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Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century

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Abstract

Managing soil organic matter (SOM) stocks to address global change challenges requires well-substantiated knowledge of SOM behavior that can be clearly communicated between scientists, management practitioners, and policy makers. However, SOM is incredibly complex and requires separation into multiple components with contrasting behavior in order to study and predict its dynamics. Numerous diverse SOM separation schemes are currently used, making cross-study comparisons difficult and hindering broad-scale generalizations. Here, we recommend separating SOM into particulate (POM) and mineral-associated (MAOM) forms, two SOM components that are fundamentally different in terms of their formation, persistence, and functioning. We provide evidence of their highly contrasting physical and chemical properties, mean residence times in soil, and responses to land use change, plant litter inputs, warming, CO₂ enrichment, and N fertilization. Conceptualizing SOM into POM versus MAOM is a feasible, well-supported, and useful framework that will allow scientists to move beyond studies of bulk SOM, but also use a consistent separation scheme across studies. Ultimately, we propose the POM versus MAOM framework as the best way forward to understand and predict broad-scale SOM dynamics in the context of global change challenges and provide necessary recommendations to managers and policy makers.

KEYWORDS: carbon sequestration, fractionation, global change, mineral-associated organic matter, particulate organic matter, soil carbon, soil fertility, soil organic matter

1 INTRODUCTION

The world's soils are increasingly recognized as a key battleground in the fights against climate change, nutrient pollution, and other pressing global change challenges. Soils have the capacity to store vast amounts of soil organic matter (SOM), which aids in provision of multiple ecosystem services (Smith et al., 2015) and is widely recognized as a viable component of a diversified strategy to address the UN sustainability goals (Keesstra et al., 2016). Managing SOM stocks to effectively address global change challenges

requires deep understanding of SOM formation, persistence, and function. Decades of research have shown that we cannot understand these aspects of SOM by studying and modeling it as a single, uniform entity (Jenkinson, 1990; Parton, Stewart, & Cole, 1988; Trumbore, 2009), and there is widespread agreement for need to separate total SOM into components with contrasting behavior.

Early efforts to separate SOM into meaningful components focused on chemical separation methods and resulted in the study of humic substances isolated by alkaline extractions. Humic substances have been the subject of much scrutiny. Recognition that they were artificial by-products of extraction and inaccurate proxies for naturally occurring SOM began to emerge as early as the 1840s (see references to Mulder and Eggertz in Baveye & Wander, 2019; Waksman, 1936), and they have more recently been dismissed by much of the SOM community (Lehmann & Kleber, 2015). In place of harsh chemical separations, physical methods of separation based on size and/or density have gained favor. Early methods were relatively simple, yielding two to four SOM forms with highly contrasting behavior (e.g., Cambardella & Elliott, 1992; Sollins, Spycher, & Glassman, 1984). Two such forms are particulate organic matter (POM) and mineral-associated organic matter (MAOM), which have very different properties and rates of turnover (Cambardella & Elliott, 1992; Christensen, 2001; von Lützow et al., 2008).

In the following decades, as the scientific community probed deeper into the complexities of SOM dynamics, SOM separation schemes evolved to accommodate studies of greater mechanistic detail. Complex separation schemes led to breakthroughs in understanding (e.g., Six, Elliott, & Paustian, 2000; Sollins et al., 2006; Stewart, Plante, Paustian, Conant, & Six, 2008), but these separations were often tailored to specific research questions or ecosystem types (e.g., agricultural systems). Together, the explosion of new knowledge—much of it context specific—and the myriad methodological approaches to studying SOM led to a muddling of ideas. Today, there is no consensus around SOM separation schemes (see Poeplau et al., 2018), hindering cross-study comparisons and leading much research on broad-scale controls of SOM storage (Chenu et al., 2019; Rasmussen et al., 2018; Wiesmeier et al., 2019), SOM responses to global change (Averill, Dietze, & Bhatnagar, 2018; Crowther et al., 2016), and effects of SOM on productivity (Oldfield, Bradford, & Wood, 2019) to treat it as a single entity.

In this critical time, when multiple global change challenges necessitate mitigating action, there is urgent need for a simple, informative way to conceptualize SOM that enables understanding and prediction across ecosystems, soil depths, and timescales. We propose separating SOM into POM and MAOM as a viable solution. Here, we present the evidence for considering POM versus MAOM as a simple, well-supported, and useful framework for scientists to better understand and predict broad-scale SOM dynamics in the context of global change challenges. We discuss the importance of investigating whether these components, and in particular

POM, are found free or occluded in aggregates, but ultimately argue that the POM versus MAOM framework is the best way forward to conceptualize results from SOM studies, identify drivers of and forecast SOM stock changes, and inform policy and management practices aiming to protect and regenerate SOM.

2 POM AND MAOM: TWO FUNDAMENTALLY DIFFERENT SOM COMPONENTS

When considering mechanisms of formation, persistence, and function, POM and MAOM are fundamentally different SOM components (Table 1). Generally speaking, POM is largely made up of lightweight fragments that are relatively undecomposed, while MAOM consists of single molecules or microscopic fragments of organic material that have either leached directly from plant material or been chemically transformed by the soil biota (Figure 1). The defining difference between them is that MAOM is protected from decomposition through association with soil minerals, while POM is not. Mineral associations include chemical bonds between SOM and mineral surfaces and occlusion within micropores or small aggregates (<50–63 μm), which all render SOM less accessible to decomposers and their enzymes (Kleber et al., 2015; Kögel-Knabner et al., 2008; Totsche et al., 2018). Because of this fundamental difference in their levels of protection from decomposition, MAOM tends to persist for much longer than POM (Kögel-Knabner et al., 2008; Poeplau et al., 2018; Trumbore & Zheng, 1996).

