

Formation of necromass-derived soil organic carbon determined by microbial death pathways

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Soil organic matter is the dominant carbon pool in terrestrial ecosystems, and its management is of increasing policy relevance. Soil microbes are the main drivers of soil organic carbon sequestration, especially through accumulation of their necromass. However, since the direct characterization of microbial necromass in soil is challenging, its composition and formation remain unresolved. Here we provide evidence that microbial death pathways (the distinct processes of microbial dying) in soil affect necromass composition and its subsequent fate. Importantly, the composition of derived microbial necromass does not equal that of microbial biomass. From biomass to necromass, distinct chemical transformations lead to increases in cell wall/cytoplasm ratios while nutrient contents and easily degradable compounds are depleted. The exact changes depend on environmental conditions and the relevance of different microbial death pathways, for example, predation, starvation or anthropogenic stresses. This has far-reaching consequences for mechanisms underpinning biogeochemical processes: (1) the quantity and persistence of microbial necromass is governed by microbial death pathways, not only the initial biomass composition; (2) efficient recycling of nutrients within microbial biomass presents a possible pathway of organic carbon sequestration that minimizes nitrogen losses; (3) human-induced disturbances affect the causes of microbial death and consequently necromass composition. Thus, new research focusing on microbial death pathways holds great potential to improve management strategies for soil organic carbon storage. Not only microbial growth but also death drive the soil microbial carbon pump.

Soil organic matter (SOM) represents the largest terrestrial organic carbon (C) stock, and thus managing this pool to balance rising atmospheric CO₂ levels is of increasing policy relevance, especially in agroecosystems¹. To achieve a lasting increase of C stored in soil, it is essential

to understand the nature of SOM and the processes that contribute to its formation. During the past century, soil science made tremendous progress in understanding basic principles. The traditional view of SOM as humic substances derived from recalcitrant plant litter was replaced

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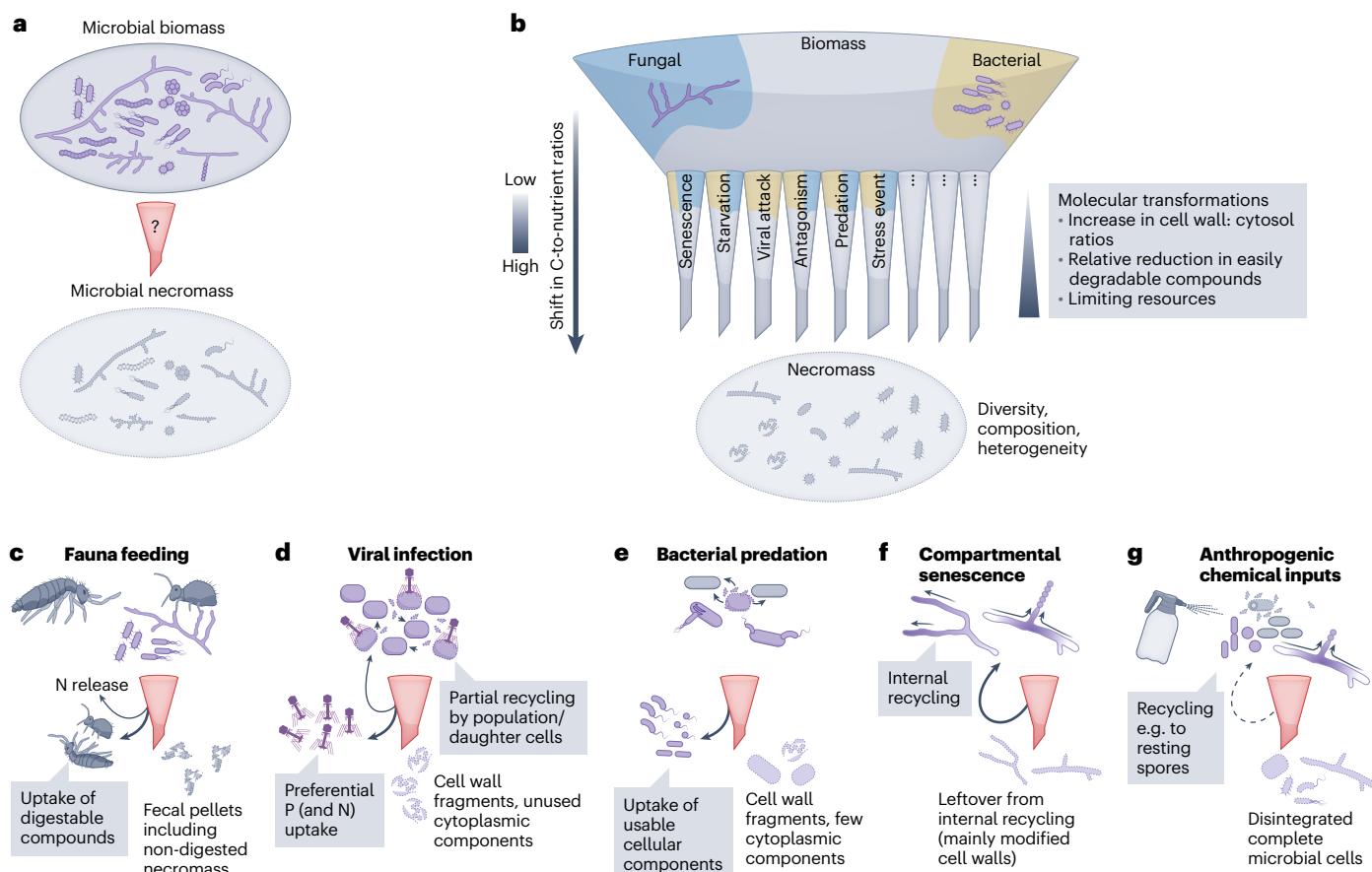


