Bridging 20 years of soil organic matter frameworks: empirical support, model representation, and next steps

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Key Points:

- Soil organic matter (SOM) research has been advanced by conceptual frameworks
- Conceptual frameworks are associated with different SOM controls with different empirical support and model representation
- Microbial properties and physical inaccessibility, as SOM controls, require more empirical work and model representation

Abstract

In the past few decades, there has been an evolution in our understanding of soil organic matter (SOM) dynamics from one of inherent biochemical recalcitrance to one deriving from plant-microbe-mineral interactions. This shift in understanding has been driven, in part, by influential conceptual frameworks which put forth hypotheses about SOM dynamics. Here, we summarize several focal conceptual frameworks and derive from them six controls related to SOM formation, (de)stabilization, and loss. These include: (1) physical inaccessibility; (2) mineral stabilization; (3) abiotic environmental limitation; (4) biochemical reactivity and diversity; (5) biodegradability of plant inputs; and (6) microbial properties. We then review the empirical evidence for these controls, their model representation, and outstanding knowledge gaps. We find relatively strong empirical support and model representation of abiotic environmental limitation but disparities between data and models for biochemical reactivity and diversity, mineral stabilization, and biodegradability of plant inputs, particularly with respect to SOM destabilization for the latter two controls. More empirical research on physical inaccessibility and microbial properties is needed to deepen our understanding of these critical SOM controls and improve their model representation. The SOM controls are highly interactive and also present some inconsistencies which may be reconciled by considering methodological limitations or temporal and spatial variation. Future conceptual frameworks must simultaneously refine our understanding of these six SOM controls at various spatial and temporal scales and within a hierarchical structure, while incorporating emerging insights. This will advance our ability to accurately predict SOM dynamics.

Plain Language Summary

Soil organic matter, the remains of plants, animals, and microbes in the soil, performs many important functions for humans and ecosystems, providing habitat for anmials, nutrients for

plants, climate change buffering, and structure for soil animals and human structures. Thus, it is important to understand how soil organic matter is formed, stabilized, and lost. Here, we review conceptual frameworks that have contributed to our understanding of soil organic matter over the past twenty years. We evaluate their support in experiments and also how well represented they are in computer models. We find the least support and representation for controls of soil organic matter associated with properties of microbes and physical barriers between microbes and soil organic matter. These and novel soil organic matter controls require more research for better understanding of soil organic matter functions.

1 Introduction

Soil organic matter (SOM) is important for both biotic and abiotic processes in ecosystems as the largest store of terrestrial carbon (C) and nutrients (particularly nitrogen [N]), an energy source for microbes, a habitat for soil biota, and a foundation for soil structure (Cotrufo & Lavallee, 2022; Anthony et al., 2023). Because of these characteristics, SOM is increasingly of interest to biogeoscientists, global change researchers, land managers, and policymakers. SOM is comprised of organic compounds that include plant and other organic inputs at various stages of decay (defined as < 2 mm) and products of soil-dwelling decomposers; it accumulates and persists in the soil when biophysical inhibition of decomposition by soil microbes (i.e., heterotrophic soil respiration; Bond-Lamberty, this issue) makes SOM decomposition rates smaller than input rates. In other words, if organic inputs to soils were easily available, consumable, and digestible to soil-dwelling decomposers, and their necromass also easily available, consumable and digestible to other microbes, there would be little accumulation of SOM. Hence, our focus here is on this accumulated SOM and its dynamics, including the processes of formation, (de)stabilization, and loss (Box 1). Our understanding of SOM dynamics has been upended in the past few decades by research showing that persistence (Box 1) is mediated by plant-microbe-mineral interactions rather than inherent chemical recalcitrance (Schmidt et al., 2011; Lehmann & Kleber, 2015; Kogel-Knaber and Rumpel, 2018). Interdisciplinary, technological advances enabling inquiry of SOM at the molecular level as well as societal needs for better understanding of SOM (due to its role in agronomy and climate) underlie this evolution in our understanding. This evolution was facilitated by the publication of several influential conceptual frameworks. These frameworks built upon empirical insights generated over several decades. We focus specifically on conceptual frameworks because of the cognitive schema they provide to integrate multidisciplinary advances, promote novel hypotheses, and stimulate new research (Derry et al., 1996).

Box 1: Terms and definitions as used in this paper

Soil organic matter (SOM) = organic compounds that include plant and other organic inputs at various stages of decay and products of soil-dwelling decomposers (defined as < 2 mm) that remain in the soil for some period of time (days to centuries) due to inhibition of their decomposition by microbes

SOM dynamics = the processes that regulate the existence and cycling of SOM

SOM formation = the transformation of plant and other organic inputs into SOM

SOM (de)stabilization = the interaction of SOM with a stabilizing force, such as a mineral surface or aggregate (stabilization), or the disengagement from that interaction (destabilization)

SOM loss = the movement of SOM out of the soil via mineralization, leaching, or erosion (note that leaching can also move organic materials downward in the soil without being lost from the soil)

SOM persistence = the amount of time SOM remains in the soil

Here, we synthesize the controls of SOM formation, (de)stabilization, and loss (hereafter, “SOM controls”) highlighted in several influential SOM conceptual frameworks of the past 20 years. The frameworks that we chose, based on expert opinion and number of citations, sought to identify unifying principles of SOM dynamics in mineral soils that moved beyond a set of case study approaches (Fierer et al., 2009). Understanding the controls of SOM dynamics in organic soils is also important but not the focus here (see Belyea and Clymo, (2001), Limpens et al. (2008), and Frolking et al. (2010) for controls of organic soils). We then use expert opinion to evaluate empirical support for the SOM controls and consider the current status of their representation in process-based models. We use this review to derive the crucial interactions and inconsistencies among SOM controls and identify potential areas of future work. As we synthesize progressive SOM science from the last two decades, we note that there have been many useful and interesting recent SOM reviews that have focused broadly on SOM dynamics (Paul, 2016), the ecology of SOM (Jackson et al., 2017), mechanisms of soil C gains and losses (Basile-Doelsch et al, 2020), SOM analysis and biochemistry (Weng et al., 2022), SOM dynamics informed by SOM fractions (Cotrufo & Lavallee, 2022), plant and microbial source attribution (Whalen et al., 2022), microbial processes in soil C models (Chandel et al., 2023), and validation of soil C models (Le Noe et al., 2023). We are unique in our focus on SOM conceptual frameworks, which have not been explicitly and holistically evaluated, despite their important role in shaping our current understanding of SOM dynamics.

2 Formation of frameworks

SOM was historically thought to consist primarily of chemically recalcitrant (e.g., bioenergetically unfavorable conditions for decomposition associated with molecular complexity) litter inputs and/or complex “humic” macromolecules formed via condensation reactions, which were persistent because of their resistance to microbial decomposition (Tan, 2003; Allison, 2006). However, pioneering research in the late 1900s and early 2000s questioned these ideas (e.g., Elliot et al., 1980; Tisdall and Oades 1982; Elliot and Coleman 1988; Hassink et al. 1993). These humic substances, thought to be large, difficult-to-characterize compounds, were present in mixtures of recognizable plant and microbial compounds (e.g., carbohydrates, lipids, proteins, lignin; Burdon et al., 2001). Support was also slowly developing for the idea that microbes can decompose humic substances, suggesting inherent chemical structure was not preventing microbial decomposition of SOM (Ekschmitt et al., 2005). Additionally, evidence mounted that the soil matrix (e.g., mineral surfaces) protects from decomposition a diversity of molecules, many of which are small and microbial-derived (Oades, 1988; Sollins et al., 1996; Gleixner et al., 1999, 2002; Baldock and Skjemstad, 2000). Thus, multiple lines of evidence showed that SOM largely consists of recognizable plant and microbial compounds persisting in a complex three dimensional mineral matrix in mineral soils.

Given this emphasis on the soil mineral matrix for stability, rather than chemical recalcitrance, physical separations, or fractionations, were commonly used to characterize SOM (Cambardella & Elliot, 1992; Christensen et al., 2001; von Lutzow et al., 2007, 2008). Physical fractionations are separated on the basis of size and density, before or after aggregate dispersion (see Leuthold et al., 2022 for detailed review). Physical fractions that are small (<50-63 µm) or dense (>1.6-1.85 g cm^{-3}) are associated with silt and clay minerals and are assumed to have greater protection from decomposition compared to those that are large and light (Lavallee et al., 2020). We refer to these small and dense fractions as “mineral-associated organic matter” or “MAOM” where protection is conferred by “mineral-organic associations". The larger and lighter fraction is generally referred to as the “particulate organic matter” or “POM”. These primary physical fractions can then experience further physical protection within aggregates (e.g., secondary physical fractions; *sensu* Christensen et al., 2001). Chemically characterizing these physical fractions was an important turning point in how we thought about SOM dynamics (Baldock and Skjemstad, 2000). For example, updated chemical characterization showed ample small microbial-derived amino acids and sugars, as well as lipids and proteins, in MAOM, suggesting that SOM persistence was not dependent on the presence of hard-to-decompose, recalcitrant compounds (Guggenberger et al., 1995; Kiem & Kogel-Knaber, 2003; Six et al., 2006; Grandy et al., 2007; Kleber et al., 2010; Kleber et al., 2011).

These new insights began to collate into conceptual frameworks that updated our understanding of SOM from which we derive six main SOM controls (Figure 1;Table 1). We emphasize that while the work highlighted here has been influential in the field of SOM research, each framework relies on many other studies and ideas and was selected by the authors based on citations and perceived influence on the field. The frameworks are highlighted here chronologically from the past two decades and include six main categories of SOM controls (bolded words):

- Six et al (2002) elucidated the mechanisms of SOM persistence as **physical inaccessibility** through SOM occlusion in microaggregates and **mineral stabilization** via chemical binding of SOM to silt and clay minerals, proposing the saturation of mineral stabilization. They also conceptualized the POM as an unprotected pool composed dominantly of plant and also microbial residues.
- Davidson & Janssens (2006) suggested that inherent temperature sensitivity of compounds was not sufficient for understanding temperature sensitivity of SOM. Rather, substrate availability, as dependent on mineral protection and water content, was a key consideration for temperature sensitivity, shaping our understanding of **abiotic environmental limitations** as controls on SOM.
- Kleber at al. (2007) suggested the zonal model of mineral-organic associations, which formalized understanding that microbial materials were found in physically protected

SOM into the idea that organic compounds sorbed onto minerals in layers, with N-rich and microbially derived biochemicals forming an inner layer and exchangeable SOM forming the outer layer. This framework suggested specific stabilization processes depend on mineral composition and compound chemistry, highlighting **biochemical reactivity and diversity** and **mineral stabilization** as controls of SOM persistence.