TABLE 1 The general properties of particulate (POM) and mineral-associated (MAOM) organic matter discussed in this review with references of relevant studies

	POM	MAOM	References
Protection mechanisms	None or occlusion in large aggregates	Mineral associations (occlusion in fine aggregates, organo-mineral clusters, and micropores; sorption to mineral surfaces)	von Lützow et al. (2007)
Mean residence time	<10 years—decades	Decades—centuries	Kleber et al. (2015), Kögel-Knabner et al. (2008), von Lützow et al. (2007)
Dominant formation pathway	Fragmentation, depolymerization	In vivo transformation or ex vivo modification of low molecular weight compounds	Cotrufo et al. (2015), Liang et al. (2017)
Subject to saturation?	No	Yes	Castellano et al. (2015), Cotrufo, Ranalli, Haddix, Six, and Lugato (in press), Stewart et al. (2008)
Dominant chemical constituents	Plant-derived (e.g., phenols, celluloses, hemicelluloses), fungal-derived (e.g., chitin, xylanase)	Low molecular weight compounds of microbial (e.g., microbial polysaccharides, amino sugars, muramic acid) and plant origin	Baldock and Skjemstad (2000), Christensen (2001), Kögel-Knabner et al. (2008), Sanderman et al. (2014), Six et al. (2001)
C/N ratio	10–40	8–13	Cotrufo et al. (in press), von Lützow et al. (2007)
Nutritional role	<ul style="list-style-type: none"> • More complex compounds with high activation energies • Not assimilable by plants, few or no assimilable compounds for microbes 	<ul style="list-style-type: none"> • More simple compounds with low activation energies • More assimilable compounds for microbes and plants 	Jilling et al. (2018), Kleber et al. (2015), Williams et al. (2018)

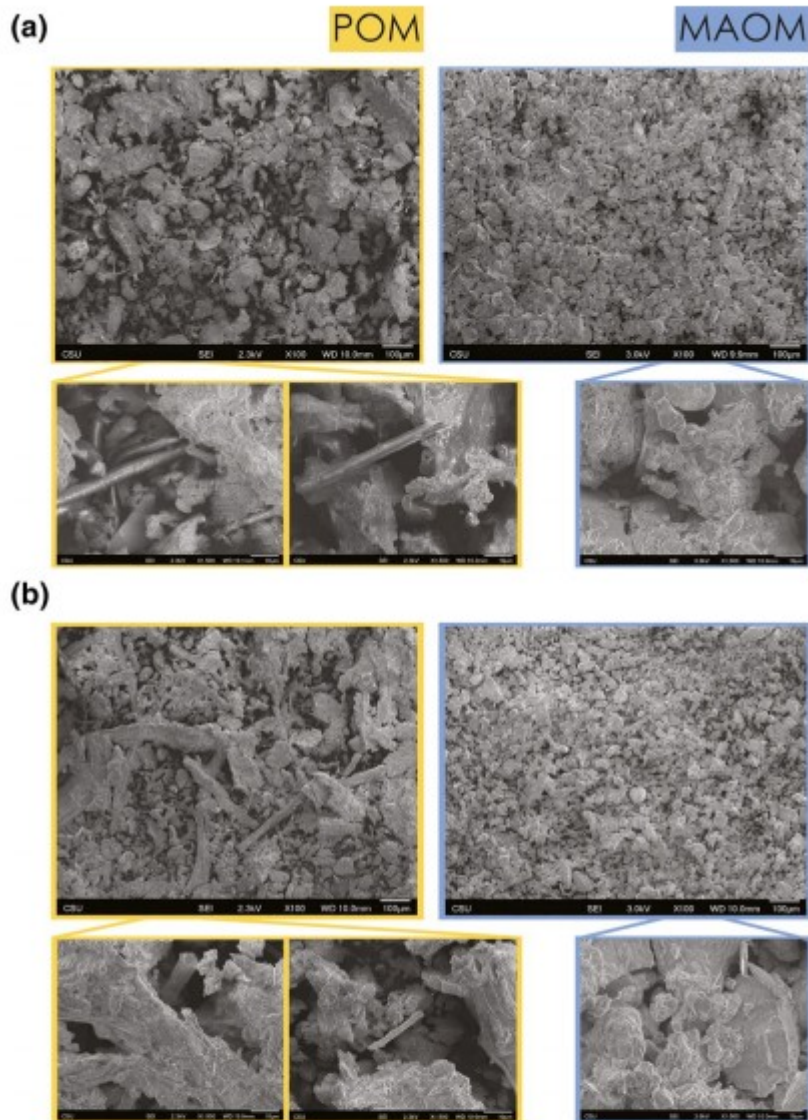


FIGURE 1 Scanning electron microscope images of particulate (POM; left) and mineral-associated (MAOM; right) organic matter, including larger overviews and closer details, from (a) deciduous forest and (b) grassland. Samples are from A horizons collected by the National Ecological Observatory Network (NEON) from the Bartlett Experimental Forest in New Hampshire and the Northern Great Plains Research Laboratory in North Dakota, respectively, and separated at Colorado State University by size (53 μm) and density (1.8 g/cm^3). Detail images show distinct plant and/or fungal structures in POM samples and clustered organo-mineral structures in MAOM samples

Chemically, POM and MAOM are fairly distinct, and it is hypothesized that this is because they are formed through different pathways (Cotrufo et al.,

