formation efficiency of residue placed on the soil surface or incorporated within the soil have observed higher efficiency of both POM and MAOM formation when residue is incorporated within the bulk mineral soil (Leichty et al., 2021; Mitchell et al., 2018). Additionally, live roots were shown to accelerate both the decomposition of litter residues (Subke et al., 2004) and soil organic matter, as well as to enhance the formation of stable SOM in forest ecosystems (Adamczyk et al., 2019). Surely these findings highlight the importance of studying SOM formation in an intact system with live roots and rhizosphere community, enabling the *in vivo* transformation of above and below ground inputs. Since proposed by Rasse et al. (2005), roots have been proven to be the major contributor of C to soil (Avera et al., 2020; Sokol et al., 2019a). However, our understanding of SOM formation from root inputs is typically derived from experiments following the fate of root residues in the bulk soil (e.g., Bird and Torn, 2006; Fulton-Smith and Cotrufo, 2019). Additionally, root C inputs besides forming new SOM, can also destabilize the existing SOM, requiring a study framework that takes into account both formation and turnover (Dijkstra et al., 2021). More rhizotron facilities enabling the study of SOM formation *in vivo* through root exudate inputs and root turnover, as well as the study or their impact of SOM turnover, are required to improve our mechanistic understanding of root C inputs for SOM accrual.

Climate, soil texture and initial C content have also been shown to play a key role in the formation of new SOM (Haddix et al., 2020). Specifically, across a climatic and soil texture gradient in Canada, MAOM formation was promoted under higher mean annual precipitation and lower sand content, possibly because of higher residue C loss via leaching and mineral surface availability for the formation of organo-mineral associations. On the other hand, new occluded POM formation was promoted by higher initial soil C content, possibly indicating higher aggregation. Macroaggregates, in fact, promote the formation of POM protected inside microaggregates, as well as of C accumulation in MAOM (Fig. 7; King et al., 2019).

Climate and initial C content controls on new SOM formation were observed at a large scale analyses in Australia (Luo et al., 2017). This study

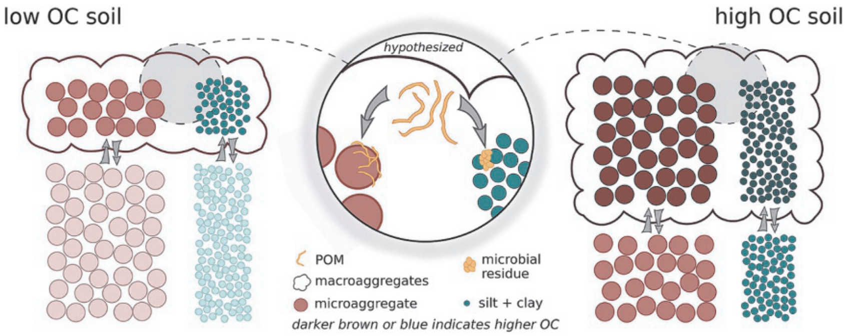

Fig. 7 Conceptual representation of the relationships between soil organic C amounts, their presence in mineral-associated (MAOM) and particulate (POM) organic matter, and distribution between macroaggregates and free and occluded micro-aggregates. These relationships suggest lower turnover of macroaggregates stimulates the accumulation of soil organic C and its stabilization via occlusion in macro- and micro-aggregates. *Reused with permission from King, A.E., Congreves, K.A., Deen, B., Dunfield, K.E., Voroney, R.P., Wagner-Riddle, C., 2019. Quantifying the relationships between soil fraction mass, fraction carbon, and total soil carbon to assess mechanisms of physical protection. Soil Biol. Biochem. 135, 95–107.*

also showed amounts of C inputs explaining the largest proportion (27%) of new total organic C accrued in soil over time (Luo et al., 2017). Amount and chemistry of specific C compounds entering the soil clearly drive SOM formation in controlled experiments (Oldfield et al., 2018a). However, the relationship between inputs and new SOM formation is not straight forward when studied in the field, as demonstrated by the Detritus Input and Removal Treatment (DIRT) project (Lajtha et al., 2014a). Increased litter addition both above and below ground do not necessarily result in increases in SOM formation, while extant SOM storage can be highly impacted by removal of litter inputs. Within the SOM pools, POM appeared to be more responsive than MAOM to increased litter inputs even after 50 years of litter manipulation, while both POM and MAOM were vulnerable to losses from litter removal (Fig. 8; Lajtha et al., 2014b). Besides not being linear, the response of SOM to litter input manipulation is also system-dependent (Crow et al., 2009). These results challenge the long-standing vision of SOM turnover as a first order process (Jenkinson et al., 1990) and highlight the need for a broader investigation across different ecosystem domains of the effect of organic matter inputs and input limitations on SOM formation and storage, including between POM and MAOM (Cotrufo et al., 2021).

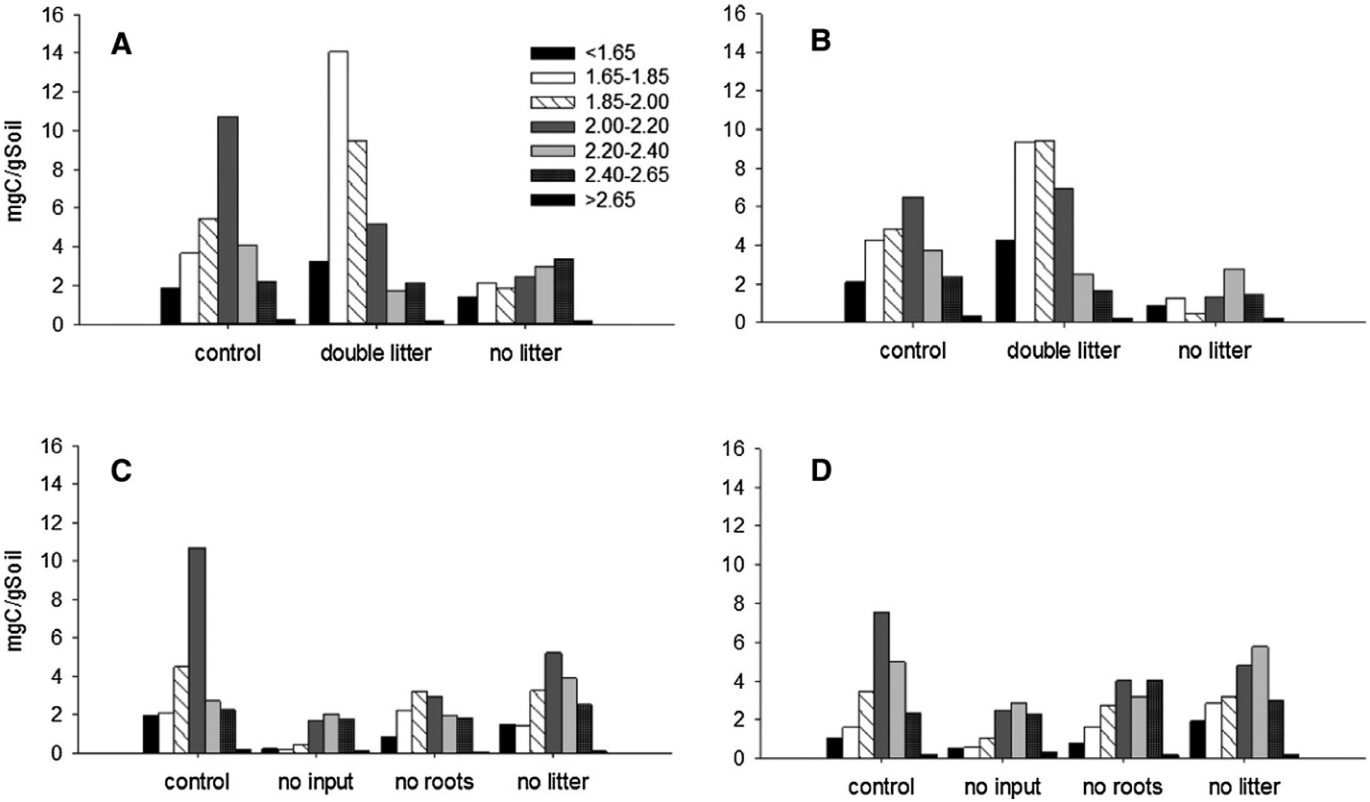

Fig. 8 Soil organic carbon concentration (mg C/g soil) in soil organic matter density fractions at Noe Woods (A), Wingra Woods (B), Curtis Prairie 1 (C), and Curtis Prairie 3 (D) plots which received different litter inputs for 50 years as part of the DIRT experiment. Using our framework (Figs. 1 and 5), density fractions $<1.85\,\text{g cm}^{-3}$ can be considered POM and density fractions $>1.85\,\text{g cm}^{-3}$ can be considered MAOM. *Reused with permission from Lajtha, K., Townsend, K.L., Kramer, M.G., Swanston, C., Bowden, R.D., Nadelhoffer, K., 2014b. Changes to particulate versus mineral-associated soil carbon after 50 years of litter manipulation in forest and prairie experimental ecosystems. Biogeochemistry, 119, 341–360.*

3. The persistence of soil organic matter

3.1 Time metrics of soil organic carbon persistence

Possibly the most studied question regarding SOM has been: What is the SOM turnover time? This question specifically refers to the turnover time of C in soil, which Torn et al. (2009) defined as the time it would take for a C pool to be depleted in the absence of new inputs. However, the concept of turnover time has not been used or measured consistently, and it often overlaps with other concepts like age, residence time, or transit time. Sierra et al. (2017) provided an elegant clarification of all these concepts and advised on appropriate calculations for these different metrics depending on the state of the system where they are applied. We embrace their suggestion to focus on the concepts of *age* to describe the time elapsed from the moment the particle entered the system to a generic time t, and *transit time* to describe the time it takes a particle to transit the system (or the age at which it leaves the system), since these are simple terms, and independent of assumptions regarding the systems (Sierra et al., 2017). Bulk soil C as well as any soil C fractions have age distributions and mean ages which describe the distribution of times and the average time, respectively, since SOM C molecules have entered the pool of interest. Similarly, the transit time will have a distribution and an average (Fig. 9; Sierra et al., 2017). However, this may differ from that of the age, since the majority of C transiting the system has a fast transit time, while the average soil C age is typically much older, because of the contribution from even millennial old C (Shi et al., 2020).

