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The importance of anabolism in microbial control over soil carbon storage

Chao Liang[1]*, Joshua P. Schimel[2] and Julie D. Jastrow[3]

Studies of the decomposition, transformation and stabilization of soil organic matter (SOM) have dramatically increased in recent years owing to growing interest in studying the global carbon (C) cycle as it pertains to climate change. While it is readily accepted that the magnitude of the organic C reservoir in soils depends upon microbial involvement, as soil C dynamics are ultimately the consequence of microbial growth and activity, it remains largely unknown how these microorganism-mediated processes lead to soil C stabilization. Here, we define two pathways—*ex vivo* modification and *in vivo* turnover—which jointly explain soil C dynamics driven by microbial catabolism and/or anabolism. Accordingly, we use the conceptual framework of the soil 'microbial carbon pump' (MCP) to demonstrate how microorganisms are an active player in soil C storage. The MCP couples microbial production of a set of organic compounds to their further stabilization, which we define as the entombing effect. This integration captures the cumulative long-term legacy of microbial assimilation on SOM formation, with mechanisms (whether via physical protection or a lack of activation energy due to chemical composition) that ultimately enable the entombment of microbial-derived C in soils. We propose a need for increased efforts and seek to inspire new studies that utilize the soil MCP as a conceptual guideline for improving mechanistic understandings of the contributions of soil C dynamics to the responses of the terrestrial C cycle under global change.

Soil carbon (C) stabilization has become an important topic in recent years owing to changes in global climate and atmospheric chemistry[1,2]. Globally, soil contains a large amount of C—twice that in the atmosphere and more than the C in vegetation and the atmosphere combined[3–5]. Owing to its large size, small changes in the balance between inputs to and outputs from the soil C pool would have a significant impact on atmospheric CO_2, and could either reduce or exacerbate the consequences of burning fossil fuels[6–8]. Because soil C cycling is ultimately the consequence of microbial growth and activity, understanding organic matter decomposition, transformation and sequestration in soils demands improved knowledge of how microbial physiology regulates the processes controlling biogeochemical cycling, climate change and ecosystem sustainability[9,10].

Microorganisms have two critical, contrasting roles in controlling terrestrial C fluxes: promoting release of C to the atmosphere through their catabolic activities, but also preventing release by stabilizing C into a form that is not easily decomposed[10]. To date, research has focused on microbial sources of CO_2 with less attention paid to the role of microbial anabolism in generating products that can be sequestered[11,12]. This has stimulated research considering the direct incorporation of microbial residues (cellular components from both living and senesced biomass) into the stable soil C pool[13–16]. For example, recent studies showed that fungal and bacterial necromass are the primary C-containing constituents contributing to the stable soil organic matter (SOM) pool[17,18]. Thus, the main driver of SOM accumulation under some conditions may not be litter decomposition and transformation *per se*, but microbial growth that leads to deposition of microbial-derived C into the SOM reservoir via biomass turnover and necromass accumulation[14,15,19]. Accordingly, any attempt to manage soils for long-term C storage will require an understanding of how to manage microbial-derived C in soil.

To this end, we present a conceptual framework, in which we stress the notion of the microbial carbon pump (MCP, a concept developed in marine systems[20]) to integrate recent insights into our understanding of how microorganisms regulate soil C dynamics. This framework balances the contrasting functions of microorganisms as agents of SOM decomposition and formation, and it highlights the role of long-term microbial assimilation in the production of organic compounds that are stabilized in soils. Here, we focus on the role of microbial metabolism in soil C dynamics, particularly the contributions of microbial anabolism to soil C storage. We first discuss evolving views on SOM and the metabolic controls of soil microorganisms in soil C turnover. We then discuss microbial anabolism and the soil MCP that control microbial necromass accumulation and stabilization. Finally, we propose areas where we see promise to advance the state of our relevant knowledge.