Fig. 1 | Visual illustration of MDPs, including molecular transformations from microbial biomass to necromass. a, The general question addressed. **b**, Overview of different forms of MDPs, with simultaneous chemical modifications. Funnels depict the different types of MDPs described; narrower, lower funnel parts reflect higher internal recycling activity (Table 1). Blue and yellow colour schemes visualize the likely relevance of MDP for fungi and

bacteria, respectively. **c–g**, Specific examples for individual types of MDPs that are discussed in the literature: fauna feeding (**c**), viral infection (**d**), bacterial predation (**e**)^{76,77} compartmental senescence (**f**) and anthropogenic chemical inputs (**g**). Known cellular and molecular transformations are illustrated, as well as directions of resource flow (black arrows).

by an emerging understanding that large portions of C compounds in soil are channelled through microorganisms. Major parts of SOM, in fact, consist of microbial residues, especially necromass². This phenomenon is referred to as the soil microbial carbon pump³. Indeed, recent global assessments of biomarkers in soil indicate that, while living microbial biomass makes up less than 5% of soil organic carbon (SOC), microbial necromass accounts for more than half^{4,5}. This several-fold increase indicates that residues of dead microorganisms accumulate in soil, persisting over time. Mineralization of these residues, as well as interactions with mineral soil surfaces and the formation of bio-organic complexes, are regarded as main factors driving necromass stabilization in soil, mechanisms that are dependent on soil type but also on the chemical composition of necromass^{6,7}. Thus, further insights into the formation and chemical nature of necromass are urgently needed to conceptually integrate it into the existing framework of biogeochemical cycles and C sequestration dynamics. Developing this fundamental line of research may also reveal how soil management strategies can be adapted to exploit microbial pathways for optimizing soil C storage⁸.

