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Hyphae move matter and microbes to mineral microsites: Integrating the hyphosphere into conceptual models of soil organic matter stabilization

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Abstract

Associations between soil minerals and microbially derived organic matter (often referred to as mineral-associated organic matter or MAOM) form a large pool of slowly cycling carbon (C). The rhizosphere, soil immediately adjacent to roots, is thought to control the spatial extent of MAOM formation because it is the dominant entry point of new C inputs to soil. However, emphasis on the rhizosphere implicitly assumes that microbial redistribution of C into bulk (non-rhizosphere) soils is minimal. We question this assumption, arguing that because of extensive fungal exploration and rapid hyphal turnover, fungal redistribution of soil C from the rhizosphere to bulk soil minerals is common, and encourages MAOM formation. First, we summarize published estimates of fungal hyphal length density and turnover rates and demonstrate that fungal C inputs are high throughout the rhizosphere–bulk soil continuum. Second, because colonization of hyphal surfaces is a common dispersal mechanism for soil bacteria, we argue that hyphal exploration allows for the non-random colonization of mineral surfaces by hyphae-associated taxa. Third, these bacterial communities and their fungal hosts determine the chemical form of organic matter deposited on colonized mineral surfaces. Collectively, our analysis demonstrates that omission of the hyphosphere from conceptual models of soil C flow overlooks key mechanisms for MAOM formation in bulk soils. Moving forward, there is a clear need for spatially explicit, quantitative research characterizing the environmental drivers of hyphal exploration and hyphosphere community composition across systems, as these are important controls over the rate and organic chemistry of C deposited on minerals.

KEYWORDS
carbon cycling, carbon sequestration, fungal ecology, MAOM, microbe mineral interactions

1 | INTRODUCTION

Soils store the majority of organic carbon (C) in terrestrial systems, and a mechanistic understanding of the formation of soil organic matter (SOM) with long residence time will be crucial to predicting future atmospheric C concentrations (Sulman et al., 2018). Recent work has focused extensively on the formation of mineral-associated organic matter (MAOM) due to its potential to persist for decades to millennia (Dungait et al., 2012; Schmidt et al., 2011). Broadly defined, MAOM consists of low molecular weight organic molecules that are chemically or physically bound to soil mineral surfaces (Lavallee et al., 2019), although both the molecular species and bond types vary considerably (Kleber, et al., 2015; Kögel-Knabner et al., 2008). While plant-derived compounds represent the ultimate source of new soil

C, there is growing recognition that microbial residues are the proximate source of the majority of MAOM in many soils (Angst et al., 2021; Castellano et al., 2015; Cotrufo et al., 2013; Grandy & Neff, 2008; Liang et al., 2017; Miltner et al., 2012; Sokol et al., 2019a).

The rhizosphere, defined as the zone of biological influence surrounding the root, serves as a spatially explicit point of entry for newly fixed C into mineral soils and a nexus of microbial activity (Kuzyakov & Blagodatskaya, 2015). Accordingly, the spatial extent of the rhizosphere has been proposed as a dominant control over the location of new microbially derived MAOM in soil (Rasse et al., 2005; Sokol & Bradford, 2019). Although conceptually attractive, focus on the rhizosphere as the dominant location of new microbially derived MAOM is hard to reconcile with observations from CO_2 pulse-labeling studies, which often recover large proportions (c. 30%–50%) of belowground plant C allocation outside of the rhizosphere within days of label addition (Huang et al., 2020; Leake et al., 2001; Norton et al., 1990). Much of this C flux from the rhizosphere into non-rhizosphere soils likely occurs via mycorrhizal fungal hyphae, which can explore soil centimeters away from the root (Agerer, 2001; Friese & Allen, 1991). Similarly, saprotrophic soil fungi can redistribute C from high- to low-organic matter soil regions while searching for patchily distributed nutrients (Frey et al., 2003). Fungal hyphae and the zone they influence (the "hyphosphere," Figure 1b) represent a ubiquitous and dynamic network of labile C, but have not been explicitly included in conceptual models of MAOM formation which assume that the rhizosphere is the point of conversion of plant C to MAOM (Miltner et al., 2012; Schmidt et al., 2011; Sokol et al., 2019). While the rhizosphere is undoubtedly an important entry point of newly fixed C to soils, we believe that conceptual omission of the hyphosphere fundamentally hinders understanding of microbial processes critical to the rate and spatial extent of MAOM formation.

Due to their micron-scale filamentous growth form, standing stocks of hyphae from all fungal trophic modes fill meters of pore space within a single cubic centimeter of soil, and hyphal turnover represents a large flux of labile organic matter at spatial scales relevant to MAOM formation (Godbold et al., 2006). Mycorrhizal hyphal growth, in particular, is increasingly recognized as an important mechanism for the incorporation of newly fixed C into SOM (Cairney, 2012; Clemmensen et al., 2013; Ekblad et al., 2013; Frey, 2019; Godbold et al., 2006; Leake et al., 2004). Estimates of ectomycorrhizal (EcM) fungal hyphae production range from 40 to 1000 kg ha^{-1} year^{-1} in the top 10 cm of soil (Ekblad et al., 2013), while Miller et al. (1995) found arbuscular mycorrhizal (AM) fungal hyphal production of 339–457 kg ha^{-1} year^{-1} at the same soil depth. These estimates suggest that hyphal production is potentially comparable to fine root production (c. 400–1500 kg ha year^{-1}; Jackson et al., 1996, 1997a; McCormack et al., 2015). Although hyphal densities are typically assumed to be higher inside the rhizosphere, both rhizosphere and non-rhizosphere soils often have similar fluxes of newly fixed C into fungal biomass (Huang et al., 2020). Thus, the hyphosphere, which is more spatially extensive and temporally dynamic than the rhizosphere, likely plays an underappreciated role in the underlying processes driving MAOM formation.