Soil organic matter and microbial metabolic controls

Long-term C storage in terrestrial ecosystems occurs primarily when plant biomass is stabilized in soils as SOM. SOM is key in maintaining ecosystem productivity and sustainability through its physical, chemical and biological soil functions: as a source of plant nutrients, by increasing infiltration and water-holding capacity, and by enhancing soil structure. Changes in SOM quantity and quality are mainly determined by three factors: abiotic environmental and edaphic variables, types of organic input, and biological activity[21].

Historically, studies have focused primarily on relating the magnitude and composition of SOM to non-biological environmental constraints that drive SOM fluctuations[1,4], with less emphasis on biological controls over C transformations[4,22]. There is a huge body of literature on humification and humic substances[23], but many aspects of this classical concept of SOM formation are being re-evaluated and displaced as modern analytical tools provide new insights into the chemical nature of SOM[22,24,25]. Evolving analytical approaches,

[1]Key laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China. [2]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106, USA. [3]Environmental Science Division, Argonne National Laboratory, Argonne, Illinois 60439, USA. *e-mail: cliang823@gmail.com

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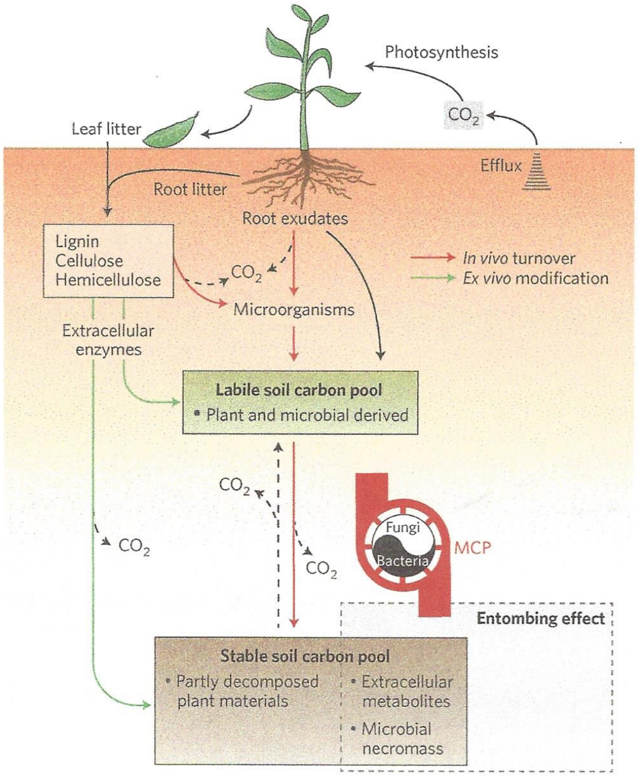

Figure 1 | Schematic diagram of microbial metabolic processes involved in C cycling in terrestrial ecosystems. Primary production inputs to soils occur through two pathways—*in vivo* turnover and *ex vivo* modification—that jointly explain soil C dynamics driven by microbial catabolism and/or anabolism before entering the stable soil C pool. Even though the relative importance of *in vivo* turnover (red lines) and *ex vivo* modification (green lines) vary with different environmental scenarios, we argue that the majority of C that is persistent in soils occurs through coupling of the soil microbial carbon pump (MCP; associated with the *in vivo* turnover pathway) to stabilization via the entombing effect. The soil MCP is a conceptual object to demonstrate the fact that microbial necromass and metabolites can be the precursors for persistent soil C, which particularly highlights the importance of microbial anabolism in soil C storage. The *yin–yang* symbol is used to create a sense of movement and illustrate that the movement is driven, but driven differently, by both bacteria and fungi with different trophic lifestyles.

coupled with studies using physical fractionation as an alternative to traditional alkali extraction, have implied that microbial-derived materials comprise a significant component of SOM[26–29]. Yet, the number of experimental studies designed to elucidate the nature of mechanistic controls on microbial contributions to soil C stabilization remains relatively limited[4,15]. Furthermore, we still struggle to understand processes as fundamental as the partitioning of C among microbial biomass, respired CO_2 and stored soil C (ref. 30). Although molecular biological tools have enhanced our appreciation of the dynamics of soil communities, it has remained difficult to relate the vast diversity of these communities to soil C cycling and stabilization[10].

