Evidence for the existence and ecological relevance of fast-cycling mineral-associated organic matter

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Longstanding theories and models classify mineral-associated organic matter as the large (~ 60%) but slow-cycling and persistent portion of soil organic matter. Strong physico-chemical interactions and diffusion limitations restrict the turnover of mineral-associated organic matter, allowing carbon and nitrogen bound therein to persist in soil for as long as centuries to millennia. However, mineral-associated organic matter is a chemically and functionally diverse pool with a substantial portion cycling at relatively fast (i.e., minutes to years) timescales. Despite a growing body of evidence for the heterogenous and multi-pool nature of mineral-associated organic matter, we lack consensus on how to conceptualize and directly quantify fast-cycling mineral-associated organic matter and its ecological significance. We demonstrate that the dynamic qualities of fast-cycling mineral-associated organic matter vary based on 1) the chemistry of the mineral particles and organic matter, 2) the complex set of interactions between organic matter and the mineral matrix, and 3) the presence and strength of destabilizing forces that lead to decomposition or loss of mineral-associated organic matter (i.e., plant-microbe interactions, agricultural intensification, and climate change). Finally, we discuss potential implications and research opportunities for how we measure, manage, and model the dynamic subfraction of this otherwise persistent pool of soil organic matter.

Soil organic matter (SOM) plays a central role in terrestrial ecosystem functioning, providing nitrogen (N) and other nutrients to plants, and holding the largest pool of organic carbon (C) on land. A portion of the SOM pool cycles slowly – with turnover time ranging from decades to millennia. Our understanding of SOM persistence has evolved from an emphasis on chemical complexity and recalcitrance towards a growing appreciation for the interactions between relatively simple plant and microbial inputs and reactive mineral surfaces as key controls on SOM persistence[1]. As such, there is considerable focus on characterizing and measuring the mineral-associated organic matter (MAOM; see Box 1) pool, the fraction of SOM which holds the majority of organic C and N in the terrestrial biosphere (60–65% of C and 75% of N)[2,3]. Strong physico-chemical interactions and diffusion limitations restrict the turnover of some MAOM, allowing C within this pool to persist for centuries to millennia[4].

Particulate organic matter (POM) is considered a more bioavailable and faster cycling pool of soil C and N, relative to MAOM. POM is dominated by larger fragments of plant and microbial residues, which are at early stages of decomposition. The POM pool responds rapidly to changes in tillage or plant inputs and often correlates strongly with whole soil measures of decomposition[5], contributing to the view of POM as an SOM pool that is particularly sensitive to disturbances and physically accessible to decomposers. However, the decomposition of POM, in addition to litter decomposition, is also needed to build MAOM[6]. The leaching and depolymerization of POM and litter releases OM compounds into solution, which can then adsorb to a reactive mineral surface before or after cycling through microbial biomass[7–9]. While microaggregates provide further protection to MAOM[10], aggregate turnover and disturbance can promote MAOM formation as well[11]. MAOM formation is also more efficient within the rhizosphere relative to the bulk soil, which suggests MAOM forms under highly dynamic conditions[12]. MAOM formation is fast: transfer of ^{15}N or ^{13}C-labeled plant residues into MAOM fractions can occur within days to months[13–16].

The abundance of fine mineral particles and high mineral specific surface area are strong predictors of soil C storage[17,18]; emerging evidence

Box 1 | MAOM definitions and characteristics

Mineral-associated organic matter (MAOM) is the term used to describe both a conceptually-defined and methodologically-defined fraction of soil organic matter (SOM). Conceptually, MAOM is defined as a fraction of SOM where OM exists in some degree of association with soil minerals, such as via sorption, co-precipitation, encapsulation in fine, micro-aggregates[48], or via organo-organic interactions. MAOM is typically defined in contrast to sand-sized and/or lighter, less protected plant and fungal fragments known as particulate organic matter (POM). The methodological definition of MAOM is material collected from soil (generally, operationally defined as <2 mm) with aggregates dispersed by physical (i.e., glass beads), chemical (i.e., dispersing agents like sodium hexametaphosphate), or energetic (i.e., sonication) methods and then

collected as the fraction passing through a 50-63 μm sieve (i.e., the silt- and clay-sized particles) and/or with a density greater than 1.6–1.85 g cm^{-3} (i.e., the heavy fraction). Operational definitions of MAOM (e.g., as defined by a small particle size or heavier density) are not always fully aligned with conceptual definitions. A limitation of size-based separations is that they may combine partially decomposed plant and fungal components (POM) with a heavy POM fraction comprised of coarse plant and microbial residues associated with mineral particles. A limitation of density separations is that they may combine this heavy POM with OM associated with the fine fraction (MAOM). Recent work has found that separating POM, heavy POM, and MAOM through combined size and density-based methods can minimize these artifacts[194].

suggests that so too are existing MAOM stocks and the overall MAOM saturation deficit[19,20]. As such, MAOM is often examined for its capacity to store and sequester C and nutrients, with less attention to the heterogeneity underlying the MAOM fraction and its implications for potential destabilization following disturbance[21,22]. Although the majority of MAOM is likely persistent and long-lived, there is increasing evidence for a dynamic, fast-cycling MAOM pool.

Given the vast quantity of C and N stored in MAOM, the presence of even a small active MAOM pool can substantially influence ecosystem processes. For example, a hypothetical and very conservative annual MAOM turnover rate of 1% in a grassland with 3000 kg MAOM N ha^{-1} in the top 10 cm of soil[23] would supply 30 kg N ha^{-1} per year, which is approximately a third of the N uptake by grassland species[24]. The fast-cycling MAOM pool may function as a distinct SOM pool with essential roles in ecosystems, including retaining nutrients prone to loss and supplying nutrients to plants and microbes. At the same time, this fast-cycling MAOM pool may become a larger source of greenhouse gas emissions over time, especially under accelerated land use and climate change, as we discuss below.