Radiocarbon (^{14}C) is arguably the most powerful tool to determine SOM age and transit time (Trumbore, 2009) and soil ^{14}C data are now available online at a global scale, for bulk soils and different SOM fractions, and along the soil profile in the International Radiocarbon database (ISRad; Lawrence et al., 2020). Globally, gross soil C age varies across ecosystems and soil depths (Balesdent et al., 2018; Mathieu et al., 2015). Using the ISRaD database, Shi et al. (2020) estimated the mean C age of global soils, obtaining an overall value of 4830 ± 1730 years, with topsoils (0–30 cm) being younger (1390 ± 310 years) than subsoils (30–100 cm; 8280 ± 2820 years). The youngest soil C is in tropical topsoils (390 years) while the oldest is in tundra subsoils (16,890 years). However, these averages are skewed by the fact that most of the C in soil is relatively young

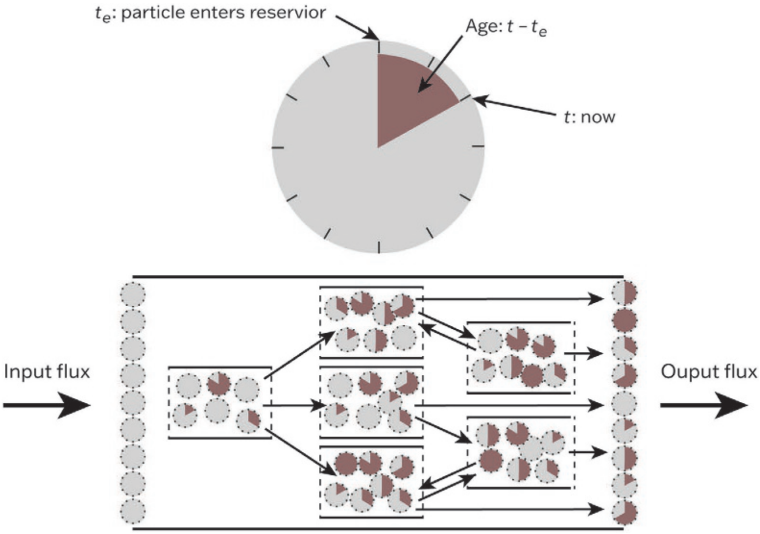

Fig. 9 Conceptual representation of pool age, system age, and transit time. The age of each particle or C molecule in the systems is represented by a clock. A soil system (largest box) can be conceptualized as a set of C pools (smaller boxes) which transfer C molecules among each other (arrows), with an input flux in which molecules enter with age = 0. At any given time, t, C molecules in each pool have different ages, generating a pool-age distribution with a corresponding mean pool age. Similarly, at any given time t, the entire soil system of C molecules will have a system age distribution with a corresponding mean system age. C molecules in the output flux will also have different ages, with their transit time representing the age at which they leave the system. The output flux will have a distribution of transit times and a mean transit time. *Redrawn after Sierra, C.A., Müller, M., Metzler, H., Manzoni, S., Trumbore, S.E., 2017. The muddle of ages, turnover, transit, and residence times in the carbon cycle. Glob. Chang. Biol. 23, 1763–1773.*

(Fig. 10), while smaller amounts of C have ^{14}C ages of 25,000 years and older (Shi et al., 2020), supporting the suggestion that tracking fluxes and transit times rather than ages of C pools may offer a better approach to resolve the probabilistic nature of the fate of C molecules in soils (Waring et al., 2020).

Within a soil, different SOM fractions have different ^{14}C ages, with the light POM fraction typically being the youngest and having mean ages that increase as it becomes occluded in aggregates (Schrumpf et al., 2013). However, old ages can also be observed in the light POM fraction when it is contributed by PyOM (Lavallee et al., 2019). The MAOM fraction typically has older ^{14}C mean ages, and a wider distribution, than POM (Fig. 10), with the acid unhydrolyzable portion of MAOM being the oldest (Schrumpf et al., 2021).

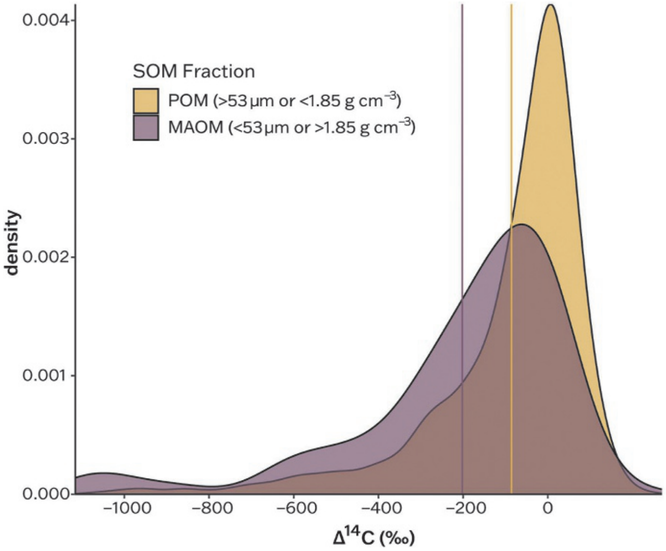

Fig. 10 Density distribution of Δ^{14}C values for particulate (POM) and mineral-associated organic matter (MAOM) as defined by size or density using 53 μm and 1.85 g cm^{-3}, respectively, as cutoffs. Lines show mean values for POM (orange) and MAOM (maroon). Data are for all reported soil fraction from the International Soil Radiocarbon Database (ISRaD), v1.9.10.2021-04-26 (Lawrence et al., 2020).

Besides radiocarbon, SOM diagnostic times have also been studied using stable isotope (^{13}C) tracing, CO_2 mineralization (mostly in laboratory incubations), and by simply relating C stocks in SOM to C inputs with estimates often varying depending on the approach used (Paul, 2016, and reference therein). Despite some C can stay in soil for millennia, the idea of an inert soil C pool (Jenkinson et al., 1987) has been dismissed (Schmidt et al., 2011), and old ^{14}C ages have been measured in active microbial biomass biomarkers in deeper soils (Rethemeyer et al., 2005). These findings support the idea that no C pool in soil is passive, but some C atoms may be recycled in the subsoil through microbial activity (Rumpel and Kogel-Knabner, 2011), without escaping the system and causing the fractions they reside in to appear to be passive if this recycling is not taken into account. Additionally, in soils developed from sedimentary parent material, older ^{14}C ages may be due to contributions of ^{14}C from inactive, geogenic C (Rumpel and Kogel-Knabner, 2011).

While accurate quantification of the diagnostic time metrics of C in soils is key to quantify SOM persistence, it may not aid in the understanding of the mechanisms of SOM stabilization resulting in such persistence. Thus, we believe that focusing exclusively on determining soil C age and transit times or defining SOM pools by their turnover times (Paul et al., 2001) does not necessarily help in predicting how SOM dynamics may change in the future. For example, two soil C molecules could have similar ages but be subject to different mechanisms of stabilization, as defined below. Thus, their ultimate transit times in the soil will vary depending on the specific response of their individual mechanism of stabilization to future environmental conditions. Understanding the mechanisms of formation and stabilization of SOM and their sensitivities to disturbance and environmental changes, in addition to representing SOM pools as defined by their formation and stabilization mechanisms are of critical importance to study and predict future SOM dynamics. Quantifying the ^{14}C ages of these mechanistic SOM fractions (e.g., DOM, POM and MAOM) at scale (Lawrence et al., 2020) will further help elucidating their properties and behavior.

3.2 Mechanisms of soil organic matter stabilization

Soil organic matter can be defined as stable when its outflux rate is low relative to the pool size. Organic C flows out of soils by aerobic SOM mineralization resulting in CO_2 efflux to the atmosphere, anaerobic fermentation resulting in CH_4 and other volatile organic C emissions, and DOM leaching. Given SOM mineralization (estimated globally at ~ 60 Pg C year^{-1}) is over an order of magnitude larger flux than the other soil C outfluxes (Schlesinger and Bernhardt, 2013), the mechanisms controlling it can be considered the main mechanisms controlling SOM stabilization at global scale. SOM mineralization is carried out by the soil biota, and overwhelmingly by the catabolic activity of the microbial community. Consequently, the mechanisms controlling microbial respiration are ultimately responsible for SOM stabilization. There have been several descriptions of SOM stabilization mechanisms (e.g., Jastrow and Miller, 1998; Trumbore, 2009). Here we rearrange previous concepts under three main types of SOM stabilization mechanisms: *microbial physiological inhibition*; *microbial metabolic limitation*, and *microbial access constraint*. We define physiological inhibition as conditions inducing overall microbial inactivity or dormancy; metabolic limitation as conditions modulating microbial catabolism, including C use efficiency (CUE); while access constraint refers to the physical barriers for microbes or their exoenzymes to reach and metabolize a SOM substrate (Fig. 11). Microbial physiological inhibition and metabolic limitation can be considered as spanning a continuum, in which

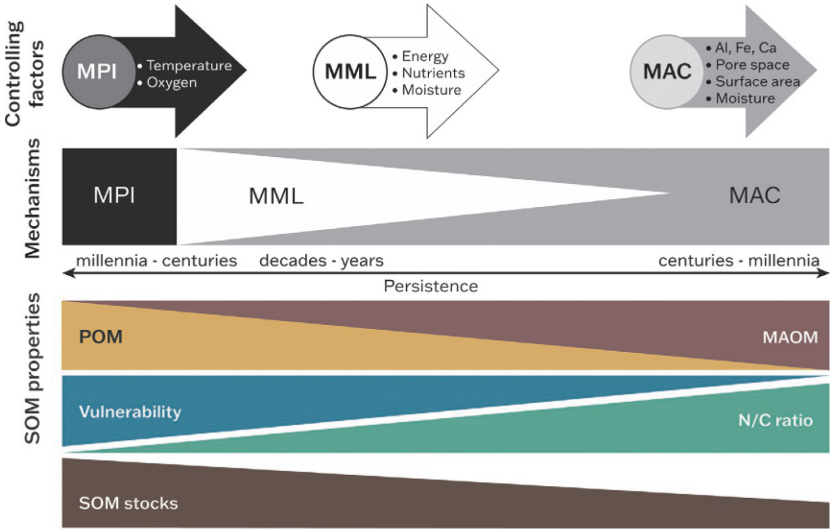

Fig. 11 Schematic representation of the mechanisms of stabilization of soil organic matter. Microbial physiological inhibition (MPI) is caused by freezing temperatures or lack of oxygen, and results in extremely low microbial processing of plant inputs, which thus accumulate largely as particulate organic matter (POM) and can persist for millennia, forming C-rich organic soils characterized by low C:N ratios. This mechanism is extremely sensitive to climate change and drainage of waterlogged soils. MPI transitions to microbial metabolic limitation (MML) when conditions still limit but do not entirely inhibit microbial activity. Thus, MML is controlled by the availability of energy, nutrients, and moisture to microbes. High levels of MML result in higher accumulation of soil organic matter (SOM) in POM, higher soil C:N, relatively low SOM persistence (years-decades), and high SOM vulnerability to changes that may release MML. Microbial access constraints (MAC) limit the access of microbes and their enzymes to SOM. Since organo-mineral associations and protection within small pores are the main spatial constraints on microbial access to SOM, MAC is controlled by the soil mineral capacity to form strong organo-mineral bonds (i.e., Al, Fe, Ca, and available reactive surface area), and by pore space and moisture. Most of the SOM protected by MAC is in MAOM, which may persist in soils for up to millennia and is generally less vulnerable to environmental changes. In soils with lower overall SOM stocks, where available SOM is likely have undergone microbial processing, MAC is the prevailing mechanism of SOM persistence.

when conditions that determine inhibition pass a threshold allowing microbes to break dormancy and become active, the rate of SOM mineralization will become controlled by the factor(s) limiting microbial activity. On the other end, if SOM is protected from microbial access by spatial impediments, it will be less sensitive to microbial metabolic limitations. Microbial physiological inhibition and spatial constraint are responsible for SOM persistent on the long term (century to millennia), while microbial metabolic limitation controls short-term SOM persistence (years to decades).

