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The Microbial Necrobiome Involved in the Soil Decomposition Process

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REVIEW

Abstract

Soil microorganisms play a key role in carbon and nutrient cycling processes, which includes the creation and decomposition of soil organic matter (SOM). At the same time, microorganisms use organic C as an energy source, for their development, and to support their functions. Based on our literature search we identified only one model proposed to date for necromass cycle which includes four key stages of the necromass continuum: production, recycling, stabilization, and destabilization. We further scrutinized factors to better understand/explain the processes related to this vital cycle. Microbial necromass is a significant and enduring part of the soil organic carbon (SOC), which is the primary C reservoir in terrestrial ecosystems. Assessing microbial necromass C stocks and understanding how they respond to global changes has become a standard approach in soil C cycle research. Nevertheless, the conventional proxies used to estimate necromass C levels do not provide insights into the dynamic processes and transformations that occur within the soil, ultimately shaping the persistence of microbial necromass.

Keywords: Soil microorganism; soil organic carbon (SOC); soil organic matter (SOM); necromass cycle.

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INTRODUCTION

Soils contain the most substantial quantity of organic carbon (C) within terrestrial ecosystems (Bernard et al., 2022). Consequently, even a minor alteration in soil C cycling could have substantial implications for atmospheric CO2 levels and the overall stability of the global climate system (Whalen et al., 2022; Zeng et al., 2022). Estimates indicate that the global soil organic carbon (SOC) pool, up to a depth of 1 meter, comprises approximately 1,417–1,469 Pg of C (Chandel et al., 2023). This is nearly three times the amount of C found in plant biomass (Smith et al., 2008) and twice the amount of C present in the Earth's atmosphere (Bernard et al., 2022; Kou et al., 2023; Schmidt et al., 2011).

Soil organic matter (SOM) encompasses a wide range of organic materials, including recently added plant, microbial, and animal-derived residues, as well as the microbial biomass responsible for breaking down these entries (Gougoulias et al., 2014). It is a primary product of microbial activity and plays an important role in the development and functioning of terrestrial ecosystems (Khatoon et al., 2017; Stoian et al., 2018). The prominent influence of SOM for the structure and stability of ecosystems underscores the importance of preserving existing levels and implementing management practices to enhance soils with declining SOM content. Organic matter (OM), especially the humus component, is essential for soil fertility (Senesi and Loffredo, 2018). Soil organisms, such as microorganisms and fauna (Berg and Laskowski, 2005), actively contribute to its decomposition and transformation, shaping the soil's physical, chemical, and biological properties (Sofo et al., 2020; Chenu et al., 2015; Păcurar et al., 2020; Vidican et al., 2016). The content in soils varies widely, ranging from less than 0.2% in arid soils to more than 80% in peat soils. In temperate regions, SOM levels typically fall within the range of 0.4% to 10.0%, with humid regions averaging around 3-4%, and semiarid areas typically having 1-3% SOM content (Smith et al., 2014). As most of the terrestrial organic C and N, SOM contains a significant portion originating from the remains of microorganisms (Dong et al., 2021). This resource plays a major role in the global C cycle (Islam et al., 2022; Koch et al., 2007; Corcoz et al., 2021) and serves as a vital source of nutrients like nitrogen (N) and phosphorus (P) for supporting plant growth as well as various soil microbial and animal activities. Traditional perspectives and models have long held that SOM primarily originates from tough, hard-to-break-down plant remains, with soil microorganisms being the primary drivers responsible for breaking down SOM through decomposition processes (Wang et al., 2020).

Soil microorganisms play a dual role in the decomposition of OM (Sokol et al., 2022). They break it down by secreting extracellular enzymes, and their remains become significant contributors to SOM (Wang et al., 2022). When plant-derived OM is metabolized by soil microbes, it transforms into microbial biomass and, upon microbial death, becomes stabilized within SOM as microbial necromass (Hu et al., 2020). Their metabolic functions are shaped by interactions with other soil microbes, fauna, plants, and environmental factors (Sokol et al., 2022). Microbial communities are the central part of C and nutrient cycling in ecosystems (Hopkins and Dungait, 2010). They both decompose (OM), releasing carbon (C), and contribute to stable C through their microbial necromass. This microbial necromass can make up a substantial part of soil C (Gross and Harrison, 2019), but the exact processes of microbial necromass production, consumption, and their role in SOM formation are not fully understood (Hu et al., 2023).

