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REVIEW

Clarifying the evidence for microbial- and plant-derived soil organic matter, and the path toward a more quantitative understanding

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Abstract

Predicting and mitigating changes in soil carbon (C) stocks under global change requires a coherent understanding of the factors regulating soil organic matter (SOM) formation and persistence, including knowledge of the direct sources of SOM (plants vs. microbes). In recent years, conceptual models of SOM formation have emphasized the primacy of microbial-derived organic matter inputs, proposing that microbial physiological traits (e.g., growth efficiency) are dominant controls on SOM quantity. However, recent quantitative studies have challenged this view, suggesting that plants make larger direct contributions to SOM than is currently recognized by this paradigm. In this review, we attempt to reconcile these perspectives by highlighting that variation across estimates of plant- versus microbial-derived SOM may arise in part from methodological limitations. We show that all major methods used to estimate plant versus microbial contributions to SOM have substantial shortcomings, highlighting the uncertainty in our current quantitative estimates. We demonstrate that there is significant overlap in the chemical signatures of compounds produced by microbes, plant roots, and through the extracellular decomposition of plant litter, which introduces uncertainty into the use of common biomarkers for parsing plant- and microbial-derived SOM, especially in the mineral-associated organic matter (MAOM) fraction. Although the studies that we review have contributed to a deeper understanding of microbial contributions to SOM, limitations with current methods constrain quantitative estimates. In light of recent advances, we suggest that now is a critical time to re-evaluate long-standing methods, clearly define their limitations, and develop a strategic plan for improving the quantification of plant- and microbial-derived SOM. From our synthesis, we outline key questions and challenges for future research on the mechanisms of SOM formation and stabilization from plant and microbial pathways.

KEYWORDS
amino sugars, biomarkers, microbial-derived organic matter, mineral-associated organic matter, molecular fingerprinting, plant-derived organic matter, soil carbon

1 | INTRODUCTION

Soil organic matter (SOM) is the largest actively cycling reservoir of carbon (C) on Earth, serving as an important terrestrial C sink, as well as a source of carbon dioxide (CO_2) to the atmosphere (Batjes, 1996; Jobaggy & Jackson, 2000). Climatic changes (e.g., warming) and human alteration of landscapes (e.g., land-use change for agriculture) can stimulate the loss of C from soils, accelerating already rising levels of atmospheric CO_2 (Crowther et al., 2016; Melillo et al., 2017; Sanderman et al., 2017). The management of soils for SOM accumulation is therefore seen as a necessary effort in mitigating climate change and in maintaining soil fertility (Minasny et al., 2017; Paustian et al., 2016). For instance, regenerative land management practices have been promoted as one key strategy for sequestering atmospheric CO_2 and building SOM (e.g., Jordon et al., 2022). However, the identification of specific approaches that are likely to result in SOM accumulation at scales relevant to climate change mitigation is hindered by fundamental uncertainties around the primary mechanisms of SOM formation and its proximate sources (Cotrufo & Lavallee, 2022).

Over the last two decades, the conceptual model of SOM formation and persistence has shifted from a focus on the selective preservation of seemingly recalcitrant plant C to a microbial-centric model that emphasizes decomposer access to substrates in soils, regulated by biotic (e.g., microbial traits) and abiotic factors, including soil mineralogy, pore architecture, and environmental conditions (Baldock & Skjemstad, 2000; Lehmann & Kleber, 2015; Schmidt et al., 2011). Under this new model, plant inputs are extracellularly decomposed by soil microorganisms into simpler plant compounds, as well as assimilated by microbes and transformed to various microbial products. These partially decomposed plant compounds, as well as the microbial cells and extracellular products (i.e., microbial "necromass") generated through microbial assimilation and biosynthesis go on to form plant-derived and microbial-derived SOM, respectively (Liang et al., 2017; Schmidt et al., 2011).

Recent approaches developed to quantify the microbial contribution to SOM have suggested that microbial necromass is the direct source of as much as ~30% and 80% of SOM, with variation observed across different ecosystems and soil types (Angst et al., 2021; Khan et al., 2016; Liang et al., 2019; Simpson et al., 2007), soil depths (Kaiser & Kalbitz, 2012; Kalbitz & Kaiser, 2008), and across different soil fractions (Angst et al., 2021). For this reason, the microbial contribution to SOM has gained widespread recognition in recent years (Liang et al., 2020), and increasingly, its primacy is emphasized in putatively stable pools of SOM, such as mineral-associated organic matter (MAOM) (Bradford et al., 2013; Buckeridge et al., 2020; Cotrufo et al., 2013; Cotrufo & Lavallee, 2022; Creamer et al., 2019; Liang et al., 2020; Oldfield et al., 2018; See et al., 2022). Current SOM theory therefore posits that microbial physiological traits (e.g., growth efficiency) are major controls on SOM formation (Buckeridge et al., 2020; Cotrufo et al., 2013; Kallenbach et al., 2016; Malik et al., 2019), and this perspective has been incorporated into a new generation of microbially explicit SOM models (Sulman et al., 2014; Wieder et al., 2014). However, the role of direct plant contributions to SOM should not be overlooked. Current quantitative estimates suggest that plant-derived SOM can comprise between 20% and 70% of SOM (e.g., Angst et al., 2021; Liang et al., 2011, 2019), and the direct sorption or occlusion of plant-derived compounds to soil minerals or within soil aggregates may decouple certain microbial physiological traits from these more persistent pools of SOM (Craig et al., 2022). Indeed, a recent meta-analysis of amino sugar data across various ecosystems indicated that on average ~60% of MAOM-C is directly plant-derived (Angst et al., 2021), suggesting that the direct incorporation of plant compounds into SOM may play a greater role in its formation than is currently recognized by dominant conceptual paradigms.

An accurate accounting of plant- versus microbial-derived SOM is necessary because these two pathways imply different controls on SOM formation and persistence (Cotrufo & Lavallee, 2022; Liang et al., 2017; Sokol et al., 2022). Although microbial SOM formation is controlled by microbial traits involved in the assimilation and anabolism of plant inputs (e.g., growth rates and efficiency; Kallenbach et al., 2016), the formation of plant-derived SOM may instead be controlled by microbial traits related to the depolymerization and extracellular transformation of plant inputs (e.g., extracellular enzyme activities) or, independent of microbial transformation, by the sorptive affinity of plant compounds (Sokol et al., 2019, 2022). Accurately accounting for the quantitative importance of these two pathways, and the processes that control them, has critical implications for modeling and projections of SOM cycling under global change (Blankinship et al., 2018; Wieder et al., 2014), and in the effective management of SOM stocks in natural and agricultural ecosystems (Cotrufo & Lavallee, 2022; Kallenbach et al., 2019).

To date, much of the data characterizing the plant and microbial origins of SOM remain qualitative, whereas explicitly quantitative data are sparse and derive from a limited suite of methods (Liang et al., 2020). Critically, there are known limitations with the common methods used to parse plant- and microbial-derived SOM (Joergensen, 2018; Liang, 2020), and no comprehensive analysis of the accuracy of all methodological approaches used to quantify plant- versus microbial-derived SOM has been conducted. To this end, we critically review the evidence for microbial- and plant-derived SOM, examining the different methodologies from which these estimates derive, which range from biomarker analyses (e.g., amino sugars, lipids) to molecular fingerprinting studies (e.g., nuclear magnetic resonance spectroscopy, NMR) and mathematical modeling (e.g., absorbing Markov chain model). Although we focus on published quantitative estimates, we also discuss the qualitative evidence for microbial-derived SOM that emerged over time, lending support for the shift in SOM theory toward an emphasis on the role of microbial necromass as a source of SOM.

From our synthesis, we argue that all major methods used to parse plant- and microbial-derived SOM have key shortcomings that must be addressed to improve the accuracy of quantitative estimates. In particular, we focus on potential overlap between plant- and microbial-derived compounds in the MAOM pool, given evolving understanding

of SOM formation processes, which includes greater emphasis on the contributions of plant rhizodeposits, dissolved organic C (DOC), and microbial extracellular products (Craig et al., 2022; Redmile-Gordon et al., 2020; Sokol & Bradford, 2019; Villarino et al., 2021). We identify several shortcomings common to the methods used to quantify SOM sources: (1) assuming that specific biomarkers will accumulate in soils in similar proportions as they are found in plant or microbial biomass, and that these biomarkers are representative of total plant and/or microbial contributions to SOM; (2) calculating relative contributions based on the assumption that an entire compound class (e.g., proteins) is predominantly derived from one group (microbes *or* plants); (3) using uncertain conversion factors or ratios; and (4) indirectly quantifying plant-derived SOM as the difference between total and microbial SOM. We conclude our review with a discussion of key future directions that would help resolve the quantitative importance of plant and microbial contributions to SOM.