2015). POM enters the bulk mineral soil from the litter/organic layer and the rhizosphere mainly through fragmentation and has generally experienced only partial processing by soil organisms. MAOM can form in multiple ways, but the main pathways pertain to the mineral adsorption of relatively low molecular weight compounds (Lehmann & Kleber, 2015), which are thought to be the main component of the most persistent portion of MAOM. Low molecular weight compounds can become MAOM in two ways: they can leach from plant litter or be produced by exoenzyme depolymerization of plant litter and associate directly with the mineral phase (the “ex vivo modification pathway” sensu Liang, Schimel, & Jastrow, 2017, and see Sanderman, Maddern, & Baldock, 2014), or they can be produced by the “in vivo microbial turnover pathway” sensu Liang et al. (2017) whereby microbiota decompose and transform organic material, resulting in necromass or exudates which are then incorporated into MAOM. Compared to POM, MAOM has a lower C/N ratio, fewer plant-derived compounds, more microbial-derived compounds, and a higher natural abundance $\delta^{13}\text{C}$ (Baldock & Skjemstad, 2000; Christensen, 2001; Poirier et al., 2005; von Lützow et al., 2007; Williams, Fogel, Berhe, & Plante, 2018; Table 1).

The functioning of SOM is key to its role in providing certain ecosystem services, and POM and MAOM tend to function very differently. While SOM performs many functions in soil (Smith et al., 2015), we focus here on two key functions which require SOM to turn over rather than accrue and persist (Janzen, 2006): fueling microbial growth and thereby the entire soil food web, and providing nutrients to microbiota and plants. Compared to POM, the compounds in MAOM tend to be more nutrient dense (Tipping, Somerville, & Luster, 2016), have lower activation energies of decomposition (Williams et al., 2018), and require less depolymerization prior to microbial or plant assimilation (Kleber et al., 2011, 2015). As a result, MAOM that dissociates from minerals and becomes available will likely be quickly assimilated or decomposed, and MAOM turnover may be an important source of N for plants and microbiota (Jilling et al., 2018). In contrast, POM is more readily available, but its quality for decomposers is less consistent than that of MAOM. On average, POM contains larger, insoluble molecules that require depolymerization prior to assimilation (Kleber et al., 2015) and have higher activation energies (Williams et al., 2018). Many compounds in POM are N-poor (von Lützow et al., 2007) and may require more N (in the form of exoenzymes) to decompose than they yield (Mooshammer, Wanek, Zechmeister-Boltenstern, & Richter, 2014). The quality of POM for microbiota depends on its chemistry and nutrient content and generally follows the quality of the plant inputs. Overall, MAOM is useful to microbiota and plants as a source of labile carbon and nutrients, but only once it is destabilized. POM is more readily available but its usefulness or quality for decomposers varies. These basic differences in functioning highlight the need to quantify and characterize POM and MAOM separately.

3 OPERATIONAL DEFINITIONS OF POM AND MAOM

The reality of soil separation procedures is that they necessitate operational definitions of soil components, including POM and MAOM. Both POM and MAOM go by many different names throughout the literature (e.g., “light fraction” for light POM) and are operationally defined in various ways (Christensen, 2001; Curtin, Beare, Qiu, & Sharp, 2019; Elliott & Cambardella, 1991; Marzaioli et al., 2010; Poeplau et al., 2018; von Lützow et al., 2007). By definition, MAOM is associated with silt and clay minerals, and these are operationally defined as smaller than 20–63 μm (the upper size limit specification varies by region; Totsche et al., 2018). Because of its mineral association, the MAOM component of soil also typically has a density greater than 1.6–1.85 g/cm^3 (the ideal density of separation varies by soil type and can be determined with testing; Cerli, Celi, Kalbitz, Guggenberger, & Kaiser, 2012). By contrast, in most soils, the majority of POM is lighter than 1.6–1.85 g/cm^3 , larger than 20–63 μm , and not water-extractable. The SOM that is heavy but larger than 20–63 μm , sometimes termed “heavy POM” or “sand-sized SOM,” is generally a relatively small portion of total SOM that may display unique behavior compared to light POM and MAOM (Soong et al., 2016). Similarly, dissolved SOM (DOM), which is operationally defined as water-extractable and smaller than 0.45 μm , typically makes up less than 2% of total SOM (von Lützow et al., 2007) and is highly dynamic (Kalbitz, Solinger, Park, Michalzik, & Matzner, 2000). Because they are relatively small and more difficult to characterize, we suggest that the explicit separation of heavy POM and DOM may not be necessary for understanding broad-scale SOM stock changes, their drivers, and responses to management and disturbance.

Different separation procedures can yield very different SOM components (Gregorich, Beare, McKim, & Skjemstad, 2006), so the use of consistent operational definitions for interstudy comparisons is critical. Here, we suggest relatively simple operational definitions of POM and MAOM that may aid in combining or comparing multiple definitions and provide some broad consistency moving forward: we define MAOM as denser than 1.6–1.85 g/cm^3 and smaller than 50–63 μm (Figure 2), and POM as lighter than 1.6–1.85 g/cm^3 (light POM) and heavier than 1.6–1.85 g/cm^3 but larger than 50–63 μm (heavy POM). Light and heavy POM may be combined to understand overall POM dynamics as contrasted to MAOM (Cotrufo et al., 2015). This approach may be particularly useful in studies with large sample sizes (Cotrufo et al., in press), because it allows separation of POM and MAOM based on size alone (Gregorich et al., 2006) and avoids the costly and more time-consuming density separation. However, we caution against this method if small, light POM contributes significantly to the recovered small fraction. POM and MAOM have also been separated by density alone (e.g., Mikutta et al., 2019), but this method should be avoided in sandy soils where sand-sized particles and heavy POM contribute significantly to the recovered heavy fraction and may affect interpretation of MAOM dynamics. A combination of density and size approaches isolates distinct light and heavy POM components from MAOM,

which most closely reflect the differences in formation, persistence, and functioning that we review here.