The idea of a fast-cycling MAOM pool is not new (e.g., Kleber et al. and Torn et al.)[25,26], but the concept is rarely acknowledged in research and policies related to the management of MAOM (e.g., natural climate solutions-oriented work) or in Earth system models. In this review, we seek to clarify the existence and ecological importance of fast-cycling MAOM with a targeted summary of research on this crucial SOM pool. Others have synthesized relevant geochemical and plant-mediated mechanisms of MAOM cycling[27,28], and the land use and climate change implications of POM versus MAOM[29] but have not focused explicitly on the fast-cycling MAOM pool. Here, we synthesize recent studies that confirm the existence of a fast-cycling MAOM pool across various ecosystem types and provide insight into its size, stability, and mechanisms of turnover. We describe its key role in ecosystem functions such as nutrient provisioning, soil C cycling, and plant-microbe interactions, and suggest implications for how we measure, manage, and model this dynamic subfraction of MAOM.

MAOM is chemically heterogeneous

MAOM is a large and heterogenous pool of SOM, containing mineral particles and organic molecules that vary widely in age, size, and reactivity. Variations in MAOM binding mechanisms and chemical characteristics determine how this pool of OM cycles through terrestrial ecosystems, by influencing its availability to microbes, turnover rate, and potential to serve as a plant nutrient source. At the scale of mineral surface-OM associations, the behavior of MAOM and the chemical bonds therein will depend largely on characteristics of the interacting organic compounds, mineral particles, and soil solution[27,30–33] (Fig. 1). Minerals can have permanent and/or variable charges of varying strength, distribution, and density and such differences will impact the type and number of binding sites, adsorption-desorption

behavior, and hence, the bioavailability of associated molecules[34,35]. For example, minerals with a relatively high point-of-zero-charge that are positively charged under neutral and acidic conditions, such as goethite, may be able to bind SOM more strongly via ligand exchange reactions compared to negatively charged clay minerals that bind to OM via cation bridging[36]. Mineral types that bind compounds more weakly may harbor more vulnerable and accessible forms of MAOM.

Characteristics of organic substrates expected to influence the mechanism and strength of association include molecular size, hydrophobicity, acidity, and abundance of carboxylic, phenolic and aromatic constituents, which interact with mineral surface chemistry to influence the mechanism and reversibility of organo-mineral associations[37–39]. For example, stronger covalent bonds tend to form between organic substrates enriched in aromatic acid and phenolic groups and mineral fractions with a high abundance of reactive Fe and Al (oxy)hydroxide phases, especially under acidic soil solution conditions[38,40]. Stoichiometry (e.g., the C:N ratio) of organic matter will also influence its potential for adsorption or desorption[41]. Empirical work and direct imaging of organo-mineral interfaces at sub-micron scales indicate that N-rich organic compounds (e.g., N-containing groups in proteins) bind preferentially to mineral surfaces[42–47], and it is often suggested that MAOM-N is more stable than MAOM-C as a result.

The stability and turnover dynamics of MAOM are also shaped by its fine-scale spatial and compositional heterogeneity[45,48–52]. Several lines of evidence support the existence of spatially or chemically distinct portions of MAOM that are more vulnerable to mineralization. Kleber et al. proposed a model suggesting that OM binds to mineral surfaces in a zonal structure[25]. In this multi-layer model, the outermost zone is referred to as the kinetic zone and hosts organic molecules that are weakly bound via van der Waals forces, hydrogen bonding, and cation bridging interactions. Secondary interactions among organic molecules (i.e., organo-organic interactions[45]) are consequently an important mechanism within this kinetic zone, and provide a mechanism for loading of new organic substrates to pre-existing MAOM[33,52]. In the zonal model, the more weakly-associated kinetic material is hypothesized to exchange readily with the soil solution. Similarly, Kaiser and Guggenberger argued that the potential bioavailability of MAOM depends on the degree of OM loading on mineral surfaces[53,54]. As more organic molecules occupy binding sites, a proportion of MAOM may become more susceptible to degradation due to fewer functional groups being involved in sorption. Further, the enrichment of N-rich OM at the mineral surface is consistent with a zonal model driven by preferential retention of N-containing functional groups (e.g., through hydrogen bonding, cation bridges, or ligand exchange)[30]. However, in batch adsorption experiments using dissolved organic matter (DOM) and goethite, N-containing compounds were the last to adsorb, populating the kinetic zone, which is hypothesized to constitute the most dynamic, exchangeable fraction[55]. Variations in mineral-organic interactions, including those regulated by

Controls on MAOM chemical heterogeneity

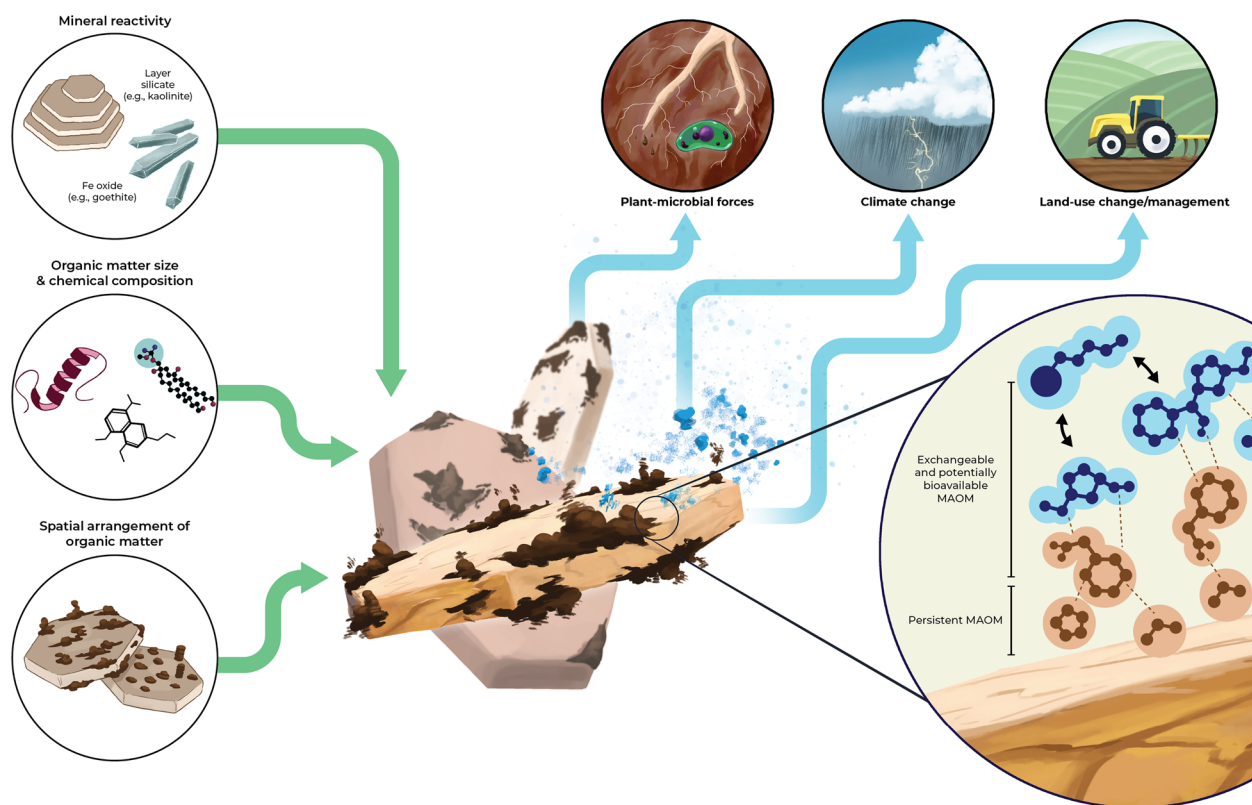**Ecological drivers of destabilization**