2 | QUALITATIVE EVIDENCE FOR MICROBIAL-DERIVED SOIL ORGANIC MATTER: HISTORICAL AND CURRENT EFFORTS

It is often suggested that microbial contributions to SOM were not recognized until recently due to the relatively small (<5%) contribution of living microbial biomass to SOC; however, a careful review of the literature demonstrates that this view has emerged over the last century (McGill et al., 1973, 1975; Oades, 1984; Waksman, 1925a, 1925b). As early as 1925, Waksman suggested that humic acids were derived in part from the cells of soil microorganisms, and that microbes contribute to SOM ("humus") stability by synthesizing "resistant substances" (Waksman, 1925b). Bremner (1958, 1965) examined amino sugars in soils, and early isotopic labeling studies demonstrated microbial formation of carbohydrates, amino acids, and amino sugars with longer retention times than the original substrate, and low rates of subsequent nitrogen (N) mineralization (Mayaudon & Simonart, 1963; McGill et al., 1973, 1975; Shields et al., 1973, 1974; Sorensen & Paul, 1971; Wagner, 1968). From such isotopic labeling incubations, McGill et al. (1973) suggested a relationship between microbial substrate use efficiency and the C retained in SOM.

In the context of microaggregate formation, Oades (1984) described the potential for microbial residues to interact with soil minerals and accumulate as an important pool of C and N in soils over time. While these studies remained largely qualitative, advances made with molecular fingerprinting approaches (e.g., NMR) allowed for increasing quantitative resolution of the microbial contribution to SOM. Solid-state ^{13}C NMR studies by Baldock et al. (1989, 1990) and Golchin et al. (1996) demonstrated the capacity of microbes to generate chemically complex organic matter from simple C substrates (e.g., glucose) and to thus contribute to the chemistry of SOM. Although the concept of "humic substances" is now recognized to encompass operational categories of SOM that are artefacts of the extraction process (Lehmann & Kleber, 2015; Schmidt et al., 2011), the humic acid and fulvic acid extraction procedures made possible the early characterization of soil molecular structure. In this context, Duchaufour (1998) described "microbial humins" and Schnitzer (1999) discussed the process of "microbial humification," or the synthesis of microbial residues in soils, contributing to SOM (see also Schnitzer & Monreal, 2011). Researchers also observed significant quantities of microbial polysaccharides and proteinaceous N in humic acid extracts (Gleixner et al., 1999; Kelleher & Simpson, 2006; Ladd & Brisbane, 1967; McGill et al., 1973, 1975; Schulten & Schnitzer, 1997). Over time, these discoveries led to shifts in SOM theory toward the "continuum model" (sensu Lehmann & Kleber, 2015), where SOM was recognized as a complex mixture of plant and microbial residues at various stages of decomposition (Kelleher & Simpson, 2006; von Lützow et al., 2006; Marschner et al., 2008; Piccolo, 2001; Sutton & Sposito, 2005).

The detailed characterization of SOM chemistry was extended to soil size and density fractions, the simplest approach being the fractionation of SOM into particulate organic matter (POM; >20–63 μm or <1.6–1.85 g cm^3) and MAOM (<20–63 μm or >1.6–1.85 g cm^3), which were found to have distinct properties and turnover times (Baldock & Skjemstad, 2000; Christensen, 2001; Lavallee et al., 2020). Although POM was accepted to be largely plant-derived (Grandy & Neff, 2008; Six et al., 2001), emergent data on the chemical and isotopic signatures of MAOM pointed toward a more microbial origin (Gleixner et al., 2001; Grandy & Neff, 2008; Sollins et al., 2006). Such evidence included high concentrations of N-containing compounds in MAOM (e.g., proteins, peptides) (Clemente et al., 2011; Dümig et al., 2012; Grandy et al., 2007; Kögel-Knabner, 2002), and correspondingly, a low C:N ratio that aligned closely with that of microbial biomass (Baldock et al., 1992; Schmidt & Kögel-Knabner, 2002; Sollins et al., 2006, 2009). Biomarkers attributed to microbial origins (e.g., proteins, hexoses) were observed to have longer mean residence times in soils than plant-derived compounds (e.g., lignin phenols) (Gleixner et al., 1999, 2002), and the $\delta^{15}N$ and $\delta^{13}C$ ratios of MAOM corresponded closely with those of microbial biomass (Baisden et al., 2002; Boström et al., 2007; Dijkstra et al., 2006; Sollins et al., 2006). Imaging techniques provided additional evidence for the microbial contribution to SOM (Herrmann et al., 2007; Keiluweit et al., 2012; Miltner et al., 2012), with SEM images showing patchy organic matter from microbial cell debris attached to mineral surfaces (Miltner et al., 2012; Schurig et al., 2013). Together, these streams of evidence led many researchers to infer that microbes were a dominant source of SOM, and potentially the primary source of MAOM (e.g., Bol et al., 2009; Gleixner et al., 2001; Grandy & Neff, 2008; Miltner et al., 2012).

3 | QUANTITATIVE ESTIMATES OF PLANT- AND MICROBIAL-DERIVED SOIL ORGANIC MATTER

Although the qualitative or semiquantitative evidence clearly shows an important microbial contribution to SOM formation and

stabilization, truly quantitative evidence continues to lag behind. There are three primary approaches that have been used to derive quantitative estimates of the relative plant and microbial contribution to SOM: (1) biomarker analyses and the use of conversion factors for extrapolation; (2) "molecular fingerprinting" approaches to characterize the chemistry of whole soils, where spectra or peaks are compared with those observed in plant and microbial biomass; and (3) mathematical modeling.

In total, there are five independent studies, plus three meta-analyses that have proposed formal quantitative estimates of the relative plant versus microbial contribution to SOM (Table 1). The three meta-analyses synthesized amino sugar biomarker data across ecosystems (Liang et al., 2019; Wang et al., 2021) or soil size fractions (Angst et al., 2021). The other quantitative estimates derive from NMR (Simpson et al., 2007), pyrolysis field ionization mass spectrometry (Py-FIMS; Ludwig et al., 2015), and mathematical modeling (Fan & Liang, 2015; Liang et al., 2011). Isotope tracer studies provide additional semiquantitative estimates of the microbial contribution to SOM (e.g., Miltner et al., 2012). There is wide variation in the range of estimates of microbial contributions to SOM, and this variation likely derives from differences in ecosystem type, climate, and soil properties (Angst et al., 2021; Liang et al., 2019), and from methodological constraints. The lowest estimate of microbial-derived SOM (5%) was obtained for an acidic pine forest soil using NMR and analyses focusing on protein biomarkers (Simpson et al., 2007). The highest estimates were proposed by Liang et al. (2011) and Fan and Liang (2015) using mathematical modeling, which both emphasized the potential of microbes to contribute directly to up to 80% of SOM. Meta-analyses based on amino sugar data have reported average values for microbial-derived SOM between 33% and 62% across different ecosystems, with forests exhibiting the lowest estimated microbial contributions, and grasslands the highest (Liang et al., 2019; Wang et al., 2021). Such a wide variation in values indicates that estimates of microbial and plant contributions to SOM are method- and context-dependent. In the following section, we review each method that has been used to derive formal quantitative estimates. We discuss limitations associated with each approach in light of evolving understanding of the importance of different SOM sources (e.g., rhizodeposits, EPS) (Redmile-Gordon et al., 2020; Villarino et al., 2021).