- Grandy & Neff (2008) extended the ideas of Kleber et al. (2007) beyond the physically protected pool and posited a consistent decomposition sequence of SOM, where more plant-like material dominant in larger physical fractions of SOM (sand-sized) was processed by microbes and microbial materials were enriched in small size fractions (silt- and clay-sized). Notably, this framework suggested less complex microbial compounds were more likely to be protected from decomposition than more complex plant materials, in opposition to the theory of chemical recalcitrance as a persistence mechanism. This framework also emphasized **biochemical reactivity and diversity** and **mineral stabilization** as important controls of SOM formation and loss.
- Schmidt et al. (2011) synthesized how SOM emerges from biotic and abiotic influences in the ecosystem (i.e., it is an ecosystem property) and emphasized the importance of **physical inaccessibility, abiotic environmental limitations,** and **mineral stabilization** as forms of SOM persistence.
- The Microbial Efficiency Matrix Stabilization (MEMS; Cotrufo et al., 2013) framework bridged litter decomposition and SOM formation, suggesting that stable SOM emerged from mineral stabilization of SOM efficiently processed by microbes originating from high quality (low C:N and low lignin) plant inputs. This work concurred with Grandy & Neff (2008) and Schmidt et al. (2011) that microbial materials are present in SOM that

persists through **mineral stabilization** and therefore on the importance of the inherent soil matrix capacity to form stable (mineral-associated) SOM, but also emphasized importance of the **biodegradability of plant inputs** and **microbial properties** (specifically carbon use efficiency [CUE]).

- The Soil Continuum Model (Lehmann & Kleber, 2015) also strongly contrasted with historical understanding (where compound size increased with humification or condensation) to provide a framework where compound size is dominantly reduced with microbial decomposition, and as SOM is more oxidized, it interacts more strongly with aggregates and mineral surfaces and persists through mineral protection. This work contrasted with Grandy & Neff (2008) in that it focused on molecular size rather than origin (e.g., plant or microbial) and provided another framework for combining the ideas of **biochemical reactivity and diversity** with **mineral stabilization.**
- The importance of the physical nature (i.e. structural versus water soluble) and **biodegradability of plant inputs** to soil was formalized into a conceptual model in Cotrufo et al. (2015) which suggested there are distinct pathways for the formation of POM and MAOM, where POM forms from physical transfer of structural residues, whereas MAOM forms from dissolved OM (DOM) inputs to soil and their microbial processing. This two pathway model contrasted with ideas from Grandy & Neff (2008) and Lehmann & Kleber (2015) which emphasize a more continuous decomposition pathway.
- Liang et al (2017) built upon the importance of **microbial properties** from Cotrufo et al. (2013) to suggest that the composition of the stable SOM was controlled by two input pathways: extracellular enzyme depolymerization of biochemically larger compounds

that produces biochemically modified compounds (the *ex vivo* pathway) and microbial anabolism of DOM that produces microbial necromass (the *in vivo* pathway).

- Jilling et al., 2018 focused on the dynamic nature of SOM **mineral stabilization**, describing biological (e.g., plant and microbial) mechanisms of destabilization.This work contextualized pathways of destabilization mentioned in other frameworks (e.g., Schmidt et al., 2011; Lehmann & Kleber, 2015), emphasizing that the MAOM pool could be disrupted by plant and microbial processes, creating a source of bioavailable N.
- Sokol et al. (2019) extended ideas from Liang et al. (2017) by suggesting that direct sorption of DOM to form MAOM is more efficient in the microbe-poor bulk soil where minerals are largely not colonized by microbes, whereas the in vivo pathway of MAOM formation is more efficient in the microbe-rich rhizosphere. This work combined ideas of **physical inaccessibility** (Schmidt et al., 2011) and **microbial properties** (Cotrufo et al., 2013; Liang et al., 2017) with a focus on **mineral stabilization** in the rhizosphere versus bulk soils.
- Lehmann et al. (2020) expanded on the importance of **biochemical reactivity and diversity** and **physical inaccessibility**, suggesting that diversity of SOM compounds and spatial heterogeneity of soil confer SOM persistence. This work aligned with ideas that microbial processing altered biochemistry (Grandy and Neff, 2008) and physical separation of microbe and substrate as a SOM persistence mechanism (Schmidt et al., 2011).
- The Rhizo-Engine framework (Dijkstra et al. 2021) suggests the stabilization or destabilization of root inputs in the soil are dependent on microbial turnover and the physicochemical matrix, largely aligning with the description of destabilization in Jilling

et al. (2018). This work focuses on the **biodegradability of plant inputs** from roots**,** with **microbial properties** and **mineral stabilization** determining their stability in the soil.

- See et al. (2022) contrasted with Sokol et al. (2019) in that they suggested that fungal hyphae can move SOM from the rhizosphere throughout the bulk soil such that hyphal density is an important control on SOM formation, extending our understanding of **microbial properties**.

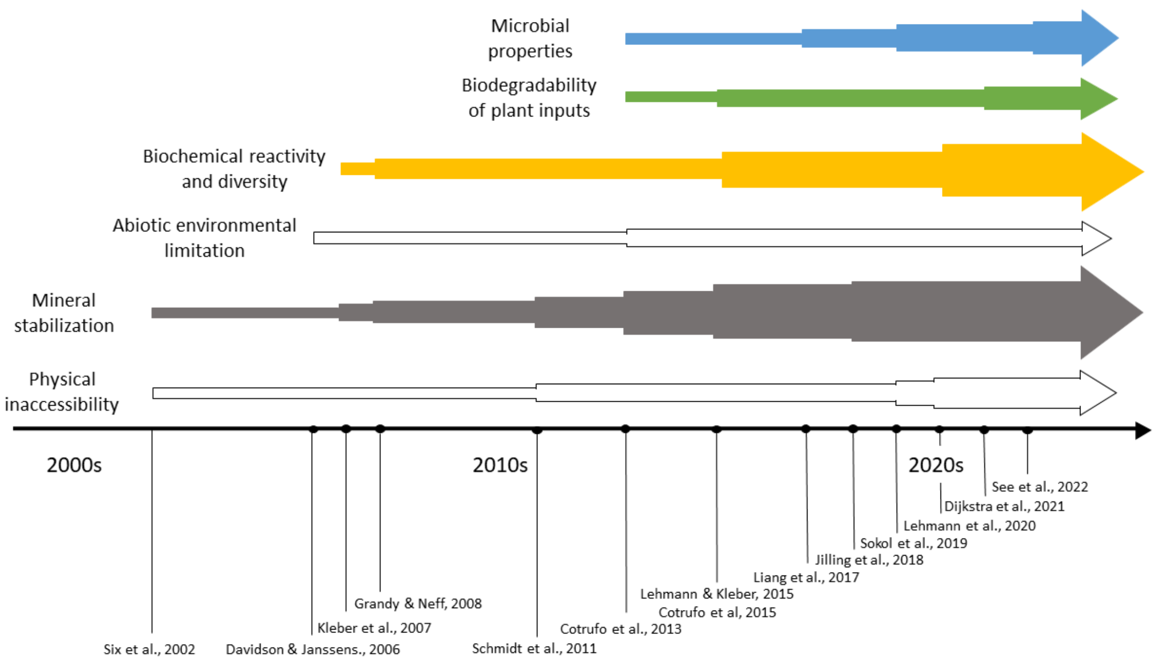

Figure 1. Timeline of conceptual frameworks and the SOM controls derived from them. Arrows get bigger as the ideas are incorporated into more frameworks.

From these frameworks we distill six primary controls for SOM dynamics: physical inaccessibility, mineral stabilization, abiotic environmental limitation, biochemical reactivity and diversity, biodegradability of plant inputs, and microbial properties (Table 1). We combine these ideas into a consolidated framework summary (Figure 2) that is inspired by the Soil Continuum Model in Lehmann & Kleber (2015) that was updated by Basile-Doelsch et al. (2020) to include the biodegradability of plant inputs (Cotrufo et al., 2013, 2015; Dijkstra et al., 2020) and updated in this paper to include abiotic environmental limitations and physical inaccessibility (Six et al., 2002; Schmidt et al., 2011; Sokol et al., 2019; Lehmann et al., 2020). The consolidated framework summary highlights non-linear connections and microbial transformations as major processes in SOM dynamics in mineral soils. Microbial transformations, dependent on microbial properties and the biodegradability of plant inputs, change the biochemical reactivity and diversity of SOM compounds which determines their potential for stabilization via mineral-organic associations or aggregation. However, microbial transformations are mitigated by physical inaccessibility and environmental limitations, which can reduce the influence of microbial processing on SOM persistence.

Table 1. Soil organic matter (SOM) controls and their definitions as used in this paper and as derived from the focal conceptual frameworks.