Fig. 1 | Conceptual figure illustrating the controls on MAOM chemical heterogeneity and three known drivers of MAOM destabilization. The distribution of MAOM into persistent or fast-cycling forms will depend largely on the properties of the minerals and associated organic matter. Key ecological drivers of MAOM destabilization include plant-microbial forces, climate change, land use change, and agricultural management. Original artwork by Elena Harley (www.elabarts.com).

variation in chemical bonds, organic matter composition and fine-scale spatial heterogeneity, warrants deeper engagement with the idea of MAOM containing a fast-cycling and bioavailable subfraction.

MAOM contains young and mineralizable compounds

MAOM is generally characterized as old and slow-cycling due to a consistent increase in SOC mean residence time (aka mean system age)[56] with decreasing particle size. Radiocarbon analyses demonstrate that silt- and clay-associated OM has a longer estimated turnover time than sand-associated OM[57]. However, a small but fast-cycling portion of MAOM (i.e., days to years) may be obscured in these estimates by much slower-cycling compounds (i.e., centuries to millennia) that substantially shift the mean estimate of residence time in these observational studies[58,59]. Radiocarbon tracer studies can more accurately track the rate of incorporation of new inputs to MAOM, though they are rarely employed. However, one site in an oak forest with accidental radiocarbon release found that up to 37% of MAOM is replaced on an annual basis and has a mean residence time of four years[60]. In the same soils, the steady-state mean residence time estimated from natural abundance radiocarbon measurements was 108 years, which suggests that natural abundance-based averages may not be a reliable measure of typical MAOM residence times in topsoil[60].

Recent work suggests that a primary driver of skewness in radiocarbon-based SOM and MAOM age data may be organic fossil C in sedimentary soil parent materials, including kerogen, lignite, and coal, which could contribute substantially to MAOM C pools. The presence of fossil C may skew radiocarbon ages in MAOM and other SOM fractions[61–63]. The use of ramped thermal analysis has proved an effective means of illustrating how the average radiocarbon value of a MAOM fraction may obscure the strongly contrasting ages of its constituent compounds, which may range from post-bomb (modern) to nearly radiocarbon dead (~ 60,000 years old or older)[64]. Thus, the reliance on radiocarbon dating alone to infer the mean age or persistence of MAOM may lead to spurious conclusions regarding MAOM durability in the context of climate change and its potential to store new C additions over long timescales.

Mineral surfaces provide MAOM with some protection from decomposition, but they are also host to active microbial communities. Mineral surfaces support high microbial biomass and accelerated rates of microbial turnover and enzyme production[65–67]. The abundance of low-molecular weight and low C:N compounds support a high mineralization potential within MAOM[68]. The intrinsic bioavailability of MAOM is illustrated by several incubation-based experiments. In a study of 156 diverse soils from across the United States, both MAOM and POM were strong predictors of whole soil C decomposition dynamics[69]. They suggest that the large pool size of MAOM may compensate for its lower decomposition rates in some soils creating similar overall contributions to CO_2 flux as POM. When SOM fractions are incubated under ideal temperature and moisture conditions, MAOM can even exhibit higher N and C mineralization potential compared to POM or light fractions[70–75]. This was recently observed for soils collected from forest, grassland, and cropland land uses[76].

Two main methodological approaches provide direct estimates of the potentially bioavailable and fast-cycling portion of the MAOM pool: (1) incubation experiments to trace the mineralization of clay or MAOM-bound organic compounds (Table 1) and (2) batch adsorption-desorption experiments (Table 2). In the former, DOM (either an isotopically labelled substrate or DOM extracted from soil or plant litter) is added to pristine minerals or to isolated MAOM fractions, and the decomposition of the newly formed MAOM is monitored over the course of a days or weeks-long incubation. Many of these studies demonstrate an intrinsic capacity for

Table 1 | Results of mineralization experiments that provide evidence for the fast-cycling MAOM pool