4 | LIMITATIONS OF CURRENT QUANTITATIVE ESTIMATES

4.1 | Amino sugars

Amino sugar analyses have emerged as the most widespread approach to estimate microbial necromass contributions to SOM, providing insight into the quantitative distribution of microbial-derived SOM across ecosystems (Angst et al., 2021; Liang et al., 2019; Wang et al., 2021). However, to generate estimates of the microbial contribution to total SOC from amino sugar concentrations, the assumptions required for extrapolation introduce error (Joergensen, 2018). One potentially large source of error arises from the formation of common conversion factors for bacterial and fungal necromass C. Bacterial necromass C is calculated by multiplying the concentration of soil muramic acid (an amino sugar specific to bacteria) by a conversion factor of 45 (Appuhn & Joergensen, 2006). This value is based on the average concentration of muramic acid in cultured bacterial biomass (10.3 $mg\,g^{-1}$ dry weight; Appuhn & Joergensen, 2006), and is calculated assuming a constant ratio of Gram-positive to Gram-negative bacteria of 65% to 35% (derived from a single grassland site; Joergensen & Potthoff, 2005) as well as an average C content of bacterial biomass (~46%; Jenkinson, 1988). The 95% confidence limits around this conversion factor range from 30 to 90 (Appuhn & Joergensen, 2006), meaning that the estimate of bacterial necromass C could either be greatly over- or underestimated. To constrain this error, the ratio of Gram-positive to Gram-negative bacteria would ideally be measured (e.g., via phospholipid fatty acid analysis or molecular methods) to calculate a soil-specific conversion factor (Joergensen, 2018); however, we are not aware of any studies that have done this.

Fungal necromass C is calculated in two steps: (1) by estimating fungal glucosamine as the difference between total and bacterial glucosamine, assuming a molar ratio of 1:2 for muramic acid to glucosamine in bacterial cells (Engelking et al., 2007) and (2) multiplying by a conversion factor of 9, assuming 46% C content of fungal biomass (Jenkinson, 1988) and an average glucosamine concentration in fungal biomass of 49 $mg\,g^{-1}$ dry weight (Appuhn & Joergensen, 2006). According to Appuhn and Joergensen (2006), the 95% confidence limits around this fungal conversion factor range from 8 to 10, suggesting that these estimates may be more constrained than those of bacterial necromass C.

Yet, it is important to acknowledge general limitations of the amino sugar approach that apply broadly to both the estimate of fungal and bacterial necromass C. First, a central assumption of this approach is that all microbial necromass components will be retained in soils to the same extent, and thus converting from a single component (amino sugars) to total microbial necromass C will be representative of the accumulated microbial contribution to SOM. However, emerging evidence suggests that certain microbial necromass components are preferentially retained in mineral soils (e.g., proteins and other N-rich compounds) (Dümig et al., 2012; Kopittke et al., 2018, 2020; Miltner et al., 2009), indicating that this may not be an accurate assumption. Just considering amino sugar residues themselves, the average mean residence times of their component parts vary considerably—from ~4 years for the whole amino sugar structure (Derrien & Amelung, 2011; Glaser et al., 2006) to ~6 years for the C in glucosamine (Glaser et al., 2006), and up to 75–160 years for amino sugar-N (Liu et al., 2016).

Second, conversion factors are based on amino sugar concentrations in fungal and bacterial biomass and, therefore, are only designed to account for microbial cell debris contributions to soils. Extracellular products of microbes (e.g., EPS, metabolites, enzymes) also make substantial contributions to SOM (Costa et al., 2018;

TABLE 1 Formal quantitative estimates of microbial- versus plant-derived SOM from the literature. The methods used in each study are listed alongside a summary of the limitations associated with each approach. Miltner et al. (2012) is included as an example of semiquantitative stable isotope-based approaches. The Liang et al. (2019), Angst et al. (2021) and Wang et al. (2021) publications are meta-analyses that performed extrapolations to estimate microbial necroma C from amino sugar concentrations. Values presented from these publications are averages for each ecosystem type or soil fraction. *Common limitations key*: (1) assuming that specific biomarkers will accumulate in soils in similar proportions as they are found in plant or microbial biomass and that these biomarkers are representative of total plant and/or microbial contributions to SOM; (2) calculating relative contributions based on the assumption that an entire compound class (e.g., proteins) is predominantly derived from one group (microbes *or* plants); (3) using uncertain conversion factors or ratios; (4) indirectly quantifying plant-derived SOM as the difference between total and microbial SOM.

Author and year	Microbial-derived (%)	Plant-derived (%)	Method	Common limitations	Study-specific limitations
Simpson et al. (2007)	52% (Grassland) 39% (Grassland) 50% (Aspen Forest) 5% (Pine Forest)	48% (Grassland) 61% (Grassland) 50% (Aspen Forest) 95% (Pine Forest)	Solution-state ^{1}H NMR	1, 2, 4	Analyzed operationally defined humic acid extracts; quantification of the microbial contribution relied on two peaks characteristic of proteins/peptides rather than entire NMR spectra
Liang et al. (2011); Liang and Balser (2011)	Up to 80%	20%+	Absorbing Markov chain model	3, 4	Values for model parameters (e.g., CUE, probability of death, recycling/reuptake rate of necromass C) are assumed, generally from one to two studies. Use of fixed rather than variable parameter values. Estimates represent *possible* microbial contribution
Miltner et al. (2012)	40%	60%	^{13}C labeling, NMR, protein amino acids, fatty acids	1, 4	Results represent proportion of added ^{13}C label retained in SOM; experiment does not directly quantify microbial- versus plant-derived SOM in situ in natural soils. Calculations based in part on avg. protein content of microbial biomass
Ludwig et al. (2015)	50% (Cropland) (>50%, MAOM)	50% (Cropland) (<50%, MAOM)	Py-FIMS	1, 2, 3	Pyrolysis products that do not occur in soils; estimates based on fatty acid C chain length and hexose: pentose ratios may be skewed by decomposing plant compounds and rhizodeposits
Fan and Liang (2015)	47%–80%	20%–53%	Mathematical modeling	3, 4	Estimates represent *possible* microbial contribution to SOM, where range derives from simulated variation in environmental conditions; some parameter values assumed from one to two studies
Khan et al. (2016)	48% (Grassland) 48% (Cropland) 30% (Cropland) 30% (Forest)	52% (Grassland) 52% (Cropland) 70% (Cropland) 70% (Forest)	Amino sugars	1, 3, 4	Conversion factors used to estimate microbial residue-C based on series of assumptions that are not accurate for all soils; assumes retention of amino sugars in soils represents total microbial contribution; cannot accurately capture EPS
Liang et al. (2019)	62% (Grassland) 56% (Cropland) 33% (Forest)	38% (Grassland) 44% (Cropland) 67% (Forest)	Amino sugars (meta-analysis)	1, 3, 4	Conversion factors used to estimate microbial residue-C based on assumptions not accurate for all soils; assumes retention of amino sugars in soils represents total microbial contribution; cannot accurately capture EPS

(Continues)

TABLE 1 (Continued)

Author and year	Microbial-derived (%)	Plant-derived (%)	Method	Common limitations	Study-specific limitations
Angst et al. (2021)	47.2% (Macroaggregates)	52.8% (Macroaggregates)	Amino sugars (meta-analysis)	1, 3, 4	Same issues described above for amino sugar-based studies. Angst et al. also synthesized data on lignin and plant lipid concentrations in MAOM; however, quantitative plant contributions were estimated as the difference between total and microbial-derived SOM based on amino sugar data
	49.7% (Microaggregates)	50.3% (Microaggregates)			
	38.6% (MAOM)	61.4% (MAOM)			
	44% (Cropland, MAOM)	66% (Cropland, MAOM)			
	15.2% (Forest, MAOM)	84.8% (Forest, MAOM)			
Wang et al. (2021)	47% (Grassland)	53% (Grassland)	Amino sugars (meta-analysis)	1, 3, 4	Issues surrounding conversion factors described above; assumes retention of amino sugars in soils represents entire microbial contribution; cannot accurately capture EPS
	51% (Cropland)	49% (Cropland)			
	35% (Forest)	65% (Forest)			

Gunina & Kuzyakov, 2015; Op De Beeck et al., 2021; Redmile-Gordon et al., 2020; Wang et al., 2017), suggesting that the amino sugar approach is insufficient to capture the entire microbial contribution. Lastly, in amino sugar-based estimates, plant-derived SOM is commonly inferred as the difference between total and microbial-derived SOM (i.e., 100% − microbial SOM), rather than via an independent estimate of the plant contribution. Therefore, an inaccurate approximation of microbial-derived SOM necessarily leads to an inaccurate prediction of plant-derived SOM. Additional caveats of the amino sugar approach have been raised, including variation in amino sugar extraction efficiency and detection across different substrates (Liang, 2020). These limitations should give researchers pause, as extrapolations based on amino sugars are quickly becoming the most common method for approximating the microbial, and by extension, the plant contribution to SOM.