Here, we summarize multiple lines of evidence to demonstrate that fungal hyphae are crucial to the transport and stabilization of
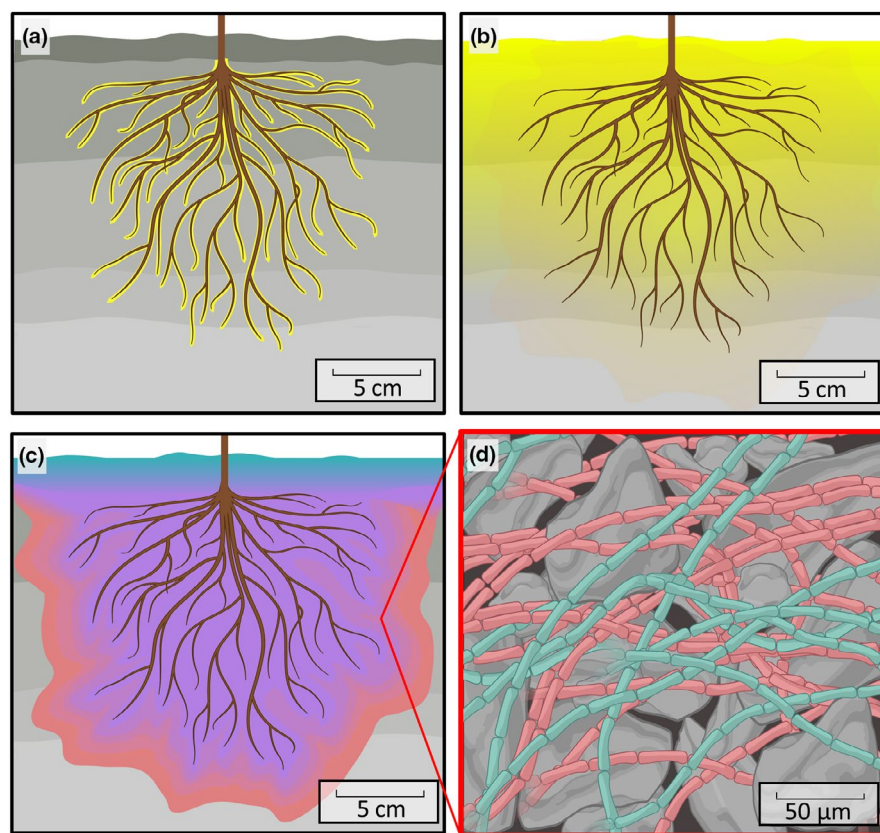

FIGURE 1 A generalized soil profile showing the spatial extent of the rhizosphere (in yellow, panel a), contrasted with the spatial extent of the hyphosphere (in yellow, panel b). New leaf litter inputs are dominated by saprotrophic fungi (in blue, panels c and d), while regions of lower organic matter in deeper soils are dominated by mycorrhizal fungi (in red, panels c and d). A co-dominance of both fungal guilds is present in multiple parts of the hyphosphere (in purple, panel c). Fungi transport of carbon to mineral soil particles that are spatially distant (i.e., mm to cm) from the rhizosphere (panel d) [Colour figure can be viewed at wileyonlinelibrary.com]

organic matter throughout the soil matrix. First, we contend that because of the high density, rapid turnover, and rapid decomposition rate of hyphae, a large proportion of organo-mineral interactions in soil originate from hyphosphere- rather than rhizosphere-derived C. Second, we describe mounting evidence suggesting that hyphae act as "highways" upon which unicellular microbes travel or are transported, helping disperse these organisms to reactive mineral sites beyond the rhizosphere. Third, we identify three distinct sources of organic matter transferred from hyphae to mineral surfaces upon colonization. Collectively, these properties of the hyphosphere suggest that hyphal movement of matter and microbes through soil drives rates of MAOM formation. We briefly discuss predictions for how environmental controls on hyphosphere function might affect rates of MAOM formation, and conclude with a set of research priorities that will be key to integrating the hyphosphere into conceptual and process-based models of MAOM formation. Although our focus is on drivers of organo-mineral interactions, the hyphosphere properties reviewed here also have implications for particulate organic C accumulation and organic matter decomposition.

2 | HYPHAE DISTRIBUTE CARBON TO MINERALS

Soil hyphal growth and turnover are difficult to accurately quantify in situ (Fernandez, 2021), but estimates of standing stocks of hyphae clearly demonstrate their importance relative to roots in distributing C throughout the soil matrix. Fungi explore more pore space than roots, and modeling efforts suggest that plant investment into mycorrhizal hyphae (per unit mass) results in several-fold higher length and surface area for resource acquisition than the same investment in roots (McCormack & Iversen, 2019). Based on a literature search of field studies ($N = 26$ studies, 43 sites), hyphal length density in EcM-dominated soils averaged 175,000 cm cm^{-3} (Table 1, Data S1 for calculation methods). For studies that measured only AM hyphae (i.e., that excluded other fungi), densities averaged 2000 cm cm^{-3} (Table 1). In contrast, global estimates of root length density average just 6.8 cm cm^{-3} (Jackson et al., 1997). Thus, the surface area of potential mineral binding sites in contact with standing stocks of soil hyphae considerably exceeds the number of sites in direct contact with root surfaces in most soils.