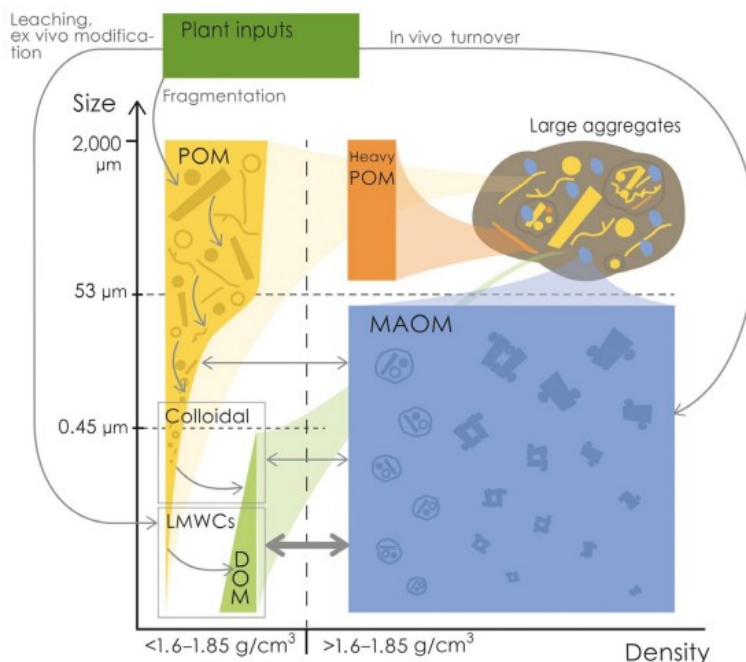


FIGURE 2 Conceptual representation of major soil organic matter (SOM) components discussed in this review. These SOM components are physically defined based on size and density, shown on the y and x axes, respectively. The upper size limit specification for MAOM varies by region, from 20 to 63 μm; we show 53 μm here for simplicity. Dissolved organic matter (DOM) is generally defined as <0.45 μm and water-extractable. Mineral-associated organic matter (MAOM) has multiple forms, including small particulate organic matter (POM)-like structures encapsulated by minerals, organo-mineral clusters, and primary organo-mineral complexes. Large aggregates can contain all other components to varying degrees. LMWCs are low molecular weight compounds. Arrows leading from plant inputs to different components represent hypothesized SOM formation pathways [Correction added on 22 November 2019 after first online publication: the DOM value has been changed from 45 μm to 0.45 μm in Figure 2 and text throughout the article.]

Defining POM and MAOM in this way does not allow explicit consideration of aggregates. This framework assumes that larger aggregates (>50–63 μm) have been dispersed prior to separation and therefore focuses on “stable” components that remain intact after such dispersion. Note that we do not refer to these as “primary” soil components—generally taken to mean individual POM or organo-mineral particles—because there are still aggregated complexes of organic and inorganic particles of various sizes after large aggregate disruption (Chenu & Plante, 2006; Sollins et al., 2009; Totsche et al., 2018). These fine stable aggregates (<50–63 μm) are included in MAOM. The implications of large aggregate disruption are further discussed later in this review (Aggregates section).

4 CONTRASTING RESPONSES OF POM AND MAOM TO GLOBAL CHANGE FACTORS

Contextualizing the responses of POM and MAOM to global change factors requires further elaboration on mechanisms of persistence. SOM persistence mechanisms can be broadly divided into two categories: spatial constraints (e.g., separation of decomposers and enzymes from substrates, and low

oxygen diffusivity inside aggregates; Keiluweit, Wanzek, Kleber, Nico, & Fendorf, 2017) and microbial inhibition. The latter refers to broad inhibition of microbial activity such as freezing temperatures and waterlogging resulting in anoxia. These microbial inhibition mechanisms are more relevant for decomposition of SOM that is not subject to spatial constraints. All SOM has the potential to be subject to spatial constraints; MAOM is protected by mineral association, and both POM and MAOM can be occluded within large aggregates (Table 2). Occlusion in large aggregates slows decomposition, but to a lesser degree than mineral association (Kögel-Knabner et al., 2008; Poeplau et al., 2018; Puget, Chenu, & Balesdent, 2000; Schrumpf et al., 2013). Given this, the persistence of POM is controlled mainly by microbial and enzymatic inhibition (plus some short-term occlusion in aggregates), while that of MAOM is controlled mainly by mineral association.

TABLE 2 Common definitions of aggregate size classes and the soil organic matter (SOM) components they contain, with examples of studies that use each definition. MAOM is mineral-associated organic matter and POM is particulate organic matter, as defined in Table 1

Name	Constituents	Upper size limit	Lower size limit	References that use this definition
Macroaggregates	Smaller macroaggregates, microaggregates, POM, MAOM ^a	2,000 μm	250 μm 212 μm 200 μm	Totsche et al. (2018) Jastrow (1996) Puget et al. (2000)
Microaggregates, or large microaggregates	Smaller microaggregates, POM, MAOM ^a	250 μm	50 or 53 μm 20 μm	Jastrow (1996), Lobe, Sandhage-Hofmann, Brodowski, Preez and Amelung (2011), Pulleman et al. (2005), Six et al. (2000, 2004) Tisdall and Oades (1982), Totsche et al. (2018)
Small microaggregates	MAOM ^a	50–53 μm 20 μm	20 μm –	Lobe et al. (2011) Totsche et al. (2018)
Silt-sized aggregates	MAOM ^a	50–53 μm 20 μm	2 μm 2 μm	Virto et al. (2008, 2010) Lobe et al. (2011)
Clay-sized aggregates	MAOM ^a	2 μm	–	Chenu and Plante (2006)

^aMAOM contains silt- and clay-sized aggregates, organo-mineral clusters, and primary organo-mineral complexes.