4.2 | Molecular fingerprinting approaches

Molecular fingerprinting approaches, such as NMR, py-GC/MS, and py-FIMS, generate a detailed picture of SOM chemical composition, providing quantitative information on bonding structures and/or relative abundances of individual molecules and chemical compound classes in SOM (Grandy et al., 2007; Ludwig et al., 2015; Simpson et al., 2007). Historically, these approaches were limited by an inability to characterize the chemistry of SOM in whole soils due to inconsistent pyrolysis, limitations in compound databases, or reliance on soil extraction into a liquid phase for analysis (Kelleher & Simpson, 2006; Leinweber et al., 1999; Schulten et al., 1996). Today, methodological developments have allowed for increasingly comprehensive characterizations of SOM chemistry (Chassé et al., 2015; Grandy et al., 2007; Kallenbach et al., 2016; Neurath et al., 2021; Olivelli et al., 2020); however, such approaches are still hindered by their inability to assign origins to compounds that are produced by both microbes and plants. To circumvent this issue, the chemical fingerprints of SOM have been compared with those of microbial and plant reference materials, often relying on specific compound classes or biomarkers from within the larger dataset to infer a plant or microbial origin (e.g., Ludwig et al., 2015; Simpson et al., 2007). Yet, this approach also introduces uncertainty. We offer two examples that illustrate these broader challenges with approaches based on molecular fingerprinting.

In a pioneering study, Simpson et al. (2007) used ^{1}H NMR to characterize SOM chemistry, comparing its chemical profile to that of microbial biomass (cultured and extracted) and plant biomass (native prairie grass). The authors provided early evidence of a significant microbial contribution to SOM using a subtraction-based approach, which suggested that microbial-derived compounds comprised >50% of NMR signal intensity in some soils. Drawing on the widely held assumption that soil proteins were primarily microbial-derived, the calculation of microbial-derived SOM was based on the total signal intensity of two peaks indicative of protein and peptide structures—phenylalanine (amino acid) and methylated side chains

(another resonance associated with proteins/peptides)—rather than on the entire NMR spectra. As a complementary analysis, total correlation spectroscopy (TOCSY) was used to demonstrate that protein/peptide structures accounted for up to 50% of the total NMR signal in some samples, offering this as further evidence of a microbial contribution to SOM of ~50%. Therefore, while Simpson et al. (2007) present detailed data on the chemical structure of SOM, their quantitative estimates rely on similar assumptions about protein origin as some of the more correlational and inferential studies described in previous sections (e.g., Grandy & Neff, 2008; Kögel-Knabner, 2002; Miltner et al., 2012).

The idea that SOM chemistry is comparable with that of plant or microbial biomass relies on the assumption that compounds will accumulate in SOM in similar proportions as they are found in their source materials, which we increasingly recognize is unlikely to be the case (Kleber et al., 2015; Kopittke et al., 2020). Furthermore, biomass reference materials are unlikely to encompass the full range of compounds derived from plant litter with varying chemistries (e.g., low vs. high C:N litter, and litter DOC) and are unable to account for the suite of compounds produced by living roots (e.g., rhizodeposits) and microbes (e.g., EPS, metabolites), which may accumulate in soils over time. Lastly, the accuracy of individual methods may vary by ecosystem type. Based on protein/peptide abundances, Simpson et al. (2007) proposed microbial contributions to SOM ranging from 52% in a grassland soil down to 5% in an acidic pine forest soil. Protein/peptide abundance may be low in certain soils due to dominant vegetation, edaphic properties, feedbacks to microbial community composition and soil mineralogy, not necessarily because of low microbial contributions to SOM. As such, the potential for ecosystem and soil characteristics to confound comparisons across sites should be considered.

In a later study, Ludwig et al. (2015) used Py-FIMS to characterize SOM chemistry and similarly focused on a subset of molecular data (in this case, carbohydrates and fatty acids). To estimate microbial and plant contributions to carbohydrates, the ratio of galactose + mannose to arabinose + xylose (i.e., GM/AX) was calculated (sensu Oades, 1984). The GM/AX ranged from 1.3 to 2.5 across their bulk soil samples, and generally increased from POM (~1.7) to MAOM (2.3) fractions. Values <0.5 are traditionally attributed to plant dominance and >2 to microbial dominance (Oades, 1984), and values intermediate to this range require interpretation. In this study, the authors interpreted intermediate values as representing a relatively equal contribution from plants and microbes to total SOM (~50% each). Consistent with previous studies, the high GM/AX ratio of MAOM (>2) was interpreted as an indication of its dominant microbial origin (e.g., Cheshire & Mundie, 1981; Guggenberger et al., 1995; Solomon et al., 2000; Spielvogel et al., 2007). As a second metric, Ludwig et al. (2015) calculated the chain-length ratio of even-numbered *n*-fatty acids as the sum of ion intensities from C_4 to C_{26} fatty acids (assumed to largely represent the microbial contribution) divided by the sum of ion intensities from C_{26} to C_{38} fatty acids (assumed to represent the plant contribution; sensu Schnitzer et al., 1986). The authors concluded that the C_{4-26}/C_{26-38} further corroborated an important microbial contribution to SOM, especially MAOM, with ratios between 5.8 and 12.4 observed in POM and up to 240 in the MAOM fraction.

There are several notable limitations associated with the use of GM/AX and the chain-length ratio of fatty acids. First, using GM/AX as a proxy of the relative microbial versus plant contribution to SOM relies on the assumption that the galactose and mannose in soils derive primarily from microorganisms; however, galactose and mannose are also present in some plant tissues, as well as in root exudates (especially galactose; Gunina & Kuzyakov, 2015; Sher et al., 2020). Ludwig et al. (2015) addressed this limitation by comparing the GM/AX of their soils to local plant biomass reference materials; however, as previously discussed, the use of biomass reference materials cannot account for the contributions of rhizodeposits or microbial extracellular products and their potential accumulation in soils over time. Second, short-chain fatty acids can derive from varied sources, not just microbial biosynthesis. Plant roots produce short-chain lipids directly (Angst, John, et al., 2016), and microbial exocellular modification of plant materials has been shown to reduce the C chain lengths of plant lipids into at least the C_{16}–C_{24} range (Holloway, 1983; Saiz-Jimenez et al., 1996), causing overlap with that of microbial-derived compounds. The incorporation of these heavily transformed compounds into MAOM could help to explain the dominance of short-chain fatty acids in fine fractions, which is instead attributed to microbial biosynthesis (Amelung et al., 2008; Jandl et al., 2004). Taken together, these persistent limitations may help explain why more researchers have not ventured to propose formal quantitative estimates of the relative plant and microbial contributions to SOM, despite collecting similar data.

4.3 | Isotope tracer and artificial soil experiments

In isotope tracer experiments, isotopically labeled material is added to soils to trace its incorporation into SOM. In cases where labeled microbial necromass or simple substrates assumed to be fully incorporated by the microbial community (e.g., glucose) are added to soil, the ^{13}C that is incorporated into SOM can be assumed to derive from microbial cells or the products of microbial activity (Creamer et al., 2019; Golchin et al., 1996; Throckmorton et al., 2012, 2015). For example, Miltner and colleagues incubated soils with ^{13}C-labeled *Escherichia coli* cells for 224 days and evaluated the fate of ^{13}C using a C mass balance approach (Kindler et al., 2006) as well as its specific redistribution into microbial amino acids (Miltner et al., 2009) and fatty acids (Kindler et al., 2009). Drawing on these data, Miltner et al. (2012) concluded that ~40% of the ^{13}C label had been incorporated into SOM, either through the direct sorption of labeled *E. coli* cells, or through microbial recycling of this necromass and biosynthesis of new biomass and other microbial products. Although ^{13}C tracer studies clearly point to the large potential of microorganisms to contribute to SOM formation, their quantitative insight is limited, as they do not directly measure the relative abundances of plant and microbial compounds present in situ in natural soils.