In addition to the large spatial extent of standing hyphal biomass, the ephemeral nature of fungal hyphae means that they explore more soil volume than roots do per unit time. Although published estimates of hyphal turnover rate are sparse, methodologically inconsistent, and largely focused on mycorrhizal fungi, some patterns have emerged. For example, the turnover rates of AM hyphae appear to be much faster than those of EcM hyphae (Table 2). Multiple studies have found that the lifespan of absorbent AM hyphae is less than 1 week (Table 2), suggesting turnover rates as rapid as five times per month, although rates are slower during the dormant season (Treseder et al., 2010). Turnover rates of AM have either been assessed visually by following individual hyphae through time (using a soil window or

TABLE 1 Estimates of hyphal length density (mean and range to the nearest hundred, number of sites) and fine root length density averaged by vegetation type in the top 30 cm of soil

Density in soil (cm cm^{-3})	Woody systems	Non-woody systems	Croplands	Mean
Total hyphae	175,400 (EcM biased[a]) (900–1,255,400; n = 8)	28,200 (5300–61,800; n = 4)	4600 (2800–6600; n = 3)	102,000 (900–1,255,400; n = 15)
AM only	2400 (100–13,000; n = 6)	2700 (300–15,000; n = 15)	300 (200–600; n = 7)	2000 (100–15,000; n = 28)
Fine roots[b]	1.6	19.2	3.1	6.8

Note: Total hyphal estimates reflect studies where the length of all fungal hyphae was quantified. Arbuscular mycorrhizal fungi (AM) estimates reflect studies where AM hyphae were measured using AM-specific protocols.

[a]Estimates of total hyphae in woody systems include data from studies that used sand in-growth cores intended to quantify EcM hyphae, and are thus an underestimation of the entire hyphosphere because they underestimate the contribution of saprotrophic fungi.

[b]Fine root length density estimates were derived from Jackson et al. (1997). Data and calculation methods available in Data S1.

TABLE 2 Literature estimates of monthly mycorrhizal hyphal turnover rates (i.e., the number of times the hyphal pool replaces itself in 1 month; inverse of hyphal lifespan), plant host community, and method of estimation

Host species or community	Hyphal type	Turnover rate	Method	Source	Study location
Plantago lanceolata	AM	4.3–5 month^{-1} (5–6 day lifespan)	Repeated hyphal extraction after $^{14}CO_2$ pulse label	Staddon et al. (2003)	Pot study
Artemisia tridentata and *Oryzopsis hymenoides*	AM	4.3–6.3 month^{-1} (5–7 day lifespan)	Direct observation (soil window)	Friese and Allen (1991)	Pot study
Lycopersicum esculentum	AM	5.8 month^{-1} for branched structures	Direct observation (soil window)	Bago et al. (1998)	Pot study
Prunus pennsylvania, Rubus spp. woodland	AM and saprotrophs	1.3–10 month^{-1} (majority >4.3 month^{-1})	Direct observation (soil window)	Atkinson and Watson (2000)	Field study
Plantago lanceolata	AM	5.8 month^{-1} for branched structures, <1 month^{-1} for runner hyphae	Repeated fatty acid sampling after $^{13}CO_2$ pulse label	Olsson and Johnson (2005)	Pot study
Bromus diandrus, Bromus hordaceous, Avena fatua	AM and saprotrophs	median 0.2 month^{-1} during dormant season	Direct observation (minirhizotrons)	Treseder et al. (2010)	Field study
Mixed *Pinus* & *Quercus* forest	EcM	0.4 month^{-1}	Direct observation (minirhizotrons)	Allen and Kitajima (2014)	Field study
Pinus sylvestris	EcM (ergosterol)	0.3 month^{-1}	Sequential ingrowth bags	Hagenbo et al. (2017)	Field study
Pinus taeda	EcM (ergosterol)	1.1 month^{-1}	Sequential ingrowth bags	Ekblad et al. (2016)	Field study
Pinus palustris	EcM (ergosterol)	0.8 month^{-1}	Sequential ingrowth bags	Hendricks et al. (2016)	Field study
Temperate deciduous AMF and EMF forests	EcM and saprotrophs (ergosterol)	0.3 month^{-1}	Sequential ingrowth bags	Cheeke et al. (2020)	Field study
Pinus pinaster, Pinus sylvestris and *Quercus ilex*	EcM (ergosterol)	0.6–0.8 month^{-1}	Sequential ingrowth bags	Hagenbo et al. (2021)	Field study

minirhizotron) or by repeated measurements of hyphal C isotopes following $^{13}CO_2$ pulse labeling (Table 2). These two methods have largely yielded similar turnover rates, suggesting that these estimates are robust. In general, EcM hyphal turnover rates have been assessed less directly than AM turnover, and are typically estimated by combining hyphal production rates from sand-filled ingrowth cores with estimates of standing hyphal biomass from ergosterol extractions (Cheeke et al., 2020; Ekblad et al., 2016). This approach assumes that the sand substrate within the ingrowth cores limits the presence of saprotrophic fungi and therefore targets EcM hyphal turnover, but this assumption may be problematic (Branco et al., 2013; Fernandez, 2021). EcM-focused studies conducted in the field estimate turnover rates ranging from 0.3 to 1.1 month^{-1} (Table 2). These lower estimates of monthly hyphal turnover are still notably higher than annual estimates of fine root turnover, which average 0.84 ± 0.03 year^{-1} globally (or 0.07 month^{-1}, calculated using the Fine Root Ecology Database (FRED); Iversen et al., 2017; Appendix S2).