3.2.1 Microbial physiological inhibition

The most and oldest C in soil is stored in cold and wet conditions (Shi et al., 2020), because of microbial physiological inhibition to decomposition due to freezing temperatures and lack of oxygen. Thus, microbial inhibition could be considered the most important mechanism of SOM stabilization at the global scale. While soil microbes can stay viable and active at sub-zero temperatures and in low oxygen microsites, their activity is extremely low under these conditions (Clark and Kemper, 1967; Steven et al., 2006). Similarly, under severe drought microbes cease their activity and may dehydrate, enter a state of dormancy, or even die (Schimel, 2018). However, dormant microbes can return active when the stress is removed (Lennon and Jones, 2011). Microbial physiological inhibition is, therefore, a mechanism of stabilization very vulnerable to change (Fig. 11), with aerating of gleysols and warming of gelisols activating microbes to mineralize the large soil C stores of these soils (Feng et al., 2020; Minick et al., 2019). With the exception of dry soils where plant stress precedes microbial stress (Schimel, 2018) resulting in low POM accumulation (Cotrufo et al., 2021), the inhibition of microbial decomposition results in the persistence of soil C primarily as light POM, largely of plant origin (Angst et al., 2018).

3.2.2 Microbial metabolic limitation

In ecosystems where climate and oxygen do not inhibit microbial activity, they can still limit it. In this sense, temperature and moisture (including wet, oxygen-limited conditions) can be considered hierarchically the first controls of microbial activity, and therefore of SOM persistence (Cotrufo et al., 2021), as we will discuss in the section on controls below. Besides climate, microbial metabolic limitation refers primarily to energy and nutrient limitations. These limitations control both the rate and efficiency of SOM mineralization, with higher rates of microbial activity but also higher CUE when microbes utilize molecules with high energetic return on investment (i.e., low C:O or C:H ratios) and nutrient availability that matches microbial stoichiometric demand (i.e., low C:nutrients ratios). In the longer term, CUE is deemed more important than modulations in microbial activity rates in determining SOM persistence, thus labile organic

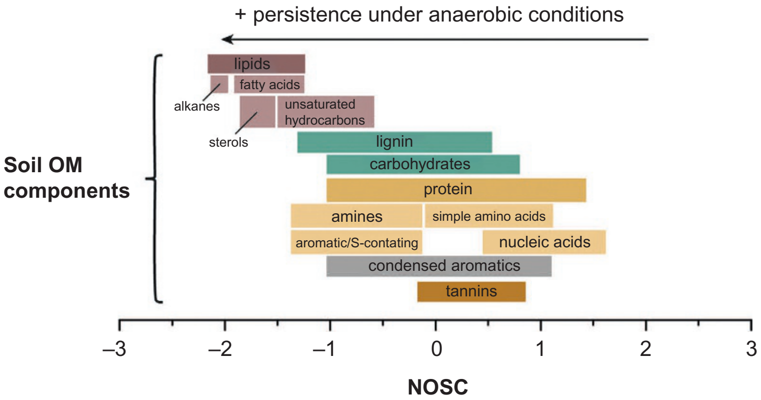

Fig. 12 For a variety of most common soil organic matter compounds, nominal oxidation state of carbon (NOSC) values are estimated based on their approximate positions in Van Krevelen diagrams. Their persistence under anaerobic conditions increases as their NOSC decreases. *Reused with permission from Keiluweit, M., Nico, P.S., Kleber, M., Fendorf, S., 2016. Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? Biogeochemistry, 127, 157–171, with modified colors.*

matter inputs (i.e., low C:O, and C:nutrient ratios) were proposed and observed to be the main precursors for persistent SOM (Cotrufo et al., 2013; Kallenbach et al., 2016). Energy limitations are controlled by the interplay of oxygen availability and substrate chemistry, with molecules characterized by low nominal oxidation state of C (e.g., aliphatics) becoming selectively preserved under low oxygen availability (Fig. 12; Keiluweit et al., 2016). Besides wetlands, oxygen limitation is also an important mechanism of soil C persistence in microsites of highly structured mineral soil, where organic matter occlusion in aggregates limits the oxygen availability required for its microbial utilization (Keiluweit et al., 2017).

In aerobic environments, limitation of microbial activity by energy and nutrient shortages is ascribed to the biochemical recalcitrance and/or chemical diversity (*sensu* Lehmann et al., 2020) of the SOM. While biochemical recalcitrance has long been considered a main driver of SOM persistence, its importance has more recently been dismissed (Dungait et al., 2012; Kleber et al., 2011; Marschner et al., 2008). Only highly condensed aromatic organic matter structures, such as those in PyOM and biochar, are found to be selectively preserved in soils for centuries (Lavallee et al., 2019; Schmidt et al., 2011), while free POM stabilized only by biochemical recalcitrance rarely exceeds 50 years of age (Marschner et al., 2008). The current view is that all polymeric structures can be progressively broken down by exoenzymes in the soil matrix until they are reduced to soluble monomers, which can be assimilated and metabolized by microbes to CO_2 or protected by mineral associations (Lehmann and Kleber, 2015).

The modulation of microbial limitation to decomposition also determines the distribution of SOM between POM and MAOM (Fig. 11). For example, higher nitrogen availability would stimulate microbial activity reducing POM while enhancing MAOM storage (Averill and Waring, 2018; Cotrufo et al., 2019) . We recently proposed that the relative balance between microbial and plant limitation controls the distribution of SOM between MAOM and POM, with relatively more MAOM in systems where microbial activity is less limited than plant primary productivity, and *vice versa* for POM (Cotrufo et al., 2021). Like microbial inhibition, microbial limitation is also determined by the environmental conditions (e.g., climate, oxygen, plant input chemistry, nutrient availability) and therefore it is highly sensitive to changes of these conditions. SOM which has accumulated because of microbial limitation may be readily lost if the environmental conditions limiting microbial activity are released, for example by climate, land use, or management changes. Understanding microbial responses to global changes and incorporating this understanding into prediction tools is, thus, critical for providing accurate estimates of SOM changes in the coming decades (Treseder et al., 2012).

3.2.3 Microbial access constraint

On the longer term, SOM persistence in soils where microbial activity is not inhibited is controlled by its accessibility to microbes, with organo-mineral associations (Torn et al., 1997; Von Lutzow et al., 2006) and protection within micro pores (Ekschmitt et al., 2008; Kravchenko and Guber, 2017) being the main spatial constraints on microbial mineralization of SOM. The association of organic matter to minerals through various binding mechanisms determines MAOM accessibility to microbes, with low molecular weight compounds of plant and microbial origin and microbial extracellular polymeric substances being the main chemical compounds bound to mineral surfaces (Kleber et al., 2015).

Microbial access to substrates requires their coming into contact, making soil pores—the spaces through which microbes and substrates travel and in which they reside—critical drivers of microbial accessibility to SOM (Kravchenko and Guber, 2017). While micropores ($<30\,\mu m$) generally limit accessibility, pores ranging in size from 30 to 150 μm were found to be ideal for microbial proliferation and activity, increasing microbial transformation of SOM but also potentially stimulating efficient MAOM formation in these microsites (Kravchenko et al., 2019). Pore size

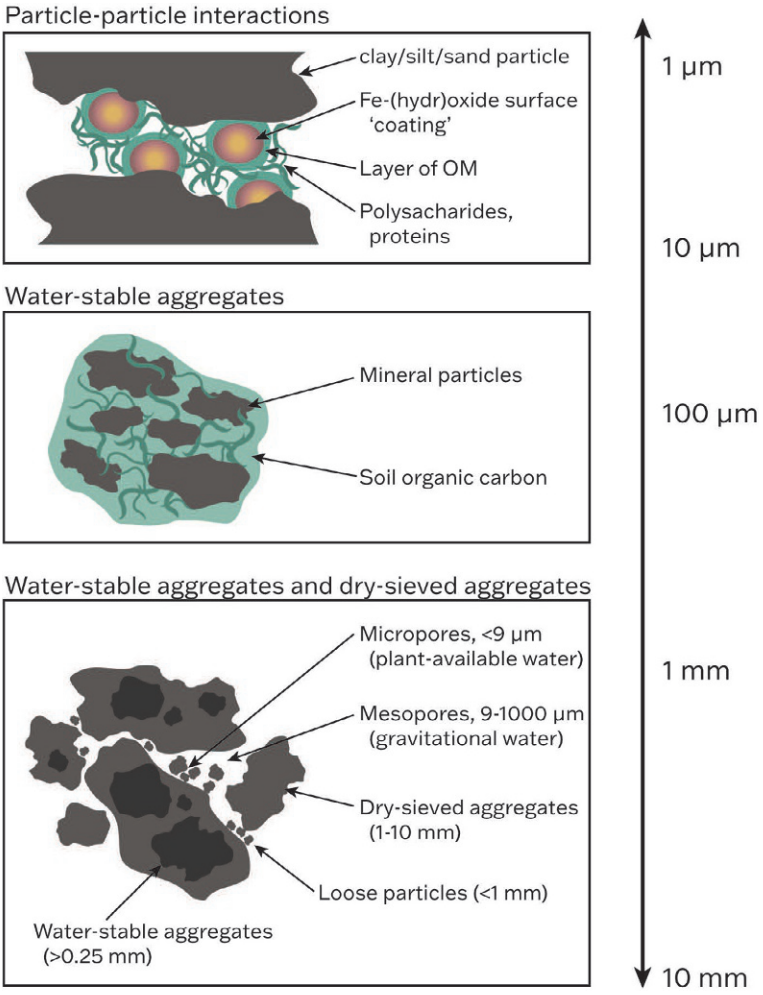

Fig. 13 Conceptual representation of the pore space size in relation to water-stable and dry-sieved aggregate sizes, interactions between mineral particles, and interactions between organic matter (OM) and minerals. *Adapted from Regelink, I.C., Stoof, C.R., Rousseva, S., Weng, L., Lair, G.J., Kram, P., Nikolaidis, N.P., Kercheva, M., Banwart, S., Comans, R.N.J., 2015. Linkages between aggregate formation, porosity and soil chemical properties. Geoderma, 247–248, 24–37.*

distribution is linked to aggregation, texture and Fe-(hydr)oxides along a size-scale gradient (Fig. 13; Regelink et al., 2015). Given microbes, and in particular bacteria, require water to access and metabolize their substrates, a lack of water in the soil environment reduces microbial access to their substrates. For mineral soils, a water potential of about -14 MPa was found to be the threshold below which microbial access to substrate would cease

(Manzoni et al., 2012). However, soil pore space (Carter, 1988) and in particular water availability vary over time (Brocca et al., 2010), and drying-rewetting cycles may stimulate decomposition rather than increase SOM persistence (Schimel et al., 2007). Therefore, Lehmann et al. (2020) proposed that the interplay between spatio-temporal variations in soil moisture and pore space would control microbial accessibility to SOM and its mineralization rate. Water saturation fluctuations during drying-rewetting cycles was also shown to determine the chemical composition of the organo-mineral fraction in addition to its degradability (Possinger et al., 2020).