Considering the metabolic activities of microorganisms during C transformations, we categorize two major pathways by which microorganisms influence SOM formation: *ex vivo* (extracellular) modification, in which extracellular enzymes attack and transform plant residues, resulting in deposition of plant-derived C that is not readily assimilated by microorganisms; and *in vivo* turnover of organic substrates via cell uptake–biosynthesis–growth–death, resulting in deposition of microbial-derived C. Through these two pathways, compounds that are more resistant to further degradation or more readily stabilized are produced by modifying compounds in the original tissues or by forming new compounds through microbial synthesis, such as polymers associated with degradative lignin products and amino sugars. In any event, *ex vivo* modification implies restructuring or altering molecules by microbial degradative enzymes (that is, purely catabolic processes), while *in vivo* turnover implies breakdown and resynthesis of molecules, and can suggest a mix of both catabolic and anabolic processes. We regard all C compounds that are deposited to SOM through the *in vivo* turnover pathway as products of microbial anabolism, as these compounds exclusively originate from constituents of microbial cells.

In the *ex vivo* modification pathway, transformations of plant materials and residues occur without actual assimilation by microorganisms. Variability in the degree to which plant-derived C is modified depends largely on plant traits[31]. Additionally, microbial groups may use and modify the structures of plant materials differently, leading to distinct patterns of C use and stabilization, depending on plant and tissue type and which microbial populations are active. For example, microbial communities in forests are better adapted to degrading complex C compounds than microorganisms in grassland[32]. Yet grassland microorganisms degrade grass litter more effectively than forest litter, while microorganisms in forests do not preferentially degrade forest litter[33]. Poll *et al.*[34] suggested that fungi preferentially degrade fresh plant litter by releasing a more potent suite of exoenzymes that break down complex materials.

The other key pathway of microorganism-mediated SOM transformation/formation is *in vivo* turnover, which leads to the deposition of microbial-derived C. Changes in the anabolic capacity of microorganisms and their activity rates directly affect microbial contributions to SOM, regulating the amount of microbial-derived C and the proportion of microbial- versus plant-derived C in the soil C pool. The importance of microbial anabolism is not only embedded in the production of biomass, but also in processing accessible organic compounds and their re-synthesis into the novel forms present in microbial biomass and necromass. For the latter, there is a chance that the C might be reformed into molecules that are relatively more chemically stable or that can be stabilized through associations with soil minerals, such as cell wall fragments, exoenzymes and osmolytes[35]. The consequences of *in vivo* turnover are ecosystem specific and dependent on how *in situ* fungal and bacterial groups grow and assimilate organic substrates. For example, forest soils contain higher microbial biomass than agricultural soils, because fungal groups active in forest ecosystems can contribute more biomass[36], probably leading to higher microbial necromass in forests. In forest ecosystems, bacteria contribute more to the soil C pool in broadleaf than in coniferous systems[37]. Microbial contributions to SOM may shift from fungal to bacterial dominance with increasing land degradation or land-use intensification[38]. Such changes in microbial residues may affect future C balances as fungal residues are thought to be more persistent in soils than bacterial residues[39,40]. Significant knowledge gaps regarding microorganism-mediated C preservation in soils include our understanding of the specific compounds involved, their turnover rates, and the nature of the stabilization mechanisms.

Microbial anabolism and the soil microbial carbon pump

Direct microbial contributions to sequestered C were often regarded as minimal, as living microbial biomass makes up <5% of SOM[41–43]. However, the small fraction of total soil C that is live biomass does not reflect the total amount of soil C that had, at some point, cycled through the living biomass[44]. In the *in vivo* turnover pathway, microorganisms first utilize easily degradable plant materials for biomass