Reference	Method	Clay or soil type	Substrate mineralization/bioavailability
177	^{14}C-labeled organic monomers (e.g., citric acid) adsorbed to pure minerals, mixed with soil, and incubated for three weeks; ^{14}C traced into microbial biomass. ^{14}C-CO_2 evolution was monitored during the first three weeks and for an additional three weeks after priming with glucose.	Kaolinite, illite, and goethite in loamy vs sandy arable topsoils	Substrate mineralization up to > 80% (citric acid on kaolinite and illite) and incorporation into microbial biomass up to ~65% (acetylglucosamine on kaolinite) over three weeks of incubation; subsequent glucose-induced priming, especially of organic acids, was highest in goethite
178	Particulate (POM) and mineral-associated (MAOM) fractions incubated with unlabeled or ^{14}C-labelled glucose for 150 days to measure total C and ^{14}C respiration.	Soils from five orders (Mollisol, Ultisol, Oxisol, Andisol, Gelisol) over four climate zones (temperate, tropics, sub-arctic, and arctic)	62–70% of glucose added to MAOM and 3–11% of native C from MAOM were respired over 150 days.
179	^{14}C-labeled citrate or glucose were equilibrated with minerals then incubated for 24 h in oxygenated suspension with or without bacteria cultured from grassland soil to quantify ^{14}C recovery in respired CO_2, in the solid phase (bacteria and minerals), and in supernatant	Synthetic illite-mica; pure kaolinite; synthetic ferric hydroxide (ferrihydrite); and a mixed clay subsoil containing kaolinite, illite/smectite, and goethite	40-60% of glucose C in all mineral treatments and 65% of citrate C sorbed to illite-mica were microbially respired within 6 h, but only 25%, 12%, and 1% of citrate C were respectively respired from kaolinite, mixed subsoil clay, and ferric hydroxide treatments
180	A ^{14}C-labeled organic compound (herbicide 2,4-D [dichloro-phenoxyacetic acid]) was sorbed to a mineral complex and incubated with cultured *Pseudomonas* sp.; ^{14}C in respired CO_2, solid, and liquid fractions measured after 28 days	An Al(OH)x-montmorillonite (chlorite-like) complex	Over 28 days, the bacteria desorbed or mineralized 80% of the sorbed 2,4-D, compared to 45% released by abiotic desorption alone
181	Organic matter (OM) extracted from forest floor O-horizon was sorbed onto minerals in the presence of different electrolytes to model the relative contributions of Ca^{2+} bridging and ligand exchange to organo-mineral binding mechanisms in solution, and aerobically incubated with O-horizon microbial inocula for 90 d to measure substrate respiration as CO_2	Synthetic goethite (iron oxide); and purchased pyrophyllite and vermiculite	24-77% of OM was bioavailable after sorption to the minerals tested, and OM mineralization increased by 42-62%. Ca^{2+} bridging slightly increased OM bioavailability in goethite, but decreased OM bioavailability by 40-55% in pyrophylite and vermiculite; ligand exchange reduced OM bioavailability by 12%, 46%, and 66% respectively in vermiculite, pyrophylite, and goethite
182	Dissolved organic carbon (DOC) from plant residue loaded onto minerals was inoculated with soil extracts and incubated for 120 d to assess OC mineralization as CO_2	Kaolinite, illite, and smectite, with and without coatings of goethite, hematite, and ferrihydrite	13–24% of sorbed OC was mineralized over 120 days; mineral associations reduced OC bioavailability by 27–43%
183	An organo-clay complex of fenamiphos, an organophosphorus pesticide, was incubated in aqueous suspension in abiotic conditions or with added *Brevibacterium* sp., and pesticide desorption and hydrolysis was monitored by HPLC over 24 h	Cetyltrimethylammonium (CTMA)-exchanged montmorillonite clay	Bacteria hydrolyzed fenamiphos at a rate 77% greater than the abiotic desorption rate over 24 h, indicating high bioavailability despite strong interlayer sorption; 82% of the pesticide was hydrolyzed in inoculated samples versus 3% and 4.6% respectively degraded and desorbed in abiotic controls. Added enzymes penetrated the mineral interlayer and retained hydrolytic activity even when sorbed

Examples of studies that measured respiration of organic compounds adsorbed to a pure clay or MAOM fraction. The method used in each paper is described alongside the clay or soil typed studied, and the primary results of said experiment.

MAOM to supply C (Table 1). Over half of adsorbed organic compounds in such experiments were bioavailable and mineralizable, with the magnitude of decomposition often mediated by mineral type.

Batch adsorption-desorption studies highlight how rapidly compounds may desorb from mineral surfaces (Table 2). Such experiments quantify the equilibrium partitioning of a sorbate between solid and solution phases, in a liquid suspension over 24-48 hours[77] and using a wide range in soil:solution ratios (1:4 to 1:10,000). Results demonstrate the rapid and largely irreversible adsorption of organic compounds. However, approximately half of adsorbed OC can be removed with water within a few hours, which highlights the high potential bioavailability of MAOM. Reported rates of desorption and mineralization vary widely due to the variety of experimental conditions including mineral type, desorption agents, background electrolytes, and pH. Likewise, the short duration, highly disturbed, and often artificial context limit our ability to interpret and translate results to natural soil systems. Another major limitation of the experimental approaches highlighted in Tables 1, 2 is that the newly formed MAOM may not behave like MAOM formed under months or years of incubation, which

would better capture the suite of biotic and abiotic pathways of MAOM stabilization. Nonetheless, the selected laboratory experiments tracing the desorption and mineralization of OC from clays highlight the potential for microbes and plant roots to access and decompose MAOM. As discussed below, there are certain ecological contexts and processes that may allow for this mineralization potential to be realized at the ecosystem scale.

Ecological drivers of MAOM destabilization

While there has been much emphasis on the controls of SOM formation and persistence, a growing body of research has focused on the drivers of SOM destabilization[21]. Forces of destabilization have been categorized into those that disrupt soil physical structure (such as soil aggregates), those that disrupt mineral-organic associations, and those that enhance C metabolism[21]. Below, we focus on three proximal drivers of MAOM destabilization: plant-microbial interactions, climate change, and agricultural intensification. The transfer of OM from mineral-associated to more bioavailable pools will depend on the presence and strength of particular environmental conditions that favor MAOM destabilization.

Table 2 | Results of batch (ad)sorption-desorption experiments that highlight the wide-ranging rate of OM desorption from minerals