The direct characterization of necromass is analytically impeded by the complex nature of soil⁹. However, microbiological research offers insights into necromass characteristics and relevant knowledge about the processes of microbial dying. By taking a microbial perspective, it becomes apparent that microbial biomass is not exposed to ‘sudden death’ but experiences a series of controlled events during its transformation to necromass, here referred to as microbial death

pathways (MDPs). MDPs comprise distinct chemical transformations dependent on the cause of death and the organisms involved but inevitably result in microbial necromass that differs from microbial biomass (Fig. 1); hence, we posit that microbial necromass does not equal microbial biomass in soil. In this Perspective, we explore how soil microorganisms die and, on the basis of microbial physiology, elaborate the chemical transformations during MDPs that influence the molecular and nutrient composition of necromass. We thereby suggest that MDPs themselves represent important determinants of soil organic C sequestration, and their implementation in concepts of soil C and nutrient cycling has far-reaching consequences for understanding the mechanisms underpinning biogeochemical processes (summarized in Box 1).

MDPs in soil microorganisms

It can easily become a philosophical question whether a microbial cell is alive, dead or even dormant¹⁰. In this Perspective, we focus on the unavoidable transition of microbial biomass to necromass, with awareness that the duration and complexity of this transition are highly variable. Current biogeochemical models use microbial biomass and different compartments of SOM as individual pools¹¹. Accordingly, we treat living biomass as one pool, describe possible MDPs that vary in extent and speed of chemical transformation and subsequently define necromass as an end product of the completed MDPs. Microorganisms in soil (biomass pool) are exposed to a range of mortality

Table 1 | Summary of described MDPs and their characteristics

MDP	Affected organismal groups	Attacking/antagonistic agent	Internal resource recycling	Necromass characteristics ^a			Estimates of death rates and relevance
				C/nutrient ratio ^b	Cell wall/cytoplasm ratio	Easily degradable compounds	
(Compartmental) senescence	Mostly fungi	n.a.	High	↑	↑	↓	Average hyphal length estimates for soil: 102 μm cm ⁻³ ; turnover rate estimates: 0.3–6.3 month ⁻¹ (ref. ¹⁵)
Starvation/stress-induced PCD	Bacteria; in fungi similar to senescence	n.a.	High	↑	↑	↓	No data
Predation (soil fauna)	Bacteria and fungi	Fauna, protozoa	Reuse by attacking agent	↓	?	↓	Soil fauna abundance: 60–11 × 10 ⁷ individuals m ⁻² soil ⁷⁰ (for individual groups, see ref. ⁷¹); 16% reduction in microbial biomass by protozoa and nematodes ⁷²
Predation (bacterial)	Bacteria	Predatory bacteria	Reuse by attacking agent	?	↑	↓	7.4% of bacteria belong to (facultative and obligate) predator groups ³⁶ ; death rates unknown
Viral attack	Bacteria	Bacteriophages	Medium	↑	↑—	↓—	10 ³ –10 ¹⁰ virus particles (g ⁻¹ soil) ³⁸ ; 30–80% of bacteria in soil carry prophages ³⁷ ; death rates unknown
Interspecific competition	Bacteria and fungi	Bacteria and fungi	Medium	↑	↑	↓	No data
Anthropogenic stress	Bacteria and fungi	n.a.	Low	—	↑—	↓—	Mostly unknown; drought events 25% death within 3 hr (ref. ⁶⁰); fire reduces microbial biomass by 33% (ref. ⁷³); pesticide effects on microbial biomass depend on chemicals and systems involved ^{74,75}

^aNecromass characteristics are described in direct comparison with microbial biomass. Arrows indicate expected transformations by MDPs; dashes no anticipated changes. Combined signs indicate several possible (context-dependent) outcomes. ^bOutcomes may change depending on the limiting element in the system—selective internal recycling of limiting elements.

risks, including not only natural developmental aging (senescence) but also starvation, desiccation, predation, viral attack, competition and anthropogenic disturbances. The relative contributions of each are so far unknown but probably depend on environmental conditions, soil types and organism groups involved (Table 1 and Fig. 1). To understand the underlying mechanisms, we will first focus on senescence and other forms of programmed cell death (PCD) and then elaborate the link to other relevant pathways affecting necromass characteristics.