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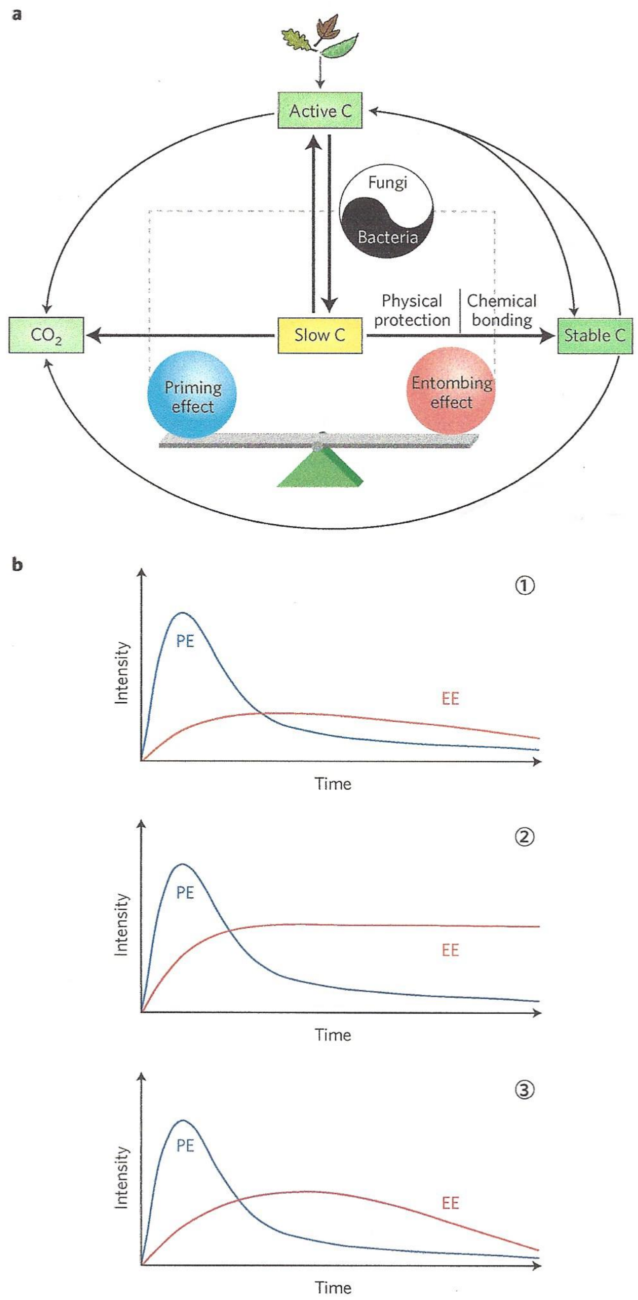

Figure 2 | Priming effect versus entombing effect regulates fluctuation of the stable soil C pool. a, The fundamental mechanistic framework. **b**, Model predictions for an assumed ecosystem under different scenarios. In each model, the vertical axis represents the rate of C response, and its corresponding curves exhibit the size of primed or entombed C, as denoted by the integrated area under each curve over the entire time. Together, the net balance (as a difference of areas) associated with changes in the priming effect (PE) versus entombing effect (EE) determines changes in the magnitude of stable C in soil. In theory, changes to the stable C pool in soil can be positive, negative or zero. As shown in **b**, PE/EE > 1 results in stable C loss (1); PE/EE < 1 results in stable C gain (2); PE/EE = 1 results in no stable C change (3). Note that if plant cover, environment and management remain relatively stable for a long time, then the stored soil C content will ultimately reach a new equilibrium level.

production. Driven by their rapid turnover, microorganisms thus contribute directly to the soil's stable C pool in an iterative process of cell generation, growth and death. In addition, microbial cellular components and their degradation products may be selectively preserved because of their chemical structure and by being sorbed to mineral surfaces, incorporated into organo-mineral complexes or occluded within inaccessible pore spaces at the submicron scale[45,46]. While the specific C forms stabilized by these mechanisms vary depending on factors such as clay mineralogy, pH and available cations, modern spectro-microscopic techniques are providing evidence that amide, aliphatic, carboxylic, aromatic and *O*-alkyl C forms stabilized at this scale generally have spectral signatures more indicative of microbial metabolites and residues than plant-derived compounds[25,47–50]. The direct transformation by microorganisms of labile C to stabilized forms allows them to contribute disproportionately to persistent C in soils. The role of microorganisms is not simply a question of 'leaving behind' senesced biomass, but includes their ability to continuously and gradually 'process' C and produce new microbial-derived compounds that ultimately accumulate in soils. Therefore, microbial necromass rather than standing biomass may be a better indicator of microbial contributions to soil C pools; research increasingly shows a substantial microbial role in the sequestration of C into stable soil C pools[14–16,19,51].