Reference	Mineral type	Organic compounds	Experimental conditions	Results
184	Commercial iron oxide powder	Natural organic matter (NOM), collected from wetland pond	Acid (HCl), base (NaOH), or inorganic salts (NaCl, Na$_2$SO$_4$, Na$_3$PO$_4$) added before adsorption	Hysteresis coefficient (h) between 0.72 and 0.86 for pH 4.1 and between 0.78 and 0.92 for pH 6.0, indicating that desorption was very limited
185	Iron oxide powder	NOM from wetland pond, separated into hydrophobic and hydrophilic fractions	Acid (HCl), base (NaOH), or inorganic salts (NaCl, Na$_2$SO$_4$, Na$_3$PO$_4$) added before adsorption	Hysteresis coefficient (h) between 0.81 and 0.91 for hydrophobic NOM, h between 0.821 and 0.984 for hydrophilic NOM, indicating desorption was very limited
186	Uncoated, FeO(OH)-coated, and Al$_2$O$_3$-coated sands	Terrestrial humic acid extracted from commercially available peat	Uncoated vs (hydr)oxide coated sands	At pH 4.1, hysteresis coefficient (h) between 0.70 and 0.96 for metal (hydr)oxide coated sands, indicating limited desorption. For uncoated sands, h was between 0.41 and 0.78, suggesting higher desorption potential
187	Soils (Vitric Phaeozem, Haplic Chernozem, Chromic Luvisol, Calcaric Phaeozem, and Chromic Cambisol) and phyllosilicate clay fractions (Ca-montmorillonite, kaolinite, and illite)	Dissolved organic carbon (DOC) extracted from pine forest floor	Near-neutral pH; phosphate treatment used to block reactive hydroxyl groups	In samples without phosphate treatment, between 13% and 50% of DOC was desorbed, with greater desorption in the phyllosilicate clay compared to the soil clay fractions
188	AmorphousAl(OH)$_3$, goethite, and low organic C subsoil	NOM, extracted from Oa horizon of an Entic Haplorthod	Desorption using solutions with a range of pH and inorganic anions (Cl$^-$, SO$_4^{2-}$, and H$_2$PO$_4^-$)	Under normal conditions, desorption of NOM was <3%, desorption reached 60% in the presence of high concentrations of H$_2$PO$_4^-$
177	Kaolinite, illite, and goethite	14C-labelled monomers (glucose, acetylglucosamine, phenylalanine, salicylic acid, and citric acid)	Also measured microbial carbon use efficiency (CUE)	40–99% of monomers across all treatments were retained after desorption with NaN$_3$, the range was reduced to 3–55% after subsequent desorption using PO$_4^{3-}$
189	Vertisol soil from crop field (bulk soil and its clay size fraction)	Carbamazepine (CBZ)	No CBZ, CBZ co-introduced, or CBZ introduced after DOM pre-adsorption	The hysteresis coefficient (HI) for CBZ-clay was 0.91 versus 0.64 in CBZ-bulk soil, HI decreased following pre-adsorption of DOM
39	Organic matter-poor, alkaline soils (Fluvent, Rhodoxeralf, and Loess)	DOM extracted from mature composted biosolids	Four sequential desorption steps	Up to 83% of sorbed DOM was retained after desorption
190	Pure clays (kaolinite, illite, smectite) with and without Fe oxide (haematite, goethite, ferrihydrite) coatings	DOC extracted from medic shoot	Effect of goethite coating on different clay types, effects of different Fe oxide coatings on illite	Across all treatments, 5.7–14.4% of sorbed DOC was desorbed
191	Soil clay fractions (kaolinite-illite, smectite, and allophane)	DOC extracted from wheat straw	Adsorption measured under varying electrolyte conditions: 0.1 M and 0.01 M Ca(NO$_3$)$_2$ and NaNO$_3$	6.4% to 55.3% of adsorbed DOC was desorbed
192	Soil clay fractions (kaolinite-illite, smectite, allophane)	DOC extracted from wheat straw	Untreated clay, C removed, and sesquioxide removed	30% to 71% of adsorbed DOC was desorbed across clay type; highest desorption in kaolinite-illite
193	Pure minerals (kaolinite, illite, montmorillonite, ferrihydrite, and goethite)	14C-labelled carboxylic acids and amino acids		For carboxylic acids: Fe oxides retained 83–100%, while phyllosilicates retained 31–85%. For amino acids: glutamic acid retention was 53–98% on Fe oxides versus 0–48% on phyllosilicates; lysine retention was 41–99% on phyllosilicates and 13–50% on Fe oxides

The mineral type employed in each study is presented alongside the organic compounds that were sorbed/desorbed to said minerals, the experimental conditions, and the primary results of each study. For studies that report a hysteresis coefficient: this metric refers to the ratio of the slope of the sorption curve to the slope of the desorption curve. It is a measure of adsorption-desorption reversibility where an h of 0 indicates completely reversible and an h of 1 indicates completely irreversible.

Plant-microbial forces

Rhizosphere environments provide conditions that can facilitate the destabilization and turnover of MAOM. MAOM in the rhizosphere is more likely to be released from mineral surfaces than MAOM in bulk soil due to a higher concentration of plant and microbial exudates in the soil near active roots[78,79]. These exudates may stimulate specific extracellular enzymes or more generally stimulate decomposition (i.e. glucose, organic acids). Additionally, plant and microbial exudates can form associations with soil minerals directly, contributing to the MAOM pool[80]. In fact, root-derived organic matter, particularly root exudates, is suggested to be a dominant source of mineral-associated C and N[12,81–84]. As a result, rhizosphere MAOM acts as both a source and sink for organic compounds and is likely more dynamic compared to MAOM in the bulk soil.

MAOM may be particularly vulnerable to destabilization by plant exudates in ecosystems with rapidly growing vegetation and high demand for soil nutrients. These conditions are common in early successional forests, agricultural systems, and ecosystems recovering from disturbance or responding to global change[85–87]. Some evidence for these patterns comes from analyses of MAOM radiocarbon content where in the eastern U.S., MAOM turns over more quickly in ecosystems with higher root mass[88]. This suggests that ecosystems with high plant nutrient demand may have a higher proportion of fast-cycling MAOM compared to other ecosystems, particularly in the rhizosphere.

The rhizosphere is also characterized by the presence and enrichment of mineral-weathering soil bacteria. Rhizosphere activity can accelerate the formation of metal oxides[89] or facilitate rock weathering and clay transformation processes[90–92]. Phosphate-dissolving bacteria have been reported in the rhizosphere of agricultural soils[93] and around the roots of mangrove trees[94]. Similarly, the dissolution of clay particles was highest in rhizosphere of Norway spruce and oak compared to bulk soil[95]. Although mineral weathering is generally seen as a slow pedogenic process, it can occur over short time scales, especially in the microbially-active zone around roots. Processes occurring at the root-soil interface can significantly accelerate pedogenesis such that mineral dissolution or alteration can occur within 20 years[95,96] or even within a growing season[97]. It is unclear how these localized, accelerated alterations to clay particles in the rhizosphere alter the formation and cycling of MAOM specifically.

