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Forum

Rethinking assumptions about plant litter decomposition

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Abstract

Plant litter decomposition is the breakdown of dead plant biomass by abiotic and biotic means. In terrestrial ecosystems, decomposition regulates the fate of fixed plant carbon, contributing both to its release into the atmosphere and its long-term storage in soil organic matter. In the present article, we revisit four assumptions about decomposition in light of advances in microbiology. First, we consider fungi as primary decomposers, noting bacterial contributions to breaking down lignin and cellulose and overcoming nitrogen limitation. Second, we discuss evidence of the role of microbial communities on litter decomposition, challenging assumptions of microbial redundancy. Third, given these functional consequences of their composition, we examine whether surface litter and bulk soil microbial communities are interchangeable. Finally, we reevaluate the idea that soil organic matter originates from plant litter, emphasizing the pivotal role of microbial necromass. We highlight the importance of integrating microbiological findings into ecosystem ecology to accelerate research on carbon cycling in terrestrial ecosystems.

Keywords: plant litter, microbial communities, carbon cycling, fungal and bacterial traits

Plant litter decomposition and plant growth are the yin and yang that balance biogeochemical cycling in natural terrestrial ecosystems. Decomposition converts dead plant tissues into carbon dioxide while stimulating plant growth through the release of inorganic nutrients. Decomposition also releases smaller organic molecules into the soil that influence the formation and persistence of soil organic matter. Together, these processes play a key role in regulating the carbon balance in terrestrial ecosystems (Chapin et al. 2012). The classic book *Decomposition in Terrestrial Ecosystems* (Swift et al. 1979) established a foundational framework for decomposition research in ecosystem ecology. Swift and colleagues (1979) discussed the importance of a primary suite of factors controlling litter decomposition: the plant community (determining litter chemistry), the physicochemical environment, and the soil biota including invertebrates and microorganisms (primarily, bacteria and fungi). This framework, rooted in the study of temperate forests in the Northern Hemisphere, has been instrumental in shaping our understanding of terrestrial carbon cycling.

Over the past two decades, advances in methodological developments—spanning -omics, chemical analyses, and field experiments—have challenged some of the inherent assumptions of this framework, revealing a more complex and diverse role of microorganisms in the decomposition of plant litter (dead plant biomass). In light of these advancements, in the present article, we revisit four tightly held assumptions about the role of microbes in litter decomposition. Although most researchers do not hold these assumptions unequivocally, the ideas still permeate ecosystem research. We therefore find it useful to contrast these past ideas with newer, emerging views and highlight some outstanding questions that deserve further consideration. Moving beyond these assumptions is essential for developing effective carbon conservation strategies and informing climate change mitigation policies.

Assumption 1: Fungi are primary decomposers, and bacteria, secondary decomposers

Fungi have long been considered the primary—that is, rate limiting—decomposers of plant litter for at least three reasons. First, fungi can degrade lignin, a major component of plant litter and the most abundant form of complex aromatic carbon in the biosphere (Kamimura et al. 2019). Because lignin is mainly located in the plant cell wall, its breakdown is considered a rate-limiting step of litter decomposition. Second, fungal hyphae—the physical structure that most fungi use for vegetative growth—can access cellulose fibers embedded in the polymeric matrix of the plant cell wall (van der Wal et al. 2013). Finally, hyphae can scavenge nutrients from distant sources and thereby alleviate nutrient scarcity that often limits decomposition (Fricker et al. 2017). Together, these features have been interpreted to mean that fungi are the primary drivers of litter decomposition in terrestrial ecosystems, an assumption further supported by high fungus to bacteria ratios in topsoil (He et al. 2020). In contrast, bacteria have been considered the cheaters of the litter community: fungi break down complex carbon molecules releasing smaller byproducts that bacteria consume, whereas bacteria do not provide fungi with resources in return. In contrast, it is assumed that bacteria do not contribute to the limiting reactions of lignin or cellulose degradation or help to access limiting nutrients (De Boer et al. 2005, Rousk and Frey 2015) except for soils with frequent anoxic conditions and fluctuating redox states