SOM control	Description of control based on frameworks	Focal conceptual framework(s) that shaped control
Physical inaccessibility	Disconnection and protection of substrates from microbes reduces SOM mineralization.	Six et al. (2002); Schmidt et al. (2011); Sokol et al. (2019); Lehmann et al. (2020)
Mineral stabilization	Physical and chemical sorption of otherwise easily decomposable organic molecules to soil minerals, preventing SOM loss via mineralization and/or leaching.	Six et al. (2002); Kleber et al. (2007); Grandy & Neff (2008); Schmidt et al. (2011); Cotrufo et al. (2013); Lehmann & Kleber, (2015); Jilling et al. (2018)
Abiotic environmental limitation	Climate (temperature and moisture) and chemical variables (pH and oxygen availability) interact to alter formation, (de)stabilization, and loss of SOM.	Davidson and Janssens (2006); Schmidt et al. (2011)
Biochemical reactivity and diversity	Reactive biochemicals (smaller, N-rich, oxidized) are more effectively minerally stabilized. Greater molecular diversity reduces biological mineralization.	Kleber et al. (2007); Grandy & Neff, (2008); Lehmann & Kleber, (2015); Lehamnn et al., (2020)

Biodegradability of plant inputs	The physical structure, solubility, and stoichiometry of plant inputs determine pathways to SOM formation and (de)stabilization.	Cotrufo et al. (2013); Cotrufo et al. (2015); Dijkstra et al. (2021)
Microbial properties	Microbial properties (such as CUE, biomass chemistry, density) influence the formation, mineral stabilization, and loss of SOM.	Cotrufo et al. (2013); Liang et al. (2017); Sokol et al. (2019); See et al. (2022)

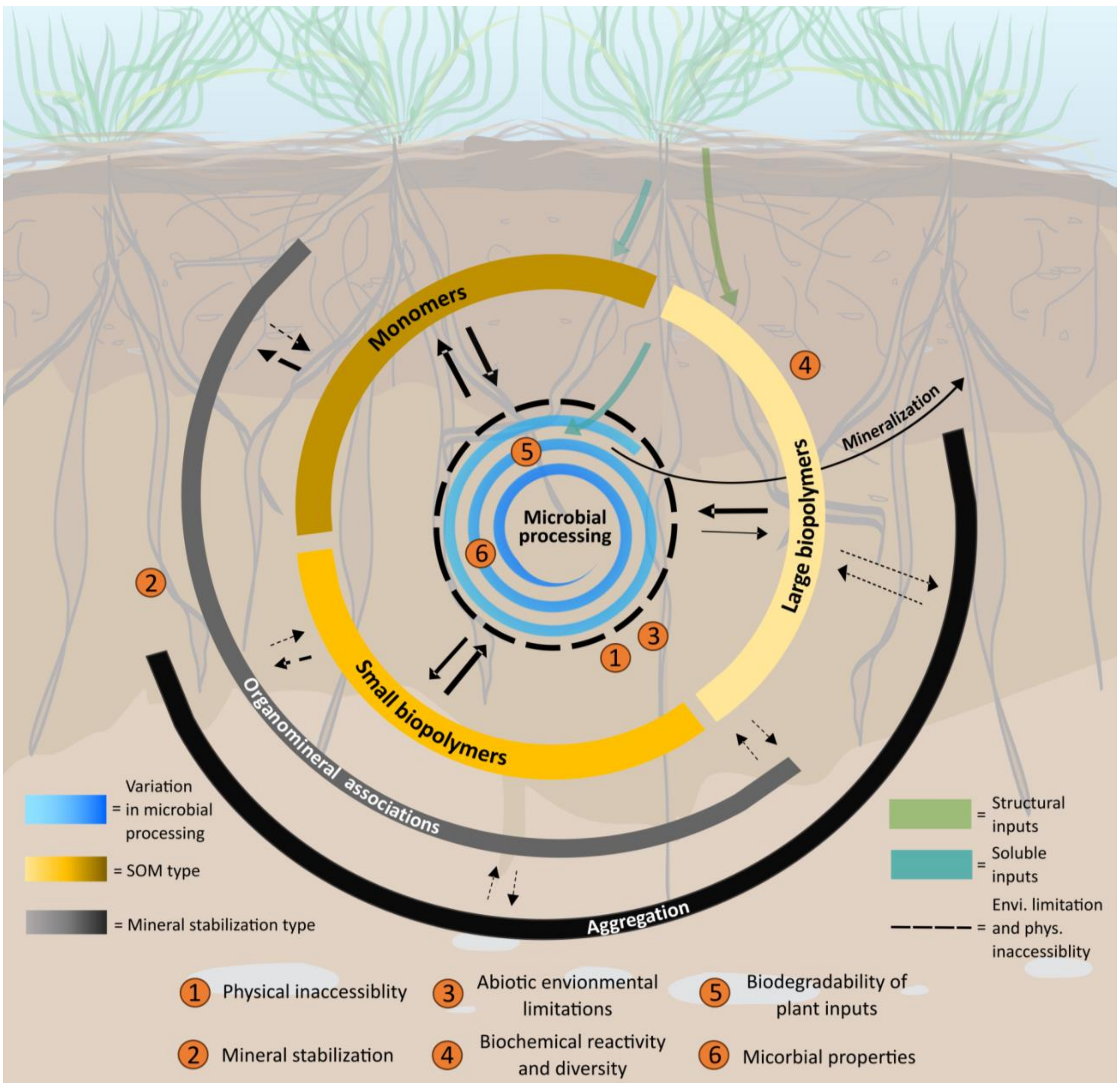

Figure 2. A consolidation of frameworks of soil organic matter (SOM) dynamics from the last two decades, that combines ideas from previous conceptual frameworks largely using the structure proposed in Lehmann & Kleber (2015) and updated in Basile-Doelsch et al (2020), and distinguishing the plant inputs into structural and soluble components (Cotrufo et al., 2015). As microbes are the main transformers of SOM, their influence is central and denoted with the blue-toned "vortex" or swirl. The strength of microbial processing is dependent on microbial properties and the biodegradability of plant inputs (blue color bar). Structural plant inputs (green arrows) are fragmented into large biopolymers by fauna. Labile plant inputs (teal arrows) directly enter the monomer pool or undergo microbial processing and are output as different SOM types (yellow bars) which can re-enter the "vortex". The types of SOM differently interact with the soil matrix (gray bars) to experience mineral stabilization. Microbial processing is constrained by physical inaccessibility and environmental limitations (dotted line) reducing the importance of microbial transformation and associated mineral stabilization mechanisms. As in Lehmann & Kleber (2015) and Basile-Doelsch et al. (2020), we maintain solid arrows as biotic processes and dotted arrows as abiotic processes. Weight of arrows represents their expected importance. Representation of the SOM controls (Table 1) derived from focal conceptual frameworks are denoted with orange circles.

Together these frameworks from the last two decades, and the previous research supporting them, are driving an evolution of our understanding of SOM. However, we note that these focal frameworks are limited in scope given our focus on the past two decades and the frameworks chosen, and thus we do not exhaustively address all possible SOM controls, such as photodegradation (King et al., 2006), for example. Nevertheless, we contend that the above conceptual frameworks and the SOM controls derived from them (Table 1) are fundamental to our current understanding of SOM dynamics. For that reason, we evaluate the empirical evidence for and model representation of these SOM controls to assess the validity of the conceptual framework hypotheses, the extent to which our current understanding is implemented in process-based models, and where more work is needed to improve our fundamental understanding of SOM dynamics.

3. Empirical contributions to and support for SOM controls

Here, we review the empirical findings that contributed to the formulation of the SOM controls (Table 1) and evaluate the empirical support following the formulation of those ideas. We emphasize that this is not a systematic review and relies on expert opinion. While we describe the influence of plant biodegradability on SOM formation and (de)stabilization, we do not evaluate the influence of the SOM controls on associated changes in plant processes that can also alter SOM dynamics (e.g., warming-induced changes in plant input associated with longer growing season lengths; Luo et al., 2007).

3.1 Physical inaccessibility

Physical inaccessibility, as a SOM control, is defined as two processes - physical protection and physical disconnection - that separate microbes from their substrates conferring stabilization and reducing loss. Occlusion of SOM in aggregates physically protects it from microbial mineralization. Aggregates, specifically microaggregates, were highlighted as a stabilization mechanism in the conceptual framework in Six et al. (2002). Tisdall and Oades (1982) provided the foundation for the hierarchy of aggregates and their differing controls, suggesting macroaggregates and microaggregates, which can exist within macroaggregates, were held together by temporary (e..g, roots and fungal hyphae) and persistent (e.g polysaccharides, metal cations, and mineral-organic associations) binding agents, respectively. Stabilization within microaggregates was strongly informed by Six et al. (2000), who put forth a conceptual model of aggregate dynamics with empirical support. This model suggested disruption of macroaggregates reduced the formation of microaggregates and that microaggregates provided greater protection to SOM than macroaggregates. Physical protection in (micro)aggregates was further supported by the basic finding that aggregation has a positive influence on SOM accumulation and more specifically by findings that microaggregates (either free or within macroaggregates) exert stronger stabilization than macroaggregates (e.g., Elliot, 1986; Cambardella and Elliot, 1993; Golchin et al., 1994; Jastrow et al., 1996; Besnard et al., 1996; Denef et al., 2001; further references in Six et al., 2002).

Microaggregates already garnered strong support as a method of physical protection of SOM before Six et al. (2002) and work following further contextualized this finding (reviewed in Totsche et al., 2017). Multiple processes of microaggregate formation have been suggested in contrast to the more classical idea of the surrounding of organic debris by mineral particles (e.g.,Tisdall and Oades, 1982). Lehmann et al. (2007) posited that microaggregates are initially formed by SOM sorption to mineral surfaces that are then further encrusted by minerals and Assano and Wagai (2014) suggested organic-metal-mineral mixtures as fundamental building blocks of microaggregates. While all of these processes likely operate, it remains unclear which is dominant; in general there is still much to understand about microaggregate biogeochemistry, stability, and temporal variability (Totsche et al., 2017). However, accumulation of SOM in microaggregates seems to be mediated by the quantity of plant inputs, faunal (especially earthworm) activity, and disturbance, which may mitigate the influence of plant inputs (Pulleman et al., 2004; Kong et al., 2005; Alvaro-Fuentes et al., 2009). Work focused on aggregates more broadly, rather than microaggregates, indicated the importance of fungi and their hyphae for formation of macroaggregates (Six et al., 2006; Witzgall et al., 2021) and confirmed these aggregates were more vulnerable to disturbance and turned over more quickly than microaggregates (Alvaro-Fuentes et al., 2009; Peng et al. 2017). Additionally, a number of studies indicate the importance of aggregates for protection of otherwise bioavailable SOM (Mueller et al., 2012, 2014; Angst et al., 2017). However, the *in-situ* dynamics of aggregates embedded in the soil are less certain (Garland et al., 2023). Overall, the physical protection that aggregates provide clearly reduces SOM loss, but the mechanistic details of aggregate, and particularly microaggregate, formation, stability, and *in-situ* dynamics are not yet fully clear.