Mycorrhizal fungi, which receive energy-rich C compounds from plant hosts, are equipped to destabilize and mobilize MAOM. The capacity for ectomycorrhizal fungi (ECM) to liberate MAOM was recently reviewed by Tunlid et al.[98]. Many ECM fungi secrete low molecular weight compounds like oxalic acid that can disrupt mineral-organic associations[99], dissolve minerals[100], release nutrients[98] and facilitate the direct assimilation of N from MAOM[101]. Some ECM species also mediate the reductive dissolution of iron-bearing minerals and the subsequent generation of reactive oxygen species[102]. MAOM was shown to be more sensitive to hydroxyl radicals than POM, which was attributed to the enrichment in MAOM of low molecular weight compounds with lower activation energies[103]. Thus, ECM-facilitated dissolution of minerals may accelerate the decomposition of MAOM. Arbuscular mycorrhizal fungi (AMF) also generate many of the same compounds with known weathering capacities[104,105] but may have more limited capacity to directly mobilize nutrients from MAOM compared to ECM[106]. AMF depend on other soil biota to mobilize and mine nutrients directly from SOM[107,108]. AMF-generated organic acids were shown to mobilize phosphorus bound to iron oxides[109], but this area of research remains highly understudied. Overall, evidence suggests that the activities of roots, mycorrhizal fungi and free-living microbes contribute substantially to MAOM mobilization, likely making the rhizosphere a hotspot for dynamic and fast-cycling MAOM.

Climate-related forces

Climate is a major driver of plant growth, microbial activity, and abiotic properties of soils. Therefore, it is also likely to alter the formation and destabilization of MAOM, with direct implications for the fast-cycling MAOM pool. Shifts in climate may disrupt and alter MAOM formation and destabilization processes, potentially limiting MAOM accrual and/or accelerating the loss of MAOM. Multiple studies report how changes in precipitation, temperature, and atmospheric CO_2 may destabilize MAOM across varied ecosystems.

Given projected shifts in climate toward intensification of hydrologic cycles, it is important to understand how shifting moisture regimes may alter fast-cycling MAOM. In arid systems where moisture limitation is a physiological control on microbial mineralization, changing precipitation patterns (and increased DOC fluxes to subsoil) may facilitate MAOM losses[88]. Moisture availability indices (e.g., MAP/PET) and correlated moisture-driven mineralogy gradients (e.g., reactive metal vs. base cation-dominated mineralogy) have therefore been applied as organizing concepts to predict differences in MAOM formation mechanisms[110–113] and susceptibility to destabilization under changing moisture availability across broad-scale climatic regions[112].

In addition to the role of moisture regime at the ecosystem scale, MAOM destabilization processes are influenced by moisture-driven changes in soil redox status at the pore scale. Most notably, the reduction of iron-bearing minerals under saturated conditions can release mineral-bound C into soluble forms, leading to potential net losses of C following a return to oxic conditions[114–118]. However, saturation may also cause more dynamic sorption-desorption events in soils less dominated by iron-bearing minerals[119]. In environments experiencing frequent wet-dry cycles, shifting aerobic to anaerobic conditions has been shown to increase the bioavailability of MAOM, possibly due to a loss of Fe-MAOM associations[45]. Wet-dry cycling was also shown to enhance the decomposition of MAOM and its vulnerability to simulated exudates[120]. This suggests that increases in moisture variability due to climate intensification may increase the proportion of the MAOM pool that cycles quickly.

Temperature is an important control on SOM decomposition rates[121], but the sensitivity of faster-cycling MAOM components to changing temperature is less well described. In general, MAOM is expected to be less temperature-sensitive overall compared to POM[122,123]. However, there have been few direct studies of the responses of different components of MAOM to changes in temperature. Available evidence suggests larger and lighter components of MAOM are more responsive to warming[124,125]. One possibility, which warrants further investigation, is that larger and lighter portions of MAOM are held more loosely to mineral surfaces, making them more susceptible to mineralization with increased microbial activity. In addition, OM protected by reactive metal associations were found to be more vulnerable to warming temperatures than OM protected by base cations, potentially due to the temperature sensitivity of biological processes involved in overcoming stable organo-metal interaction mechanisms[112].

As the CO_2 fertilization effect promotes higher rates of photosynthesis, plants require more nutrients from soil, particularly N[126]. As a result, rising atmospheric CO_2 concentrations may indirectly promote MAOM desorption and turnover as a consequence of increasing plant nutrient demand. In ecosystems without a large standing stock of bioavailable N, plants may rely on MAOM as a source of limiting nutrients to fuel higher rates of productivity. This may occur through greater root exudation[87], which could cause desorption of N-rich MAOM that would subsequently be available for mineralization. However, rhizosphere-induced priming may act on the POM pool rather than the MAOM pool[127,128]. Indeed, in support of a minimal MAOM response to CO_2 enrichment, a meta-analysis of global change manipulations found no significant effect of elevated CO_2 (eCO_2) on MAOM-C concentrations[123]. However, in studies conducted for more than five years, MAOM-C concentrations tended to decrease with eCO_2[123]. This pattern suggests that the effects of eCO_2 may not be immediately apparent, but could become more evident over time as the diminishing soil nutrient pool prompts plants and microbes to begin mining resources from MAOM. Moreover, the biotic demand by plants and their associated fungi may also mediate how elevated CO_2 affects MAOM pools. In a synthesis of 19 CO_2 enrichment experiments, MAOM pools decreased in plots where the dominant plants associated with ECM fungi but increased in plots where the dominant plants associated with AM fungi[129]. This suggests that MAOM

vulnerability may depend, in part, on the nutrient requirements and nutrient acquisition capabilities of the plants and their associated microbes.

Land use change and agricultural management

In general, land management that alters the input and microbial processing of OM will influence MAOM cycling[130]. Agricultural management systems may shift disturbance regimes, external inputs, and plant diversity, as well as the abiotic environment (e.g. temperature and moisture), with both biotic and abiotic drivers influencing MAOM[120,131,132]. For example, the physical disruption of tillage and changes in irrigation can disproportionately impact the MAOM protected within macro-aggregates[133]. MAOM turnover also depends on the C:N ratio and chemical composition of organic inputs. For example, a clover-rye mixed cover crop facilitated transfer of POM-C to MAOM-C more than a rye or clover crop alone[134]. Manure additions have been linked to faster MAOM turnover times than synthetic inputs[135], perhaps because inorganic fertilizer applications may suppress the biological mechanisms that mobilize MAOM[136].