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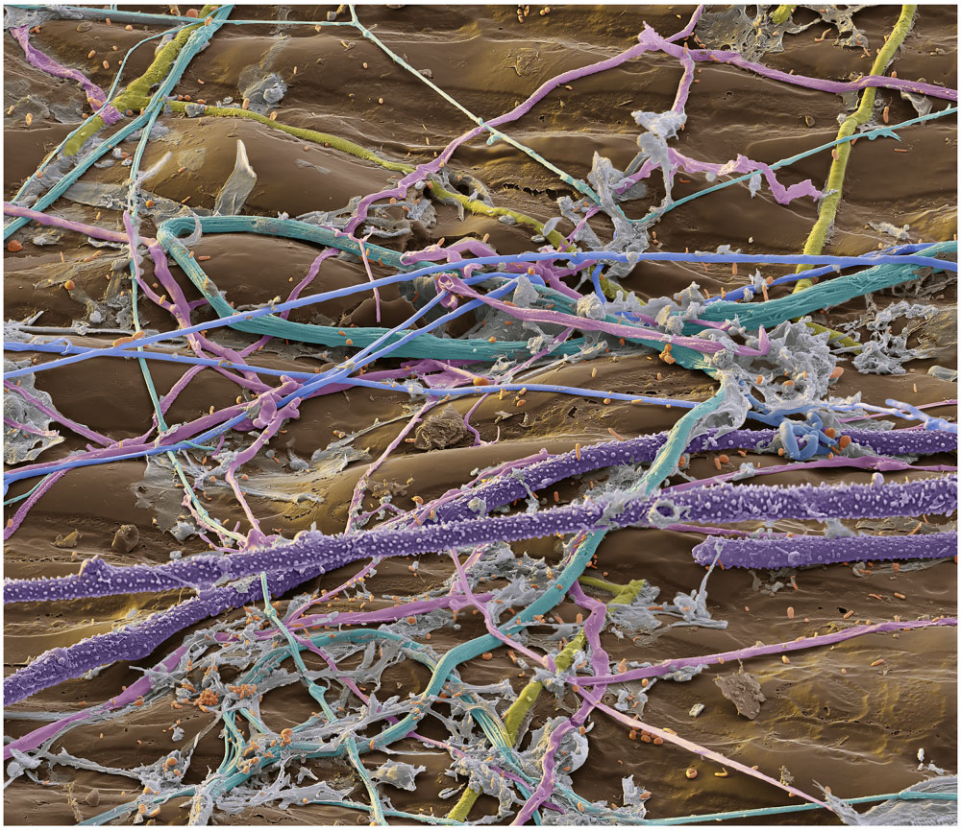

Figure 1. Fungi and bacteria contribute to leaf litter decomposition. Colored scanning electron micrograph of a fallen leaf (background) from the Northern Black Forest, Germany. Hyphae (string-like) of different fungi and bacteria (small spheres) together can drive leaf litter decomposition. Source: Sciencephoto.com.

(DeAngelis et al. 2011). In European temperate forests, for example, extracellular hydrolytic enzymes detected by metaproteomics were exclusively assigned to fungal origin with no detection of bacterial enzymes in the surface litter layer (Schneider et al. 2012). Instead, the abundance of bacteria and the abundance of fungal enzymes were strongly correlated, suggesting that bacteria proliferate on low molecular weight carbohydrates provided by fungal enzymes.