Because POM is less protected, environmental changes that may decrease microbial inhibition (e.g., thawing, draining) or disrupt aggregates (e.g., tillage) can immediately increase the POM decomposition rate. MAOM is less sensitive to decreases in microbial inhibition, because it must be destabilized before its decomposition rate can increase. However, some environmental changes could increase MAOM destabilization (e.g., changes in redox chemistry causing desorption; Huang & Hall, 2017), making it available and increasing the SOM decomposition rate regardless of whether or not inhibition has decreased (Bailey, Pries, & Lajtha, 2019; Conant et al., 2011). When studying the effects of global changes on SOM, the fundamental differences in the relevant mechanisms for POM versus MAOM persistence—

inhibition versus destabilization—as well as their different formation pathways and functional roles are necessary to form relevant hypotheses and contextualize results.

Studies of land use change, specifically cultivation of previously undisturbed soils, gave the first indications of the differences between POM and MAOM in the context of global change. Early studies showed POM to be more vulnerable to loss upon cultivation and gave researchers insight into the idea of mineral protection (Anderson & Paul, 1984; Cambardella & Elliott, 1992; Tiessen & Stewart, 1983). While POM and MAOM have been shown time and again to have highly contrasting behavior in response to cultivation (Cambardella & Elliott, 1994; Collins et al., 1999; Duval et al., 2013), this concept was deemphasized as attention grew around physical protection in aggregates, and the roles of different aggregate size classes as SOM diagnostic features (Plaza-Bonilla, Álvaro-Fuentes, & Cantero-Martínez, 2014; Six et al., 2000). The prominence of POM and MAOM as the two physical soil fractions with the largest differences in response to cultivation and mean residence times (MRTs) was recently reiterated in a comprehensive SOM fractionation methods comparison by Poeplau et al. (2018).

Further insights into differences between POM and MAOM in response to environmental change have come from litter manipulation studies, which alter plant litter inputs to understand potential impacts of plant productivity changes. In the case of increased inputs, we might expect to see increases in POM or MAOM due to increased formation, which is related to litter quality and MAOM saturation. According to the Microbial Efficiency-Matrix Stabilization hypothesis (Cotrufo, Wallenstein, Boot, Deneff, & Paul, 2013), lower quality litters should favor POM formation, while higher quality litters should result in greater MAOM formation. In a 50 year field experiment with litter addition and removal treatments, Lajtha et al. (2014) found significant increases in POM, with little change in MAOM, though the relationship to litter quality was not determined. In another study using similar methodology at different sites, Crow et al. (2009) found no detectable effect of litter manipulation on total SOM, but did detect increases in POM with doubled wood inputs, as expected from a low-quality litter. On the contrary, decreased inputs should decrease SOM formation and potentially persistence, with POM being more vulnerable to loss. In response to litter removals in the Lajtha et al. (2014) study, POM decreased, while MAOM responses varied by site. However, Lajtha et al. (2014) did not disperse large aggregates, so they may have seen clearer responses from what we term MAOM if they had included the heavy material from large aggregates in their heavy fraction.

Soil warming caused by climate change threatens to accelerate microbial SOM decomposition rates (Kirschbaum, 2000), and there is clear need to study warming responses of various SOM components, rather than SOM as a whole (Davidson, Trumbore, & Amundson, 2000; Knorr, Prentice, House, & Holland, 2005). Research for many years focused on comparing the

responses of labile versus recalcitrant substrates to warming (Davidson & Janssens, 2006), but these differences are only relevant for available SOM (i.e., POM; Wagai et al., 2013). For MAOM, the effects of warming on its decomposition are mediated by the effect on destabilization. Given this, the focus of research has begun shifting to include the role of substrate availability to decomposers (Conant et al., 2011). Still, few soil warming studies to date have explicitly separated POM and MAOM. Of those that have, a recent incubation of isolated POM and MAOM fractions showed that POM was more sensitive to warming than MAOM (Benbi, Boparai, & Brar, 2014), suggesting that MAOM destabilization was less impacted by warming than the POM decomposition rate. In contrast, a more complex field warming experiment showed no clear differences in responses of POM and MAOM, perhaps due to changes in SOM formation and redistribution between fractions, or limited statistical power (Schnecker, Borcken, Schindlbacher, & Wanek, 2016). The effects of warming on SOM components depend on the character and complexity of the study system, due to combinations of direct and indirect effects of warming on the plant-soil-microbial system (Field, Lobell, Peters, & Chiariello, 2007). The duration of warming experiments may also bias results, as short-term (i.e., <10 years) treatments may not produce detectable changes in slow-cycling MAOM (Conant et al., 2011). Targeted investigations of the direct effects of warming on persistence and formation of POM and MAOM are needed to elucidate specific mechanisms of change. These can be used in combination with studies of intact ecosystems to quantify the additive direct and indirect effects of warming on POM and MAOM and ultimately predict future SOM stocks with climate change.

Elevated CO₂ is another pressing global change challenge that causes complex, interacting belowground responses. Indirect effects of elevated CO₂ on the plant community such as changes in amount and quality of plant litter inputs (Norby, Cotrufo, Ineson, O'Neill, & Canadell, 2001) and root exudation determine SOM responses, and these processes affect POM and MAOM differently. As an example, increased root exudation, which has been observed under elevated CO₂ (Drake et al., 2011; Phillips, Finzi, & Bernhardt, 2010), may cause destabilization of MAOM (Keiluweit et al., 2015), or faster decomposition of low quality POM through so-called "priming effects" (Sulman, Phillips, Oishi, Shevliakova, & Pacala, 2014). However, few elevated CO₂ studies have separated POM and MAOM. In one such study using free-air CO₂ enrichment in a California grassland, Cardon et al. (2001) showed no significant effect on total SOC but contrasting effects on POM and MAOM fractions. MAOM turnover slowed under elevated CO₂, while POM turnover hastened (Cardon et al., 2001).