MAOM response to management depends on both MAOM formation and loss; management that increases soil microbial activity can also enhance MAOM mineralization. The balance between stabilization and destabilization processes is heavily context-dependent and may result in either increases or decreases in MAOM[21]. For example, in a study on intensively managed Mollisols, incorporating legume cover crops and adding manure did not result in increased MAOM, as was hypothesized[137]. The researchers attributed this finding to nutrient mining of MAOM by the maize crop, which offset potential gains in MAOM due to enhanced microbial efficiency and biomass production. Similarly, long-term organic fertilization increased MAOM-C turnover, but not accrual[135]. Organic cropping with manure on an Alfisol also did not increase MAOM[138], but adding a legume cover crop did increase MAOM in an arid wheat cropping systems on silt loam soils[139]. These studies highlight how measuring net changes overlooks active-cycling MAOM, which may be a large flux in systems that experience high rates of both MAOM loss and accrual. This fast-cycling MAOM may prove to be important in predicting N available to crops, as N mineralization remains an important, and poorly predicted, element of crop yield[136,140–142].

In some cases, management may not alter the quantity of POM or MAOM but rather cause shifts in the chemical composition of one or both fractions. For example, MAOM chemical composition shifted in response to contrasting cover crop functional types[143] and in organic cropping systems with cover crops and manure[138], even though MAOM-C concentration was not affected. Similarly, in a system shifting from tropical savanna to pasture, losses of savanna-derived MAOM-C were offset by gains from pasture-derived C[144]. These shifts in MAOM chemical composition or quantity may correspond with faster-cycling MAOM, but it is uncertain how to measure or manage plant access to this nutrient supply.

Implications of the multi-pool and dynamic nature of MAOM

The implications of a fast-cycling MAOM pool for both agricultural management and representation within Earth system models have largely gone unexplored. Below, we discuss the relevance of fast-cycling MAOM for these applications and highlight key research opportunities to improve our understanding and measurement of this MAOM pool's importance.

Managing fast-cycling MAOM in managed landscapes

While some management practices may destabilize MAOM, there are other practices that may be harnessed to promote fast-cycling MAOM for multiple benefits such as soil nutrient availability and accrual of soil C[145]. This perspective aligns with recent calls for more holistic stewardship of SOM that supports all forms —not only the stable forms—and accounts for the continuous flow of nutrients into and out of SOM[146]. In this context, Daly et al. outlined several key hypotheses about the potential role of the fast-cycling MAOM pool that require further testing[136]. First, fast-cycling MAOM can provide key nutrients for crops, particularly in low input systems that promote plant investment in root production and mycorrhizal

symbioses[136]. Furthermore, fast-cycling MAOM may play a key role in the accumulation of more persistent SOC. Movement of compounds into and out of the fast-cycling MAOM fraction could help equilibrate the concurrent, though seemingly opposed, processes of SOM accrual and SOM mobilization in soils. Fast-cycling MAOM fraction could briefly stabilize soluble C and N compounds during periods when their concentrations are high, thereby acting as a temporary buffer against losses of C and N via leaching, microbial respiration, and transformations like denitrification. For example, in agroecosystems, the rapid, early season movement of inorganic N fertilizers into microbial biomass and MAOM may enhance its availability later, during periods of peak crop growth. When soluble SOM pools are low, desorption and decomposition of fast-cycling MAOM could supply plants and microbes with energy and nutrients and thus may regulate short-term nutrient availability. Over time, some fast-cycling MAOM may form stronger bonds with mineral surfaces or be incorporated into larger SOM complexes like aggregates, thereby transforming it to slower-cycling MAOM. This pipeline of loss-prone dissolved compounds moving through fast-cycling MAOM into persistent SOM may be key to increasing retention of C, N, and other nutrients in the soil system.

Ultimately, the ecosystem and management implications of fast-cycling MAOM depend on the fate(s) of MAOM following desorption. Fast-cycling MAOM may be functionally similar to POM, but the lower C:N ratio of MAOM suggests that it should be utilized relatively efficiently by microbes, resulting in less CO_2 losses and greater C and N incorporation into microbial biomass and metabolites compared to POM. This cycle of SOM temporarily sorbing to mineral surfaces, undergoing microbial consumption and transformation, and re-release into soil solution as DOM, has been suggested to result in the cascade theory of SOM downward translocation[147]. This theory is supported by the observation of relatively older, more microbially-processed SOM in deeper soil horizons, as well as by empirical observations of DOM chemical composition changes during downward transport through grassland soil profiles using ultrahigh-resolution mass spectrometry[148]. Specific surface soil management strategies promoting SOC transport to, and accumulation within, deeper soils remain a critical knowledge gap[149], and fast cycling MAOM may be key to this process. Research focusing specifically on MAOM dynamics across soil depths could help clarify our understanding of the fate and importance of fast-cycling MAOM in long-term C storage.

Integrating fast-cycling MAOM into models of soil C and N dynamics

Earth system models typically conceptualize soil C as multiple pools that decompose via first-order decay kinetics and differ in their turnover times[150]. In the last decade, models that explicitly include nonlinear microbial-mineral interactions are becoming more prevalent but vary widely in their process representations and parameterizations[151–154]. Mechanisms of stabilization vary from DOC sorption only[155,156] to accumulation of microbial necromass[154,157] or chemically recalcitrant compounds[128] to a combination of the two[158–161]. As a result of these different model formulations, the predicted temporal dynamics of SOM, and the underlying pools conceptualized as MAOM can vary widely in response to disturbance[151,162].

The vast majority of SOM models, including all models used at global scales, assume that modeled pools are homogenous and that any particle within a pool has an equal probability of entering or leaving as its neighbor[150]. Within this framework, turnover time and age is estimated as a single value for each pool, such that representing MAOM of varying ages would require increasing the number of pools and defining specific stabilization mechanisms or a combination of mechanisms for each pool. However, when MAOM is explicitly represented in SOM models, it is most often defined as a single pool[155,156,158,160]. Moreover, while clay content or soil texture may partly represent organo-mineral interactions[159], this oversimplifies the spectrum of reactivity across clay types as well as secondary rock-derived minerals such as iron and aluminum oxides[163]. Multiple SOM models were found to overestimate MAOM turnover[154]. Further dividing the MAOM pool may better represent components with different turnover times[154].