Senescence and programmed cell death in microorganisms

The old paradigm of microorganisms being immortal under optimal conditions was dismantled some time ago, first by the observation of asymmetric cell division in bacterial cells and yeasts, leading to subsequent aging of mother cells^{12,13}. Likewise, filamentous fungi show a “progressive loss of growth potential” over time¹⁴. Such natural aging of individuals over longer periods probably has limited relevance in unstable soil environments, especially in unicellular organisms. However, in filamentous fungi, senescence occurs as a by-product of growth and probably represents a prominent mechanism of necromass formation due to the modular fungal growth form. Fungi move through soil by the formation of new hyphae, consequently leaving behind large amounts of hyphal fragments¹⁵. Most important, new hyphal growth as well as fungal sporulation and fruiting are subsidized by internal recycling from older hyphal parts, resulting in efficient reuse of cytoplasmic components, lipids and even cell wall fragments such as chitin^{16,17}. This mechanism is of particular relevance during nutrient limitations and starvation (Table 1)^{18,19}. We describe this whole process as compartmental senescence (Fig. 1f), an analogue to leaf senescence in which valuable resources are withdrawn as a natural developmental process up to leaf abscission²⁰. Similar to leaf litter, senescent hyphal parts diverge in their chemical composition from actively growing hyphae. Older hyphae (distant from growing tips) are characterized

by vacuolization and cytoplasmic reductions following the activity of autocatalytic enzymes^{21,22} and strong reductions in DNA content²³ and nutrient concentrations²⁴. Senescence-derived fungal necromass will therefore be depleted in cytoplasmic components, storage compounds and growth-limiting elements relative to biomass²⁵ (Fig. 1f). The relative proportion of the cell wall fraction will increase, with consequences for C/nutrient ratios and chemical complexity: fungal cell walls are rich in complex interlinked polysaccharides, with varying concentrations of chitin and melanin depending on species identity²⁶.

In bacteria, surprisingly similar recycling processes are induced under nutrient-limited or stressful conditions (common in heterogeneous soil environments) despite their unicellular growth form²⁷, especially within colonies and biofilms. This is represented in the literature by the generic concept of programmed cell death (PCD)^{28,29} and will be categorized here as starvation or stress-induced PCD (Table 1). Bacterial PCD is governed by a highly controlled genetic programme involving cellular lytic degradation^{30,31}. As a most simple mechanism, endospore formation induced under stressful conditions is supported by autocatalysis of the mother cell and even surrounding daughter cells^{28,32}. Similarly, under starvation, PCD is a strategy in *Myxococcus* to provide nutrients for fruiting body formation while individual cell death in filamentous *Streptomyces* colonies supports neighbouring cells²⁸. Such unicellular suicide may seem paradoxical, but several authors describe this widespread phenomenon as a form of altruistic behaviour with the main goal of nutrient replenishment for genetically related survivors (kin selection)^{28,29,33}. Especially in the context of recent suggestions that the majority of soil bacteria and archaea occur in colonies embedded in extracellular polymeric substances (EPS) and biofilms, these mechanisms may be highly relevant^{33,34}. Within bacterial colonies, proximity allows cellular components released by cell lysis to be recycled efficiently by survivors, especially under resource-limited conditions²⁷. Again, the resulting necromass will be depleted in

BOX 1

Implementing MDPs in the conceptual understanding of biogeochemical processes

Microbial death pathways (MDPs): The distinct processes of microbial dying, including chemical transformations dependent on the cause of death and the organisms involved

Why to implement? A short summary

- Not only microbial growth but also the process of dying represent a relevant driver of the soil microbial carbon pump.
- The chemical composition of biomass is altered during MDPs, leading to distinct characteristics of resultant necromass (see examples in Fig. 1c–g) → microbial necromass ≠ microbial biomass.
- The chemical composition of microbial necromass affects its persistence (mean residence time), having impacts on both its mineralization and stabilization rates.
- Individual types of MDPs affect necromass composition differently: SOC sequestration and microbial community dynamics depend on the types of MDPs relevant in soil.
- (Re)use of components from biomass during natural MDPs—by the species itself or attacking agents—leads to efficient channeling of C, nitrogen (N) and energy in soil.
- Under certain conditions, C sequestration via microbial pathways is not limited by N availability and does not necessarily reduce plant nutrient availability → high relevance for agricultural management.
- Global change factors have direct impacts on the process and rate of microbial death.
- Differences in MDPs among functional microbial groups explain community-driven effects, especially the increased C storage in fungal dominated systems: fungal mycelia produce large amounts of C-enriched hyphal leftovers (necromass).