Physical disconnection is informed by three conceptual frameworks that describe areas of the soil where microbes are expected to be relatively more physically disconnected from the substrates they use as energetic and anabolic resources. These include deep soils relative to surface soils (Schmidt et al., 2011), and bulk soils relative to rhizosphere soils (Sokol et al., 2019). Both deep and bulk soils are areas where microbes and SOM will experience more spatial separation, rather than co-location, due to spatially heterogeneous nature of soils (Lehmann et al., 2020). Multiple reviews pointed to physical separation between microbes and substrates as a potential SOM protection mechanism, particularly in the deep soil (Ekschmitt et al., 2008; Rumpel and Kogel-Knaber, 2011), and also noted that microbes are largely sessile and so co-location of microbes and their substrates could only occur through diffusion or mass flow of DOM (Or et al., 2007). Additionally observations of lower microbial colonization simply leading to greater distances to substrate on average further supported this idea (Young and Crawford, 2004; Rawlins et al., 2016; Prashar et al., 2013). Multiple studies also identified greater or different resource (C, N, or P) or temperature limitation in deep or bulk soils (Rovira and

Greacen, 1957; Fierer et al., 2003; Fontaine et al., 2007; Chabbi et al., 2009; Chakrawal et al., 2020), suggesting that in these microbially sparse areas of the soil SOM persists via reduced microbial substrate availability. As such, physical disconnection is also associated with the idea of microbial density as a microbial property influencing SOM formation, stabilization, and loss (see Microbial Properties section; Sokol et al., 2019).

Further theoretical and empirical work on physical disconnection additionally supported greater distances between microbes and their substrates and lower and more resource limited microbial activity in deep, heterogeneous, and bulk soils relative to surface, homogeneous, and rhizosphere soils (Gleixner et al., 2013; Raynaud and Nunan, 2014; Heitkotter and Marschner, 2018; Shi et al., 2021; Henneron et al., 2022; Li et al., 2022). However, Inagaki et al. (2023) found greater mineralization when substrate was added as a hotspot (more heterogeneous) rather than in a distributed manner (more homogenous). Given the limited number of studies on soil heterogeneity as an aspect of physical disconnection, this adds uncertainty to this aspect and also highlights the difficulty of determining an *in situ* method to compare the influence of spatial heterogeneity on co-location and spatial separation of microbes and their substrates. Thus, while there is continued support for physical disconnection reducing SOM loss, the extent of physical disconnection in certain parts of the soil (e..g, heterogenous parts) and the persistence associated with physical disconnection remains uncertain.

3.2 Mineral Stabilization

Mineral stabilization, defined as the physical and chemical sorption of otherwise easily decomposable organic molecules to soil minerals, mitigates SOM loss until desorption. The idea that soil colloids stabilize SOM has been around for decades (Allison et al., 1949). The driving support for mineral stabilization as a SOM control can be summarized in three ideas: (1) greater presence of clay minerals, cations, and metal oxides increase SOM, (2) MAOM is older and has a longer turnover time than other SOM, and (3) MAOM consists of labile, easily decomposed organic compounds. First, the relationship between SOM and mineral content appears in studies of field soils, where increased soil colloid presence or cation availability correlates to greater amounts of SOM (Hassink, 1997; Six et al., 2002; Kiem & Kögel-Knabner, 2002; Kawahigashi et al., 2006; Hobbie et al., 2007). Laboratory studies corroborate this relationship, as experiments have shown that soils with higher clay content retain more C over long-term incubations (Sorensen, 1981). Second, radiocarbon dating of SOM fractions shows increased age of C in mineral associated and aggregate-protected forms of SOM (Kögel-Knabner et al., 2008; Marschner et al., 2008; Theng et al., 1992) as well as slower turnover times (Balesdent et al., 1987). Finally, mineral fractions often consist of labile microbially-derived SOM, which further suggests that minerals protect this otherwise easily decomposable SOM from decomposition (Grandy & Neff, 2008; Poirier et al., 2005). In addition to the ideas that minerals stabilize SOM, there is also the idea that this stabilization is limited, termed C saturation, although this has been suggested to occur for organic and mineral N as well (Six et al., 2002; Castellano et al., 2012). The C saturation concept was supported by (1) the understanding that the protection mechanism of minerals is ultimately limited by its surface area and (2) the lack of increase of soil C content with doubling or tripling of plant inputs in high C soils (Kemper and Koch, 1966; Campbell et al., 1991; Hassink, 1997; Paustian we al., 1997; Solberg et al., 1997; Stewart et al., 2007).

While mineral stabilization has been supported in many threads of evidence, it requires a nuanced understanding, as various factors may influence the strength of mineral associations in protecting SOM. Because SOM binds to mineral surfaces through diverse mechanisms (von Lützow et al., 2006), the strength of mineral protection depends on properties of the organic compound (e.g. type, abundance, and charge characteristics of surface functional groups) and the mineral particle (e.g. size, shape, and surface topography; Kleber et al., 2015). Various minerals affect the strength of stabilization differently, which pH also influences (Keiluweit et al., 2015; Parfitt et al., 1997; Rasmussen et al., 2018). Work following the publication of the conceptual frameworks supporting this SOM control has re-emphasized the importance of cation and metal availability, or combinations thereof, in mineral stabilization (Rasmussen et al., 2018; Wagai et al., 2020; King et al., 2023). Additionally, minerals can contribute to more complex functions beyond sorption, including catalysis (Kleber et al., 2021). Despite general support of minerals as stabilizing forces, there are still uncertainties regarding the effective capacity of minerals to stabilize MAOM under different environmental conditions (Stewart et al., 2008; Georgiou et al., 2022; Begill et al., 2023), the spatial arrangement of MAOM on mineral surfaces (Possinger et al., 2020; Schweizer, 2022), and the temporal dynamics and methodological limitations of these associations (Cotrufo et al., 2023; Poeplau et al., 2023). These uncertainties present good opportunities for further study.

Unlike the other conceptual frameworks reviewed in this paper, which present mineral stabilization as a largely passive control of SOM persistence, Jilling et al. (2018) argues that MAOM is an actively cycling SOM pool as well as an important source of nutrients for plants and microbes. The idea that SOM may actively exchange between dissolved and mineral-associated forms is not new (Hedges & Keil, 1999; Sanderman et al., 2008) and MAOM has been conceptualized as consisting of a stable and exchangeable fraction (Kleber et al., 2007). Jilling et al. (2018) present priming, plant exudation and associated changes in soil pH as potential paths to mineral destabilization, as supported by previous work. In terms of priming, plants may stimulate microbial activity by exuding labile compounds, such as simple sugars

(Kuzyakov, 2010), which can spur N or P mining of the MAOM pool and destabilize C in the process (Rousk et al., 2016; Sharma et al., 2013; Villarino et al. 2023). Plants also release organic acids that abiotically mobilize MAOM and compete for mineral binding sites on the mineral surface (Jilling et al., 2018; Keiluweit et al., 2015). Organic acids may also modify soil pH, which can stimulate both sorption and desorption of MAOM, via changes in mineral surface charge characteristics and mineral dissolution, respectively (Avena & Koopal, 1998; Rashad et al., 2010; Singh et al., 2016).

Plant- and microbial-induced MAOM destabilization has some empirical support but studies are still limited. Addition of root exudate proxies (e.g., organic acids and carbohydrates) increased MAOM-C mineralization and ammonification, total soil N mineralization, and DOM, depending on root exudate and mineral type, potentially via desorption of N-rich MAOM (Li et a., 2021; Jilling et al., 2021; Liu et al., 2022). An organic acid, oxalic acid, was shown to increase both metals and dissolved organic N in a sterile soil that consisted of MAOM and sand, suggesting it was causing direct destabilization of SOM previously sorbed to minerals (Jilling et al., 2021). This was supported by another incubation study which found higher root exudate-induced priming of C and N and larger decreases in iron-bound SOM in a high iron soil compared to a low iron soil, suggesting abiotic desorption (Jiang et al., 2021). Despite the support in incubation studies, we know of no study that has studied plant- and microbial-induced MAOM destabilization in the field; identifying the extent to which this occurs *in-situ* and its controls are important next steps for this SOM control.

3.3 Abiotic environmental limitation

Key conceptual frameworks that contributed to our understanding of abiotic environmental limitation focus on how temperature, moisture, pH and oxygen availability interact to alter formation, (de)stabilization, and loss of SOM. The foundational understanding of abiotic climate and chemical controls on SOM decomposition began several decades ago through lab and field experiments (Greenwood 1961, Katterer et al. 1998, Motavalli et al. 1995, Walse et al. 1998). However, conceptual frameworks of the last 20 years advanced our understanding of specific environmental controls considered important for SOM dynamics (Davidson and Janssons, 2006; Schmidt et al., 2011). As research progressed on SOM protection through aggregation and sorption mechanisms (Oades, 1988; Sollins et al., 1996; Six et al., 2002), SOM responses to warming were observed to depend more on substrate availability and microenvironmental conditions, rather than solely the inherent temperature sensitivity of specific compounds (Kirschbaum et al., 2004; Eliasson et al., 2005; Knorr et al., 2006 and discussion therein). Further work identified the importance of temperature, moisture, pH and oxygen availability, that together influence biological processing of SOM, with greater biological activity expected in warm, wet, neutral, and oxygen-rich conditions (Sexstone et al., 1985; Miller et al. 2005; von Lützow and Kögel-Knabner 2009; Fierer et al. 2009). Together, these control biological access to substrate, metabolic rate and pathways, and community composition (Fierer et al., 2009; Paul 2016; Cotrufo et al., 2022). These insights provided the understanding that multiple types of environmental controls interact to directly and indirectly influence biological processing of SOM.