The MCP, a concept first raised by marine researchers[20,52], provides a formalized focus for understanding microbial processes in producing persistent organic matter. This draws attention to the microbial transformation of plant-derived C through microbial biomass and ultimately into the stable soil C pool[12,19]. In both aquatic and terrestrial systems, microorganisms can grow and turn over rapidly during organic matter decomposition, leaving necromass, part of which can be stabilized in the environment. An analogue to the marine MCP[20] has been hypothesized to operate in soils[11,13,53], but the idea of a soil MCP has received little study. Here, we couple the MCP concept with the ability of the synthesized compounds to be stabilized on mineral surfaces and within soil structures—a phenomenon we define as the 'entombing effect'.

A schematic diagram of this conceptual framework displays the relevant pathways and consequences of microbial growth, metabolism and death (Fig. 1). In this diagram, microbial controls on terrestrial C cycles, driven by catabolism and/or anabolism, are emphasized to demonstrate the microorganism-mediated C transformation process—where the soil MCP, particularly via *in vivo* turnover, strengthens the entombing effect on soil C storage. Accordingly, the efficiency of the soil MCP, as affected by factors including internal features (for example, microbial physiology, chemical stability and physical interaction) and external constraints (for example, edaphic variables and global change drivers), will play a significant role in a soil's capacity to retain persistent organic C.

Hypothesis-driven perspectives and future directions

By synthesizing knowledge on microbial C cycling in soils, we illustrate that the microbial entombing effect can drive the generation and sequestration of persistent soil C. A conceptual framework encompassing the soil MCP not only provides a theoretical structure for studying microbial anabolism in soil C storage, but also enables us to generate testable hypotheses regarding ecosystem responses to external disturbance and the determinants of SOM chemistry, as well as other promising future research directions.

The balance between microbial priming and entombing regulates the stable soil C pool. The stable soil C pool and its dynamics are an enigma that has puzzled scientists for decades. We are aware that small changes in the global balance between C inputs to and outputs from soil can alter atmospheric CO_2 concentrations. However, the heterogeneity of SOM makes detecting changes in pool sizes

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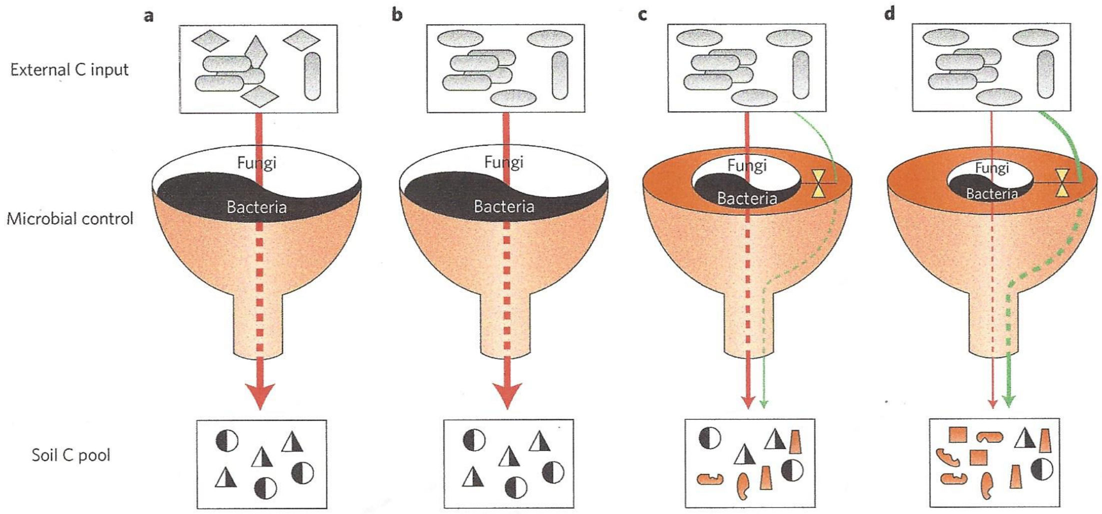