Laboratory and genomic analyses call into question some of the reasoning for fungal dominance outlined above. It is now known that many bacteria can break down both lignin and cellulose (figure 1). In addition to the members of the genus *Streptomyces*, a filamentous Actinomycetota known to degrade lignin (Bontemps et al. 2013), soil bacteria belonging to Alpha- and Gammaproteobacteria and other Actinomycetota can also depolymerize lignin (Bugg et al. 2020, Chen et al. 2024). At least four classes of lignin-degrading enzymes including dye-decolorizing peroxidases, multicopper oxidase enzyme, manganese superoxide dismutase enzyme, and the family of glutathione-dependent β-etherase enzymes have been identified in laboratory studies using bacterial strains such as *Rhodococcus*, *Amycolatopsis*, *Pseudomonas*, *Thermobifida*, *Paenibacillus*, *Ochrobactrum*, and *Sphingobacterium*. Some of these taxa are abundant in the surface litter layer (Purahong et al. 2016, Barbour et al. 2022). Moreover, a cultivation-independent study using a combination of quantitative stable isotope probing and metagenomics in forest soil, identified both Alpha- and Betaproteobacteria families (Comamonadaceae and Caulobacteraceae) that assimilate carbon from various lignocellulolytic polymers (Wilhelm et al. 2019). The result was supported by identifying the necessary suite of catabolic genes for lignin degradation in their genomes. Furthermore, the enzymatic capacity of bacteria to degrade complex plant polysaccharides including cellulose, starch, and xylan is extensive, diverse, and widely distributed among the bacterial phylogeny in both grasslands and forest soils (Berlemont and Martiny 2015, López-Mondéjar et al. 2016). Finally, bacteria, including those in leaf litter (Nelson et al. 2015), encode nitrogen assimilation pathways such as nitrogen fixation that may aid in overcoming nitrogen limitation in leaf litter, even if they cannot scavenge through hyphae (Albright et al. 2019).

Given these new insights, we hypothesize that many bacteria found on plant litter are not just cheaters but coregulators of decomposition. To test this idea, studies will need to simultaneously consider both bacteria and fungi while measuring complex polysaccharide degradation and nitrogen cycling. Coupled dynamics between fungal and bacterial communities have been observed during decomposition, with nonrandom co-occurrences among taxa, suggesting potential interactions (Purahong et al. 2016). For example, fungi may specialize in breaking down recalcitrant fractions of deadwood, whereas nitrogen-fixing bacteria alleviate nitrogen constraints for the microbial community as a whole (Vojtěch et al. 2021). In addition, active bacterial involvement in nitrogen cycling during leaf litter decomposition has been demonstrated (Likar et al. 2023). Reducing the ecosystem bias of decomposition studies is also needed, considering that the importance of bacteria for litter decomposition may depend on the ecosystem characteristics such as litter chemistry and the abiotic environment. Much of our understanding of decomposition

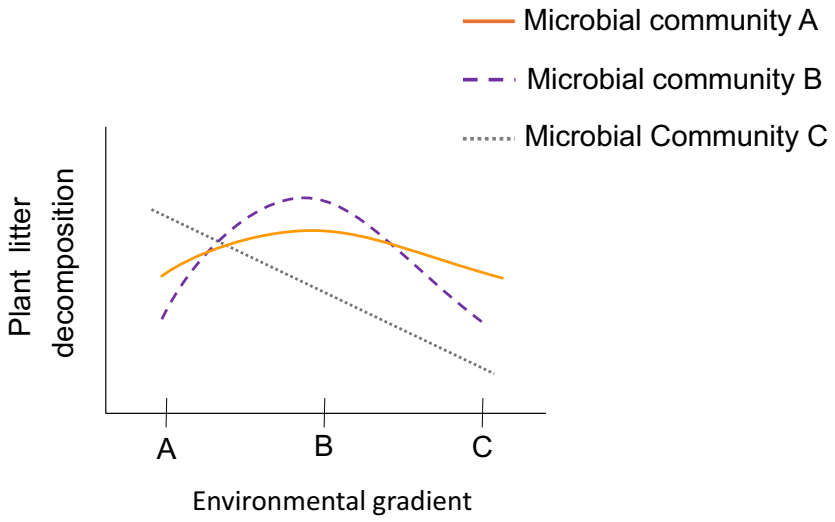

Figure 2. Functional response curves illustrate the role of microbial community composition on decomposition rates. Three hypothetical microbial communities from different points (a, b, c) along an environmental gradient that exhibit varying rates of plant litter decomposition. Such differing functional responses challenge the prevailing view that environmental conditions alone determine decomposition rates within a specific habitat.

dynamics is based on studies conducted in temperate and boreal forests, where fungi typically are more abundant (Bahram et al. 2018). In contrast, ecosystems such as tropical forests, grasslands, and deserts, where fungi are less abundant in topsoil (He et al. 2020), remain underrepresented in decomposition studies. For instance, in arid ecosystems in southern California, bacterial biomass appears to be higher than fungal biomass in leaf litter and positively related to decomposition rate (Baker et al. 2018). Ultimately, however, biomass is not a sufficient metric of a microbial group's contribution to decomposition as it does not capture activity or turnover (the balance of growth and death rates), both of which will influence the contributions to decomposition (e.g., Soares and Rousk 2019).