N availability affects nearly all ecosystem components, creating complex interactions that affect SOM through multiple mechanisms. These include changes in microbial SOM processing driven by C and N stoichiometry of inputs (Mooshammer, Wanek, Hämmerle, et al., 2014; Mooshammer, Wanek, Zechmeister-Boltenstern, et al., 2014), changes in microbial community

structure (Averill et al., 2018), and changes in pH that can coincide with N additions (Tian & Niu, 2015). All of these indirectly affect SOM storage, but act on MAOM and POM in different ways (Averill & Waring, 2017). N additions may shift the stoichiometry of inputs closer to meeting microbial N demand. This could shift SOM formation from POM to MAOM (Cotrufo et al., 2013) and increase POM decomposition by decreasing N limitation. In an incubation experiment, Kirkby et al. (2014) observed both positive and negative effects of added straw (a low-quality litter) on MAOM stocks, but consistent increases in MAOM stocks when nutrients including N were added. Bradford, Fierer, and Reynolds (2008) observed higher POM decomposition and greater MAOM formation in mesocosms with N and P additions than without. Longer term N additions, as is the case with chronic N deposition, may lead to shifts in microbial communities, for example, by favoring arbuscular-mycorrhizal (AM) trees over ectomycorrhizal (ECM) trees (Averill et al., 2018). This shift could change patterns of SOM formation, as suggested by Craig et al. (2018) who observed more subsoil C and N and more MAOM-N (but not POM-N) in AM- versus ECM-dominated forest stands. ECM dominance may promote POM formation and has been shown to positively correlate with O horizon (Craig et al., 2018) and topsoil (Averill et al., 2018) C stocks. One consequence of added N that may mediate effects on microbial decomposition and SOM formation is acidification (Tian & Niu, 2015), which can limit microbial growth. This might slow POM decomposition and MAOM formation, resulting in larger POM stocks and smaller MAOM stocks (Averill & Waring, 2017). The reverse would be expected without acidification, which agrees with the aforementioned results of Kirkby et al. (2014) and Bradford et al. (2008).

5 ADDRESSING GLOBAL CHANGE CHALLENGES USING THE POM VERSUS MAOM FRAMEWORK

There are two broad strategies to managing SOM stocks for global change mitigation: sequestration versus functioning (the latter often requires its turnover; Janzen, 2006). For example, research on mitigating rising atmospheric greenhouse gases focuses on sequestering long-lived SOM, whereas improving soil fertility requires SOM that can be accessed by soil biota (Chenu et al., 2019). In general, any efforts to address global change challenges via SOM will benefit from larger SOM stocks; it is the required character of that SOM (long-lived or quickly turning over) that differs. Since POM and MAOM form, persist, and function in different ways, conceptually separating them is key to crafting effective global change mitigation strategies involving SOM sequestration and functioning.

MAOM, being longer lived, is the focus of most research on SOM accrual and sequestration. Recent conceptual frameworks discuss increasing MAOM formation in the context of microbial efficiency (Cotrufo et al., 2013), metabolic pathway (Liang et al., 2017), saturation (Castellano, Mueller, Olk, Sawyer, & Six, 2015), and spatial dependence (Sokol, Sanderman, & Bradford, 2018). A recent study identifying broad-scale predictors of SOM stocks (Rasmussen et al., 2018) focused on MAOM without explicitly

measuring it, because it is the dominant contributor to total SOM in their dataset (they excluded histosols and organic horizons that might be POM-dominated). Studies in POM-dominated systems that do not explicitly separate POM and MAOM may come to different conclusions, because they are essentially analyzing factors that influence POM stocks. For example, in a study of the organic mor layer of an old-growth boreal forest, Kvaschenko, Clemmensen, Karlton, and Lindahl (2017) found that the abundance of saprotrophic basidiomycetes and activity of oxidative enzymes were negatively correlated with organic layer C and N stocks, but C and N stocks in the organic mor layer did not correlate with stocks in the mineral soil.

Targeting MAOM for SOM sequestration makes sense from a persistence perspective, but it may not always be feasible because MAOM can saturate (Gulde, Chung, Amelung, Chang, & Six, 2008; Hassink, Whitmore, & Kubat, 1997; Stewart, Paustian, Conant, Plante, & Six, 2007), while POM cannot. Also, MAOM sequestration requires more N than POM due to its lower C/N ratio (Cotrufo et al., in press). Certain management strategies, such as retaining low-quality crop residues on agricultural soils, may favor formation of POM over MAOM (Kirkby et al., 2014). There may be circumstances where POM could be sequestered long term and its vulnerability to global change factors minimized, such as at depth (Chenu et al., 2019; Hicks Pries et al., 2018) where its decomposition could be inhibited by lack of fresh C supply (Fontaine et al., 2007) or spatial separation from decomposers (Sokol et al., 2018). While researchers tend to focus on sequestration of long-lived soil C, it is important to note that short-lived soil C could be managed to effectively draw down C from the atmosphere despite its fast turnover, so long as there is a net increase in soil C and the size of the new C stock is maintained over time.