Figure 3 | *Ex vivo* modification versus *in vivo* turnover of microbial metabolic processes controls the chemical fate of soil C. a–d, The pathways in **a** and **b** demonstrate the chemical convergence hypothesis—initial chemical differences in external C input are expected to converge through microbial anabolism within the *in vivo* turnover channel (red lines) alone. The pathways in **b–d** demonstrate a dual control hypothesis—initial C chemistry is shaped by the relative dominance of *ex vivo* modification (green lines) versus *in vivo* turnover, where we expect that the higher dominance of *ex vivo* modification will result in diverged chemical composition of soil organic matter.

difficult, and also obscures our understanding of 'unseen' mechanistic controls on those pools.

As an ironic twist, soil microorganisms that primarily decompose SOM can also drive C sequestration by producing stable or stabilized SOM. We suggest that the magnitude of soil C storage is largely controlled by the balance between microbial catabolic activity, which releases C as CO_2, and anabolic activity, which contributes senesced microbial biomass. Therefore, these two functions must be considered simultaneously when investigating stable soil C. Following addition of new external C, CO_2 evolution may increase dramatically (for example, by up to 400%[54]) by stimulating microbial decomposition of existing stabilized SOM, a phenomenon known as the priming effect[55]. In contrast to the loss of primed C, the same microorganisms also synthesize new organic compounds as they build biomass and ultimately part of their necromass will be stabilized, a phenomenon defined above as the entombing effect. Here, we hypothesize that litter input quality regulates stable soil C pool dynamics by driving shifts in microbial community activity and composition (Fig. 2). In our conceptual framework with a particular focus on microbial control over C loss/gain in the stable soil C pool, the dynamics of the stable soil C pool are determined by the balance between microbial priming and microbial entombing (Fig. 2a). More specifically, we hypothesize that fungal dominance, driven by low-quality litter inputs[36], will lead to not only a higher rate of CO_2 release by decomposing relatively stable C, but also greater accumulation of microbial-derived C by incorporating more fungal necromass into the stable C pool. Both effects will determine the change in pool size, so the net effect on the stable soil C pool by microbial priming and entombing can be negative (C loss), positive (C gain) or zero (no change) at different temporal scales. We propose that fluctuation of stable soil C pool size, under three different priming-entombing scenarios, can be predicted by mathematical simulation[56] (Fig. 2b).

This conceptual framework is simplified and does not consider all possible C-flow channels, some of which should be included for particular systems. For example, leaching is a channel for C loss, which may translocate C deeper in the soil profile and then move it with below-ground water flow. In general, although the priming and entombing channels can be differentiated at a conceptual level, it is often difficult to discriminate between them. Consequently, while individual studies have shown that these channels all occur (probably simultaneously), we are currently unable to rank the relative importance of each acting channel and how this might vary under different conditions. In order to elucidate the mechanisms and improve our ability to predict C cycling, this hypothesis calls for more studies to investigate these processes—particularly the entombing effect.