While mineral association, by definition, controls MAOM persistence, physical constraints may affect both POM and MAOM persistence. Aggregate occlusion controls microbial community composition and accessibility to SOM (Trivedi et al., 2015), as well as oxygen availability (Keiluweit et al., 2016), slowing down the mineralization of the occluded SOM in relation to aggregate size, with higher protection offered by the finer aggregates (Bimüller et al., 2016). In their landmark review, Six et al. (2004) reconstructed the history of the research on the effects of aggregates on SOM dynamics, emphasizing the role of microaggregates ($<250\,\mu m$) for SOM protection and of macroaggregate ($>250\,\mu m$) turnover for promoting the formation of microaggregates, thus influencing overall SOM stabilization. Aggregate occlusion offers protection from fast decomposition in particular for POM, which when found free in mineral soil decomposes faster than if occluded in aggregates (Haddix et al., 2020). By contrast, we did not observe significant differences in the ^{14}C signature of silt and clay sized MAOM found free or occluded in different aggregate size fractions (Marzaioli et al., 2010), rather aggregates appeared to promote MAOM formation (Fulton-Smith and Cotrufo, 2019), possibly because of the increased proximity between DOM, microbes and MAOM within aggregates, and the creation of pore sizes between 30 and $150\,\mu m$ particularly suited for MAOM formation (Kravchenko et al., 2019).

3.3 Controls of soil organic matter persistence

In the past decade, our understanding of the controls of SOM persistence has significantly advanced. We now understand that the persistence of SOM is driven by a complexity of abiotic and biotic factors interacting with each other at the ecosystem level, such that SOM persistence becomes an emerging property of each individual ecosystem (Schmidt et al., 2011). However, while we can now list the controls of soil organic C along different spatial scales (Doetterl et al., 2015; Hobley et al., 2015; Viscarra Rossel et al., 2019; Wiesmeier et al., 2019), we cannot yet identify a hierarchical structure of controls as they operate across different ecosystems and scales. For example, climate, vegetation, and parent material are known to be major drivers of soil organic C storage (Wiesmeier et al., 2019), but their hierarchy and interactions remain largely undefined. We recently proposed the *In-N-Out* framework (Fig. 14) to overcome this knowledge gap and provide a

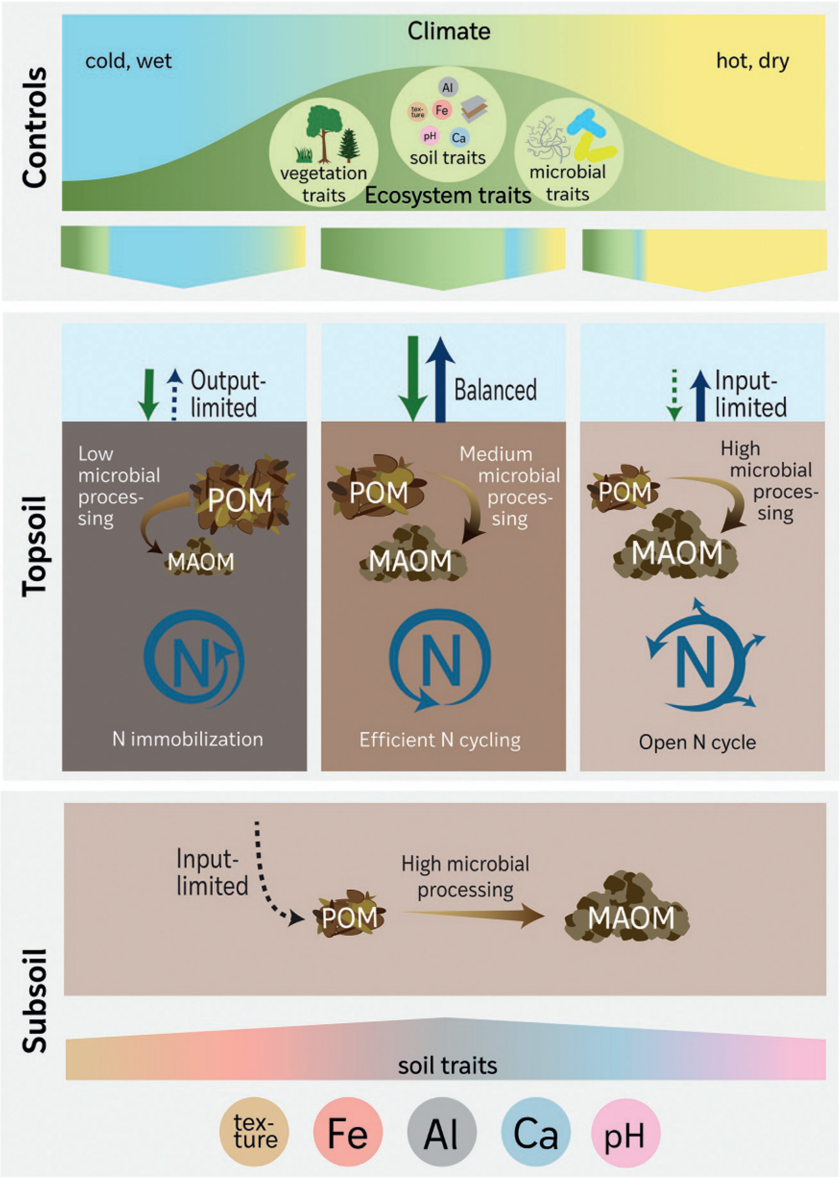

Fig. 14 See figure legend on opposite page.

hierarchical structure to test the effect of different factors on SOM persistence (Cotrufo et al., 2021). We hope that future research will adopt this framework and test the related hypotheses to advance a generalizable understanding of soil C and N cycling and storage in terrestrial ecosystems.

3.3.1 Direct and indirect climatic controls

We propose climate to be the overarching control on SOM persistence (Fig. 14) when it imposes either a physiological inhibition (freezing temperature, anoxic conditions, severe drought), or a large metabolic limitation (low/very high temperature and moisture) on microbial activity. Additionally, by modifying soil moisture, climate regimes also affect microbial access to resources (Schimel, 2018), thus controlling SOM persistence by modulating the microbial access constraint mechanism (Fig. 11). The effect of climate on SOM persistence will depend on the climatic zone, since the impact of moisture and temperature on microbial activity is not linear (Paul, 2007). However, areas with higher precipitation and humid soils are associated with higher soil organic C storage (Hobley et al., 2015; Plaza et al., 2018; see Fig. 18), likely because of the increased plant productivity and inputs (Wu et al., 2011), but possibly also because higher

Fig. 14 Conceptual representation of our In-N-Out framework. Arrows in top and bottom panel are color-coded according to potential controls. We hypothesize (right panel) that C input limits soil C and N cycling when plant photosynthesis is constrained relatively more than microbial activities. In these ecosystems, microbes process the small available plant C inputs, resulting in low soil C stocks with relatively high mineral-associated organic matter (MAOM) accumulation controlled by the availability of soil minerals for stabilization of microbial aproducts. C input-limited ecosystems are expected to have decoupled C and N cycles, with the latter being open and the excess N lost from the soil. We also hypothesize (left panel) C output limitation to control soil C and N cycling in systems where microbes are more inhibited than plants. C-output limited systems would be characterized by higher POM relative to MAOM, and the N immobilized in POM would impose N limitation on productivity. Further, we hypothesize (central panel) that balanced plant C inputs vs microbial C outputs will result in soils having more equal shares of POM and MAOM and closed N cycling. Further, we expect climate to be the main driver of C input- and C output-limited systems, while ecosystem traits emerging from the interaction of plant, microbial, and soil traits to be significant drivers of soil C and N dynamics in ecosystems with more balanced inputs and outputs. Finally, we hypothesize (bottom panel) that subsoils are input-limited and their SOM dynamics are largely controlled by soil traits, including mineral properties. *Reused with permission from Cotrufo, M.F., Lavallee, J., Zhang, Y., Hansen, P., Paustian, K., Schipanski, M.E. & Wallenstein, W.D. 2021. In-n-out: a hierarchical framework to understand and predict soil carbon storage and nitrogen recycling. Glob. Chang. Biol., In Press.*

precipitation promotes DOM leaching and MAOM formation (Haddix et al., 2020). As mentioned previously, moisture saturation also creates anoxic conditions, inhibiting SOM mineralization and resulting in gleysols with very high soil organic C storage primarily as undecomposed plant-derived light POM (Angst et al., 2021). The response of SOM persistence to temperature has been the focus of much research. Typically freezing temperatures inhibiting microbial activity are associated with very high SOM persistence, resulting in gelisols, also with very high soil organic C storage primarily as undecomposed plant-derived POM (Angst et al., 2021). Warming increases microbial activity and therefore stimulates SOM transformations. Typically POM is most vulnerable to warming (Benbi et al., 2014; Lugato et al., 2021; Rocci et al., 2021) because it's largely unprotected, and warming releases microbial energy limitation (Davidson and Janssens, 2006), which is the primary mechanism of POM stabilization (Fig. 11). Accelerated POM losses with warming may result in increased MAOM formation (Soong et al., 2021), as more microbial products are formed from POM decomposition which can associate to minerals. This may be expected to be particularly true if warming increases microbial CUE by selecting for microbes with higher CUE, as it has been inferred on the basis of model findings (Ye et al., 2019). However, laboratory incubations have indicated the temperature sensitivity of microbial CUE is mediated by the substrate biochemical recalcitrance, with lower CUE of recalcitrant compounds under warming (Frey et al., 2013). While MAOM formation may be stimulated under warming, MAOM mineralization is expected to be less sensitive to warming, because MAOM is stabilized by microbial access constraints rather than metabolic limitations, and the temperature responses of organo-mineral sorption/desorption may balance each other out (Conant et al., 2011). However, warming may also accelerate MAOM mineralization, in particular in agricultural soil where POM is scarce and MAOM represents the main source of energy to microbes (Lugato et al., 2021).

Given climate is a soil forming factor in interactions with parent material, topography, time, vegetation and other biotic factors (Jenny, 1941), in the long term it affects SOM persistence in all soils. Besides directly affecting microbial activity and access to resources by modulating soil moisture (Schimel, 2018), climate also has an indirect effect on decomposition by determining vegetation and microbial activity and traits (Aerts, 1997). For example, in northern latitudes or higher altitudes, climate not only inhibits microbial physiological activity, but determines the biome (e.g., tundra, taiga) and affects vegetation and microbial traits, which in turn affect soil C dynamics (Lynch et al., 2018). Additionally, climate controls long-term mineral weathering, and thus the interactions between geochemistry and climate need to be taken into account when studying SOM dynamics and storage (Doetterl et al., 2015). This interaction, in fact, determines mineral reactivity, thus controlling nutrient availability and microbial community composition and metabolism, and modulating the energy and nutrient availability and pathways ultimately responsible for SOM persistence (Doetterl et al., 2018). Considering this long-term indirect effect of climate on soil mineral weathering, Doetterl et al. (2018) pointed out the risk for younger soils, for example in high latitudes, of experiencing a dramatic change in SOM dynamics due to warming releasing current limitations on mineral weathering.