While we recognize that the summary estimates of both hyphal density and turnover could be better constrained, their magnitude in relation to fine root density and turnover clearly demonstrates the importance of fungal hyphae to the frequency of organo-mineral interactions in soil. Assuming a monthly EcM hyphal turnover rate of 0.6 month^{-1} (mean across studies in Table 2) and average hyphal density of 175,400 cm cm^{-3} (average of woody systems, Table 1), this suggests that fungi have the potential to explore more than 100,000 cm of pore space per cm^3 in a single month. The same calculation for AM fungi (mean hyphal turnover = 5.2 month^{-1} during the active season, average density in non-woody systems = 2700 cm cm^{-3}) suggests these hyphae have the potential to explore almost 14,000 cm cm^{-3} of soil per month. These monthly estimates of potential hyphal exploration stand in stark contrast to annual estimates of potential root exploration. Using global averages of fine root density (Table 1), and turnover rates (Appendix S2), annual root exploration potential averages only 2.1 cm cm^{-3} year^{-1} in woody systems and 11.7 cm cm^{-3} year^{-1} in non-woody systems (Appendix S2). Even with the high uncertainty associated with each of these values, the data strongly signal the importance of hyphae for distributing C through soils. While mycorrhizal hyphae are important as a flux of newly fixed C to minerals, saprotrophic hyphae also redistribute C from detritus to minerals, and are thus important in the context of MAOM formation. More accurate estimates of the hyphal length density and turnover rates for entire fungal communities (and within guilds) are needed across systems, along with a better understanding of the factors which influence these dynamics.

3 | HYPHAE DISTRIBUTE OTHER MICROBES THROUGH SOIL

As hyphae redistribute organic matter through soils, they provide resources and a physical structure allowing for the transport and establishment of microbial communities across microsites (Guennoc et al., 2018; Junier et al., 2013; Nazir et al., 2010; Warmink et al., 2011). To endure the spatial and temporal patchiness of soil water and resource availability (Vos et al., 2013), the majority of unicellular microbes are non-motile, existing as colonies anchored to surface particles by extracellular polymeric substances (EPS; Costa et al., 2018). Dispersal of motile (flagellated) microbes through the soil matrix is prevented by air pockets, with motility largely restricted to water films that connect particles (Dechesne et al., 2010). Regardless of dispersal mechanism, successful microbial establishment upon arrival at a new microsite may be limited by resource availability. In contrast, hyphae-forming fungi move freely through soil pores, providing unicellular microbes both a trail of labile C (Gorka et al., 2019) and a hydrated surface upon which to travel (Kakouridis et al., 2020). Bacterial migration along these "fungal highways" is well documented; flagellated bacteria swim along the water films on hyphal surfaces (Simon et al., 2015; Zhang et al., 2018) and biofilms of non-motile bacteria enmeshed in EPS have been observed on the hyphae of AM, EcM, saprotrophic, and plant pathogenic fungi (Guennoc et al., 2018; Hover et al., 2016; Nazir et al., 2014; Scheublin et al., 2010; Simon et al., 2015). Notably, these biofilms occur on both live and dead hyphae (Guennoc et al., 2018), but tend to concentrate along the leading tips of hyphae (Guennoc et al., 2018; Nazir et al., 2014; Otto et al., 2017), underscoring the importance of fungal exploration to new bacterial colony establishment (Warmink et al., 2011).

Bacterial assemblages associated with fungal hyphae are not random (Deveau et al., 2018; Emmett et al., 2021), which affects MAOM formation because bacterial taxa vary considerably in their chemical interactions with minerals (Huang et al., 2005). The composition of the hyphal microbiome varies phylogenetically across fungal taxa, as well as across fungal guilds (i.e., mycorrhizal vs. saprotrophic), reflecting different needs for resource acquisition (e.g., organic matter decomposition vs. mineral nutrient acquisition; Pent et al., 2020). Bacterial community composition in the hyphosphere varies with nutritional demand in both mycorrhizal (Gorka et al., 2019; Wang et al., 2019); and saprotrophic fungi (Zhang et al., 2020), and the functional genomics of bacteria residing on a single fungal taxon can be experimentally altered based on nutrient addition (Zhang et al., 2020). Multiple lines of evidence suggest that the presence of individual fungal taxa can structure the composition and function of soil bacterial communities (Jeewani et al., 2021; Liu et al., 2018; Nuccio et al., 2013; Yuan et al., 2021; Zagryadskaya et al., 2011), which can subsequently impact organo-mineral interactions (Jeewani et al., 2021). In sum, the fungal community composition of the hyphosphere affects the functional diversity of the bacterial communities colonizing soil minerals, with clear implications for the organic chemistry of MAOM formation.