In more practical terms:

- C/N estimates and conversion factors for biomarkers of microbial necromass (derived from measurements in biomass) must be corrected.
- Ecological experiments with microbial necromass should use real necromass derived from the completed MDPs (metaphorically, leaf litter decomposition experiments also do not use fresh leaves).

easily degradable cytoplasmic compounds and growth-limiting elements. In addition, starvation induces further modifications to bacterial cells, such as degradation of storage compounds and a reduction in cell size. On the basis of geometric considerations, smaller cell sizes further increase cell wall/cytosol ratios.

Together, these lines of evidence suggest that death in microorganisms leads to substantial modifications in the molecular composition of necromass compared with biomass, driven mainly by decreases in cytoplasmic components with related rising C/nutrient ratios, in parallel with a reduction of limiting and easily degradable compounds (Fig. 1).

Further types of MDPs relevant in soil

Although the relative contributions of different causes and mechanisms for MDPs in soil are currently unresolved (Table 1), it is clear that in

How to implement? Some first ideas

In experiments:

- Understand individual MDPs in more detail on the basis of controlled experiments: microbial strains/communities may be exposed to different stressors under laboratory conditions (agar media, artificial soil) and the chemical composition of derived necromass analysed. Examples: inoculation with viruses or predators, exposure to sudden drought events, pesticide additions, reduction of nutrients. Necromass may be distinguished by life/death stains or isotope tracers, but also the chemical analysis of microbial biomass under stressed conditions will improve estimates of necromass chemistry (compared with biomarker conversion factors based on microbes grown on rich agar media).
- Preparing real necromass for experiments: (1) microbial biomass exposed to different forms of MDPs (see preceding point; including ¹³C labels) can be used for subsequent experiments in soil; (2) bacterial and fungal isolates cultivated for necromass production may be not only autoclaved but also grown over longer time spans under suboptimal conditions; (3) spatial and temporal sampling of the dying part of the microorganisms may allow capture of microbial cells most closely resembling the real necromass.
- Analyse mortality rates and turnover in microbial biomass and individual groups under varying conditions⁶⁵ and determine the relevance of different MDPs under varying conditions/soil types using new techniques (stable isotope probing, microfluidic devices)^{66,67}.

In biogeochemical models:

- Simple parameters to include: (1) biomass turnover times/mortality rates → necromass quantity (relative to microbial growth); (2) adjusted relevance of pathways in the necromass continuum⁶² depending on MDP and necromass composition (for example, stabilization versus destabilization); (3) death traits of relevant microbial groups.
- Theoretical models can be used to test the relevance of MDPs for C sequestration and persistence.

natural soil environments additional (external) causes of microbial death are common. Still, parts of the mechanisms described for senescence and PCD, especially resource recycling, are also relevant for other MDPs. Soil microorganisms form the base of the soil food web and are consumed by a diverse and abundant soil fauna community³⁵. Bacteria can also be killed by other predatory bacteria³⁶ and viruses that are highly abundant in soils^{37,38} (Table 1 and Fig. 1). Evidently, predated microbial biomass is transformed in varying degrees to necromass residues³⁹. Here the physiology and resource demands of the attacking agent are important in determining the resulting chemical transformations. Predation by fauna and protozoa is known to release excess N in mineral forms, a concept referred to as the microbial loop⁴⁰ (Fig. 1c). Fauna needs to maintain homeostatic C/N/P ratios and invest C into both catabolism and anabolism, which necessitates the