Direct and indirect climate driving of SOM persistence is reasonably expected to be highest under extreme climates (Cotrufo et al., 2021). Under mesic conditions, climate exerts a more distant driving force, mostly indirectly because of its control on vegetation and microbial traits, as well as soil geochemical traits (Fig. 14). Thus, under mesic climates, we expect vegetation and microbial traits to become the primary short-term drivers of SOM persistence in topsoils, with soil geochemical traits being the primary driver in subsoil and for the long term in all mineral soils (Fig. 14). In managed systems, the role of climate is even more secondary, with management becoming a dominating driver of SOM dynamics (Paustian et al., 1997), directly through disturbance and indirectly by modifying inputs, microbial activity and traits, and soil geochemistry. SOM persistence is also controlled by fire, which creates PyOM and therefore increases the biochemical recalcitrance to microbial decomposition (Pellegrini et al., 2020) of a portion of SOM in systems subject to frequent fires, either due to management or naturally occurring wildfires.

3.3.2 Soil geochemistry controls and carbon saturation

Where plant inputs are not limiting, soil geochemical traits are the main driver of MAOM stocks and long-term persistence (Fig. 14). By determining the amount of surface area available for organo-mineral bonding and its reactivity, soil geochemical traits control microbial access constraints (Doetterl et al., 2015; Kleber et al., 2015; Rasmussen et al., 2018; Torn et al., 2009; Von Lutzow et al., 2006; Wiesmeier et al., 2019). Given MAOM is the most abundant form of C in mineral topsoil of the main terrestrial ecosystems aside from coniferous forests—particularly so for managed agricultural soils (Lugato et al., 2021)—and in all subsoils (Rumpel and Kogel-Knabner, 2011), the soil geochemical control on soil C storage is of utmost important for the future of soil C storage, and soil functioning.

Traditionally, soil texture and in particular the amount of silt and clay size particles has been considered the main control of MAOM accumulation in soils (Hassink, 1997). Since organo-mineral association requires available mineral surfaces, the availability of silt- and clay-sized minerals in soil has been postulated to impose an upper limit, or saturation level, to the amount of MAOM storage (Six et al., 2002; Stewart et al., 2007). While the MAOM saturation hypothesis found support at large scale (Cotrufo et al., 2019) for European soils across a range of ecosystem types (Fig. 15), we still lack a complete mechanistic understanding of the processes determining MAOM saturation and its upper limit across different soil types (Beare et al., 2014). The availability of mineral surfaces can explain C sequestration potential in some cases (Chen et al., 2019), but in other cases different processes may also be at play. Recently, Craig et al. (2021)

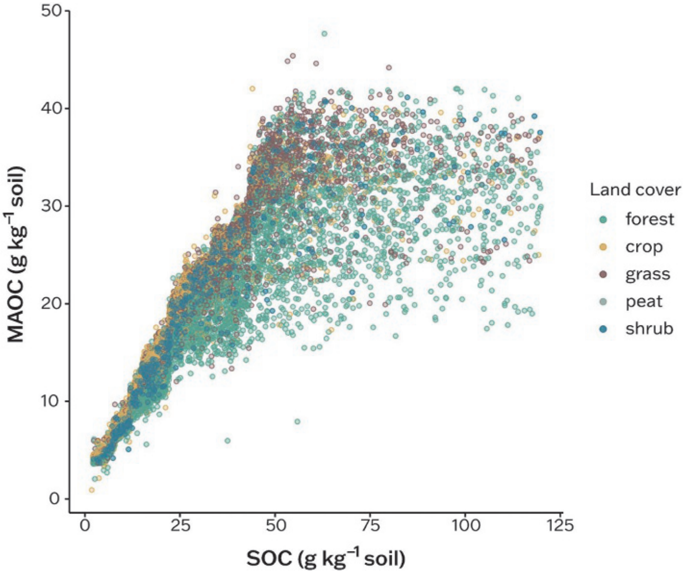

Fig. 15 Carbon (C) storage in mineral-associated organic matter (MAOM) vs total soil organic carbon (SOC) storage in European soils. The amount of soil C in MAOM increases proportionally to total SOC until a saturation plateau is reached. Data include both measured and predicted points from Lugato et al., 2021.

proposed that biological processes limiting microbial necromass production may also drive saturation dynamics. The observation that only a minor portion of the mineral surface (<19%) has organic attachments, with organo-mineral clusters sporadically distributed on key sites of rough mineral surfaces leaving large part of the mineral surface uncovered (Kopittke et al., 2020; Vogel et al., 2014), further complicates the interpretation of the mineral saturation concept.

Our current inability to fully understand MAOM saturation is likely due to our limited understanding of the physical-chemical structuring of organo-mineral associations. However, it is fast advancing thanks to the availability of nanoscale analytical methods (Kopittke et al., 2020; Possinger et al., 2020). Kleber et al. (2007) proposed that organic molecules self-assemble on mineral surfaces in aqueous solutions, creating a series of layers or zones based on chemical characteristics. However, this layered organo-mineral structure has not yet been confirmed, and nanometer-scale spatial analyses rather revealed disordered organo-mineral and organic-organic phases, differing in their N and C molecular enrichments (Possinger et al., 2020). In particular, N-rich compounds were observed to preferentially create organo-mineral bonds, while organo-organic phases form independently of the C:N ratio of the molecules (Kopittke et al., 2020). More nanometer-scale observations of the three-dimensional structure and spatial distribution of organo-organic and organo-mineral clusters are needed across a wide range of soil mineralogy to advance our understanding of organo-mineral protection and MAOM saturation.

In fact, we now recognize the importance of the geochemical nature of minerals, beside the overall soil texture, in controlling soil organic C stocks. Rasmussen et al. (2018) analyzed data from over 5500 soil samples across the US and identified the importance of variables such as exchangeable calcium (Ca), short-range-order Aluminum (Al)- and Iron (Fe)-oxyhydroxides, and Al-, Fe- organo-metal complexes in controlling soil organic C stocks. They also pointed to the possibility of using a pH scale to identify their relative importance, with exchangeable Ca as the dominant control in alkaline soil and Al- and Fe-oxyhydroxides as the best predictors in more acidic and humid soils (Fig. 16). Their study was conducted for total soil organic C, and the relationships they identified may have been even stronger if the analysis focused only on the MAOM fraction. More broad-scale studies are required to specifically link soil geochemistry, and its interactions with organic matter chemistry and soil redox, to the accumulation and persistence of C in MAOM.

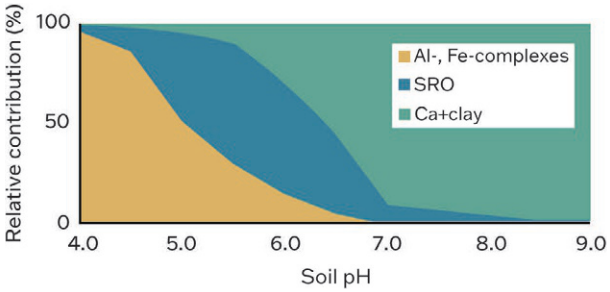

Fig. 16 Proposed relative contribution of different forms of mineral associations to carbon stabilization in mineral-associated organic matter with the increase in soil pH. SRO refers to short-range order minerals. *Reused with permission from Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C., Crow, S. E., Druhan, J. L., Hicks Pries, C. E., Marin-Spiotta, E., Plante, A. F., Schädel, C., Schimel, J. P., Sierra, C. A., Thompson, A. & Wagai, R. 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry, 137, 297-306 with modified colors.*

3.3.3 Biotic and biochemical controls of soil organic matter persistence

While climate and soil geochemistry can be considered overarching drivers of SOM persistence because they largely control the two mechanisms responsible for long-term soil C storage (i.e., microbial physiological limitation and microbial access constraint, respectively), vegetation cover represents a significant driver of short-term SOM dynamics, controlling microbial communities and their functionality (Fierer et al., 2012). Further, under temperate climates these interplay of vegetation and associated microbial communities control SOM persistence, by affecting the distribution between POM and MAOM (Lugato et al., 2021).

While the specific chemical makeup of a molecule (apart from some PyOM) is not expected to protect it from decomposition in the long term, it has been recently proposed that the diversity of chemical structures may control microbial limitations to decomposing them. Lehmann et al. (2020) proposed that high molecular diversity of SOM imposes an energy limitation on microbes, because it requires investing in a larger variety of enzymes and metabolic pathways, overall slowing down SOM mineralization. They also proposed that microbial products have a higher molecular diversity than plant inputs, implying that this driver of SOM persistence is more important after rather than before microbial processing of plant inputs (Lehmann et al., 2020). Research is required to test this novel, intriguing hypothesis. Besides C chemistry, nutrient deficiencies are well known to be a major control over microbial limitation of SOM decomposition and soil C storage (Macdonald et al., 2018), given the lower C:nutrients ratios in microbes as compared to plant inputs (Cleveland and Liptzin, 2007). However, according to the nitrogen mining hypothesis, nitrogen limitation can also promote the mineralization of older SOM characterized by lower C:N in low nutrient environments (Craine et al., 2007).

4. Soil organic matter relationships to soil properties, functions, and their outcomes

The relationships between SOM and soil functions are complex, with various interactions and feedbacks at multiple levels. We attempt to clarify these relationships by reviewing causal linkages within a multi-level framework that includes (1) properties of the soil mineral and organic phases, and SOM stocks; (2) soil properties; (3) soil functions; and (4) outcomes (Fig. 17). We consider the effects of the properties of SOM separately from the size of SOM stocks, even though they are intrinsically linked in nature. There have been several quality reviews on the links between SOM stocks, soil properties, and soil functions (Hoffland et al., 2020; King et al., 2020; Lal, 2020a). Our aim here is to complement these existing reviews and put the current state of knowledge into the context of what we see as the most useful SOM properties for understanding and predicting soil functions and outcomes: SOM availability, SOM stoichiometry, and

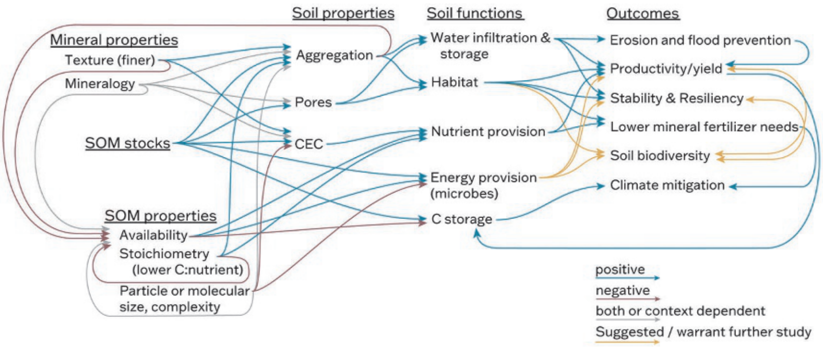

Fig. 17 Overview of the relationships between mineral properties, SOM stocks, SOM properties, soil properties, soil functions, and key outcomes described in this chapter. Causal relationships are characterized as positive (blue), negative (red), both or context dependent (gray), or suggested and in need of further study (yellow). SOM fractions (e.g., POM and MAOM) usually differ in all three of the SOM properties presented here. Relevant supporting studies are cited in the text.