4 | HYPHAL ESTABLISHMENT ON MINERAL SURFACES ENCOURAGES MAOM FORMATION

Mounting evidence suggests that a large proportion of MAOM consists of common microbial biomolecules such as polysaccharides,

lipids, organic acids, and enzymes (Grandy & Neff, 2008; Heckman et al., 2018; Miltner et al., 2012). As fungi comprise the majority of soil microbial biomass (He et al., 2020) and necromass (Liang et al., 2019; Simpson et al., 2007), they likely contribute disproportionately to microbially derived MAOM. Hyphal proliferation along soil mineral surfaces leads to the production and subsequent sorption of microbial compounds from three distinct sources: (1) exudates (e.g., sugars, organic acids, and enzymes) from live hyphae and their associated microbes (Figure 2a), (2) the direct decomposition products of the fungal necromass (Figure 2b), and (3) molecules originating from processes of microbial succession during hyphal necromass decomposition (e.g., EPS, exudates, and bacterial necromass products; Figure 2c). The relative importance of these sources likely depends on both hyphosphere community composition (Anthony et al., 2020) and soil mineralogy (Creamer et al., 2019; Heckman et al., 2018).

Both hyphae and associated microbes release organic compounds into their surrounding environment that have the potential to interact with minerals (Figure 2a). The simplest of these molecules are sugars exuded by hyphae to stimulate growth of unicellular symbionts and increase nutrient acquisition (Zhang et al., 2016). Many of the compounds produced by hyphosphere microbes are intended to degrade existing SOM for energy or nutrients, but also have the potential to form new MAOM. For instance, extracellular enzymes intended to liberate organic matter or nutrients can form stable bonds with clay minerals (Olagoke et al., 2019), and may represent an underappreciated source of MAOM in some systems. Indeed, a recent comparison across Critical Zone Observatory sites in the United States found that 80% of the enzymes present in the whole soil column were sorbed to clays in deep mineral soils (Dove et al., 2020). Similarly, mineral-sorbed organic acids are thought to originate from root exudates and leached organic matter (Sokol et al., 2019), but may in fact be derived from fungi, since hyphae produce large quantities of these acids to accelerate the weathering of minerals (Blum et al., 2002; Hoffland et al., 2004; Smits & Wallander, 2017). Given the close proximity of hyphae

to mineral surfaces, it is likely that the hyphosphere represents an important source of these exudates for the formation of MAOM in mineral soils. In the case of exudates with high mineral affinity (e.g., oxalic acid), fungal production would lead to higher rates of sorption in deeper soils than expected based solely on leaching from surficial horizons (e.g., Mikutta et al., 2019; Sokol et al., 2019).

As hyphae senesce, the decomposition products of fungal necromass present a wide range of organic molecules available for mineral sorption (Figure 2b). When fungal cells lyse, soluble components within the cell such as amino acids and sugars become available to the surrounding environment and can sorb to mineral surfaces or be consumed by decomposers for further transformation (see below). Depolymerization of beta-glucans and chitin, the dominant components of fungal cell walls, occurs over the course of days to weeks (See et al., 2020), providing opportunities for sorption of amino sugar monomers or polysaccharide chains (Keiluweit et al., 2012). As hyphal necromass decomposition proceeds, more slowly decomposing cell wall components yield more complex molecules for organo-mineral interactions. For example, many dikaryotic fungi (including many EcM species) contain melanins within their cell walls that can persist for years as particulate matter in litterbags (Fernandez et al., 2019), and melanized sclerotia have been shown to persist in soils for millennia (Scott et al., 2010). The formation of organo-mineral complexes from melanin-derived molecules remains poorly characterized. However, such complexes are likely important given the ubiquity of melanized fungi (Siletti et al., 2017; Van Der Wal et al., 2009) and the fact that other complex aromatic molecules (i.e., lignins) contribute substantially to mineral-bound SOM (Angst et al., 2021; Rasse et al., 2005). In a study of microbial growth in lignin-free model soils, increased mineral-associated phenolic and aromatic compounds were observed after 18 months (Kallenbach et al., 2016), suggesting the accumulation of fungal melanins. Thus, both labile and recalcitrant components of fungal necromass likely contribute directly to new MAOM formation.
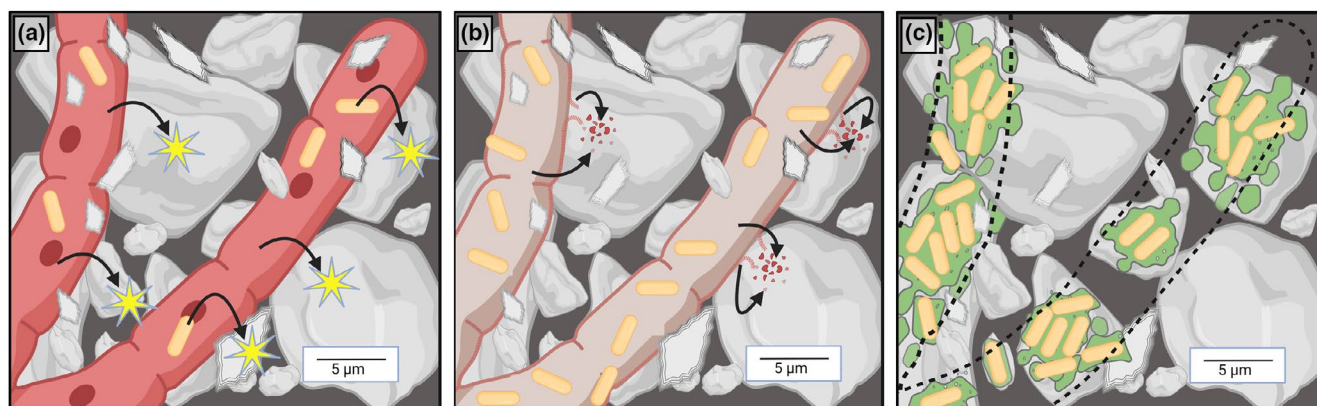