Assumption 2: Microbial composition is irrelevant to decomposition

With the exception of the ratio between fungi and bacteria (Swift et al. 1979, Strickland and Rousk 2010), a historical assumption of the terrestrial decomposition framework is that microbial communities perform decomposition in a manner independent of their composition (the relative abundance among taxa). As a result, microbial communities can be black boxed in litter decomposition models (Schimel 1995), without considering differences in their microbial composition. This is in stark contrast to plant communities, whose species identity or functional group is often considered in ecosystem research (Pérez-Harguindeguy et al. 2016). A practical demonstration of this assumption's consequences is that litter decomposition experiments often hold litter chemistry (i.e., plant community) constant across sites but ignore whether variation of the local microbial community might influence decomposition rates.

For years, evidence has been growing from both lab and field studies that the composition of litter microbial communities directly influences the rate of decomposition and changes in litter chemistry during this process (figure 2). In the lab, different combinations of microbial cultures (both fungi and bacteria) decomposed leaf litter at different rates (Strickland et al. 2009, Matulich and Martiny 2015). In the field, litter decomposition rates in native Patagonian forests differed up to 34% under the influence of different microbial communities associated with different tree species (Vivanco et al. 2018). Furthermore, reciprocal transplant experiments that disentangle the microbial community from their environment and litter substrate revealed that the presence of different microbial communities altered litter decomposition rates by up to 40% (Glassman et al. 2018). One complication with these studies is that it remains difficult to disentangle the effects of composition from overall microbial abundance; microbial abundance and decomposition rates are often positively correlated, but the direction of causality can be unclear.

Moving forward, the next step is to identify the functional traits responsible for the effect of microbial taxonomic composition on plant litter decomposition. Specifically, we hypothesize that the composition and abundance of carbohydrate active enzymes (CAZymes) in large part determines the ability of a microbial community to decompose a specific litter type. Bacteria and fungi encode a large and diverse suite of CAZymes that hydrolyze carbohydrate polymers such as cellulose and xylan (Berlemont and Martiny 2015, Rubén et al. 2022). CAZyme gene composition varies among microbial communities that differ in polysaccharide decomposition rates (Martiny et al. 2017). Furthermore, variation in CAZyme gene composition among bacterial and fungal strains is related to their degree of carbohydrate use (Chase et al. 2016). However, we are still far from understanding how variation in genomic potential among microbial communities translates into decomposition rates of particular substrates. This goal will require quantitative *in situ* studies that directly measure the processing of different litter components (e.g., through stable isotope analyses; Levy-Booth et al. 2022) while varying the composition of the microbial community. In addition, the development and application of models, both mechanistic and machine learning, could help to relate genetic potential to actual rates of decomposition (Sokol et al. 2022). For instance, trait-based models aim to model the role of extracellular enzymes and their tradeoffs with drought tolerance influence litter decomposition (Allison and Goulden 2017), which have then been supported by experiments in the field (Malik et al. 2020b). These models can integrate genomic data with environmental and functional data, providing deeper insights into how microbial traits influence ecosystem processes.