SOM particle size or molecular complexity. By "useful," we mean that these properties are most easily quantified or reflected by physical fractionation procedures, and their links to functioning are best supported by the current literature. Other aspects of SOM such as temporal variability and molecular diversity may also be important (Lehmann et al., 2020), but they are less understood at this point in time. We then review the existing knowledge linking these SOM and soil properties to relevant outcomes including plant productivity, system stability and resiliency, and climate mitigation.

4.1 Contributions of soil organic matter to soil properties

Soil is a complex mixture of minerals and organic matter, each of which has inherent properties which combine in the context of time, climate, topography, and biota to determine emergent soil properties (Fig. 17). Several quality reviews covering the relationships between SOM, minerals, and soil chemical and physical properties already exist (e.g., Hoffland et al., 2020; Krull et al., 2004; Murphy, 2015; Wander, 2004). We build on those to provide an overview and a more in-depth discussion of how SOM properties contribute to key soil properties including soil cation exchange capacity (CEC), soil aggregation, and soil porosity. Other soil properties (e.g., pH, redox chemistry) play pivotal roles in SOM dynamics and soil functioning, however their relationships to minerals, SOM stocks, and soil functions are too complex and interactive to cover satisfactorily here. Repellency is also a key soil property with regard to water dynamics, but its links to SOM stocks and properties remain unclear (Cesarano et al., 2016; Miller et al., 2017), and it often fluctuates over short timescales based on precipitation patterns and wetting events (Vogelmann et al., 2013), making it difficult to review in this context.

4.1.1 Cation exchange capacity

Soil CEC is a measure of the amount of negatively charged sites that can retain and exchange positively charged ions (e.g., Mg^{2+}, Ca^{2+}, K^{+}) and is a commonly-used indicator of soil quality and fertility. Many of the myriad organic compounds which make up SOM have pH-dependent charge (e.g., carboxyl groups; Kaiser et al., 2008) and are negatively charged at pH $\sim$4.5 and above, and hence contribute to soil's CEC. In typical predictive models of soil CEC, texture (clay content) and SOM are the main predictors, while mineralogy is a common interacting factor (Seybold et al., 2005). The estimated relative contribution of SOM to CEC varies depending on SOM amount, soil texture and mineralogy, pH, and other factors, but typical values are between 25% and 90% (Murphy, 2015; Oorts et al., 2003). Going further to relate SOM properties to CEC is methodologically difficult because it requires separating SOM with differing properties while also accounting for or eliminating contributions by the mineral phase. Researchers have approached this by treating physical size fractions with hydrofluoric acid to remove minerals (Skjemstad et al., 2008), using indirect regression approaches on physical size fractions (Oorts et al., 2003), and focusing on soluble OM fractions (Kaiser et al., 2008). Skjemstad et al. (2008) and Oorts et al. (2003) found that the MAOM fractions ($<53\,\mu$m) generally had higher CEC and contributed more to total CEC than the POM fractions ($>53\,\mu$m), while Kaiser et al. (2008) found that pyrophosphate-soluble OM fractions accounted for 0.8–11.6% of total CEC even though they only accounted for 0.3–0.9% of the total soil mass. Results of these studies support the idea that CEC of SOM tends to increase through decomposition and transformations that produce lower molecular weight SOM compounds with higher relative proportions of reactive/acidic functional groups (e.g., carboxyl, hydroxyl).

4.1.2 Soil structure

Soil structure is the result of the complex interplay between soil texture, plant roots, soil biota, and SOM. These factors all interact and feedback on each other, so mechanisms of causality of aggregation can be difficult to parse. At larger scales, when looking across soils of similar textures, higher SOM stocks correspond to higher aggregate stability (Le Bissonnais et al., 2018), but this does not inform on causality. Our current understanding of the role of SOM on aggregate formation processes comes from decades of research on SOM accrual chronosequences in the field (e.g., Jastrow, 1996) studies on the effects of isolating or removing certain aggregate-forming factors (e.g., Blankinship et al., 2016), and field and laboratory incubations of different OM additions to assess effects on aggregate formation (e.g., Bucka et al., 2021; Denef et al., 2002).

Roots and hyphae are important to the formation of macro-aggregates ($>250\,\mu$m) because they create net-like structures and produce mucilage that bring soil particles and microaggregates ($<250\,\mu$m) together (Six et al., 2004). Living roots and hyphae would not be considered SOM, but as they die and their structures become POM (while soluble compounds are released as DOM), they act as nuclei of aggregate formation (Bucka et al., 2021) through the promotion of microbial activity, leading to deposition of microbial byproducts and further proliferation of saprotrophic hyphae, which further promote aggregation (Jastrow and Miller, 1998). While larger, less decomposed organic fragments (POM) can act as catalysts in macroaggregate formation, smaller organic compounds (e.g., DOM, microbial products) are thought to act as a kind of "glue," binding multiple soil particles together or co-precipitating with metal oxides to form highly stable organo-mineral complexes (i.e., MAOM) (Wagai et al., 2020). The strength of the binding effect and the resulting stability of the aggregates depends on the soil mineralogy as well as the SOM chemistry and stoichiometry (Bucka et al., 2021; Denef et al., 2002) with lower C:N ratio compounds potentially forming stronger complexes (Sollins et al., 2009; Tipping et al., 2016; Wagai et al., 2020). The effects of small organic molecules go beyond the microscale however, based on observations that they promote macroaggregate formation and stabilization as well (Blankinship et al., 2016; Bucka et al., 2019).

Soil porosity is another aspect of soil structure which emerges from the interactions of several variables, including SOM (Kravchenko and Guber, 2017). Porosity is largely an outcome of aggregation, with pores (>10 μm; Fig. 13) forming between micro- and macro-aggregates, both of which are promoted by SOM as previously described (Zaffar and Sheng-Gao, 2015). Roots, fungal hyphae, and soil biota can also form pores by pushing soil particles aside as they grow or travel, or by leaving voids as they decompose (De Gryze et al., 2006; Young and Crawford, 2004). Smaller pores (<10 μm) are also present between primary soil particles and clay interlayer spaces, and organo-mineral associations can shape pore architecture on this scale (Fig. 13).

4.2 Contributions of soil organic matter to soil functions

4.2.1 Water dynamics and habitat

As SOM coats mineral particles, promotes aggregation, and increases porosity (Bucka et al., 2021), it changes the soil structure in ways which improve water dynamics and benefit soil biota and plant roots. The prevention of surface crusting and creation of flow paths lead to higher infiltration rates. Increased porosity and soil structure lead to improved water holding capacity (Yang et al., 2014). Murphy (2015) estimated that plant-available water increases by ~2 to 3.5 mm per 10 cm soil for each 1.0% increase in soil organic C over the range of 0.7–3.0% C, and others have given similar estimates (Lal, 2020a).

The structural effects of SOM also improve the quality of habitat that the soil can provide to microorganisms, soil fauna, and roots. Pores of various sizes can be occupied by a variety of organisms, provide refugia from predation, or create hotspots of activity (Kravchenko and Guber, 2017; Tecon and Or, 2017). Enhanced soil structure also allows roots to grow more freely and explore larger volumes of soil, thereby increasing their ability to access nutrients and water (King et al., 2020). While there is evidence for direct effects of SOM properties on water dynamics and habitat provision (for example, SOM can increase soil water retention at low matric potentials by directly absorbing water; Yang et al., 2014), the effects of SOM on these functions generally operate indirectly through its influence on soil properties (Fig. 17).

4.2.2 Nutrient provision

Another important function that SOM contributes to is nutrient provision, since SOM contains a wealth of essential nutrients including N, P, and S, that can be made available by SOM depolymerization and/or mineralization and taken up by plants and microbes. In typical agricultural soils, SOM contains 90–95% of the total N and 20–80% of the total P (Murphy, 2015). The CEC contributed by SOM also acts to store and provide other nutrients (e.g., Mg^{2+}, Ca^{2+}, K^{+}) via an indirect mechanism (Fig. 17). Recent meta-analyses of experiments using zero-fertilizer control methods or ^{15}N to track fertilizer uptake in cereal crops estimate that about 58–68% of crop N is derived from sources other than the current year's fertilizer (Quan et al., 2020; Yan et al., 2020), and the primary source is likely to be the depolymerization and mineralization of SOM-N. Laboratory experiments using zero N controls also suggest that native SOM often contributes the majority of the total mineral N in soils, even if they are relatively low in SOM and treated with external N inputs (Masunga et al., 2016). While it might be expected that N fertilization would bypass SOM-N supply to some extent, in a global meta-analysis of 43 ^{15}N laboratory and field studies, Liu et al. (2017) found that adding either organic amendments or inorganic fertilizers actually caused higher plant uptake of native soil N. These increases did not always correspond to higher microbe-mediated SOM-N mineralization, suggesting that plant-mediated mechanisms such as increased root growth and rhizosphere priming of SOM-N may be responsible (Clarholm et al., 2015; Liu et al., 2017).

The relative contributions of different SOM components to ecosystem N supply have been researched for decades. Earlier work showed higher rates of net N mineralization from MAOM than from POM (Whalen et al., 2000), and suggested that POM having higher C:N ratios ($\sim >25$)

promotes N immobilization (Compton and Boone, 2002) during the early stages of its decomposition. These results were mainly explained by the nutrient content of the SOM fractions, with MAOM having lower C:N ratios closer to the stoichiometric needs of soil microbes (Mooshammer et al., 2014) and therefore resulting in more N mineralization and less N immobilization than higher C:N POM fractions. Recently, the differences in N provision by POM and MAOM were reemphasized and put into the context of SOM accessibility (Jilling et al., 2018). Daly et al. (2021) suggest that the source of bioavailable SOM-N depends on the relative amounts of POM and MAOM, and on mineral sorption potential. In environments such as heathlands or coniferous forests where POM stocks are relatively high, POM may be the predominant source of bioavailable N because it is more easily accessed. However, in environments such as intensive agricultural systems where POM stocks are low, MAOM-N may be the primary source of bioavailable N even though it is generally difficult to access, leading plants and microbes to use strategies to liberate MAOM-N from mineral surfaces (Daly et al., 2021; Jilling et al., 2018). These ideas have yet to be tested in the field or at larger scales. Given that SOM-N is such a large source of N in agricultural systems (and even more so in unmanaged systems), it is imperative that we better understand its dynamics and controls. Future experiments to better link SOM properties to nutrient provision under various conditions can inform targeted management of SOM stocks in agricultural soils and beyond.

4.2.3 Supporting soil biota

SOM forms the base of the soil food web, providing C-rich substrates and energy to decomposers. Soil microbes are generally C-limited (Soong et al., 2018), so SOM stocks and properties are major controls on their metabolism, growth, and population dynamics. Plant inputs are also a major control on microbial growth, which then stimulates SOM formation (Prommer et al., 2020), so it is difficult to tease apart the effects of higher plant inputs vs higher SOM stocks on microbial biomass and activity in field experiments. In laboratory incubations where plant inputs can be excluded or controlled, SOM stock size is a key determinant of microbial biomass and activity (Birge et al., 2015; Follett et al., 2007). The C and energy provisioning function of SOM depends not only on its stock size, but also on its properties (Fig. 17). Substrates that are less complex require lower enzymatic investments by the microbial community to decompose, thereby better supporting the energy provisioning function (Hoffland et al., 2020).