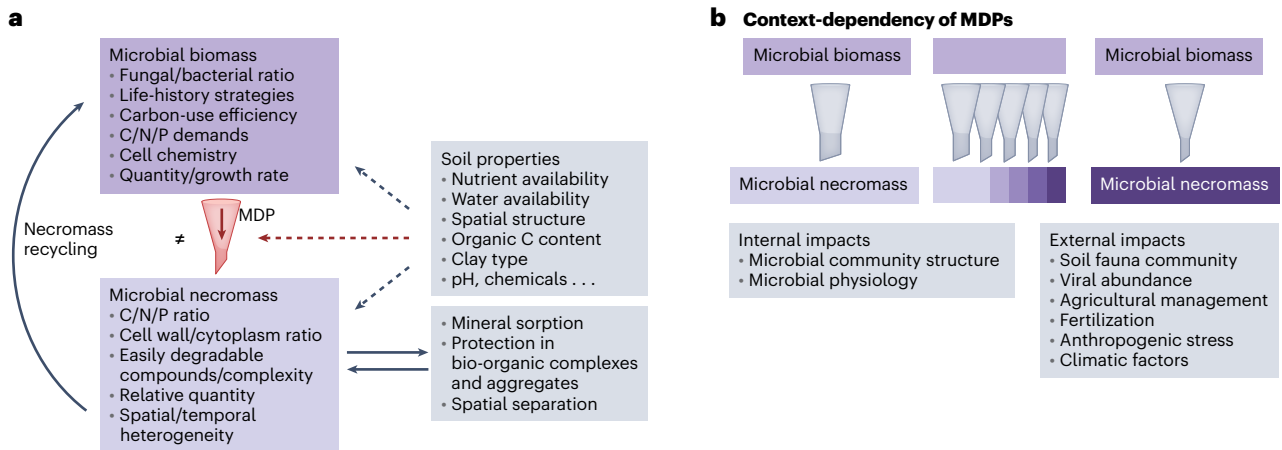


Fig. 2 | Visualizing the dependencies of MDPs on biotic and abiotic soil properties and environmental factors. **a**, Processes relevant for microbial necromass composition and its fate are illustrated (solid arrows), as well as the impact of soil properties on these processes (dashed arrows). Variables of microbial biomass, necromass and the chemical and physical soil environment

relevant for the respective processes are listed. **b**, Context dependency of MDPs. Simplified visualization of the strength of chemical transformations during MDPs and factors relevant in this context. Following MDPs, necromass may be fairly similar to the initial biomass (left) whereas certain MDPs may lead to substantial transformation of the initial biomass (right).

release of excess mineralized N, especially following ingestion of bacteria with low C/N ratios. In parallel, non-digested microbial necromass residues will be emitted in faecal pellets or excreted (in the case of protozoa), with the chemical composition of these residues depending on the digestive capacities of the predator species^{41,42} and their specificity of prey intake³⁵. The exact chemical composition depends on many factors, but relative proportions of less easily degradable compounds will generally increase (Fig. 1c). Predatory bacteria, by contrast, ingest mainly the cytoplasm of bacterial prey, leaving behind cell wall fragments as necromass residues³⁶ (Fig. 1e). Even viral attack produces modified bacterial residues that are depleted in N and especially P, and thus C enriched³⁷ (Fig. 1d). Another relevant mechanism to consider during viral or pathogenic infection is self-defence mechanisms present in bacterial colonies. Via quorum sensing, infected bacterial cells partly initiate cell lysis (PCD), which some authors also describe as a mechanism to make resources available to neighbouring daughter cells^{28,43}, again allowing resource recycling within colonies (Fig. 1d).

Other forms of MDPs exist in soil, and the list discussed here is probably incomplete (Fig. 1b). Antagonistic interactions during microbial competition can have lethal outcomes. Microbial species strongly compete for resources in soil environments. On the one hand, more efficient resource exploitation by one species may lead to starvation and subsequent (compartmental) death of another, inducing PCD mechanisms as described⁴⁴. On the other hand, interference competition involves the excretion of antimicrobial toxins with potentially lethal effects^{45,46}. Regarding chemical transformations during MDPs induced by antagonism, certain degrees of internal resource recycling in response to this stressor are likely, depending on the lethality and concentrations of toxins, especially during stress-induced spore formations in bacteria or within fungal mycelia⁴⁷.