FIGURE 2 Three sources of hyphosphere C transfer to mineral surfaces, shown chronologically beginning with initial establishment of a live hyphal tip at a new microsite. Source 1: Live hyphae and associated bacteria exude organic molecules (e.g., enzymes, sugars, organic acids, depicted by stars) into their surroundings (panel a). Source 2: During the early stages of fungal necromass decomposition, hyphal cytoplasm components, cell wall polysaccharides, and lipids originating from the necromass are released (depicted as red dots on mineral surface; panel b). Source 3: As fungal necromass decomposition proceeds, microbial succession leads to a buildup of EPS (in green) enmeshing remnants of recalcitrant fungal cell wall structures (e.g., melanins) along the mineral surface (panel c) [Colour figure can be viewed at wileyonlinelibrary.com]

Fungal necromass contains a higher proportion of labile C (e.g., cell soluble sugars, polysaccharide chains) than root litter, and decomposition rates of labile components of hyphae are commonly measured in days, while fine root decomposition is commonly measured over the course of years (See et al., 2019, 2020). As hyphal necromass decomposes, it forms the base of a complex food web of microbial decomposers dominated by bacteria (López-Mondéjar et al., 2018) that anchor themselves to the hyphal remnants and adjacent mineral surfaces with EPS (Figure 2c). This biofilm production is thought to be a dominant source of MAOM in many soils (Kleber et al., 2015). The bacterial taxa present on living mineral-associated hyphae are likely some of the earliest necromass decomposers when hyphae senesce. For instance, biofilms of *Pseudomonas* species are common on the EcM genus *Laccaria* and thought to be beneficial to the fungi (Duponnois & Garbaye, 1991; Guennoc et al., 2018; Labbe et al., 2014), and these taxa have also been observed in high numbers during the first weeks of fungal necromass decomposition in field studies (Beidler et al., 2020; Brabcová et al., 2016; Fernandez & Kennedy, 2018). As microbial succession proceeds, other decomposer taxa establish, likely arriving via new hyphae or by traveling along EPS pathways established on the decomposing hyphae. Within days to weeks little of the original hyphal necromass remains, but the microbial residues that replace it will still be composed primarily of C originally deposited by the colonizing hyphae (Figure 3; Appendix S3).

5 | DRIVERS OF HYPHOSPHERE FUNCTION RELATED TO MAOM FORMATION

The research summarized above highlights a need to understand the factors controlling the variability of hyphosphere spatiotemporal dynamics and microbial community composition across systems (Figure 4). Hyphosphere spatiotemporal dynamics (i.e., the rate and spatial extent of hyphal exploration) exert strong controls over the flux of new C to soil mineral surfaces, and thus influence the rate of new MAOM formation. Similarly, hyphosphere fungal and bacterial community composition control the molecular composition of new C deposited at sites for potential MAOM formation. Current understanding of the environmental controls over hyphosphere exploration and community composition is nascent, but some general principles have started to emerge.

The dominant fungal trophic mode of the hyphosphere (i.e., mycorrhizal vs. saprotrophic) differs spatially throughout the soil profile (Figure 2c). Saprotrophic fungi are limited by the availability of both C and soil nutrients, and their exploration will be higher in regions with higher SOM where these resources are coupled. In contrast, mycorrhizal fungi are not limited by soil C availability, and their hyphal exploration is dictated instead by the nutrient demands of the plant host (Han et al., 2020; Smith & Read, 2008), suggesting that mycorrhizal fungi may play a disproportionate role in distributing newly fixed C to mineral soil (Ekblad et al., 2013; Godbold et al., 2006). Indeed, the proportion of mycorrhizal hyphae relative

to saprotrophic hyphae increases with decreasing SOM:mineral content in soils (Carteron et al., 2020; Lindahl et al., 2007; Schlatter et al., 2018). It was recently demonstrated that the contribution of AMF-associated compounds to soil C pools increases with depth in mineral soil (Wang et al., 2017); similar patterns with depth have been observed with EcM-associated melanins (Clemmensen et al., 2015), although the latter study was conducted in a highly organic soil. It appears that EcM mycelial networks may be more extensive than those of AM fungi in their spatial exploration (Table 1), suggesting greater rates of deposition onto minerals, but this may be partially offset by the fact that AMF hyphae turn over more rapidly (Table 2). However, there is considerable variation within both EcM and AM fungi in terms of hyphal exploration (Agerer, 2001; Jakobsen et al., 1992; Joner & Jakobsen, 1995; Schnepf et al., 2008), and species composition within both of these guilds varies with soil depth and organic matter content (Bahram et al., 2015; Rosling et al., 2003). As noted above, this fungal taxonomic diversity also structures hyphosphere bacterial diversity (sensu Section 3), and likely affects not only the rate of C accumulation in mineral soils, but also the organic chemistry of the C deposited (Figure 4).