However, when paired with molecular fingerprinting approaches, isotope tracer studies have provided evidence of a significant microbial contribution to SOM chemistry. For instance, Miltner et al. (2009, 2012) analyzed incubated soils via NMR and demonstrated that the chemistry of ^{13}C-amended SOM did not differ from that of field soils, suggesting a substantial microbial contribution to the chemical composition of SOM in the field. Similarly, Baldock et al. (1989) tracked the incorporation of ^{13}C-glucose into a fine sandy loam soil during a 30-day lab incubation, finding that microbes synthesized alkyl, O-alkyl and carboxyl C with resonances similar to those found in field soil using solid-state ^{13}C CP/MAS NMR.

Laboratory incubations with artificial soils (i.e., mixtures of sand, silt and/or clay that are initially organic matter-free) are another approach that has been used to circumvent the analytical challenges associated with differentiating plant- versus microbial-derived SOM in natural soils. Golchin et al. (1996) incubated artificial soils with a microbial inoculum and a simple sugar (glucose), finding that microbes synthesized novel O-alkyl, alkyl, carbonyl, and some aromatic structures, with O-alkyl (carbohydrates/polysaccharides) and alkyl (e.g., lipid) structures dominating. More recently, Kallenbach et al. (2016) used artificial soils incubated with glucose and other simple substrates for 18 months to demonstrate microbial formation of chemically complex SOM that was biologically and chemically stable (36%–93% of SOM). Py-GC/MS analysis revealed that microbes formed SOM composed of proteins, lipids, N-bearing compounds, aromatics, and polysaccharides, which resembled the chemistry of a field soil (Kallenbach et al., 2016). Although such studies are often suggested to show that microbial anabolism can explain the chemical composition of a large fraction of SOM, potential overlap in the chemical resonances of microbial-derived compounds with heavily decomposed plant compounds, litter DOC, or root-derived compounds (as discussed above) limits the quantitative inferences that can be drawn from these studies about SOM sources in the field.

4.4 | Numerical modeling studies

In the context of plant and microbial contributions to SOM, numerical modeling studies have emphasized the vast potential for microbes to contribute to SOM formation (47%–80%; Fan & Liang, 2015; Liang et al., 2011). Numerical models integrate theoretical understanding and empirical measurements to make predictions about pool sizes and process rates, and to simulate the effects of perturbations on these pools and processes (Kyker-Snowman et al., 2021). Modeling studies can therefore provide valuable insights to guide future theoretical and empirical work (Blankinship et al., 2018). However, models are limited in their scope and generalizability, as they are parameterized with values derived from the literature—sometimes from a single study within a particular soil type or ecosystem context. For instance, the absorbing Markov chain model employed by Liang et al. (2011) to estimate the potential contribution of microbial necromass to SOM (up to 80%) used values for model parameters selected from individual publications. Such parameters included a fixed CUE value set at 0.6 (Allison et al., 2010), a fixed probability of microbial death equal to 0.5 (Feng, 2009), and a fixed probability of microbial necromass transfer to the living microbial biomass pool (0.000114; Feng, 2009).

The results of models should therefore be interpreted as representing a *possible* microbial contribution to SOM, given the suite of limitations inherent to model parameterization (e.g., selection of factors to be included implicitly or explicitly in the model structure), and under the specific ecosystem context simulated in the model. As discussed by Liang et al. (2011), such models are limited by analytical and technical challenges with quantifying pool sizes and rates of transformation between pools. Improving quantitative estimates of microbial traits (e.g., CUE) and transformation rates between pools (e.g., biomass turnover rates, or necromass decomposition and immobilization rates) in a range of ecosystems will aid in model validation, and the use of variable (e.g., probabilistic) rather than fixed parameter values will provide insight into the range of microbial contributions to SOM under different contexts.

5 | DECIPHERING THE PLANT AND MICROBIAL ORIGINS OF MINERAL-ASSOCIATED ORGANIC MATTER

Taken together, the limitations of current quantitative approaches raise fundamental questions about our ability to ascribe a plant or microbial origin to SOM. Distinguishing compound origin is particularly challenging for the MAOM pool, where compounds are more heavily decomposed, and/or derived from relatively low molecular weight compounds that can be produced directly by both microbes and plants (Grandy & Neff, 2008; Lavallee et al., 2020). Formal quantitative estimates of plant and microbial contributions to MAOM are scarce, and those that exist suggest relative contributions are context- and method dependent (Table 1) (Angst et al., 2021; Ludwig et al., 2015). Growing evidence for the importance of dissolved and low molecular weight plant compounds (e.g., root exudates, litter DOC) as sources of MAOM-C (Cotrufo et al., 2022; Craig et al., 2022; Sokol & Bradford, 2019; Villarino et al., 2021) creates uncertainty around the plant versus microbial origins of simple, low C:N compounds in MAOM. Given these uncertainties, we review data on the chemical composition of MAOM and discuss major challenges associated with determining its plant and microbial sources.

5.1 | The chemical composition of mineral-associated organic matter and its plant and microbial sources

Polysaccharides, lipids, and proteins are dominant components of the silt- and clay-sized fractions that constitute the MAOM pool. Polysaccharides and lipids can each comprise up to half of the C in the MAOM pool, with values observed between ~18% and 52% and 3%–45%, respectively (Angst et al., 2017; Angst,

Kögel-Knabner, et al., 2016; Bol et al., 2009; Geng et al., 2019; Grandy & Neff, 2008; Schnecker et al., 2016; Spielvogel et al., 2008). Amide N (proteins/peptides) commonly makes up ~10%–40% of MAOM-C and between 60% and 90% of MAOM-N (Angst et al., 2017; Bol et al., 2009; Geng et al., 2019; Grandy & Neff, 2008; Knicker, 2011; Schnecker et al., 2016). Lignin and its identifiable derivatives generally comprise <10% of MAOM-C (Angst et al., 2017; Bol et al., 2009; Geng et al., 2019; Grandy & Neff, 2008; Knicker, 2011), although this proportion may be higher in soils with abundant short-range order Fe and Al hydroxides (e.g., in Andosols developed on volcanic ejecta; Kramer et al., 2012). Compounds with aromatic and phenolic moieties not assigned to the aforementioned categories can each comprise an additional 1%–12% of MAOM-C (Dümig et al., 2012; Grandy et al., 2007; Schnecker et al., 2016). Aside from lignin, which is exclusively plant-derived, the remaining compound classes are produced by both plants and microbes, making their comprehensive assignment to particular origins a challenge (Figure 1).

5.1.1 | Carbohydrates

Carbohydrates constitute 4%–60% of microbial biomass, with the upper range generally observed in chitin-rich fungal biomass (Kleber et al., 2007; Kögel-Knabner, 2002). Cellulose and hemicellulose comprise 15%–60% and 10%–30% of vascular plant biomass, respectively (Kleber et al., 2007). While carbohydrates are therefore important constituents of both plant and microbial biomass, their presence in MAOM is commonly attributed to a microbial origin (Gleixner et al., 2002; Grandy & Neff, 2008). Microbes generate a diversity of cellular and extracellular polysaccharides (e.g., galactose and mannose) with functional groups that can sorb to mineral surfaces via cation or water bridging (Chenu, 1995; Feng et al., 2005; Kleber et al., 2015; von Lützow et al., 2007), whereas plant carbohydrates are thought to be rapidly decomposed and transformed (Amelung et al., 1997; Gleixner et al., 2002). Cellulose is the dominant structural plant carbohydrate in soils and is readily depolymerized to glucose (Amelung et al., 2008); similarly, glucose is the dominant sugar in plant exudates (Jones et al., 2004). Glucose is commonly reported to be rapidly mineralized in soils and to show low sorptive affinity (Fischer et al., 2010; Gunina & Kuzyakov, 2015); however, in soils rich in iron (hydr)oxides, glucose may be strongly protected by mineral surfaces (Porras et al., 2018). The relative abundance of glucose can also exceed that of galactose and mannose in the MAOM fraction (Dümig et al., 2012; Poirier et al., 2005), and its origin could be either plant or microbial.