***Ex vivo* modification versus *in vivo* turnover controls the chemical fate of soil C.** Decomposition drives ecosystem C cycling, and plays a central role in shaping the composition and spatial distribution of below-ground C. SOM composition and complexity have the potential to significantly alter soil characteristics and functions such as organo-mineral interactions, environmental sustainability, and soil C stabilization. Thus, it is critical to identify the factors linking the quality of organic matter inputs, residue decomposition and SOM storage, and to understand the origin and consequences of SOM chemistry. However, it remains contentious how initial litter chemistry changes during decomposition and what roles the dual microbial pathways (*ex vivo* modification and *in vivo* turnover) play in controlling these changes. One traditional opinion is that the differences in initial litter chemistry will eventually converge towards a set of common compounds that are more resistant to decay[29,57]. Contrary to this idea, another viewpoint believes that the initial differences in litter chemistry will persist into the late stages of decomposition when external C inputs are incorporated into SOM[58–61]. For example, litter rich in tannins will leave a stronger tannin signal in the soil[59]. Recently, a paradigm shift has occurred that highlights the importance of decomposer control; Wickings *et al.*[62] showed that different management regimes altered decomposer communities, which in turn altered chemistry in decomposing grass litter. We propose here that our associated conceptual framework (*in vivo* turnover and *ex vivo* modification) can be used to explain inconsistence of traditional views, and at the same time, to elucidate the underlying mechanisms of decomposer control, specifically with regards to microbial metabolic controls and the chemical complexity of SOM.

We hypothesize that microbial anabolism supports the chemical convergence such that over the course of decomposition, chemically unique inputs become more similar as they are assimilated into microbial biomass (Fig. 3a,b). In this case, the varying compositional

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chemistry of different external litter inputs would tend to converge and the distinct chemistries of the initial litter types would become indistinguishable after intensive microbial turnover via the *in vivo* turnover pathway. Further, we hypothesize that the relative contributions from *in vivo* turnover and *ex vivo* modification by microorganisms ultimately will determine the C chemical structure and complexity of SOM produced during the course of decomposition (Fig. 3b–d), enabling the chemistry of the same litter input to diverge. Specifically, greater dominance of *ex vivo* modification relative to *in vivo* turnover will result in greater C chemical complexity of SOM.

Our hypotheses on the determinants of soil C chemistry are difficult to test in field or lab studies. Natural ecosystems are open systems with continuous inputs of plant (and animal) litters, which integrate with pre-existing compounds and potentially dilute the impacts of microorganism-mediated decomposition on SOM chemistry. Although stable C isotopes have the power to disentangle the newly added C from already existing C, isotopic techniques that add labelled litters in the laboratory are not fit for long-term studies of C dynamics. Another issue we need to consider is the variance in cell C chemistry across microbial species. In our conceptual framework, we assume that the differences in C chemistry between fungal and bacterial cells are insignificant compared with the variations among diverse plant litters, which consequently leads to chemical convergence after continuous substrate assimilation by microorganisms. This convergence is plausible when microbial products become an increasingly dominant portion of the remaining mass of a particular litter cohort as decomposition proceeds since many biomass constituents are similar among different taxa[57].

Concluding remarks

Despite its importance to soil C storage, the incorporation of microbial-derived components into the stable soil C pool has not received enough attention yet. Recent research has made it clear that microbial-derived C is ubiquitous and relatively stable against decomposition when it becomes physically protected. At present, our understanding of the differentiation in C allocation and microbial processing through *ex vivo* modification and *in vivo* turnover is far from satisfactory and contributes to the uncertainties in quantifying and predicting C disposition and dynamics under global change. Hence, studies on the stabilization of microbial-derived C in soils are indispensable for advancing knowledge of soil C dynamics and stability, improving the structure of global C cycling models to reduce predictive uncertainties, and helping to inform strategies to maximize C sequestration and craft climate policy. In particular, the soil MCP conceptualizes a sequestration mechanism during microbial *in vivo* turnover—that is, microbial generation of new soil C via accumulating anabolism-induced necromass, part of which can persist in soils. Together, the soil MCP and its related entombing effects, which are mechanistically connected with the terrestrial C cycle and global climate, serve as conceptual models for guiding the multidisciplinary approaches required to integrate empirical, theoretical and predictive perspectives that will be necessary for understanding the contributions and importance of microbial necromass in the formation and stabilization of SOM, as well as its resilience and vulnerability to global change.

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Author contributions

C.L. conceived the ideas, developed the conceptual framework, and drafted the original manuscript. C.L., J.P.S. and J.D.J. contributed to concept polishing and critical revision of the manuscript. All authors read and approved the final manuscript.

Additional information

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Correspondence should be addressed to C.L.

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Competing interests

The authors declare no competing financial interests.

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