Many studies support the influence of temperature and moisture on biological processing of SOM. Broadly, expected reductions in microbial activity are most apparent at extreme ends of environmental spectrums (e.g., freezing, desiccation, acidic and anaerobic conditions) but are less apparent for moderate changes in environmental factors. For example, temperature limitation of microbial activity is supported by slowed or halted SOM decomposition in cold and frozen environments (Vaughn et al., 2019; Shi et al. 2020) and hot, dry environments (Schimel et al. 2018). However, the complex controls of temperature remain difficult to characterize, even including seasonal shits in metabolic pathways (McMahon et al. 2011). In their seminal review, Conant et al. (2011) evaluated ideas of substrate limitation formalized in Davidson and Janssens (2006) and found strong support of higher temperature increasing the rates of SOM depolymerization, microbial assimilation and death, and mineral adsorption and desorption, but uncertainties remain around covalently-bound and occluded SOM. In particular, understanding of microbial response to temperature has been analyzed using the Macro-Molecular Rate Theory (MMRT) which indicated variability in microbial temperature sensitivity and acclimation (Shipper 2014, Alster et al. 2020; Moinet et al. 2020). However, temporal dynamics - and underlying mechanisms - of microbial respiratory sensitivity to temperature remain uncertain, including specific assumptions of MMRT (Tang and Riley, 2023). Moisture control was similarly found to be strongest at extremes due to either lack of physical access to substrate or microbial desiccation in dry situations, or due to saturation creating a deficiency in oxygen, but with less clear effects at moderate moistures (Gabriel et al. 2013, Sierra et al., 2015; Wang et al. 2016).

While there has been less empirical work on pH and oxygen availability, support remains for them as drivers of SOM dynamics. Oxygen content shapes microbial communities (DeAngelis et al. 2010) and low oxygen content limits microbial mineralization of SOM to easily-decomposable compounds (Keiluweit et al. 2016; Lin et al. 2021). Regardless of the potential for some decomposition to persist in low oxygen conditions, Keiluweit et al. (2017) showed that a shift from anaerobic to aerobic conditions can increase SOM decomposition by ten fold, indicating strong limitation under anaerobic conditions. Similarly, acidity and liming were found to influence microbial community, physiology, and activity (Lauber et al. 2009; Husson et al. 2013; Shaaban et al., 2017; Sridhar et al., 2022). Although research hypothesized distinct responses of SOM fractions to soil acidity induced by N deposition (Averill and Waring 2018), there was variable support for this hypothesis, with effects of N addition and acidity on SOM mineralization sometimes disconnected (Chen et al., 2020; Lu et al. 2022; Li et al. 2021; Xing 2022). Overall, it is clear that the abiotic environment can strongly limit microbial processing of SOM at extremes that even can occur under what might be considered “typical conditions” (e.g, anaerobic microsites in upland soils; Keiluweit et al., 2017). Understanding more subtle shifts in the environment and differentiating between instantaneous and adaptive responses across individuals, communities, and ecosystems will inform expected changes to SOM dynamics under global environmental change.

3.4 Biochemical reactivity and diversity

Biochemical reactivity and diversity, the ideas that reactive biochemicals (smaller, N-rich, oxidized) are more effectively minerally stabilized and that greater molecular diversity reduces biological mineralization, is a longstanding SOM control. The conceptual frameworks describing this control were derived from multiple lines of evidence, including the following crucial findings that supported an overturning of humification as a dominant mechanism of SOM persistence: (1) Biochemical recalcitrance provides only short-term protection from decomposition, with the exception of charcoal (Skjemstad et al., 1996; Lobe et al. 2002; Schmidt and Kögel-Knabner, 2002); (2) There is scant evidence that humic substances are a distinct type of molecule or exist in soils independent of the alkaline extraction methods used to separate them (Staunton and Weissman, 2001; Tatzber et al. 2009); (3) Decomposition is inevitable and leads to reduction in molecular size and complexity and increasing oxidation and thus reactivity with charged particles in soil (Gleixner et al. 2002); (4) Interactions between organic molecules and charged colloids lead to the more important mechanisms of SOM persistence (Balesdent et al. 1996; Six et al. 2002); (5) Interactions between organic molecules and clay and iron hydroxide colloids coupled to predictable interactions among molecules contributes to distinct, patchy zones of SOM accumulation (Arnarson and Keil, 2001; Mayer and Xing, 2001). The implicit counter assumption of this SOM control is that less reactive compounds (e.g., aromatic compounds like lignin) are only protected by, and persist through, their inherent biochemical properties (Six et al., 2002; Grandy and Neff, 2008).

While there was considerable support for the above lines of evidence before the formation of these frameworks, further work has lended more support to the idea that biochemical reactivity and diversity influence the development of organo-mineral interactions and SOM persistence (Coward et al. 2019; Possinger et al. 2020; Almaida et al. 2023). Chemical properties of biomolecules such as their size, oxidation state, N content, degree of aromatic condensation (i.e., O:C and H:C ratios) and charge characteristics influence the interactions between SOM and soil particles (Zhao et al., 2022; Sparks et al. 2024). These interactions contribute to SOM persistence by physical protection, reducing contact between microbes and substrates due to occlusion in small aggregates and pores, and the formation of distinct, patchy zones of SOM accumulation (Schlüter et al. 2022; Schweizer, 2022). Biochemical properties contributing to these mechanisms of persistence, including enrichment of O and N and reductions in molecular size, arise during the microbial decomposition and transformation of plant-derived molecules (Sanderman and Grandy, 2020; Whalen et al. 2022). Thus, SOM longevity is enhanced by generation of small, oxidized, reactive molecules from decomposition of plant inputs that interact with each other and charged colloids. In addition, there has been confirmation that certain types of less reactive compounds, specifically charcoal or black or pyrogenic C, persist for decades in soil through their inherent biochemical properties (Lavallee et al., 2019), but this is not a long-term persistence mechanism for the majority of biochemicals (Bol et al., 2009).

Although research has confirmed the importance of biochemical reactivity and diversity in SOM dynamics, empirical insights also reveal the context dependency of these effects and the limitations to our understanding. For example, the architecture of SOM on soil minerals, including the spatial organization of clusters of SOM and the organo-mineral and organic-organic structures therein may influence SOM persistence. Kleber et al. (2007) argue for zonal structures of organo-mineral interactions that self organize, with a stable inner-sphere complex of hydroxyl groups, phosphate groups, and proteins, followed by a hydrophobic lipid bilayer, and a kinetic zone of freely exchanged SOM. However, recent studies add complexity and some uncertainty to these ideas. For example, while studies confirm the enrichment of N and oxidized species at the organo-mineral interface (Mikutta et al. 2010; Possinger et al. 2020) iron hydroxide surfaces may also interact with and sorb aromatic compounds (Kramer et al. 2012; Zhao et al. 2016). This highlights the potential for biochemistry to impact sorption differently depending on mineral surface characteristics. This also raises questions about what drives the low C:N ratios observed in MAOM. The lower C:N ratio of MAOM has been attributed to microbial decomposition resulting in litter C loss and production of N-rich necromass (Tipping et al. 2016). However, recent studies show that some minerals preferentially bind with N-enriched SOM (Jilling et al. 2018; Possinger et al. 2029). Therefore, mineral surface chemistry may also drive the low C:N ratio of MAOM. Additionally, the presumed dominance of microbial materials in MAOM is also under reconsideration (Angst et al., 2021). For instance, Whalen et al. (2022) shows that the overlap in the chemical characteristics of molecules derived from plants and microbes makes it difficult to attribute many compounds to distinct plant or microbial origin. This assertion aligns with conceptual and quantitative models that provide pathways for both plant and microbial inputs to enter MAOM pools (Miltner et al. 2012; Kyker-Snowman et al. 2020; Cotrufo et al. 2022). Thus, while it is clear that biochemical reactivity and diversity plays a role in determining mineral stabilization, we are not yet able to fully characterize how this role is influenced by the specific characteristics of and interactions among plant inputs, microbial decomposers and mineral surfaces.

3.5 Biodegradability of plant inputs

The biodegradability of plant inputs, defined as their physical structure, solubility, and stoichiometry, is another important control on SOM formation and (de)stabilization. Here, we first address SOM formation and stabilization, followed by destabilization. Historically, recalcitrant litter was thought to be the most important contributor to stable SOM, as it was the slowest to decompose. However, reviews, biochemical analyses, and isotope tracer studies revealed that slow decomposition did not translate to greater SOM stabilization. Rather, these found that fast-decomposing soluble compounds, including those with low C:N ratios, contributed more to minerally-stabilized SOM (e.g., MAOM) while structural materials contributed more to non-stable pools, that turned over faster on average (e.g., POM; Voroney et al., 1989; Bird et al., 2008; Marschner et al., 2008; Preston et al., 2009; Prescott, 2010; Hatton et al., 2015), as articulated in the conceptual frameworks associated with this control (Cotrufo et al., 2013, 2015; Dijkstra et al., 2021). These findings prompted the delineation of multiple pathways of formation and stabilization of soluble and low C:N plant inputs, including through microbial anabolism, direct sorption, and exo-enzymatic processing of litter residues; these were thought to depend on plant input source and chemistry (Cotrufo et al., 2013; Cotrufo et al., 2015; Liang et al., 2017; Sokol et al., 2019; Sokol and Bradford, 2019). In particular, the microbial anabolism pathway for soluble inputs relied on findings that low C:N litters were used more efficiently by microbes and that microbial materials were preferentially stabilized in MAOM compared to plant-associated compounds (Manzoni et al., 2008; Grandy & Neff, 2008; Clemente et al., 2011). For POM, the physical transfer of structural material was most clearly articulated as a formation pathway (Cotrufo et al., 2015). Root inputs, as a type of plant input that may be more efficiently and effectively stabilized than aboveground inputs (Rasse et al., 2005; Villarino et al., 2021 but see Lajtha et al., 2018), were included in these conceptualizations of the biodegradability of plant inputs, with rhizodeposition expected to contribute to stable MAOM and turnover of structural root litter contributing to POM (Rasse et al., 2005).