Adding to this uncertainty, the metric used in many studies to describe the plant and microbial sources of carbohydrates (i.e., GM/AX, or the ratio of galactose + mannose to arabinose + xylose; e.g., Amelung et al., 1999; Dümig et al., 2012; Roberson et al., 1995) may not be a robust determinant of polysaccharide origin. Hemicellulose can include galactose and mannose as constituent sugars, and rhizodeposition is an important source of hexoses in soil, especially galactose (Figure 2) (Gunina & Kuzyakov, 2015; Pett-Ridge et al., 2021). Given that rhizodeposits are increasingly recognized for their contributions to MAOM (Sokol & Bradford, 2019; Villarino et al., 2021), it may be time to revise our use of the GM/AX ratio in determining polysaccharide origin. Indeed, the higher concentrations of galactose and mannose in MAOM compared with that of arabinose and xylose could represent a preferential accumulation of these compounds through sorption, rather than definitive evidence of a dominant microbial contribution. At present, the relative plant and microbial contributions to the pool of hexoses in soils is poorly constrained. As such, Gunina and Kuzyakov (2015) recommended measuring galactose and mannose concentrations of plant materials for individual study sites and adjusting calculations accordingly. Similarly, the concentrations of these compounds in rhizodeposits should be taken into account (Sher et al., 2020).

Based on pentose biomarkers, Angst et al. (2021) estimated that plant-derived carbohydrates comprise ~10% of MAOM-C. By comparison, polysaccharides that are commonly attributed to microbial sources account for ~15%–25% of MAOM-C. These include galactose and mannose (~60–90 and 30–70 mg g^{-1} C, respectively), amino sugars (~59–66 mg g^{-1} C) and uronic acids (6–20 mg g^{-1} C) (Amelung et al., 1999; Angst et al., 2021; Dümig et al., 2012; Guggenberger et al., 1995; Solomon et al., 2000). While it may therefore be tempting to suggest that microbes are the dominant source of carbohydrates in MAOM, uncertainty around the source of hexoses in soil (discussed above) continues to limit our ability to precisely differentiate and quantify microbial and plant contributions to this pool (Figure 2).

5.1.2 | Lipids

Lipids constitute up to ~40% of microbial cell dry mass (Kleber & Reardon, 2017; Kleber et al., 2007) and 3%–20% of aboveground plant biomass (Nelson & Baldock, 2005). As illustrated by our summary of Ludwig et al. (2015) described above, the ratio of short-to-long even chain *n*-fatty acids has been applied to estimate the relative contributions of microbes and plants to the lipid pool in SOM. The ratio increases substantially from POM to MAOM, which is interpreted to represent a dominant contribution of microbial lipids to the MAOM fraction (Amelung et al., 2008; Jandl et al., 2004; Ludwig et al., 2015; Rovira & Grasset, 2019). Incubation studies where microbes are the only source of new organic matter corroborate the high potential for microbes to contribute to this lipid pool (Golchin et al., 1996; Kallenbach et al., 2016; Kindler et al., 2009; Olivelli et al., 2020). Yet, as discussed above, there can be substantial overlap in the chain lengths of even-numbered *n*-fatty acids derived from plants and microbes (Figure 2). Roots are a significant source of *n*-fatty acids in the C_{14}–C_{18} range (Angst, John, et al., 2016), which overlaps precisely with the most common *n*-fatty acids produced by microbes (Amelung et al., 2008). Microbial exocellular decomposition of plant lipids can also reduce C chain length (Quénéa et al., 2006), causing them to overlap with the range traditionally viewed as "microbial"

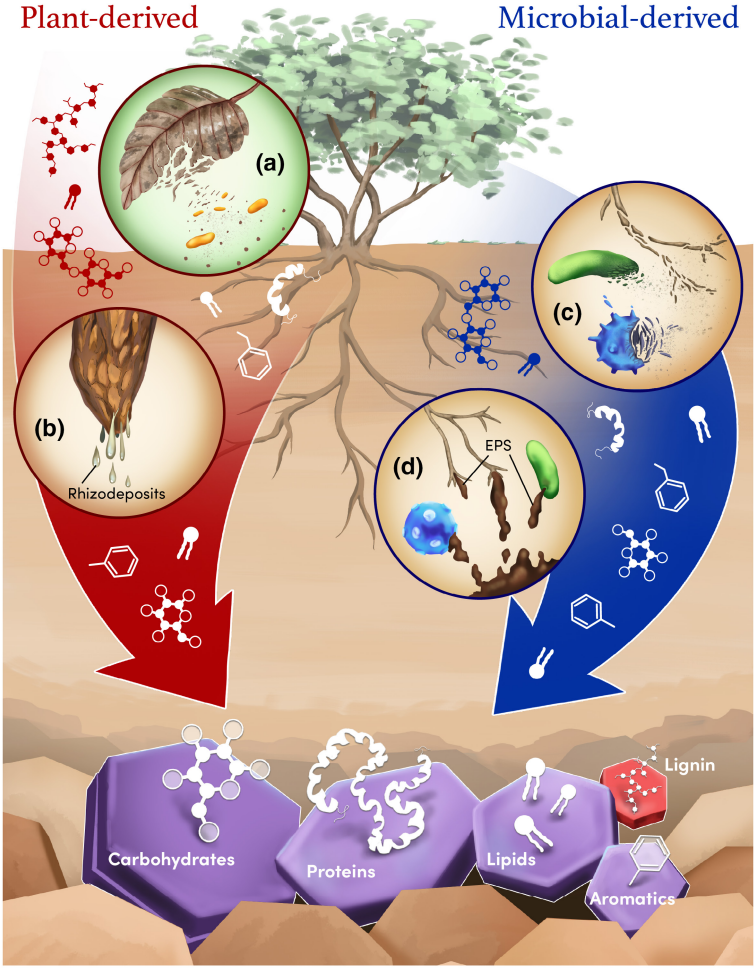

FIGURE 1 Plants and microbes as sources of the compounds commonly observed in mineral-associated organic matter (MAOM), including carbohydrates, proteins, short-chain lipids, and aromatics. Although many of the compounds in MAOM have historically been attributed to microbial sources, they could also derive directly from plant roots (e.g., galactose in root exudates), plant litter DOC, or from the extensive extracellular decomposition of plant litter, releasing compounds such as proteins and fragmented lipid chains. Although phenols have historically been associated more with plant-derived SOM (e.g., lignin), microbes also produce various phenolic and aromatic compounds (e.g., melanin) that could help explain their presence in MAOM. *Specific pathways and MAOM sources illustrated in this diagram*: (a) extracellular decomposition of leaf litter, releasing smaller structural units of plant biomolecules, as well as litter DOC; (b) root rhizodeposition of relatively low-molecular-weight compounds; (c) microbial biosynthesis of cellular residues; (d) microbial EPS production. *At bottom*: Depiction of the chemistry of MAOM, with average relative abundances of major compound classes represented by mineral size. Lignin is represented in red because it is exclusively plant-derived. All other compound classes are represented in purple, highlighting their mixed and uncertain sources.

(Holloway, 1983; Saiz-Jimenez et al., 1996), despite being directly plant-derived. Adding to this uncertainty, long-chain *n*-alkanoic acids (i.e., $>C_{20}$, even) in soils are often attributed to a plant origin; however, fungi also produce *n*-alkanoic acids with chain lengths in a similar range (C_{12}–C_{32}, even; Amelung et al., 2008), and some long-chain *n*-alkanoic acids (up to C_{30}) observed in sediments have been attributed to bacteria (Makou et al., 2018). Therefore, a ratio relying on the assumption that short-chain lipids (e.g., C_4–C_{26}) derive from microbes and long-chain lipids (e.g., C_{26}–C_{38}) derive from plants (sensu Ludwig et al., 2015; Schnitzer et al., 1986) is insufficient to delineate the microbial versus plant contribution to MAOM.