Environmental stressors play an important role in structuring the composition and function of hyphosphere fungal and bacterial communities (Lustenhouwer et al., 2020; Moore et al., 2021), likely with cascading effects on the rate and chemistry of MAOM formation. A full review of these stressors is beyond the scope of this review, but examples include edaphic factors such as soil water availability, pH, and salinity (Rath & Rousk, 2015; Schimel, 2018; Tedersoo et al., 2020). Thus, natural and anthropogenic disturbances leading to fungal stressors such as drought (Querejeta et al., 2009), fire (Hopkins et al., 2021), atmospheric N deposition (Moore et al., 2021), or mining (Kane et al., 2020) have the potential to alter rates of MAOM formation by altering hyphosphere communities. Importantly, environmental stressors not only lead to altered hyphosphere community composition, but also affect the physiology of individual taxa related to C use and MAOM formation (Schimel & Schaeffer, 2012). For instance, melanized structures in fungi are energetically expensive to produce, and protect fungal cells from environmental stressors ranging from desiccation to metal toxicity (Koide et al., 2014). Melanization of the hyphosphere has been shown to occur during periods of drought (Querejeta et al., 2009), affecting the chemistry of C deposition directly by increasing the aromatic complexity of hyphal necromass, and indirectly by structuring the community composition of bacterial decomposers (Fernandez & Kennedy, 2018). Similarly, cell walls composed of beta-glucans may be more resistant to decomposition than those composed of chitin alone, and may be more prevalent in more stressful environments (Treseder & Lennon, 2015). Thus, environmental stressors may play an important role in controlling the functional composition of hyphosphere communities, and ultimately the rate and chemistry of MAOM formation (Koide et al., 2014).

In addition to environmental stressors and fungal trophic mode, hyphal resource demand in relation to resource availability will dictate the extent of hyphal exploration along mineral surfaces. The
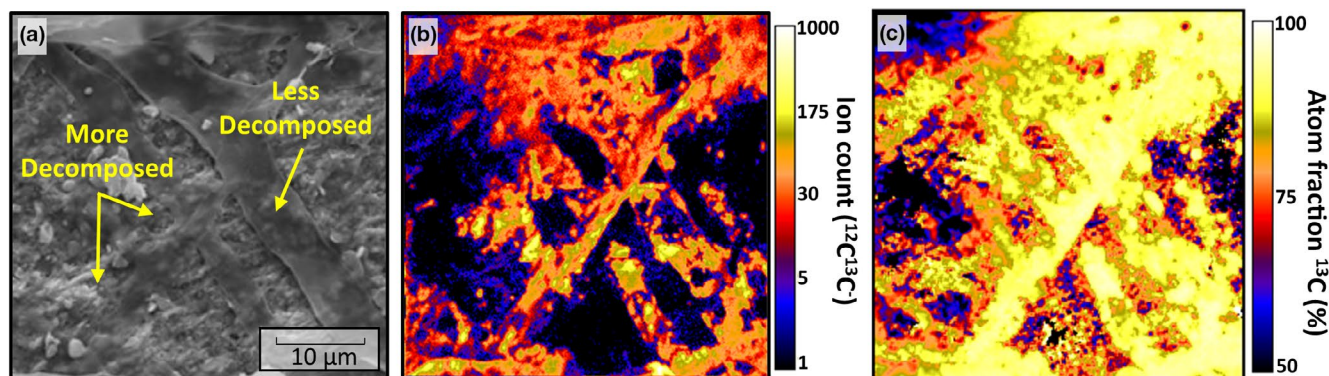
FIGURE 3 Images from a mesocosm experiment where organic matter-free goethite was incubated in live soil for 35 days underneath ^{13}C-enriched decomposing fungal necromass. Minerals were separated from the decomposing substrate by 53 μm mesh, allowing for free movement of live hyphae and soil solution. During the incubation period, living saprotrophic hyphae transferred C from the decomposing substrate to minerals in the adjacent compartment. Panel (a) shows a scanning electron microscope (SEM) image of fungal hyphae in various stages of decomposition along the surface of a goethite particle. Panel (b) shows a Nano-scale Secondary Ion Mass Spectrometry (NanoSIMS) image of the same surface, revealing that the spatial distribution of organic molecules across the microsite (as $^{12}C^{13}C^{-}$ ion counts after ~100 nm of sputtering) was concentrated along the hyphal tracks. Panel (c) is a NanoSIMS image revealing high ^{13}C enrichment (78–95 atom percent) across the surface, demonstrating that the majority of C transferred to the goethite during the incubation originated from the decomposing substrate (located ≤1 mm away). Collectively, these images suggest that the majority of C accumulation on minerals during this experiment was transferred via saprotrophic hyphal exploration, rather than by diffusion through soil water. Further details about this experiment can be found in Appendix S3 [Colour figure can be viewed at wileyonlinelibrary.com]

hyphal growth form evolved in part as an adaptation to account for heterogeneous distribution of the multiple resources required for life (Nagy et al., 2020). Fungal "mining" of mineral-derived nutrients is well documented (Burford et al., 2003; Hoffland et al., 2004), and can represent a significant input of rock-derived nutrients to ecosystem budgets (Blum et al., 2002). Similarly, mycorrhizal fungal exploitation of soil water in mineral soils is common in water-stressed systems (Augé, 2001; Lehto & Zwiazek, 2011). Thus, there may be greater hyphal exploration (and subsequent rates of C deposition) of mineral surfaces in soils where mineral resources (e.g., Ca, P, K, Mg, and water) are in higher demand (Sun et al., 2020). This hypothesis further points to the relative importance of mycorrhizal fungi in rates of MAOM formation, as their lack of C limitation allows them increased access to these regions of lower organic matter (Figure 1c). A comprehensive understanding of multiple resource limitation by fungi and their associated plants and microbes has not yet been achieved, but is an active area of research (Buchkowski et al., 2019; Zechmeister-Boltenstern et al., 2015) with clear implications for the rate of C distribution throughout mineral soils.