Substrates that more closely match microbial stoichiometry (e.g., lower C:N ratio) are decomposed and processed with higher efficiencies, which allows microbes to form more biomass per unit substrate C (Sinsabaugh et al., 2013). Higher rates of microbial biomass production and MAOM formation from less complex and lower C:N ratio plant inputs have been observed in both laboratory (Kallenbach et al., 2016; Lavallee et al., 2018) and field experiments (Bird et al., 2008; Fulton-Smith and Cotrufo, 2019; Soong and Cotrufo, 2015). In any given soil, the total stock of SOM is likely the most important contributor to the C and energy provisioning by SOM, while its properties play moderating roles.

4.2.4 Soil carbon storage

Given the current state of climate change, one of the most critical soil functions which SOM underpins is C storage (Fig. 17). Carbon storage is the sum of organic and inorganic soil C stocks (which are highest in arid regions (Mi et al., 2008) and decrease with soil acidity (An et al., 2019), but we focus only on organic C here. The previously described mechanisms controlling SOM formation and persistence determine distributions of SOM storage at different spatial scales, from the pedon to the globe. Globally, soils are estimated to store 2344 Pg of organic C in the upper 3 m (Jobbagy and Jackson, 2000). Areas with the highest soil C stocks—where plant inputs exceed SOM mineralization and other outputs due primarily to microbial physiological inhibition (see Section 3.2)—are in climates which are cold and/or wet enough to limit microbial activity while still allowing for plant growth, such as boreal forests, peatlands, and tundra (Fig. 18; Jackson et al., 2017). By contrast arid lands store the least amount of soil organic C (Fig. 18), likely because plant inputs are more limited than microbial decomposition in these regions (Fig. 14).

An estimated 30% of total global soil organic C is in the Northern Circumpolar Region (Batjes, 1996). The C in these very SOM-rich soils is predominantly found in POM and is particularly vulnerable to losses due to changes such as warming, draining, or land use change. In particular, POM decomposition has been shown to be more sensitive to changing climate than MAOM in natural ecosystems (Lugato et al., 2021; Rocci et al., 2021), stressing the urgency to address climate change before the release of microbial inhibition passes a dangerous threshold in the C-climate feedback (Luo, 2007). Soils with the lowest C stocks—where plant inputs are very limited due to climate constraints or biomass removal—tend to have higher ratios of C in MAOM, which is generally less vulnerable than POM to

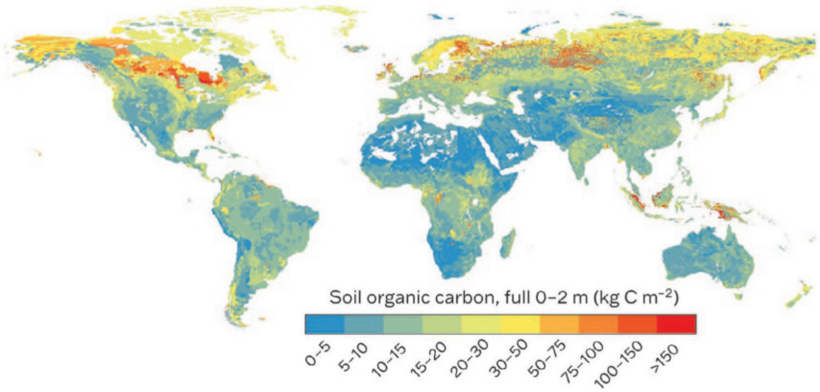

Fig. 18 Estimated soil organic carbon (SOC) stocks to a depth of 2 m using data from the WISE30sec soil property database (Batjes, 2016). *Reused with permission from Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G. & Piñeiro, G. 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. Annu. Rev. Ecol. Evol. Syst., 48, 419-445.*

change but may still be lost rapidly where it is the predominant form of C (Lugato et al., 2021).

The depth distribution of soil C also varies by ecosystem and vegetation type, with the concentration of C in the top 20 cm relative to the first meter of the soil profile being highest in forests, lower in grasslands, lower still in shrublands, and being generally higher in colder and wetter systems (Jobbagy and Jackson, 2000). Compared to forests and shrublands, grasslands store more organic C at depth (>1 m; Wang et al., 2010) and store a larger proportion of C in MAOM (Lugato et al., 2021). Agricultural soils typically store the lowest amount of C per unit area, mostly in MAOM, and with the highest relative N content (i.e., lowest C:N; Lugato et al., 2021). In Europe, we found the majority agricultural soils to be below the saturation threshold (Fig. 15), presenting high potentials for high C sequestration.

4.3 Linking soil organic matter to key outcomes

The links between SOM, soil functions, and key outcomes (Fig. 17) are well-accepted and often referenced but rarely directly demonstrated. This is largely due to the difficulty of determining causality—for example, are higher SOM contents responsible for improving soil functioning, leading to higher plant productivity, or is higher plant productivity and inputs to soil leading to higher SOM content? Controlled experiments with manipulated SOM levels (Bucka et al., 2021; Oldfield et al., 2018b, 2020) or in agricultural trials (Johnston et al., 2009) have attempted to tease these causal linkages apart. However, even when these experiments are well-designed and executed, there may be direct and indirect mechanisms operating simultaneously which are difficult to parse. King et al. (2020) posit that SOM may indirectly affect plant performance by improving root access to nutrients and water, rather than directly increasing the provision of soil nutrients and moisture. While these caveats have yet to be fully resolved, there is still a wealth of research linking SOM to soil functioning and key outcomes by various methods, with evidence in support of causal relationships is rapidly increasing.

One of the most accepted links between SOM and outcomes is that of erosion and flood prevention (Fig. 17). Improved soil structure is known to decrease erodibility (Barthes and Roose, 2002), and increase infiltration and water retention on smaller scales (Franzluebbers, 2002), which almost certainly decreases erosion and mitigates flooding risk. However, studies directly linking soil structure to erosion and flooding outcomes are relatively rare (O'connell et al., 2007). Similarly, one of the least supported links is between SOM and soil biodiversity, even though the relationship makes sense in theory (Caruso et al., 2019; Smith et al., 2015).

The relationship between SOM and plant productivity (Fig. 17), especially agricultural yields, has been studied for over a century. Early experiments using long-term trials such as those at Rothamsted suggested that soils with higher SOM tended to produce higher yields when no fertilizer N was added (Johnston, 1986), but these could not be easily replicated. More recently, the availability of larger datasets including yield and SOM variables have allowed for broader assessment of these relationships (Fig. 19; Oldfield et al., 2019). Researchers have related not only average crop yields, but also yield stability through time to SOM stocks. For example, Pan et al. (2009) synthesized data from cereal crops across mainland China and found positive relationships between soil organic C and grain yield, and strong negative relationships between soil organic C and yield variability. In a study of predominantly rain-fed corn systems in the United States, Kane et al. (2021) found that SOM stocks were positively correlated with yield, and the positive relationship strengthened when drought conditions were more severe. They also found that crop insurance payouts tended to be lower where SOM stocks were higher, suggesting higher crop resiliency (Kane et al., 2021). They attributed these effects to the improved water holding capacity

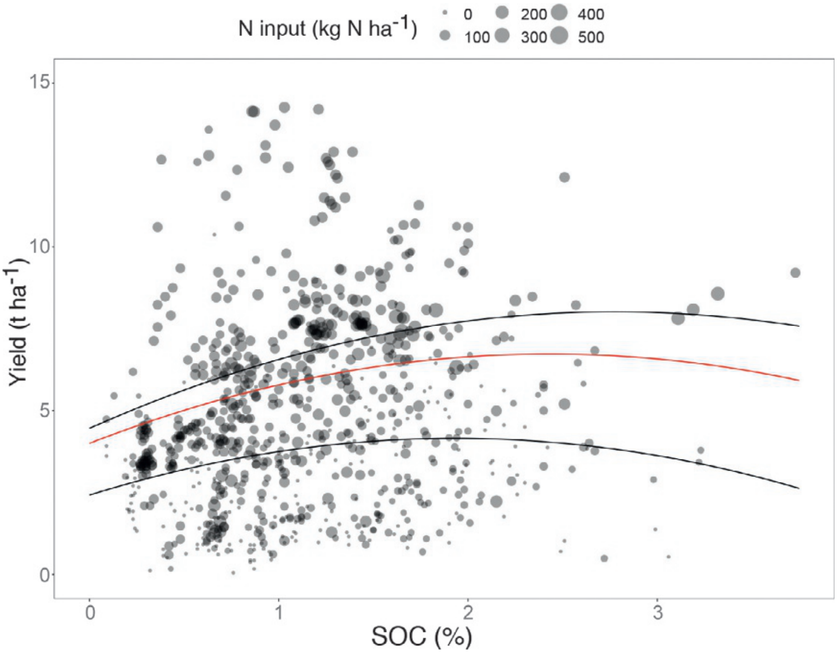

Fig. 19 Relationship between soil organic C (SOC) and maize yield for published studies presented by Oldfield et al. (2019). The regression lines represent modeled yields for rain-fed maize based on the averages of aridity, pH, texture, and latitude at different N fertilization rates in their meta-dataset. Different levels of N inputs are represented by the three lines, with the red line representing the mean N input rate (118 kg N ha^{-1} year^{-1}) across all studies, the bottom line representing 0 N, and the top line representing 200 kg N ha^{-1} year^{-1}. The sizes of the raw data points represent the full range of nitrogen inputs, from 0 (smallest circles) to 500 kg N ha^{-1} year^{-1} (largest circles). *This figure, from Oldfield, E. E., Bradford, M. A. & Wood, S. A. 2019. Global meta-analysis of the relationship between soil organic matter and crop yields. Soil, 5, 15-32, is licensed under CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/deed.ast).*

(Williams et al., 2016) and nutrient provisioning (using CEC as a proxy) of soils with higher SOM (Fig. 17), though there were other mechanisms at play which they could not pinpoint using their dataset (Kane et al., 2021).

Supply of SOM-derived nutrients to crops has been suggested to be the major mechanism explaining positive relationships between SOM and yields (Fig. 17). This makes sense given the large amounts of non-fertilizer N that crops take up, as previously discussed. In a meta-analysis of Dutch agricultural soils, Schjønning et al. (2018) estimated that the level of mineral N needed to reach potential crop production decreased by 12.3 kg N ha^{-1} for every 1% increase in soil organic C. In a global meta-analysis of SOM and crop yields, Oldfield et al. (2019) estimated that at lower rates of N input ($\leq$50 kg N ha^{-1}), fertilizer inputs could be cut in half with yields maintained if soil organic C were increased from 0.5% to 1.0% (Fig. 19). When nutrients are not limiting, the positive effects of SOM on yield have been found to diminish in some studies (Hijbeek et al., 2017; Schjønning et al., 2018). However, yield responsiveness to N additions has also been shown to increase with soil organic C (Johnston et al., 2009), which suggests the benefits of SOM to crop yields go beyond just N provisioning (King et al., 2020).