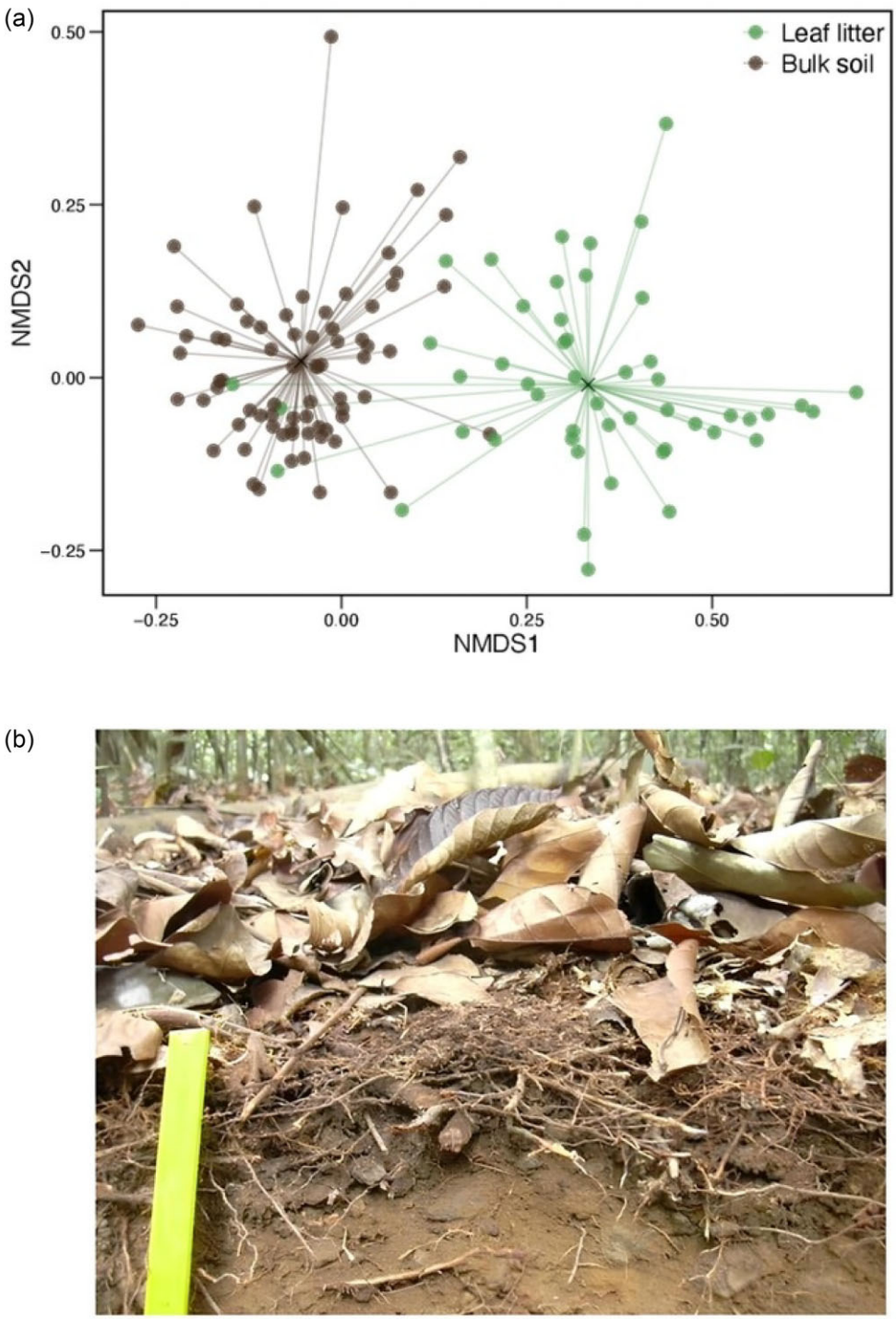

Figure 3. Microbial communities in surface plant litter differ from those in bulk soil. (a) Nonmetric multidimensional scaling ordination of bacterial community composition in leaf litter and bulk soil layers. Each point represents a sample, with leaf litter samples clustered on the right and bulk soil samples clustered on the left. Lines connect samples to their respective centroids to clarify habitat clustering. Source: The data are from the Loma Ridge Global Change Experiment in southern California, in the United States, redrawn from Barbour and colleagues (2022). (b) The litter layer and soil in the Ankasa Tropical Forest. Source: Reproduced from CarboAfrica Newsletter no. 5.