Finally, it is worth noting that soil structure and mineralogy are important determinants of MAOM formation (Wang et al., 2019; Wang et al., 2019; Figure 4), and interact with hyphosphere traits reviewed here. For instance, soil structure affects not only the number of mineral sites available for MAOM formation, but also the extent of hyphal exploration (Ritz & Young, 2004; Witzgall et al., 2021), with some proportion of soil volume often inaccessible to hyphae due to small pore sizes. Moreover, emerging evidence suggests that different fungal and bacterial taxa may preferentially colonize different mineral types (Finley et al., 2021; Sun et al., 2020; Zhang et al., 2020), implying complex interactions between soil

mineralogy and the microbes responsible for depositing the organic substrates at mineral surfaces (Jilling et al., 2018; Kleber et al., 2015). Understanding of these microbe–mineral interactions and their effects on the formation and cycling of MAOM is rapidly evolving, and will remain an important research driver for the foreseeable future.

6 | CONCLUSIONS

The task of integrating the hyphosphere into conceptual and process-based models of MAOM formation will require research across scales and disciplines. There is an urgent need for fine-scale estimates of hyphal exploration and functional community composition within and across mineral soils. Such estimates will require the use of laboratory and field-based mesocosms to provide spatially explicit measurements of hyphal length density, turnover, and microbial community composition. Incorporating buried mineral substrates and stable isotope probing approaches into these experiments would provide invaluable data relating hyphosphere function to rates of MAOM formation (Pett-Ridge & Firestone, 2017). As more studies link hyphosphere function to MAOM formation, a better understanding of the dominant controls of this functional diversity across systems will be necessary for its incorporation into global models. The use of "omics"-based approaches will be crucial to characterizing the response of hyphosphere function to environmental conditions (Romero-Olivares et al., 2021; Starke et al., 2021), but will require validation with trait measurements (Malik et al., 2020). Focusing these tools on genes related to hyphal proliferation, fungal cell wall composition and EPS production by hyphae-associated bacteria would provide a path forward for linking environmental conditions to MAOM formation.
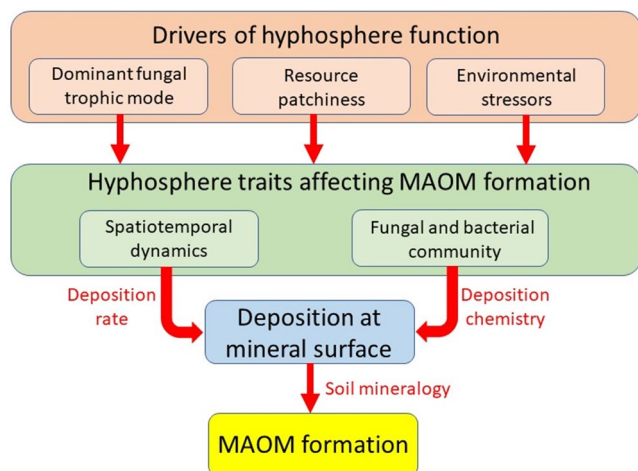
FIGURE 4 A conceptual diagram relating hyphosphere dynamics to MAOM formation. Factors affecting hyphosphere function include the dominant fungal trophic mode (saprotrophic vs. mycorrhizal), the spatial distribution of multiple limiting resources (e.g., C, nutrients, and water), and environmental stressors. The spatial extent of hyphal exploration, combined with turnover rate (i.e., spatiotemporal dynamics), control the magnitude of hyphosphere C flux to new mineral sites. The functional traits of the fungal community and associated bacterial community control the organic chemistry of hyphosphere C flux through differences in exudates, cell wall composition, and EPS production. Collectively, the hyphosphere exerts strong controls over the quantity and form of organic molecules deposited at mineral microsites, and therefore the potential for MAOM formation [Colour figure can be viewed at wileyonlinelibrary.com]

Many reviews and syntheses have highlighted the importance of hyphosphere processes in the decomposition of soil C, including MAOM (Averill et al., 2014; Frey, 2019; Read et al., 2004; Terrer et al., 2021; Wang et al., 2020; Zak et al., 2019). Here, we call attention to the importance of the hyphosphere as an input of new MAOM. We contend that although plant detritus, exudates, and allocation to symbionts are ultimately the source of new C inputs to soil, fungal hyphae are the dominant mechanism by which this C is distributed through the soil matrix. Hyphae explore many orders of magnitude more pore volume than roots (Tables 1 and 2), coming into contact with orders of magnitude more mineral surface area. Furthermore, hyphae shape the organic chemistry of C deposited on mineral surfaces through differences in hyphal chemistry and through their influence on bacterial community composition. Mycorrhizal hyphae may be of particular importance because they represent a flux of newly fixed atmospheric C and are more likely to explore areas of low-organic matter than saprotrophs. A better understanding of the drivers of MOAM formation rates will thus require better characterization of the extent and functional diversity of the hyphosphere in mineral soils.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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