There has been very little research into the specific properties of SOM and how they relate to plant productivity and yield, but we believe this could be the key to deepening our understanding of the mechanisms at play, thereby improving our ability to manage for desired outcomes. Multiple meta-analyses have shown a positive relationship between yield and soil organic C that eventually plateaus or even becomes negative beyond a certain soil organic C threshold (Oldfield et al., 2019; Waqas et al., 2020), suggesting that SOM only benefits yield up to a point. The mechanisms behind this plateau, and how best to predict the threshold level of SOM for a given site remain unknown (Lal, 2020b), but separating SOM based on its properties could provide a way forward (Dexter et al., 2008; Schjønning et al., 2018). As total SOM increases, the ratio of POM: MAOM also tends to increase (Cotrufo et al., 2019; Lugato et al., 2021). This shift in SOM character affects soil properties (Dexter et al., 2008) and likely affects the rate or mechanisms of N supply to crops (Daly et al., 2021), especially if the POM has a high C:N ratio. Schjønning et al. (2018) put their results into the context of mineral capacity (i.e., MAOM saturation), and suggested that the estimated potential yield was higher when the fine mineral fraction was closer to saturation. This aligns with the ideas of Daly et al. (2021), where N supply drops when the mineral sorption potential is high compared to SOM-N supply. Schjønning et al. (2018) were unable to investigate SOM fractions directly due to limitations of their dataset, but they recommend further analyses in the context of different SOM fractions to fully understand SOM-yield relationships and we agree.

The ability of soils to store large amounts of C, and their capacity for additional C storage, points to their great potential for climate mitigation. Sanderman et al. (2017) suggested an upper limit to potential C storage in global agricultural lands – based on estimates of C losses over the past 12,000 years – of ~133 Pg C in the top 2 m, representing a ~4% increase in the existing global soil C stock of these lands to 2 m and a ~16% reduction of atmospheric CO_2. Given the need for long-term C storage, other studies have focused on soil C sequestration potential in long-lived soil C forms including MAOM. A recent theoretical exploration of the upper limit for additional MAOM formation in global soils suggested that 107 ± 13 Pg C could be added by sorption to 1 m depth, representing a ~7% increase in the global soil C stock in the top 1 m (Abramoff et al., 2021). Realistically, constraints to plant inputs and human land use requirements limit what is realizable. Yet, global soils are still estimated to have the potential to store an additional 2–8 Pg CO_2e year^{-1} (Fig. 20; Paustian et al., 2019)—not counting avoidable losses of ~2.2 Pg CO_2e year^{-1} (Bossio et al., 2020)—with high potential storage in agricultural lands and grasslands (Amelung et al., 2020). Assuming these rates could be maintained for 20 years before decreasing and approaching equilibrium, this could amount to total soil storage of 40–160 Pg CO_2e that equates to ~10.9–43.6 Pg C (using a simple conversion of 1 tone C to 3.67 tones

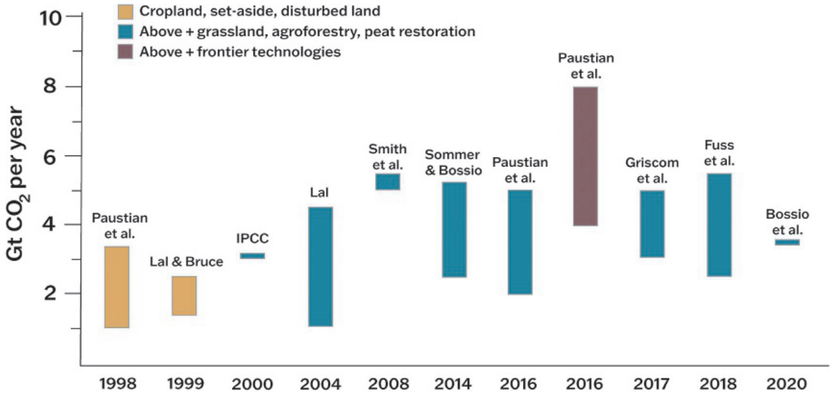

Fig. 20 Published estimates of global biophysical soil carbon sequestration potential, assuming (near) full adoption of C sequestering practices. Estimates vary in terms of which practices or land use types they included, with estimates after 2000 including a wider range of options on all agricultural lands, as opposed to pre-2000 estimates which focused on cropland and set-aside of marginal cropland to grassland. *Redrawn from Paustian, K., Collier, S., Baldock, J., Burgess, R., Creque, J., Delonge, M., Dungait, J., Ellert, B., Frank, S. & Goddard, T. 2019. Quantifying carbon for agricultural soil management: from the current status toward a global soil information system. Carbon Manag., 10, 567–587, with the addition of estimates from Bossio, D., Cook-Patton, S., Ellis, P., Fargione, J., Sanderman, J., Smith, P., Wood, S., Zomer, R., Von Unger, M. & Emmer, I. 2020. The role of soil carbon in natural climate solutions. Nat. Sustain., 1–8.*

CO_2e). Consistent with this range, Bossio et al. (2020) estimated that rebuilding depleted SOM stocks represents about 15%, and avoidable losses of existing stocks another 10%, of the total potential C sequestration of natural climate solutions, which is estimated to be 23.8 Pg $CO_2e\,year^{-1}$ (Griscom et al., 2017). Importantly, these estimates do not account for the form the accrued or existing SOC is in, or its vulnerability to unavoidable future changes including warming, but understanding potential storage of soil C in different forms will further inform on best management practices and priority areas for sequestration efforts.

5. Managing for soil organic matter regeneration

Right now, SOM is seen as a vital pathway to achieving multiple sustainability goals, with climate mitigation and food security at the forefront. Increasing soil organic C storage for climate mitigation will require both preserving existing SOM stocks and increasing SOM stocks wherever feasible, using practices which do not result in increased greenhouse gas (N_2O and CH_4) emissions (Guenet et al., 2021). On the other hand, improving soil health for food security will require the turnover of SOM, responsible for regenerating fertility and supporting soil biota (Janzen, 2006). Achieving these goals simultaneously requires careful management of SOM stocks using a systems-thinking approach which considers the interplay between environmental context, management practices, SOM formation and stabilization processes, and the contributions of SOM to soil functioning.

Regenerating SOM in managed lands has an estimated potential to store up to ~8 Pg $CO_2e\,year^{-1}$ (Fig. 20; Paustian et al., 2019), but it is also imperative to avoid losses of existing SOM stocks by avoiding land use changes which release soil C (e.g., from grasslands to row crops), minimizing soil erosion, and protecting peatlands and wetlands (Bossio et al., 2020). At the broadest level, SOM stocks are determined by the balance of inputs and outputs, and we can use our understanding of SOM formation and stabilization to manage these processes to regenerate and increase SOM stocks.

In most agricultural soils, SOM stocks have declined through time because inputs are relatively low (e.g., due to biomass harvest, small root systems of annual plants, and fallow periods) and outputs are relatively high (e.g., due to soil disturbance reducing microbial access constraints, Fig. 11).

One effective way to counteract this is by increasing inputs that are known to promote efficient SOM formation. Examples include living roots (Sprunger et al., 2019b), root exudates, high quality plant litter (Sprunger et al., 2019a), and compost (Wei et al., 2016). All these inputs can stimulate microbial activity and promote the formation of microbial metabolites and necromass, leading to aggregate and MAOM formation (Fig. 5). One caveat to this strategy is that efficient SOM formation requires relatively high amounts of nutrients (Kirkby et al., 2014). Increasing SOM stocks in agricultural soils will require N, P, and other nutrients to proceed successfully, which has been identified as a potential hinderance or downside of this management goal (Schlesinger and Amundson, 2019; Spohn, 2020; Van Groenigen et al., 2006). However, management practices that increase soil nutrient levels or tighten nutrient cycles and minimize nutrient losses, such as planting legumes (Canarini et al., 2018; Hobley et al., 2018; Schmeer et al., 2014), using enhanced efficiency fertilizers (Li et al., 2018; Xia et al., 2017), or improving grazing management (Gosnell et al., 2020; Mosier et al., 2021; Teague et al., 2011), have the potential to provide these necessary nutrients without requiring increased inputs of synthetic fertilizers. Other strategies to combat nutrient limitation to C storage could include decreasing the nutrient demand of C storage, for example by increasing the direct sorption of C-rich, plant-derived DOM to MAOM. According to the C-surplus hypothesis (Prescott et al., 2020), plants exude C-rich soluble compounds when photosynthetic C uptake exceeds plant biosynthetic capacity, for example under conditions of nutrient or water limitation. Promoting this influx of C-rich material to the soil could increase its contributions to MAOM, possibly through organo-organic bonding (Kopittke et al., 2020), thereby increasing the C:N ratio of MAOM and reducing the N cost of persistent MAOM storage (Cotrufo et al., 2019).

In conjunction with increasing inputs which promote SOM formation, the key to regenerating SOM lies in promoting its persistence, by increasing the proportion of SOM that is stabilized in soil. Practices that are likely to increase persistence include reducing tillage to maintain soil structure, prioritizing inputs that lead to relatively more MAOM than POM formation, and increasing inputs to deep soils so long as priming is avoided. This can also be achieved by focusing regeneration efforts on soils which have high capacities for additional MAOM storage, and which are likely to have higher SOM persistence. Most agricultural soils have sustained significant SOM losses through time (Sanderman et al., 2017) and are therefore far from physicochemical saturation thresholds and have high MAOM storage capacities (Angers et al., 2011), making them ideal for regeneration of persistent SOM from that standpoint. Soils which are more likely to support regeneration of persistent SOM include fine-textured soils, soils with higher reactive mineral/metal concentrations, areas with low disturbance, or even cold or waterlogged soils.

While fundamental research will need to continue discovering the much which is left unknown of SOM dynamics, we now have enough of an understanding to move forward with concerted actions to preserve and restore SOM world-wide. Global maps of C and N distribution in POM and MAOM (e.g., Lugato et al., 2021; Viscarra Rossel et al., 2019) and of MAOM saturation deficits (e.g., Angers et al., 2011) will be needed to provide baselines to inform and direct SOM conservation and regeneration programs. Advancement in the use of spectroscopy and artificial intelligence to increase throughput of estimation of soil C and N distribution between POM and MAOM will aid in this mapping effort (Baldock et al., 2018; Lugato et al., 2021; Ramirez et al., 2021; Sanderman et al., 2021). Organic soils, in particular peatlands and wetlands, with high C stocks in POM will require specific protection to avoid land conversion and disturbance. Incentives will need to be devoted to accelerating the large-scale adoption of regenerative management principles to increase SOM stocks, both in POM and MAOM and along the soil profile of managed mineral soils. New generation models which represent the current understanding of SOM dynamics and are verifiable by the growing wealth of data must be included in ready-to-use decision support tools to enable accurate forecasting of best site-specific regenerative management principles to adopt. If the specific environmental benefits associated with those practices (e.g., C sequestration, water and nutrient provision, increased biodiversity) will be remunerated by markets, they will need to be accurately quantified via rigorous efforts requiring both modeling and measurement verification that accounts for the persistence of such benefits. The scientific community has the knowledge and are developing the tools to follow this path, with long-lasting benefits for the future of humanity on our planet.

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