Additional lipid biomarkers that are commonly used to assess plant lipid contributions to soils are the *n*-alkanes, *n*-alkanols, α-hydroxyalkanoic acids, ω-hydroxyalkanoic acids, and the α, ω-alkanedioic acids. Although the latter two categories are exclusively plant-derived, there is some uncertainty around the sources of *n*-alkanes, *n*-alkanols, and α-hydroxyalkanoic acids in soils. For instance, long-chain, odd-numbered *n*-alkanes are commonly said to derive from the waxes of higher plants (e.g., Mueller et al., 2012; Otto et al., 2005); however, some longer chain *n*-alkanes (C_{23}–C_{35}, odd) may also be present in fungal tissues (Feng & Simpson, 2007; Huang et al., 2012) and in fungal spores (Oró et al., 1966). Similarly, C_{18} *n*-alkan-1-ol is present in both suberin and microbial spores (Naafs et al., 2004; Quénéa et al., 2006), and there is substantial overlap in the C chain lengths of α-hydroxyalkanoic acids produced by fungi and plants (Amelung et al., 2008). Synthesizing lipid biomarker data,

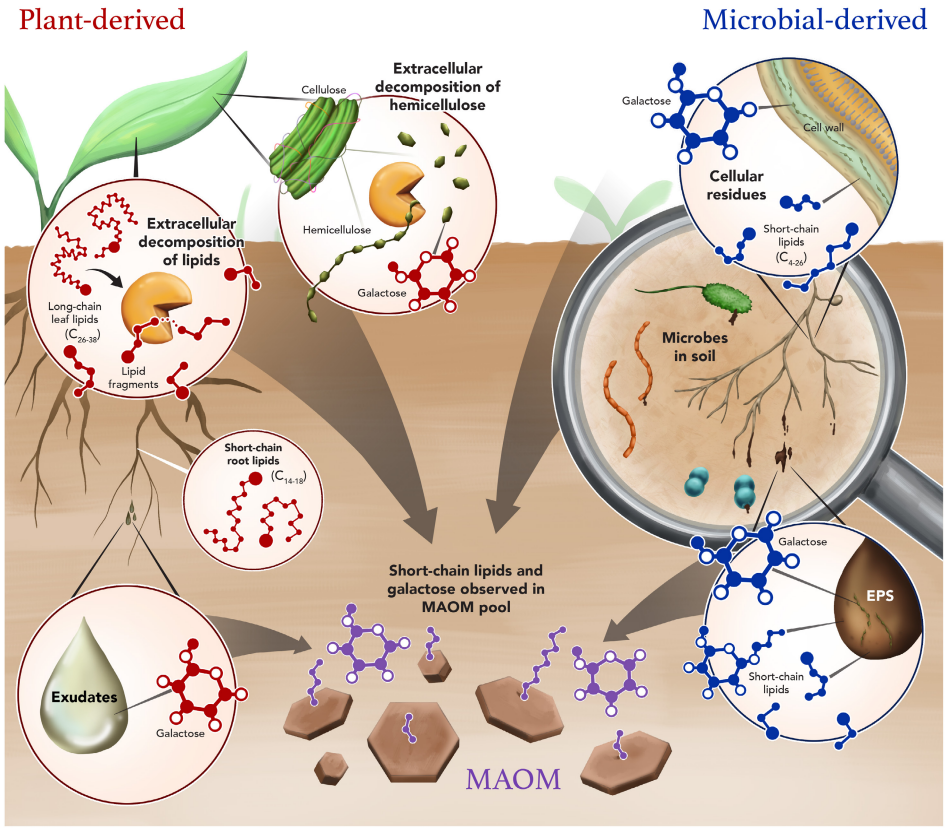

FIGURE 2 Plant and microbial pathways of MAOM formation for two example compounds: galactose and short-chain lipids. Galactose in soils is assumed to be primarily microbial-derived, and this assumption is embedded in common ratios for determining carbohydrate sources (i.e., GM/AX ratio; Oades, 1984). However, galactose can also derive from plant root exudates and from the decomposition of hemicellulose in plant tissues, making its origins in MAOM uncertain. Similarly, the presence of short-chain lipids in MAOM is commonly attributed to microbial sources, as the average chain lengths of lipids observed in the MAOM fraction are more similar to those of microbial tissues (~C_{4-26}) than plant tissues (~C_{26-38}; sensu Schnitzer et al., 1986 for *n*-fatty acids). However, roots produce short-chain lipids (C_{14-18}) directly, and small plant lipid fragments (<C_{26}) are released when microbes decompose longer-chain plant lipids extracellularly.

Angst et al. (2021) suggested that plant lipids comprise 2%–10% of MAOM-C. Limitations of lipid biomarkers aside, if total lipids comprise 3%–45% of MAOM-C as molecular fingerprinting data suggest, then microbial lipids make substantial contributions to the MAOM pool in systems where lipids are abundant. However, given overlapping chain lengths for microbial and especially root-derived lipids, there is still a fair degree of uncertainty around lipid origins in soils (Figure 2).

5.1.3 | Proteins and N-containing compounds

A crux of the correlational evidence for microbial contributions to MAOM is its low C:N ratio (Nelson & Baldock, 2005). As Paul (2016) observed, the low C:N of MAOM fractions, ranging from ~20 in some forest soils (e.g., Angst et al., 2017; Grandy & Neff, 2008) to as low as ~6 in some agricultural soils (e.g., Paul et al., 2011), does not allow for the presence of many N-free plant compounds. Because proteins only comprise 1%–15% of plant biomass, and up to 60% of microbial biomass (Kleber et al., 2007; Kögel-Knabner, 2002), and are generally not thought to diffuse across the root plasma membrane like other root exudates (Jones et al., 2004), microbes have historically been considered the primary source of proteinaceous N in MAOM (Simpson et al., 2007). Furthermore, MAOM is enriched in ^{15}N relative to POM and plant biomass (Sollins et al., 2006, 2009), and its isotopic signature is closely aligned with that of microbial biomass (Dijkstra et al., 2006). This pattern is now primarily attributed to the incorporation of microbial necromass into MAOM (Boström et al., 2007; Dijkstra et al., 2006; Melillo et al., 1989) and is supported by nanoscale evidence of ^{15}N-enriched compounds on mineral surfaces, posited to be microbial residues (Keiluweit et al., 2012; Kopittke et al., 2018, 2020; Possinger et al., 2020). However, this view ignores other potential direct plant contributions to the proteinaceous N in MAOM.

Whereas the proportion of proteins in plant litter is low relative to structural carbohydrates, proteins are the most abundant compounds inside plant cells (e.g., RuBisCo; Kögel-Knabner, 2002). Thus, plant cell lysis could introduce proteins, peptides and amino acids directly into mineral soil. Structural litter inputs can also form MAOM, especially when they decompose in direct contact with mineral surfaces (Rumpel et al., 2015; Sanaullah et al., 2011). Proteins and amino acids have high sorptive affinities (Feng et al., 2005; Kleber

et al., 2007; McKnight et al., 1992; Rillig et al., 2007) and their liberation from plant litter could thus contribute directly to MAOM if mineral sorption outcompetes microbial uptake (Dippold et al., 2014; Zimmerman et al., 2004). Root exudates can also include large quantities of amino acids (Canarini et al., 2019; Dietz et al., 2020) which can sorb directly to mineral surfaces, especially in soils with abundant Fe and Al (hydr)oxides (Kaiser et al., 2004; McKnight et al., 1992). Such N-rich DOM—produced from rhizodeposits and through the decomposition of low C:N plant litter (Soong et al., 2015)—is likely to be an important direct source of plant inputs to the MAOM-N pool (Craig et al., 2022). The extracellular modification of plant litter by microbes could also help explain increasing δ^{15}N and δ^{13}C values in clay and silt-sized fractions if microbes preferentially incorporate lighter isotopes during metabolism (Connin et al., 2001; Kramer et al., 2003). Although the extent of isotopic fractionation during microbial mineralization varies and is sometimes undetectable (Boström et al., 2007; Craine et al., 2015), it is likely that this process contributes to the isotopic enrichment of MAOM alongside incorporation of enriched microbial necromass (Connin et al., 2001; Dijkstra et al., 2006; Kramer et al., 2003; Lichtfouse et al., 1995).

While it therefore seems likely that plants contribute directly to the pool of N-containing compounds in MAOM, including those which are isotopically enriched, more research is needed to elucidate the likelihood of plant versus microbial contributions to MAOM quantity and persistence, and how this may differ across different soil regions. For instance, fungal hyphal lengths in soils are estimated to be 15,000 times greater than those of fine roots, suggesting that fungi occupy a considerably greater surface area of soil minerals compared to plant roots (See et al., 2022). This may increase the likelihood that microbes contribute to the accumulation of N-rich (and other) compounds in MAOM. Alternatively, in certain regions of bulk soil where microbial densities are low, direct plant contributions to these pools in MAOM may be higher, especially for compounds with high sorptive affinities (Sokol et al., 2019).