Support for the influence of the biodegradability of plant inputs on SOM formation and stabilization can be derived from studies following the pathways of litter to SOM formation via examination of individual compounds, isotopically labeled litter, or litters of varying chemistries. These studies supported formation of MAOM from soluble litter and POM from structural litter (Haddix et al., 2016; Lajtha et al., 2014; Cordova et al., 2018; Lavallee et al., 2018; Hicks Pries et al., 2018; Fulton-Smith & Cotrufo, 2019; Haddix et al., 2020; Pierson et al., 2021; Villarino et al., 2021; Huys et al., 2022; Cotrufo et al., 2022; Even & Cotrufo, accepted). Furthermore, high quality litters (e.g., low C:N) facilitated MAOM formation, but not necessarily through an anabolic or efficient microbial pathway, suggesting direct sorption could underlie this connection in some circumstances (Aponte et al., 2013; Tamura & Tharayil, 2014; Cyle et al., 2016; Craig et al., 2018; Cordova et al., 2018; Craig et al., 2022; Cotrufo et al., 2022). Inefficient MAOM formation from high quality litters has been suggested to be related to the C saturation deficit (i.e., how far the MAOM pool is from saturation; Castellano et al., 2015) but the limited testing of this hypothesis has found mixed results (Li et al., 2022; Rodrigues et al., 2022). Other studies, in contrast to those above, have found relationships between structural compounds and MAOM (Huys et al., 2022), and MAOM and POM (Witzgall et al., 2021), as well as no relationship between litter chemistry and POM and MAOM formation (Schmatz et al., 2016; Tamura et al., 2017). Additionally, soluble OM inputs were shown to result in POM formation (Cotrufo et al., 2022) supporting the concept of microbial contribution to the formation of larger SOM components (Lehmann & Kleber, 2015). These findings suggest the paths of SOM formation and stabilization may be multiple and context dependent.

While the biodegradability of plant inputs can influence formation and stabilization of SOM, it can also influence destabilization of SOM. Dijstra et al. (2021) articulated this for different types of root inputs, which can contribute directly to SOM stabilization as described above, but also cause destabilization through two pathways: priming of existing SOM by stimulated rhizosphere microbial activity (Huo et al., 2017; Kuzyakov, 2002; Cheng et al. 2014) and disruption of organo-mineral bonds in aggregates by organic acids in root exudates (Clarholm et al., 2015; Keiluweit et al. 2015). Notably, destabilization does not necessarily mean a net loss of SOM but likely modifies the nature of SOM if, for example, an organic acid replaces an amino acid on a mineral surface.

Both priming and MAOM destabilization can clearly occur due to different types of root inputs but the extent of these responses and their importance in SOM turnover remain uncertain. Root input-induced destabilization was supported by a 20-year experiment that excluded live roots and found increased MAOM pools, suggesting MAOM was destabilized by priming or desorption when live roots were present (Pierson et al. 2021). However, an analysis of 35 isotopic labeling studies found rhizodeposition increased MAOM pools, suggesting soluble root inputs likely favor MAOM formation and stabilization in most contexts, while reducing POM pools, likely due to increased decomposition associated with priming (Villarino et al., 2021). Priming of SOM due to rhizodeposition is likely a short-term response, and rarely exceeds new plant input to SOM, but it does affect the net SOM balance, making it important to better understand in the future (Perveen et al., 2019; Schiedung et al., 2023). Further it remains unclear if plant input biodegradability is the key control on the influence of root inputs on formation and (de)stabilization of SOM; soil properties may play a more important role (Cusack and Turner, 2021). Understanding the relative influence of different types of root inputs on formation and stabilization versus destabilization will be important for soil management and predicting SOM responses to global change.

Overall, while it is clear the biodegradability of plant inputs influences SOM formation and stabilization, and likely to some extent destabilization, the pathway associated with different types of plant inputs is not always consistent. Ultimately, on ecosystem and broader scales it is highly likely that altered plant input quantity and quality will influence SOM nonlinearly over time, particularly due to the transient nature of the priming effect (Perveen et al., 2019; Schiedung et al., 2023). Determining the relative importance of formation pathways or when stabilization versus destabilization might occur remains an important research gap for understanding the relevance of the biodegradability of plant inputs for SOM formation and loss.

3.6 Microbial properties

Microbial properties, in the context of a SOM control, refer to characteristics of microorganisms that influence the formation, mineral stabilization, and loss of SOM. Several frameworks have explored how microbial properties (e.g., physiological, morphological, biochemical) contribute to the formation and persistence of SOM, though most have focused on a small set of traits for microbes broadly, rather than specific taxa. The main traits that have been highlighted in the literature thus far are CUE, also referred to as substrate use efficiency (SUE), allocation, referring to biochemical characteristics of microbes based on the types of compounds they produce (e.g., cell walls, proteins), and microbial, and specifically hyphal, density, where higher CUE and density are hypothesized to be associated with greater MAOM formation from incorporation of microbial materials (Cotrufo et al., 2013; Liang et al., 2017; Sokol et al., 2019, 2022; See et al., 2022). Liang et al. (2017) also address exo-enzymatic processing (termed the *ex vivo* pathway) but this pathway was missing a clear empirical underpinning, so we do not address that mechanism specifically here. The ideas of CUE and allocation contributing to SOM formation largely derive from findings of efficient microbial substrate use and biosynthesis being associated with SOM formation as well as the contribution of microbial materials of specific biochemistry to stable SOM (Kindler et al., 2006; Bradford et al., 2013; Schweigert et al., 2015). Microbial density, as a trait, derived from studies showing greater microbial abundance in the rhizosphere compared to the bulk soil coupled to the understanding that microbial colonization is associated with greater anabolism (Guggenberger and Kaiser, 2003; Young & Crawford, 2004; Prashar et al., 2013). Whereas, the specific control of hyphal density stemmed from studies showing that (1) a large proportion of plant C allocation is found outside of the rhizosphere (Huang et al., 2020; Leake et al., 2001; Norton et al., 1990); (2) saprotrophic fungi can redistribute C from SOM patches to other regions of the soil while searching for nutrients (Frey et al., 2003); and (3) mycorrhizal hyphae incorporate newly fixed C into SOM (Cairney, 2012; Clemmensen et al., 2013; Ekblad et al., 2013; Frey, 2019; Godbold et al., 2006; Leake et al., 2004).

While work suggesting the importance of microbial properties has received considerable attention and citations, few direct tests of the proposed mechanisms have been conducted, and available results are mixed. Positive correlations between CUE and SOM or MAOM content have been observed (Luo et al., 2020, Wang et al., 2021, Tao et al., 2023; Kallenbach et al., 2015, 2016). Tao et al. (2023) demonstrated that CUE was the most important predictor of SOC in comparison to other biophysical factors using data synthesis and modeling approaches, though critics of this approach argue that CUE is treated more as an ecosystem property than a microbial trait, that the results are dependent on choice of model structure, and that some controls are overlooked (e.g., plant inputs; Xiao et al., 2023; He et al., preprint). Ernakovich et al. (2021) similarly found that CUE was related to new MAOM formation, but the measure of CUE employed in this study reflected both soil and microbial properties. In contrast, Craig et al. (2022) found that while the decomposition of fast decaying litter promoted SOM formation, CUE, along with microbial growth and turnover, were negatively correlated with MAOM, suggesting that the transfer of C to MAOM might instead be due to other pathways and controls (e.g., necromass chemistry, direct sorption with or without enzymatic processing, priming effects, and abiotic conditions). Similar to CUE, support for the importance of microbial density is mixed. The only clear test of microbial density we are aware of suggested that the higher microbial density of the rhizosphere was associated with more efficient MAOM formation (Sokol et al., 2019). However other studies find greater microbial necromass biomarker abundance in the bulk soil than the rhizosphere or associated with living biomass, soil pH, and DOC rather than belowground biomass, suggesting that microbial density in the rhizosphere does not always confer MAOM formation via a microbial anabolic pathway (Zheng et al., 2021; Yang et al., 2022; Jia et al., 2023). There has been limited testing of the importance of hyphal density as of yet, but current evidence suggests hyphal density may be particularly important for stable SOM formation in arbuscular mycorrhizal and N-rich systems but may reduce MAOM formation in ectomycorrhizal systems (Zhu, Zhang et al., 2022; Hicks Pries et al., 2023; Horsch et al., 2023). A comprehensive evaluation of traits had not occurred until Whalen et al. (in review) directly tested whether a suite of physiological, morphological, and biochemical traits of soil fungi are linked to SOM formation potential. While total SOM and MAOM formation were highly correlated with CUE, the formation of stable, chemically diverse SOM fractions was promoted by ‘multifunctional’ species with intermediate investment across a group of traits (i.e., CUE, growth rate, turnover rate, and biomass protein and phenol contents). This emphasized the importance of synergies between microbial properties, rather than tradeoffs, for the formation of complex SOM. Further work should build from these findings with single cultures to consider the impact of microbial interactions (viral-bacterial-fungal, bacterial-bacterial, fungal-fungal, etc.) on how the expression of multifunctional traits and trait investments alter SOM dynamics. It is clear that microbial properties are important for SOM formation, but there is still much to learn about which traits or groups of traits are associated with SOM formation and under which biophysical conditions.

4 Implementation of framework ideas in SOM models

The theoretical frameworks summarized in Figure 2 are partly or fully reflected within numerical models of SOM turnover and persistence (Blankinship et al. 2018). These models allow us to project the responses of SOM under global change; but they can also be seen as hypothesis testing tools, because they make explicit assumptions in their structures and parameterizations that can be informed by and evaluated with conceptual understanding and observational and experimental data (Sulman et al. 2018). Given that our theoretical understanding and model calibrations are incomplete, numerical models also provide opportunities to explore sensitivities to process and parametric uncertainty (Zhang et al. 2020, Abramoff et al. 2022; Pierson et al. 2022). We note that recent reviews provide excellent resources for readers looking for detailed summaries of the diversity of modeling approaches (Chandel et al., 2023; Le Noe et al., 2023). Our aim in this section is to briefly highlight how different aspects of the frameworks are implemented into numerical models, given the value of models noted above.