Assumption 3: Bulk soil microbes are responsible for surface plant litter decomposition

The idea that decomposers of plant litter at the soil surface are the same as those in the bulk soil is implicit in the ways in which surface litter is studied. Indeed, so far in this perspective, we have not distinguished between these communities as many studies discuss decomposers generally even if focusing on just bulk soil, surface litter, or wood. Studies of plant litter decomposition commonly use litterbags placed on the ground, where the litter layer is removed to ensure direct contact between the litterbags and the bulk soil. This practice seems to reflect the assumption that decomposers live belowground and colonize fresh plant litter that

falls on the soil surface. Similarly, bulk soil respiration is often used as a proxy for microbial abundance on litter (e.g., Bradford et al. 2017), and bulk soil properties such as moisture, pH, total carbon, and nutrient availability are sometimes reported to describe the environment for the surface litter (Vivanco and Austin 2008). Finally, bulk soil (rather than leaf litter) is often used to inoculate leaf litter in lab incubations for studying litter decomposition (e.g., Strickland et al. 2009, Liu et al. 2023).

An accumulation of evidence now suggests that the composition of microbial communities on surface litter is quite distinct from those in the bulk soil in a variety of ecosystems (figure 3). For instance, in temperate forests, fungal and bacterial composition differs between the litter layer and bulk soil (Urbanová et al. 2015, Mašínová et al. 2017), and fungal community composition in the litter layer is associated with nearby tree species (Vivanco et al. 2018), a relationship that decreases with soil depth (Baldrian et al. 2012, Urbanová et al. 2015). In boreal forests, saprotrophic fungi are primarily confined to surface litter, and mycorrhizal fungi dominate in the underlying, more decomposed litter and humus (Lindahl et al. 2007). Even in grasslands, where the surface litter layer can be much thinner than in temperate forests, microbial community composition in the surface litter differs from that of the bulk soil (Griffiths et al. 2003, Seaton et al. 2022, Barbour et al. 2023). Beyond composition, bacterial abundance (cell counts) can also differ by an order of magnitude between leaf litter and bulk soil (higher in leaf litter when expressed per gram or higher in bulk soil when expressed per gram organic matter content), as has been observed across a gradient of ecosystems (Khalili et al. 2019).

Such striking differences in microbial abundance and composition indicate that the communities are specifically adapted to the surface or bulk soil environment, raising the question *What makes a plant litter decomposer different from a bulk soil decomposer?* Clearly, there are differences in the chemical makeup of the organic matter in these two environments, perhaps leading to selection for different types of resource acquisition traits, as was discussed in assumption 2. However, we further hypothesize that microbial traits related specifically to the abiotic environment may contribute to the local adaptation of these communities. In particular, the surface soil experiences dramatic daily and seasonal fluctuations in moisture, temperature, and exposure to sunlight. In the phyllosphere, these fluctuations select for microbial traits that resist abiotic stress such as the ability to produce of polymeric substances, biosurfactants, and pigments (Vorholt 2012). Similarly, in seasonally dry environments and many crop systems, plant litter can remain in a standing dead position that may not directly contact the bulk soil for years. Importantly, the assembly of microbial communities in plant litter is not only shaped by selection of different environmental conditions but also by its sources of dispersal. In a Californian grassland, plant litter communities assemble from the surrounding litter rather than the bulk soil beneath it (Walters et al. 2022), but bulk soil becomes a more important source after fire removes the litter layer (Barbour et al. 2023). Airborne and phyllosphere microorganisms also contribute to the colonization of surface litter, providing a distinct inoculum compared to bulk soil (Voříšková and Baldrian 2013, Walters et al. 2022). In addition, invertebrates can transport microorganisms internally or externally, facilitating microbial dispersal and further influencing microbial community assembly (Seibold et al. 2019). Therefore, the contribution of microbial processes to surface litter or bulk soil decomposition will depend not only on differences in resource acquisition traits but also on other traits, including stress tolerance (Wood et al. 2018, Malik et al. 2020a), dispersal abilities, and interactions with fauna. These processes and trait trade-offs will likely be important for understanding the relationship between surface litter microbial communities, their rates of plant litter decomposition, and ultimately, the composition of microbial and plant biomass that enters into the bulk soil, contributing to the formation of soil organic matter.