Another relevant mortality agent in light of global change is MDPs induced by anthropogenic disturbances. Examples are pesticide applications and other forms of soil pollution (Fig. 1g), soil compaction, more intense drought or heat events as a consequence of climate change, or osmotic stress induced by salinity (as a consequence of inappropriate management). Water stress also occurs regularly under natural conditions, and microorganisms have adapted to such soil conditions over evolutionary time⁴⁸—abiotic stresses are probably relevant MDPs in soil (including desiccation, starvation, freezing, anoxia and oxidative stress). However, sudden and severe stress events, including xenobiotic chemicals, may lead to more rapid death and subsequent

release of complete cell components, characterized by lower resource retention and less efficient reuse than observed in natural MDPs⁴⁹ (Table 1, Fig. 1g).

Relevance of MDPs in environmental contexts

Different types of MDPs differ not only in the relative amount of necromass produced but also in the chemical transformations induced, with further contrasts created among different microbial groups. For example, while compartmental senescence in fungal mycelia produces necromass residues dominated by complex, C-rich cell wall fragments, lysis of bacterial cells probably releases more cytoplasmic compounds and cell wall fragments containing more N, since bacterial cell walls contain higher proportions of peptides^{26,50}. Predation, by contrast, will retain more C within the soil food web but also release complex necromass residues together with mineral nutrients available to plants. Thus, it can be expected that fungal/bacterial ratios, predator load, viral abundances and competitive dynamics in soil communities will affect the relative importance of different MDP types, with consequences for necromass quantity and quality (Fig. 2a). Since the community composition of soil microbes, fauna and viruses varies among soils and further responds to environmental change, MDPs and the strength of chemical transformations will vary accordingly (Fig. 2)^{38,51,52}. In parallel, the efficiency of C versus nutrient recycling within microbial biomass will respond to soil nutrient limitations⁵³, affecting the C/N and N/P ratios of microbial necromass (Fig. 2a). Anthropogenic (lethal) stressors, especially extreme events⁵⁴, may have even more substantial impacts on necromass formation and composition. Rapid, uncontrolled death of microorganisms in soil not only increases the quantity of necromass produced but also reduces its chemical transformation as opposed to natural MDPs (Fig. 1g and Table 1).

Not only microbial growth rates are affected by environmental parameters but also MDPs, which subsequently determine the amount of C (1) remaining within microbial biomass or the soil food web, (2) being retained as SOC by mineral and organic interactions or (3) available for mineralization by necromass-degrading microbes. Predictions of the long-term persistence of necromass-derived SOC are important research priorities, although challenging to conduct due to the different mechanisms and high context dependency involved (Fig. 2)⁶. According to metabolic theory, necromass that is richer in easily available C and nutrients (alongside C-rich molecules) will be more exposed to microbial mineralization than will more transformed

complex polymeric necromass⁵⁵. Indeed, meshbag experiments indicate that necromass mineralization rates are positively correlated with N content and negatively correlated with the abundance of highly complex components such as melanin⁵⁶. However, mineral sorption is discussed as a more prevalent factor determining necromass persistence, which acts most strongly on proteinaceous and phosphorylated molecules⁵⁷. Thus, MDPs and resulting necromass chemistry are relevant to all stages of the necromass continuum⁵⁸, namely, production, recycling and stabilization, although the relevance of each stage will probably depend on microbial necromass composition and diversity, together with soil properties (Fig. 2a).