4.1 Model representation of physical inaccessibility

The idea that substrates are physically protected or disconnected from microbial decomposers is variably represented in soil biogeochemical models. Despite decades of evidence of the importance of aggregates for physical protection of SOM, explicit consideration of aggregates is represented in only a few models (Segoli et al. 2013; Abramoff et al., 2018; 2022). Aggregate dynamics therefore represent an important frontier in soil biogeochemical models. Physical disconnection is better represented in models and is expected to be more prevalent in deep, bulk, and heterogeneous soils, as compared to surface, rhizosphere, and homogeneous soils (Schmidt et al., 2011; Sokol et al., 2019; Lehmann et al., 2020). In depth-resolved soil models, turnover times are often reduced in deeper soil horizons to implicitly represent the physical disconnection between substrates and decomposers and consequent energy limitations that slow decomposition processes (Koven et al. 2013). However, not all depth-resolved models impose reductions in turnover times with depth, but rather, some allow the underlying mechanisms to drive differences in SOM persistence with depth (Dwivedi et al. 2017; Druhan et al. 2021; Ahrens et al. 2020; Zhang et al., 2021). For instance, Ahrens et al. (2015) found that even without imposing longer C turnover times in deeper soils, older ^{14}C ages emerged from the interplay of mineral stabilization and microbial recycling in their model and that vertical transport by DOC prevented SOM from being too old compared to site-level observations. Ultimately, only a small subset of ecosystem- or global-scale soil models are fully depth-resolved (Ahrens et al. 2015; Koven et al. 2013; Grant et al. 2014; Zhang et al., 2021), while many others represent at most topsoil (0-30cm) and subsoil (30-100cm) intervals (Wieder et al. 2013; Sulman et al. 2018).

Besides depth, the physical disconnection of microbes and substrates can occur with the heterogeneous distribution of SOM in bulk soils or because of gradients in plant inputs in soil affected by rhizosphere processes. For example, recent modeling work demonstrates that the spatially heterogeneous distribution of SOM can cause different respiration rates compared to a model configured with homogenous SOM distribution (Chakrawal et al., 2020), suggesting larger scale models may need effective equations and/or parameterizations to capture these emergent dynamics. With respect to representing greater microbe-substrate co-location in the rhizosphere compared to the bulk soil, Sulman et al. (2014) and Zhang et al. (2021) are some of the few models that represent dynamics of rhizosphere and bulk soil separately. Despite these advancements, capturing dynamics of aggregate formation, destruction, and distribution, implementing fully depth-resolved models, capturing spatial heterogeneity of microbes and substrates in computationally efficient model formulations, and defining the volume of soil that experiences spatial heterogeneity or rhizosphere effects remains challenging to quantify and parameterize in models that are used at ecosystem- to global-scales.

4.2 Model representation of mineral stabilization

Mineral stabilization has been included as a SOM persistence mechanism in soil biogeochemistry models for decades. This concept is reflected in the parameterization of turnover times for SOM pools that are considered ‘passive’, or stable (formulated as, or comparable to, MAOM), especially when the allocation to or turnover of these pools are modified by soil physical properties like texture (Parton et al. 1994; Sulman et al. 2018). Soil texture (i.e., clay and silt content) may be a relatively crude proxy for mineral stabilization, but it is likely still a useful (and widely measured) integrator variable for complex SOM interactions with the mineral soil matrix (Bailey et al. 2018; Rasmussen et al. 2018).

Other model parameterizations include variation in mineral stabilization due to mineral composition by representing different mineral types or relationships between pH and MAOM (Grant et al. 2012, Aherns et al. 2020, Abramoff et al. 2022), as well as modeling separate exchangeable and stable MAOM pools (Zhang et al. 2021). The period for which C or N remains in a pool formulated as MAOM is generally dependent on desorption rates, microbial decomposition capacity, and environmental controls, and this period exceeds that of more POM-like pools (Sulman et al., 2018). Since these MAOM-like pools are generally parameterized with a lower C:N ratio and they protect otherwise decomposable SOM (Rocci et al., accepted), they largely align with the conceptual frameworks of mineral stabilization (Kleber et al., 2007; Lehmann & Kleber, 2015). While models broadly represent exchange of MAOM-like pools, the destabilization of mineral-sorbed SOM by explicit plant and microbial processes – which is relatively new to the SOM paradigm (Keiluweit et al. 2015; Jilling et al., 2018; Bailey et al. 2019) – is virtually absent from ecosystem-scale models. This presents an exciting opportunity for empirical and modeling work to feedback on each other as our understanding of the dynamic nature of MAOM exchange and destabilization develops.

4.3 Model representation of abiotic environmental limitation

The abiotic environmental limitation of microbial activity can be seen in the rate scalars used to modify the turnover of SOM pools. For both temperature and moisture, these environmental scalars are intended to represent the kinetics of substrate diffusion and microbial activity on SOM decomposition and rates of heterotrophic respiration. The shapes of these functions are highly variable across models and can generate substantial uncertainty in simulated rates of heterotrophic respiration (Sierra et al., 2015; Zhou et al., 2021; Evans et al. 2022). For example, while freezing temperature should reduce microbial activity, the limitation of liquid water may actually limit decomposition rates in some model formulations. Similarly, under saturated conditions, oxygen availability may ultimately slow rates of heterotrophic respiration, which can be implicitly represented with a hump shaped water scalar, or explicitly represented with an oxygen scalar in models that consider porosity and gas diffusion in soils (Ghezzehei et al. 2018; Evans et al 2022). Beyond temporally varying temperature, water, and oxygen availability, static soil physical properties like soil pH or texture (see below) may modify rates of SOM turnover (Rasmussen et al. 2018; Zhang et al., 2021; Abramoff et al., 2022). The extent to which changing environmental conditions influence the turnover of SOM and rates of heterotrophic soil respiration shows a high dependency on the model assumptions and parameterizations of these environmental scalars, as well as their interactions with other mechanisms of persistence in models (Wieder et al. 2013; Koven et al. 2017; Wieder et al. 2019).

4.4 Model representation of biochemical reactivity and diversity

Foundational ideas about biochemistry are broadly implemented in soil biogeochemical models, although both have evolved over the past several decades. The foundational idea we highlight here, which posits that smaller, N-rich and oxidized biochemicals are more effectively minerally stabilized and thereby persistent (Table 1) have been represented in several models through the parameterization of SOM stoichiometry and fluxes between pools, such as the low C:N ratio of the passive pool (Schimel et al. 1994; Parton et al. 1994) and the flux from microbial necromass to more persistent SOM (Wieder et al 2014; Sulman et al 2014; Abramoff 2018; Ahrens et al. 2020; Zhang et al., 2021). The latter models include microbial explicit representations of decomposition dynamics and generally assume that some fraction of low molecular weight SOM and/or polymeric microbial residues persist because they are strongly sorbed to minerals. Such formulations vary across microbial explicit models, where some models form minerally stabilized SOM only from microbial necromass (Wieder et al. 2014), and others represent both low molecular weight and microbial residue pools that can each sorb/desorb at different rates (Sulman et al. 2014; Ahrens et al. 2020; Abramoff et al. 2022; Zhang et al. 2021). Moreover all of the sorbed compounds may be assigned the same turnover rate (Abramoff et al. 2018; Sulman et al. 2014), or some models explicitly distinguish microbial necromass turnover and DOM sorption pathways of mineral stabilization that vary rates of exchange or desorption (Ahrens et al. 2020; Zhang et al. 2021).

Despite these complexities, no ecosystem-scale models represent the complete SOM functional diversity (e.g., sugars, lipids, organic acids, lignin-derived compounds, and amino acids) due to inherent difficulties in parameterizing and validating underlying model pools at large scales, although some ecosystem models do represent select SOM compound classes explicitly (e.g., non-structural carbohydrates, proteins, lignin, cellulose; Grant et al. 2014). At the site-level and within strictly theoretical studies, however, reactive-transport models have been used to represent an extensive suite of polymeric and monomeric organic compounds, where compound classes are selected based on properties relevant for metabolic processing (e.g., oxygen to C ratio, positive or negative charge, and degree of polarity; Riley et al. 2014; Dwivedi et al. 2017). The PROMISE framework (Waring et al., 2020) and prior work by Sierra et al. (2017) further illustrates that SOM dynamics are driven by probabilities of interactions at the molecular scale and, therefore, underlying pools can be heterogeneous in their persistence and depict a distribution of carbon ages (Azizi-Rad et al., 2021). Ultimately, differences between these model formulations allow the opportunity to probe our scientific understanding, but we also highlight the difficulty in parameterizing increasingly complex representations of biochemistry effects on SOM dynamics.

4.5 Model representation of biodegradability of plant inputs

Some aspects of the influence of the biodegradability of plant inputs have been fundamentally represented in models but other aspects of this control are still underrepresented. For example, the importance of litter quality has long been recognized in determining litter decomposition rates, a pattern that is also well established in models, often using C:N ratios and/or lignin content as proxies (Parton et al. 1987; Aerts et al. 1997; Adair et al. 2008; Bonan et al. 2013). These proxies generally cause separation of litter into metabolic and structural components which are differently incorporated into distinct SOM pools; some of these model structures are well-aligned with the expectation that soluble and structural materials preferentially form MAOM and POM, respectively (Parton et al., 1987; Wang et al., 2010; Wieder et al., 2014; Zhang et al., 2021; Cotrufo et al., 2015). While the metabolic and structural components previously mentioned broadly match our current understanding, few models have represented measurable litter pools which can directly connect models and empirical work (but see Zhang et al., 2021). As mentioned in the mineral stabilization section, the influence of different types of root inputs on mineral destabilization is poorly represented in models.

Rhizosphere priming has been investigated by Sulman et al. (2014) and Keuper et al. (2020) using process-based models, but not considering different types of root inputs. Thus, while some aspects of plant input effects on SOM have a long history of representation in soil biogeochemical models, others deserve more attention in future work.

4.6 Model representation of microbial properties

The expression of microbial properties can be simulated in models that implicitly or explicitly represent heterotrophic microbial activity. For example, CUE is a common, albeit highly uncertain, feature in soil biogeochemical models (Manzoni et al. 2018). Explicit consideration of microbial-mediated decomposition rates or enzyme activity has become more common in recent decades (summarized by Chandel et al., 2023; Le Noe et al., 2023). These microbially-explicit models allow for consideration of how microbial properties influence the rate (catabolism) and fate (anabolism) of SOM turnover (Schimel and Schaefer 2012). This growing diversity of model formulations (e.g. Wang et al. 2013; Wieder et al., 2014; Sulman et al. 2014; Tang et al. 2015; Ahrens et al. 2015) provides opportunities to consider how microbial trait-environment relationships influence SOM turnover and rates of heterotrophic respiration (Frey et al. 2013; Wieder et al. 2013; Abramoff et al., 2018; Zhang et al., 2021).