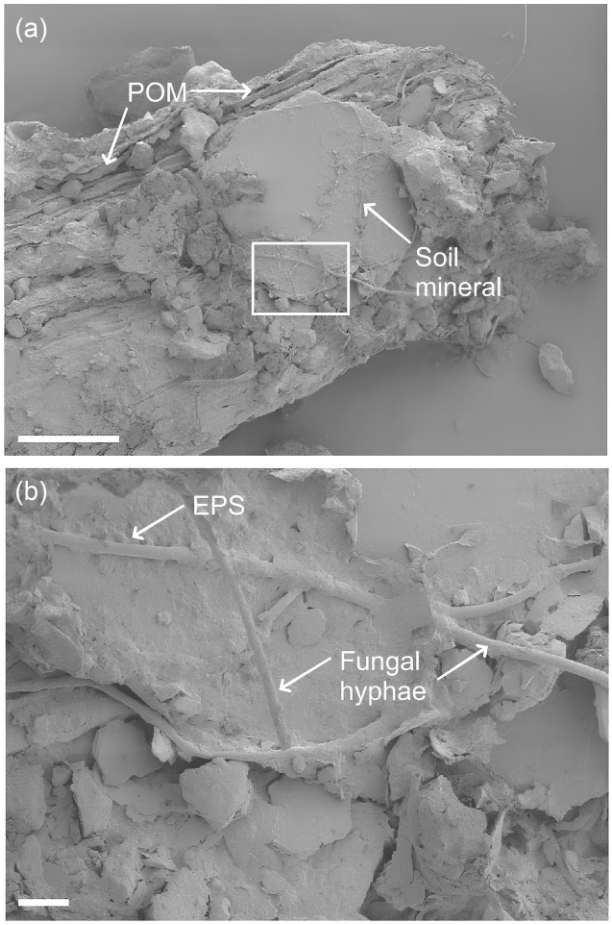

Figure 4. Soil organic matter originates from both plant litter and microbial debris. Scanning electron microscopy images of the interface of plant litter and soil minerals, where soil minerals are (a) attached to the litter surface (scale bar = 100 micrometer [μm]) and (b) enmeshed with fungal hyphae and extracellular polymeric substances (scale bar = 10 μm). Source: Reproduced from Witzgall and colleagues (2021).

Assumption 4: Soil organic matter is leftover plant litter

Past ecology textbooks explained that simple compounds in plant litter are readily consumed by microbes releasing carbon dioxide to the atmosphere, whereas more complex compounds resist microbial degradation and contribute to the formation of soil organic matter in the form of humus. Humus is described as a collection of large and complex chemical compounds that last hundreds or thousands of years underground and is, therefore, the leftovers of microbial degradation (Stevenson 1994). This notion was reinforced by the resemblance in chemical complexity between humus and lignin (Weil and Brady 2017).

Advances in microscopy, nuclear magnetic resonance, and X-ray spectroscopy have challenged this traditional understanding of soil organic matter for at least two decades (Schmidt et al. 2011, Lehmann and Kleber 2015), but the idea still persists. The new techniques have revealed that soil organic matter consists of

Table 1. A summary of four traditional assumptions and updated views on microbial roles in decomposition, along with key questions that remain to be addressed.

Assumption	Emergent view	Outstanding questions
Fungi are primary decomposers, and bacteria, secondary decomposers	Bacteria are coregulators of decomposition	How do bacteria and fungi interact to affect decomposition dynamics? What are the quantitative contributions of particular types of microbes to decomposition and do they vary by ecosystem?
Microbial composition is irrelevant to decomposition	Microbial traits correlate with the ability of microbial communities to decompose plant litter	Which microbial traits contribute to differences in decomposition by different microbial communities?
Bulk soil microbes are responsible for surface plant litter decomposition	Plant litter decomposers are different from bulk soil decomposers	What makes a decomposer of plant litter different from a decomposer of soil organic matter? Do litter decomposers differ in their ability to break down specific compounds or are they adapted to the litter environment?
Soil organic matter is leftover plant litter	Microbial traits play a pivotal role in soil organic matter formation	Which microbial traits influence the formation and persistence of soil organic matter?