Another relevant factor for C persistence is the heterogeneity introduced by spatial and temporal diversity in soil⁵⁹, with this complexity further enhanced by diverse and spatially differentiated MDPs. The latter affect molecular composition and diversity of microbial necromass as well as nutrient release from biomass and its spatial distribution. The way cells disintegrate, for example, leakage of cytosolic compounds, altered particle size distributions and the spatial arrangement of cellular remains within soil particles further increases spatial heterogeneity (Fig. 1). In addition, temporal effects on MDPs will be present at various scales, from short-term to seasonal fluctuations⁶⁰. In conclusion, diverse MDPs, chemical transformations and their responses to spatial and temporal fluctuations will increase molecular diversity, spatial heterogeneity and temporal variability—all relevant factors determining SOC sequestration⁵⁹.

Conclusions and future research directions

We have detailed how microbial dying represents a distinct process with consequences for the quantity and molecular composition of microbial necromass. Despite a lack of direct measurements in soil, knowledge derived from (1) microbial physiology, (2) trophic interactions and (3) soil community ecology provides strong evidence for the mechanisms of MDPs described. At the current stage, the relation between microbial parameters and soil organic C storage is not fully resolved, often related to missing information on microbial traits, interactions of necromass with soil minerals and responses to environmental change^{61,62}. In this Perspective, we argue that an understanding of the processes and rates of microbial death and resulting necromass characteristics will improve the implementation of microbial contributions to SOC sequestration in biogeochemical models. Microbial death, interactively with microbial growth, drives the soil microbial carbon pump, where the correlations among biomass and necromass abundance and composition are highly context dependent (Fig. 2). Current SOM research takes microbial growth and carbon-use efficiency as a proxy for microbial C inputs⁶³. However, as presented here, mortality rates and chemical transformations will also determine the quantity and composition of microbial necromass in soil (Box 1).

The insights provided on biomass-to-necromass transformations add important new perspectives on soil biogeochemical processes (Box 1). Still, it is clear that MDPs represent only one component of a complex multifactorial soil system, which affects SOC sequestration interactively with microbial biomass characteristics and soil chemical properties (Fig. 2). An important opportunity provided by these new insights is to rethink the energy-efficient channelling of C within microbial communities as well as high nutrient-use efficiencies due to resource recycling mechanisms. It was proposed that C sequestration in microbial residues may be limited by N demands⁶⁴. However, if N is reused or released in mineral forms before necromass formation, N (or other nutrients) may, under certain conditions, not limit C sequestration. In line with this, increases in C sequestration also do not necessarily decrease nutrients available to plants, an aspect especially relevant for the management of agricultural soils with untapped C storage potential^{4,5}.

Future research must test these concepts experimentally in soil and microbial systems and establish whether the incorporation

of MDPs improves predictive strength of biogeochemical models (Box 1). We hope this Perspective will stimulate deeper exploration of the topic, exploiting new techniques and interdisciplinary approaches, and motivate a new research focus in the field of SOC cycling and microbial ecology. As the direct analysis of microbial necromass in soil is challenging, this also applies to the examination of MDPs. However, analytical tools in soil science and microbiology are evolving rapidly. Detailed applications of stable isotope probing allow analyses of microbial growth and death within highly resolved food web dynamics^{60,65}, while higher resolution in imaging and spectroscopic techniques may provide insights on microbial interactions and processes at the level of individual organisms and populations^{66,67}. Furthermore, by integrating MDPs, we hypothesize that experiments with real necromass—not autoclaved biomass—will provide more detailed insights into its fate and stabilization (Box 1). Most likely, the often observed biphasic mineralization (two-pool model) is an artefact derived from this experimental bias driven by easily mineralizable cytosolic compounds^{68,69}. Future experiments should also address responses of MDPs to global change scenarios. Such knowledge and conceptual insight hold great potential to improve mechanistic understanding of organic C storage via microbial necromass, increase the precision of biogeochemical models and develop agricultural management strategies to exploit the C storage potential of soils.

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Author contributions

T.C. and J.L. generated the initial conceptual ideas. T.C. led the writing and literature search. K.M.-J., I.M., M.C.R., J.L. and T.C. developed the final concepts. All authors contributed to writing and editing.

Competing interests

The authors declare no competing interests.

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