A major global change challenge that will require improved soil functioning and SOM turnover is increasing soil fertility while reducing nutrient pollution. Doing so requires understanding how POM and MAOM contribute to N cycling in soils, though to date few studies have explored the two fractions explicitly (Boone, 1994; Sollins et al., 1984; Whalen, Bottomley, & Myrold, 2000). Since POM is available for microbial decomposition and turns over quickly, POM-N may be the dominant source of N to microbiota even though it contains less N than MAOM (this is generally the case on both a concentration and total stock basis; Cotrufo et al., in press). Microbiota will use POM less efficiently (respiring more CO₂ due to its higher C/N ratio and greater chemical complexity; Mooshammer, Wanek, Zechmeister-Boltenstern, et al., 2014), and recycle the N more tightly with lower gaseous or leaching losses. MAOM contains more N and is a better match for microbial stoichiometric needs. There is evidence that some MAOM is exchangeable on short timescales (e.g., Hall, McNicol, Natake, & Silver, 2015), and that its turnover is an important source of N to microbiota (Jilling et al., 2018; Turner et al., 2017). Its low C/N ratio and lower chemical complexity will lead microbiota to process MAOM more efficiently, producing less CO₂. However, N in excess of

microbial requirements will be mineralized, and could cause gaseous or leaching N losses from the soil. Therefore, accrual and turnover of POM versus MAOM could have very different impacts on soil fertility, N leaching, and greenhouse gas production. Successful global change mitigation efforts will require careful evaluation of the implications of SOM management strategies, which SOM components they target, and the knock-on effects for soil functioning and ecosystem service provision. Management practices that might target both POM and MAOM, such as diversification, intensification, or perennialization of crop production, have the potential to address the soil “C dilemma” (Janzen, 2006) and meet both C sequestration and soil fertility goals.

6 CAVEATS OF THE POM VERSUS MAOM FRAMEWORK

6.1 Aggregates

Aggregates of various size classes have been heavily studied as important regulators of SOM turnover (Feller & Beare, 1997; Jastrow & Miller, 1997; King et al., 2019; Six, Bossuyt, Degryze, & Denef, 2004; Tisdall & Oades, 1982) and early indicators of environmental change, in particular land use and soil disturbance (Six & Paustian, 2014). Various aggregate size class definitions exist in the literature, but the most common definitions are shown in Table 2. We recommend large (>50 μm) aggregate dispersion for questions of SOM stock changes related to global changes for three reasons: (a) they are a mixture of POM and MAOM (Table 2); (b) they do not confer long-term (i.e., decades to centuries) protection from decomposition; and (c) excluding them from fractionation procedures saves a great deal of time, cost, and complication.

Aggregates of various sizes interact with one another in complex ways, conceptualized as the “aggregate hierarchy” in which aggregates form around smaller aggregates (Tisdall & Oades, 1982), and facilitate formation of smaller aggregates (Jastrow & Miller, 1997; Six et al., 2000) and MAOM (Fulton-Smith & Cotrufo, 2019; Grandy & Robertson, 2007; King et al., 2019) within themselves. As a result, larger aggregates (>50 μm) contain mixtures of POM, MAOM, and smaller aggregates (Figure 2), all of which are subject to different levels of protection from decomposition (Jastrow & Miller, 1997; Tisdall & Oades, 1982) and are difficult to interpret when lumped together.

Large aggregates themselves are relatively short-lived, so the level of protection that they provide is low compared to mineral associations. The turnover of POM within large aggregates is only slightly longer than that of free POM (Besnard, Chenu, Balesdent, Puget, & Arrouays, 1996; Poeplau et al., 2018; Puget et al., 2000; Tisdall & Oades, 1982), or in between that of POM and MAOM (Schrumpf et al., 2013). It is not until the level of fine microaggregates (<50 μm) that significant, long-lived protection from decomposition is observed (Virto, Moni, Swanston, & Chenu, 2010), which is why we include these fine microaggregates in our definition of MAOM. In fact, studies that have observed the <50 μm fraction directly suggest that the

majority of SOM in the <50 μm fraction is associated with clusters of soil particles (Asano et al., 2018; Chenu & Plante, 2006; Vogel et al., 2014), and that primary silt and clay particles account for relatively little MAOM.

One of the most convincing reasons to disperse large aggregates is a practical one; proper separation of aggregates and the fractions within is a laborious procedure that requires a high level of expertise and prior testing (Cerli et al., 2012). While aggregate separation can result in valuable information about SOM formation and may yield diagnostic indicator fractions for SOM responses to land use change (Del Galdo, Six, Peressotti, & Cotrufo, 2003; Grandy & Robertson, 2007; Six & Paustian, 2014), they are not feasible in the context of broad-scale soil analyses such as for C markets. Taken together, the complexity of large aggregates, their relatively small effects on SOM MRTs, and the labor required to separate fractions within them justifies their dispersion when the aim is a simple, clear method of characterizing SOM dynamics across many soils.

6.2 Composite fractions

POM and MAOM are both composite fractions, in that they are not completely uniform in terms of their chemistry, rate of turnover, and vulnerability to loss. For example, MAOM contains larger organic particles encrusted in minerals or in mineral-organic clusters (Chenu & Plante, 2006; Pulleman, Six, van Breemen, & Jongmans, 2005; Totsche et al., 2018; Vidal et al., 2019; Virto, Barré, & Chenu, 2008). Those organic particles may resemble POM chemically, but they are small and protected enough from decomposition to be considered MAOM (Virto et al., 2010). At the same time, POM can contain microbial compounds such as chitin (Baldock & Skjemstad, 2000) and xylanase (Marhan, Kandeler, & Scheu, 2007), or highly decomposed OM if it is of low density (Six et al., 2001). No matter the fractionation scheme, all soil fractions have some degree of non-uniformity due to the heterogeneity of SOM and the methodological limitations of SOM fractionation procedures (von Lützwow et al., 2007). POM versus MAOM is a relatively simple separation that yields two highly contrasting SOM components in terms of their formation, persistence, and function. We see it as the best compromise between feasibility and distinctness of the resulting fractions. However, one important consideration is PyOM, which has been thermally altered by fire. PyOM can be present in both POM and MAOM fractions (Brodowski, John, Flessa, & Amelung, 2006; Glaser, Balashov, Haumaier, Guggenberger, & Zech, 2000; Leifeld, Heiling, & Hajdas, 2015), but largely forms and persists by different mechanisms than other SOM; inherent recalcitrance is a more important mechanism for PyOM persistence (Knicker, 2011; Lavalley et al., 2019; Singh, Abiven, Torn, & Schmidt, 2012; Wang, Xiong, & Kuzyakov, 2015). Therefore, its presence in both POM and MAOM may confound results in systems where it makes up a large portion of total SOM. We would not recommend that all studies account for it because it is difficult to separate and quantify (Hammes et al., 2007); however, experimenters should be aware of its influence and consider quantifying it when possible and relevant.