5.1.4 | Lignin, aromatics, and phenolics

Lignin makes up 5%–25% of leaf litter and ~15%–40% of wood, and its presence in soils is exclusively plant-derived (Berg & McClaugherty, 2003; Campbell & Sederoff, 1996). In contrast, compounds in MAOM identified as "phenolics" or "aromatics" could derive from either plants or microorganisms. Phenols in soils may derive from varied sources, including fungal melanins (Fernandez et al., 2019) and other phenolic microbial metabolites (Kallenbach et al., 2016; Solomon et al., 2012; Wang et al., 2017), as well as plant tannins or unidentified components of the lignin polymer (von Lützow et al., 2006). Phenols (e.g., flavonoids) and aromatic acids (e.g., *p*-coumaric acid) are also present in root exudates (Pett-Ridge et al., 2021; Zhalnina et al., 2018). If decomposed or oxidized to a significant extent, aromatic components of proteins and lipids may be included in the general aromatics or phenolics pools (e.g., aromatic R-groups of amino acids or phenolic ring structures from suberin or cutin; Kögel-Knabner, 2002). Knicker (2011) estimated that non-protein aromatic C accounted for only 7%–15% of SOC in soil clay fractions. Similarly, our summary of molecular fingerprinting data suggests that aromatic and phenolic compounds not assigned to lignin or protein sources comprise between 1% and 12% of MAOM-C (Dümig et al., 2012; Grandy et al., 2007; Schnecker et al., 2016).

Phenolic and aromatic compounds can undergo strong sorption to mineral surfaces via ligand exchange reactions, especially when they associate with Fe and Al (hydr)oxides and short-range order minerals (Mikutta et al., 2007; Sanderman et al., 2014). Although a number of studies have highlighted the particular sorptive affinity of lignin-derived phenols in this context (Chassé et al., 2015; Kaiser et al., 2004; Kaiser & Guggenberger, 2000; Kramer et al., 2012; Sanderman et al., 2014), molecular fingerprinting analyses not relying on soil extraction still generally show lignin contributions of <10% of MAOM-C (Angst et al., 2017; Bol et al., 2009; Geng et al., 2019; Grandy & Neff, 2008). Rather, it is likely that the phenolic and aromatic compounds present in MAOM are derived from the various plant and microbial sources discussed above, including but not limited to lignin phenols. Owing to its low C:N ratio, there are clear stoichiometric limitations on the relative abundance of N-free plant compounds in MAOM. If aromatics and phenolics are abundant in MAOM, and the C:N of MAOM is low, then aromatic protein derivatives and other N-containing compounds likely comprise a substantial portion of this pool (Knicker, 2011), and the origin of these compounds may be either plant or microbial.

6 | SUMMARY

- There is compelling evidence for both significant plant and microbial contributions to SOM, with variation likely across ecosystems and soil types. However, all major methods used to quantify plant versus microbial contributions to SOM have substantial limitations, highlighting the uncertainty in our current estimates.
- We identify four key limitations common to the methods used to parse plant- and microbial-derived SOM (Table 1).
- A major source of uncertainty derives from challenges associated with parsing plant and microbial-derived compounds in the MAOM pool (e.g., proteins, hexoses, short-chain lipids, phenols). The number of truly quantitative studies examining the plant and microbial origins of MAOM is limited; more studies are needed using a variety of methodological approaches.
- Resolving the direct sources of MAOM (e.g., root exudates, plant litter DOM, microbial cell residues, EPS) will help to elucidate the dominant controls on SOM formation.
- Future research would benefit from a strategic plan for improving quantification of plant- versus microbial-derived SOM. Below, we outline several tangible steps, as well as key challenges and open questions for further research.

7 | FUTURE DIRECTIONS

- *Methodological recommendations*:
  - Given limitations inherent to individual methods, we call for future studies to use integrated approaches that draw on a combination of methods (e.g., amino sugars and molecular fingerprinting analysis). Researchers should evaluate whether the results of each analysis corroborate one another, and the specific limitations of each method should be considered within the context in which it is used. Plant-derived SOM should be quantified directly using plant-specific biomarkers, rather than indirectly as the difference between total and microbial-derived SOM, and other potential sources of SOM (e.g., soil fauna, pyrogenic OM) should be considered.
  - To constrain error in amino sugar analysis (the most common approach for quantifying microbial-derived SOM), researchers should measure the ratio of Gram-positive to Gram-negative bacteria in their samples and calculate a site-specific bacterial conversion factor. Novel approaches that pair amino sugars with stoichiometric calculations (Deng & Liang, 2022) or isotopic methods (Hu et al., 2018) should be considered. Given that the amino sugar method targets microbial cell wall components, it may be particularly well paired with methods that assess extracellular microbial compounds (e.g., EPS).
  - In molecular fingerprinting studies, novel reference materials should be used that integrate the chemistry of plant or microbial biomass alongside their extracellular products (e.g., root exudates and other forms of plant DOC, microbial EPS). Data from artificial soil experiments may be especially useful toward this aim. The potential for preferential accumulation of specific compounds (e.g., proteinaceous N, phenolics) in soils over time should be considered when making comparisons between experimental samples and reference materials.
  - Novel approaches should be considered for their application to the question of plant- versus microbial-derived SOM (e.g., POST-C7 NMR, Ernakovich et al., 2021; lipidomics, Neurath et al., 2021). Long-term isotope tracer studies in field or laboratory mesocosms with living plants and labeled microbial necromass may be a particularly promising approach, especially if combined with molecular fingerprinting and/or biomarker approaches to corroborate estimates of plant- and microbial-derived SOM.
- *Key research questions and priorities*:
  - Our synthesis reveals that both plants and microbes could be sources of the compounds commonly found in MAOM (Figures 1 and 2). This observation raises questions about the relevance of the plant versus microbial origin of SOM. Some compound classes, due to shared physicochemical properties, may be more soluble and/or have a stronger affinity to soil minerals, regardless of their plant or microbial origin. In this case, the total rate of production and availability of specific compounds (e.g., certain polysaccharides, short-chain lipids, proteins, phenols) may matter more to MAOM formation than the plant or microbial origin of these compounds.
  - However, if research reveals that either plants or microbes have a greater likelihood of contributing to the MAOM pool, then the origin of SOM has important practical implications for its management and representation in models. More research is needed to resolve the likelihood of plant versus microbial contributions to MAOM across different ecosystem contexts, and within vertical and horizontal soil space (e.g., surface vs. deep soil, sensu Kaiser & Kalbitz, 2012; rhizosphere vs. bulk soil, sensu Sokol et al., 2019).
  - **Addressing the following knowledge gaps will help to resolve some of these uncertainties:**
  - On average, does the persistence of microbial-derived SOM differ from that of plant-derived SOM?
  - Do microbes contribute more to MAOM formation than plants because they interact over a larger surface area with mineral surfaces than do plant roots (e.g., ~102,000 cm fungal hyphae cm^{-3} soil vs. ~6.8 cm fine roots cm^{-3} soil; See et al., 2022)?
  - What is the direct quantitative contribution of plant rhizodeposits to MAOM (Figure 1b)? Although rhizodeposits are increasingly recognized as an important source of plant C to the MAOM pool (Sokol & Bradford, 2019; Villarino et al., 2021), it is unclear what proportion of these plant inputs are directly sorbed within MAOM versus microbially assimilated and transformed before incorporation.
  - What is the quantitative contribution of microbial EPS to MAOM (Figure 1d)? Microbial EPS are comprised of polysaccharides, proteins, uronic acids and lesser quantities of DNA and glycolipids (Flemming & Wingender, 2010), and thus encompass many of the major compound classes found in MAOM. EPS appear to be abundant in mineral soils (e.g., Chenu & Jaunet, 1992; Chenu & Stotsky, 2002), and continued advancements in EPS extraction techniques (Redmile-Gordon et al., 2014; Wang et al., 2019) and other methods of quantification will help resolve their overall contribution to SOM.

AUTHOR CONTRIBUTIONS

Emily D. Whalen, A. Stuart Grandy, Noah W. Sokol, and Serita D. Frey conceived of the concept for this review. Emily D. Whalen led the data and literature synthesis, figure concepts and writing. Emily D. Whalen and A. Stuart Grandy contributed to the artistic development of figures. All authors contributed to idea development, writing, and editing of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this review article as no new datasets were generated or analyzed in this study.

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