diverse biomolecules, some of which originate from the microbes themselves that, potentially, can be degraded by microbes (Kögel-Knabner 2002, von Lützow et al. 2006). These biomolecules can be classified in two distinct pools, particulate organic matter and mineral associated organic matter, with different properties and turnover times (Lavallee et al. 2020). Large plant litter fragments are often classified as residues and are removed prior to density or size fractionation, which results in the separation of particulate and mineral associated organic matter pools. Particulate organic matter is largely made of undecomposed plant fragments that decompose relatively quickly, except when trapped in soil aggregates. In contrast, mineral associated organic matter consists of single molecules or microscopic fragments of organic material tightly bound to minerals or trapped in small microaggregates. Because mineral associated organic matter is less readily available to microbes, it represents the most stable component of soil organic matter and has therefore received attention because of its impact on soil carbon storage (Piazza et al. 2024). Mineral associated organic matter has both plant and microbial origins. Its plant origin involves leaching from plant litter or the exoenzyme depolymerization of plant litter. The microbial origin of mineral associated organic matter consists of the remnants of cells (microbial necromass) and exudates that are produced by microbes during decomposition (Cotrufo et al. 2013, Castellano et al. 2015). Although a variety of approaches, including microbial biomarker analysis, molecular fingerprinting, stoichiometric approaches, and mathematical modeling, have been employed to quantify these contributions, uncertainty remains about the relative contribution of plant and microbial pathways of mineral associated organic matter formation (figure 4; Whalen et al. 2022, Chang et al. 2024, Rocci et al. 2024).

The result of the accumulation of this work on the origin of soil organic matter places microbes at the forefront, shifting the idea of their role from mere decomposers to builders of soil organic matter. The current hypothesis therefore is that microbial traits play a pivotal role in soil organic matter formation, regardless of whether it originates from plant or microbial pathways (Whalen et al. 2022). In plant-derived soil organic matter formation, microbial traits relevant to the breakdown and transformation of plant inputs, such as microbial enzyme diversity, come into play. Conversely, microbial-derived soil organic matter formation hinges on microbial traits associated with the assimilation and anabolism of plant inputs, such as maximum growth rates and efficiency (Liang et al. 2017). Indeed, evidence suggests that, as for decomposition, microbial communities and their respective traits influence the formation of stable soil organic matter. For example, Domeignoz-Horta and colleagues (2021) inoculated different microbial communities into a model soil matrix amended with simple carbon (cellobiose) and measured the thermal stability of the resultant soil organic matter. Communities consisting solely of bacteria were associated with the formation of more thermally labile soil carbon pools than were communities consisting of both bacteria and fungi. Notably, the fungal community's specific composition appeared to exert less influence on the soil organic matter's distinct fingerprint, although the abundance of fungi exhibited a positive correlation with the thermal stability of soil organic matter. They concluded that although fungi played a critical role in decomposing soil organic matter, bacteria influence the composition and persistence of soil organic matter. These intriguing results indicate the need for future studies that further resolve the role of microbial composition in soil organic matter decomposition and its persistence.

Conclusions

In revisiting four assumptions about litter decomposition, we identified opportunities to advance our understanding of terrestrial decomposition by placing microbes at the forefront of this research (table 1). Microbes play critical roles in controlling the rate of carbon release to the atmosphere and the fate of litter carbon, which are key aspects determining carbon storage in terrestrial ecosystems. By shifting our focus to microbes—who they are (assumption 1, fungal versus bacterial), what they do (assumption 2, community composition), where they live (assumption 3, litter and soil environment), and how do they contribute to soil organic matter (assumption 4, microbial contribution to soil organic matter)—we can integrate microbial insights into our general understanding about litter decomposition and further accelerate research in this area. This exercise in the present article also illuminates a number of yet unanswered questions about the role of microbes in litter decomposition (table 1). Addressing these questions will enhance our understanding of the role of microbes in carbon cycling and predictions of carbon dynamics in ecosystems (Lennon et al. 2024).

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Author contributions

Lucía Vivanco (Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing), and Jennifer B.H. Martiny (Conceptualization, Funding acquisition, Writing - review & editing)

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