6.3 Mechanistic detail

Depending on the level of inquiry, the POM versus MAOM framework may not be detailed enough to allow novel insights. For example, separating one pool of MAOM complicates or prevents studying fast-cycling MAOM (Hall et al., 2015), which is increasingly thought to play a key role in plant-soil-microbial interactions (Jilling et al., 2018; Keiluweit et al., 2015). We readily acknowledge that this is a coarse separation that leaves much uncharacterized, but this is the appropriate level of detail for our current need to identify general patterns at large spatial scales and address global change challenges. Finer detail is necessary for novel scientific inquiry, and those studies must continue. However, we encourage authors of such studies to additionally present the broad results for POM and MAOM fractions, whether by doing a second separation or combining data from smaller fractions that make up POM or MAOM, to enable cross-study comparison and broader generalization of results.

7 MOVING FORWARD WITH THE POM VERSUS MAOM FRAMEWORK

Despite widespread agreement among experimenters and modelers that understanding and predicting SOM stock responses to global changes requires separating it into multiple pools, much broad-scale SOM research still treats it as a single entity (Averill et al., 2018; Chenu et al., 2019; Crowther et al., 2016; Oldfield et al., 2019; Rasmussen et al., 2018; Wiesmeier et al., 2019). We posit that moving beyond bulk SOM to the POM versus MAOM framework will help to clarify complicated SOM responses and lead to novel insights regarding SOM formation, persistence, and function. Furthermore, we stress the importance of adopting consistent operational definitions of POM and MAOM to streamline interstudy comparison and avoid miscommunication. Additional studies that explicitly separate responses of MAOM and POM to global change factors are needed to better constrain them and generalize their responses across ecosystems, soil depths, and timescales. The POM and MAOM separation requires less labor than more complex separation schemes (Cambardella & Elliott, 1993), but it is still costly and slow compared to analyzing bulk soil. A high-throughput, low-cost fractionation method to separate POM and MAOM could encourage more widespread adoption of the separation, especially in studies with large numbers of samples. Adding measurements of POM and MAOM across systems and under different conditions from past and future studies to a readily accessible database, such as the International Soil Carbon Network (Harden et al., 2018), would facilitate model development and broad-scale analyses of controls on POM and MAOM behavior.

Many new hypotheses and frameworks for SOM sequestration focus on MAOM over POM, but MAOM accrual requires more N and is only possible in soils where MAOM is not saturated. Accrual of POM may be an underrated player in future C sequestration strategies, but POM will only accrue if its decomposition does not increase enough to counteract its formation.

Successful sequestration strategies will target POM and/or MAOM taking into account ecosystem properties such as microbial community structure, pH, N availability, and MAOM saturation level (Chenu et al., 2019; Cotrufo et al., in press). Lessening or avoiding SOM losses is equally important as accrual for efforts to sequester SOM. Mechanisms of SOM loss (e.g., priming and N mining), and conditions under which they favor losses of POM versus MAOM deserve further study. While microbiota are increasingly included in conceptual frameworks and biogeochemical models as key contributors to SOM formation and turnover, soil fauna have largely been ignored. Soil fauna contribute to both POM and MAOM formation (Filser et al., 2016; Soong et al., 2016; Vidal et al., 2019), and regulate SOM decomposition through soil food web interactions. Quantifying their contributions across systems is a topic for potentially high-impact research.

The POM versus MAOM framework can serve to improve ecosystem models with explicit SOM dynamics. The use of physically defined SOM pools in the place of theoretical, kinetically defined pools is quickly gaining traction in the modeling community. In fact, several newer models use POM and MAOM (Faticchi, Manzoni, Or, & Paschalis, 2019; Robertson et al., 2018; Sulman et al., 2014), while there is debate on whether or how to include other fractions (Filser et al., 2016; Sulman et al., 2018; Wieder et al., 2015). Including too many SOM pools can cause difficulty during parameterization and validation, and is not justifiable without sound evidence that doing so improves model performance (Sulman et al., 2018). Using fewer pools that are highly contrasting (i.e., POM and MAOM) is the most parsimonious method, and is also the easiest to parameterize, validate, and use at ecosystem to Earth system scales.

8 CONCLUSION

We are at a critical time when natural solutions to global change challenges are gaining traction in the non-scientific community, yet there is little consensus among scientists in terms of specific recommendations. Finding consensus requires a consistent way to measure and model SOM components and reliably predict how they will change with global change factors. This must be a parsimonious approach that is grounded in sound science but is also capable of being translated into understandable answers for land managers and policy makers. The POM versus MAOM framework achieves this. POM and MAOM are easy to conceptualize and understand, relatively quick and inexpensive to separate, and are already incorporated into newer generation SOM models. Scientific understanding and lines of inquiry continue to evolve beyond just POM and MAOM—as they should and must—but we have demonstrated that we currently have sufficient scientific evidence on which to base broad-scale measurement and predictions of POM and MAOM, with the ultimate goal of guiding policy and management for positive impacts.

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