Select models do include a second MAOM pool that is considered faster cycling – for example, the exchangeable MAOM pool in the MEMS v2 model[164], the Q pool in the MEND model[161], and the Q_DOM pool in the COMISSION model[159], which all represent DOC sorbed to minerals that can readily exchange with DOC in solution. Moreover, fast-cycling MAOM is expected to interact with minerals in ways that differ from more persistent MAOM, which suggests potential benefits of separately representing these pools. However, parameterizing sorption/desorption rates and specific mineral relationships for these distinct MAOM pools, and benchmarking their relative sizes, remains a challenge due to data limitations especially at larger scales. Alternatively, other modeling frameworks exist that focus on a continuum of individual particles traveling through model pools, with the ability to estimate the distribution of ages and transit times within a single pool[56,165,166]. Models can also represent the fast-cycling MAOM pool by allowing for MAOM desorption at relatively high rates. For instance, a study using the SOMic model, which represents microbial dynamics and allows for rapid MAOM desorption, found that this modeling framework generated predictions of global SOC distribution and long-term SOC dynamics that were closely aligned with empirical data[167]. Enhanced representation of mineral composition may improve predictions of fast-cycling MAOM. Although data on soil minerology exists at global scales, understanding of how specific mineral interactions affect MAOM cycling rates is still emerging[168,169]. Regardless of the modeling framework, the existence of fast-cycling MAOM suggests that modeling MAOM as a single homogenous, passively cycling SOM pool is likely insufficient for accurately capturing temporal dynamics.

Measurement of fast-cycling MAOM

Although SOM fractionation methods drive our operational and conceptual understanding of POM and MAOM pools, we lack a standard method for directly quantifying the fast-cycling MAOM pool. MAOM can be further separated along physical (density, particle size) and chemical (solubility in acid or base, oxidation, thermal lability) gradients, which may, in theory, be able to isolate a more bioavailable subfraction. However, these methods also often require further dispersion and disruption that may facilitate the inter-fraction transfer of C and N. Common procedures for isolating SOM fractions may remove or obscure the fast-cycling portion of MAOM. Fractionation procedures require a degree of mixing and dispersion in liquid that will release and redistribute DOM between POM and MAOM. The quantity of DOM leached during fractionation can be significant[170] and it is currently not possible to distinguish between POM or MAOM in leached compounds. MAOM that desorbs and enters dissolved pools during fractionation may be an important component of fast-cycling MAOM. More studies are needed to identify the extent of leaching under contrasting fractionation and dispersion conditions as it is possible that certain methods favor the transfer of POM C or N into the MAOM pool, potentially inflating the stabilization capacity of this fraction.

Sequential chemical extractions can isolate phases of MAOM that differ in solubility and potentially bioavailability. Selective dissolutions with Na-pyrophosphate, hydroxylamine, and dithionite-HCl can be used to target organo-metal complexes, short-range order Al and Fe hydroxides, and crystalline Fe hydroxides, respectively[171]. These well-stabilized forms of MAOM are still vulnerable to loss, such as the iron-associated C that is destabilized and released by low molecular weight organic acids or under saturated conditions[116,172]. Physical and chemical fractionation methods can also be combined with thermal and/or chemometric approaches to estimate the chemical and biological stability of particle size fractions of SOM[173]. Otherwise, a combined chemical and biological assay is a potentially promising method for simulating destabilizing agents and the conditions that accelerate MAOM cycling. For example, by incubating isolated MAOM fractions with organic acids and glucose to simulate root exudates, one can estimate the destabilization potential of MAOM[172,174]. However, this has not been examined comprehensively across soil types and experimental conditions to generate a standard method.

Radiocarbon and ^{13}C-based experiments can provide estimates of pool turnover times. However, these methods provide an average turnover time, which may obscure the smaller, faster cycling subfraction, unless paired with ramped thermal analysis techniques that can quantify an underlying distribution of turnover times. MAOM generally has a wide distribution of radiocarbon mean ages, with considerable overlap with the distribution for POM[9,113]. Measurements of CO_2 respiration in long-term incubations can be used to calculate the size and turnover rate of active and slow pools of C[175] although calculated residence times may vary based on experiment duration[176] and these incubations are unable to determine the origin of the CO_2. Isotope tracer-based experiments in which POM and MAOM fractions are incubated separately or differentially labelled would allow for the tracing of fast-cycling MAOM and provide critical, mechanistic insights into the potential size of and controls on this pool. If using stable isotope labelling to target MAOM subfractions, researchers should ensure that newly-formed MAOM reflects both abiotic and biotic pathways of stabilization (i.e., not relying exclusively on short-term, adsorption-based approaches to labelling MAOM, which favor abiotic pathways). In general, future work should identify a consistent method and guidance for how to pair fractionation methods with isotope tracer and/or spectroscopic/imaging methods to isolate the various MAOM subfractions.

Conclusion

For decades, the soil science community has acknowledged the existence of fast-cycling MAOM. Although the majority of MAOM is highly persistent and cycles on decadal and millennial time-scales, a portion is bioavailable, exchangeable, and an active contributor to C and N fluxes. As we have summarized, the size of this pool will likely depend on the intrinsic properties of the MAOM – namely, the availability and physicochemical properties of minerals as well as the composition, quantity, and structure of the associated OM. In addition, fast-cycling MAOM will likely respond readily to drivers of destabilization, such as plant-microbe interactions, climate change, agricultural intensification, and land use change. Therefore, clarifying its size and responses in varying ecological scenarios is important to improve model predictions and make better recommendations for land managers. While counterintuitive to the goals of soil C sequestration, within certain contexts, especially agroecosystems that could benefit from MAOM's potential to supply N, it may be beneficial to promote the existence of a fast-cycling MAOM pool[146]. Accurate quantification of this pool and its role in ecological processes will enhance our understanding of these contexts and could inform agricultural management approaches. Likewise, our previous understanding of MAOM as a persistent, slowly-cycling pool is clearly oversimplified, and including more realistic representations of fast-cycling MAOM in Earth system models is needed to accurately quantify both the current and future size of this SOM pool. These applications are currently hindered by methodological limitations that have made it challenging to characterize this dynamic pool of MAOM. Continued development of methods to isolate and trace fast-cycling MAOM will enable better quantification of this pool and subsequent integration of these insights into modeling and soil management practices.

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