Some of these microbial-explicit models have been expanded to represent different microbial functional groups and/or explicit extracellular enzymes (Wieder et al., 2014; Sistla et al., 2014; Grant et al., 2014; Wang et al., 2013; Wutzler et al., 2023), affording opportunities to explore how changes in microbial community composition and community-weighted mean traits may influence SOM turnover. For instance, several ecosystem-scale models represent two or more microbial constituents, including r vs. k strategists (Wieder et al. 2015), rhizosphere vs. bulk microbes (Sulman et al. 2014; Zhang et al. 2021), and a suite of 10+ functional groups

(Grant et al. 2014). At smaller (pore to core) scales, individual- and trait-based models are widespread and often depict emergent system behavior that may not be captured in ecosystem-scale models (Kaiser et al. 2015; Allison et al. 2014, 2017; Bouskill et al. 2012; Marschman et al. 2023). For example, Kaiser et al. (2014) show that microbial community interactions can lead to community-level adaptations that accelerate N cycling in high C:N litter and alleviate N limitation without decreasing CUE. Kaiser et al. (2015) further illustrate the importance of different microbial groups (e.g., enzyme producers and cheaters) in regulating emergent SOM decay rates and N retention through an accumulation of N-rich necromass.

While microbial properties are important for influencing the biochemical nature and mineral stabilization of SOM at smaller spatial and temporal scales, it is still an open question how much complexity is needed within ecosystem- to global-scale models. Omics data may be a useful tool for constraining trait-based models at larger scales (Graham & Hofmockel, 2021). However, an increasing number of microbial functional groups and traits may be difficult to parameterize at larger spatial scales. As such, effective equations and parameterizations that implicitly incorporate community-level controls (e.g., Georgiou et al. 2017), may be a tractable way to add complexity and capture emergent dynamics.

5 Summary and looking forward

Overall, the primary SOM controls, as defined in Table 1, were supported by empirical work (albeit with considerable context dependency) and represented in models to varying extents, but there remain gaps in our understanding (Figure 3). For example, more empirical work on physical disconnection in different parts of the soil (e.g., bulk vs. rhizosphere, surface vs. deep, homogeneous vs. heterogeneous) will be important for determining whether these differences deserve wider representation in models, whereas wider model representation of the physical protection provided by aggregates would likely be useful in ensuring process-based models match our empirical understanding. Our review highlighted that MAOM has largely been conceptualized as a passive pool, but both recent empirical work and model representations have supported it as more actively cycling (Jilling et al., 2021; Zhang et al., 2021; Ahrens et al. 2020). Understanding the extent to which MAOM is active or passive and whether saturation limits this pool will be important advances. Environmental limitation is perhaps the most fundamental of the SOM controls but there remains lingering uncertainty around temperature sensitivity of both microbes and associated SOM pools and acclimation and adaptation, as well as variable representation of temperature and moisture controls in models. Despite its long history in advancing our understanding of SOM controls, we are still unsure whether biochemical reactivity and diversity causes consistent layering of compounds and whether this fine-grained detail is important to incorporate into models. While it is clear the biodegradability of plant inputs influences SOM formation and stabilization, it is unclear what drives the variable pathways of MAOM formation (e.g., direct sorption or microbial anabolism); implementing different pathways into models may allow for efficient testing of relationships between the biodegradability of plant inputs and pathways of formation and stabilization. Whereas, the influence of biodegradability of plant inputs on destabilization requires greater investigation in observational, experimental, and modeling studies. The exploration of microbial properties in conceptual frameworks and models is largely limited to CUE; recent work highlights the need to consider a broader suite of microbial properties as SOM controls (Sokol et al., 2022; Whalen et al., in review). Altogether, conceptual frameworks have provided us with important framing for the past couple decades of SOM research but there are clear gaps that will be important avenues of pursuit for the next couple of decades.

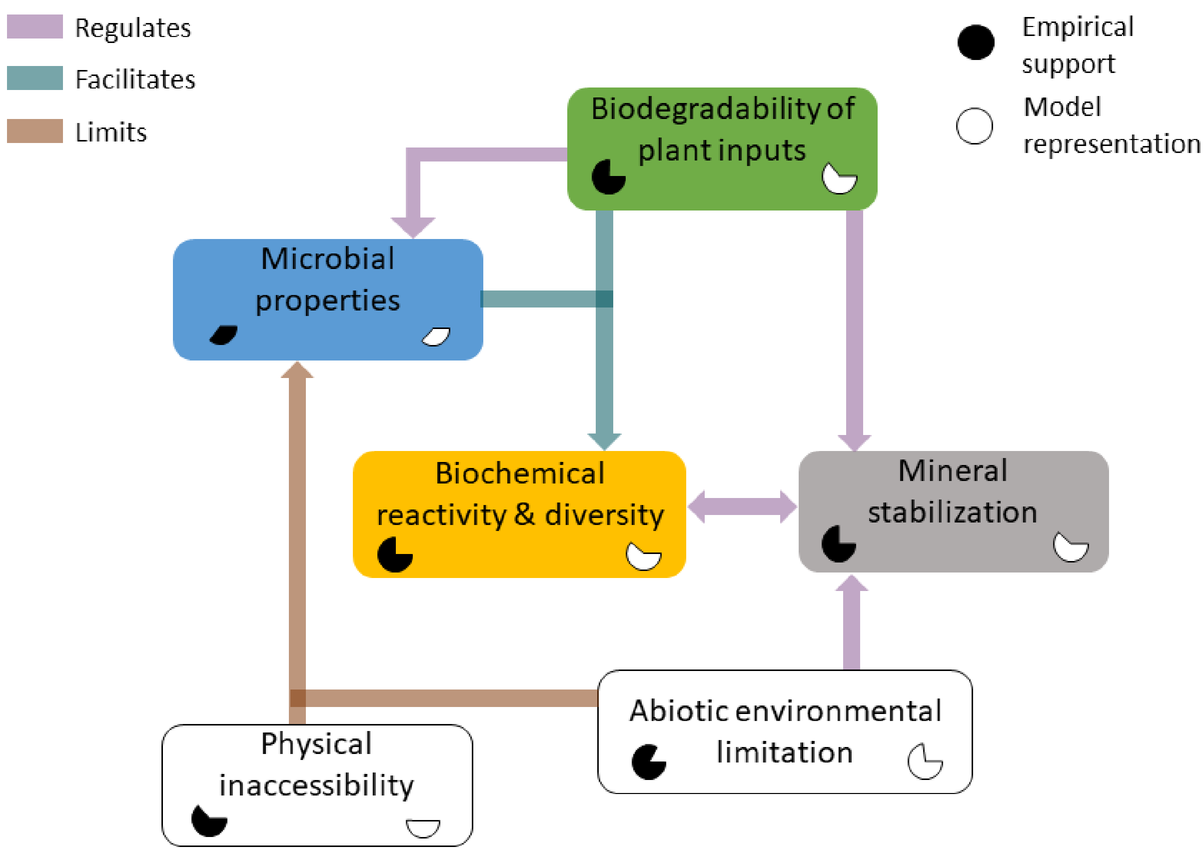

Figure 3. Empirical support (black semi-circles) and model representation (white semi-circles) of the SOM controls (rounded boxes) identified in Figure 1 based on the review in this paper. A full circle represents the strongest empirical support and model representation. Colored arrows (pink = regulates; teal = facilitates, orange = limits) show how the SOM controls relate to one another. Note that the color of each rounded box relates to the color in Figures 1 and 2.

While we discuss each SOM control in separate sections above, they are inextricably connected (Figure 3) and also present some inconsistencies when evaluated together. For example, the low C:N ratio of (Rocci et al., accepted) and the dominance of small and often oxidized molecules in (Mooshammer et al. 2022) MAOM provides support for the dominance of microbial materials in MAOM (e.g., Grandy and Neff, 2008; Cotrufo et al., 2013) but other ideas suggest direct pathways for plant materials to become MAOM (Liang et al., 2017; Sokol et al., 2019; Cotrufo et al., 2022) and the presence of an unstable, N-rich MAOM fraction (Jilling et al., 2018; Dijkstra et al., 2021). These inconsistencies can be reconciled with the understanding that our methods for distinguishing plant and microbial compounds in MAOM are limited (Whalen et al., 2022) and the rates MAOM formation and destabilization geographically vary with climate, soil, and vegetation (Cordova et al., 2018; Yu et al., 2022; Sokol et al., 2022). The conceptualization of mineral stabilization as a persistence mechanism (Six et al., 2002; Lehmann and Kleber, 2015) can be seen as at odds with MAOM as a partially exchangeable pool. This can be better understood by comparing conceptualizations of MAOM to how MAOM is measured; separating a small or dense fraction of SOM may include non-stabilized material, despite the assumption of mineral association given the name of the pool. Additionally, the frameworks described above both suggest largely continuous formation pathways of POM to MAOM (though this framework allows for microbial feedbacks; Grandy and Neff, 2008) and two distinct formation pathways of POM and MAOM (Cotrufo et al., 2015). These can be reconciled by separately considering formation from plant litter and SOM cycling within the soil. When derived from plant litter, there is strong evidence for POM largely forming from structural material and MAOM largely forming from soluble material. However, once formed, POM can be a source for MAOM formation (Witzgall et al., 2021), although how prevalent this is remains uncertain. Determining the hierarchy or context dependency of these controls moving forward may further help reconcile perceived inconsistencies in our understanding of SOM dynamics (Cotrufo et al., 2021).

In conclusion, building upon more than a century of soil science, researchers in the past 20 years have provided important conceptual frameworks regarding controls of SOM formation, (de)stabilization, and loss. These frameworks have variable empirical support and model representation with particularly important gaps in microbial properties and physical inaccessibility (Figure 3). By focusing on six primary SOM controls derived from the focal conceptual frameworks, we were able to identify interactions and inconsistencies between these controls and important areas for future empirical and modeling work. We are excited to see the forthcoming conceptual frameworks of the following decades and how they continue to shape the evolution of our understanding of SOM dynamics.

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Open Research

There were no data or code used in this manuscript.

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