The aim of this paper is to analyze the importance of microbial necromass in the decomposition process of OM from soil. Each stage of the microbial necromass cycle was assessed in relation to the factors that shape it. The primary goals include the understanding of processes involved in microbial necromass formation, by analyzing its impact on decomposition patterns. Secondary goals are related to the identification of the diverse factors, substrate availability, microbial community composition, and environmental conditions, which collectively contribute to shape the entire microbial necromass cycle.

FACTORS AFFECTING NECROMASS CYCLE

Soil organic matter (SOM) plays a pivotal role as the primary C reservoir within terrestrial ecosystems, and its management has gained significant policy importance (Camenzind et al., 2023). Due to the current climate change pressure, the single and combined influence of biotic and abiotic factors on microbial necromass cycle is increasing in importance (Dong et al., 2021). While there is substantial research on how external factors like drought, elevated CO_2 levels, and changes in land use affect microbial necromass degradation, our understanding of the intrinsic determinants of necromass degradation, particularly the microbial characteristics of various microorganisms, is limited. Soil microorganisms are the primary agents responsible for sequestering SOC, particularly through the buildup of their deceased biomass.

Precipitation, temperature, and soil pH are the key factors that influence the microbial necromass content and its role in SOC and the microbial necromass accumulation coefficient (Wang et al., 2021). Temperature plays a determining role in regulating the mineralization of SOM (Wang et al., 2020). In the context of global warming, understanding how temperature influences SOM mineralization becomes extremely important (Wang et al., 2016). As temperatures rise, the mineralization of microbial-derived SOM tends to increase due to the heightened microbial activity. However, at the same time, the production of necromass by microbial activity may also increase. This complex interaction means that the net contribution of microbial-derived SOM to total SOM becomes uncertain as temperatures increase. In essence, while higher temperatures can accelerate the breakdown of OM by microorganisms, they can also stimulate the production of new microbial necromass, making it challenging to predict the overall impact on SOM dynamics (Wang et al., 2020).

Microbial necromass, a key component of SOM, is also strongly influenced by global change factors such as human-driven nutrient inputs, climate warming, elevated CO_2 levels, and periodic drought, which in turn impact soil microorganisms and their activity (Hu et al., 2023).

STAGES OF NECROMASS CYCLE

The necrobiome can be described as a relatively concentrated group of organisms that have undergone evolutionary adaptations to detect, utilize, and ultimately gather around decaying OM, either for nourishment or as a habitat resource (Benbow et al., 2019). Microbial necromass plays a major role in shaping the composition of SOM, and effectively controlling it could be a key approach in addressing atmospheric CO_2 levels and mitigating climate changes. The common agreement is that the amount of microbial necromass produced largely depends on how efficiently microorganisms use carbon (C). This efficiency, in turn, is significantly affected by the type and quality of the OM that these microorganisms feed on (Angst et al., 2022).

The factors that affect the microbial necromass cycle and the four stages of this cycle (Figure 1), also the functions of necrobiome involved need to be explored as a flow for a correct understanding:

1. Formation or production (microbial death): this phase involves the initial generation of necromass through the demise of microbial communities.
2. Recycling (utilization of necromass by other microorganisms): in this stage, a different community of microorganisms consume the necromass, recycling its organic material.
3. Preservation or stabilization (necromass attachment to soil minerals): during this phase, the microbial necromass becomes attached to soil minerals, leading to its preservation in a stable form.
4. Decomposition or destabilization (release of necromass from a stable condition): the final phase involves the breakdown and release of microbial necromass from its stable condition, completing the cycle.

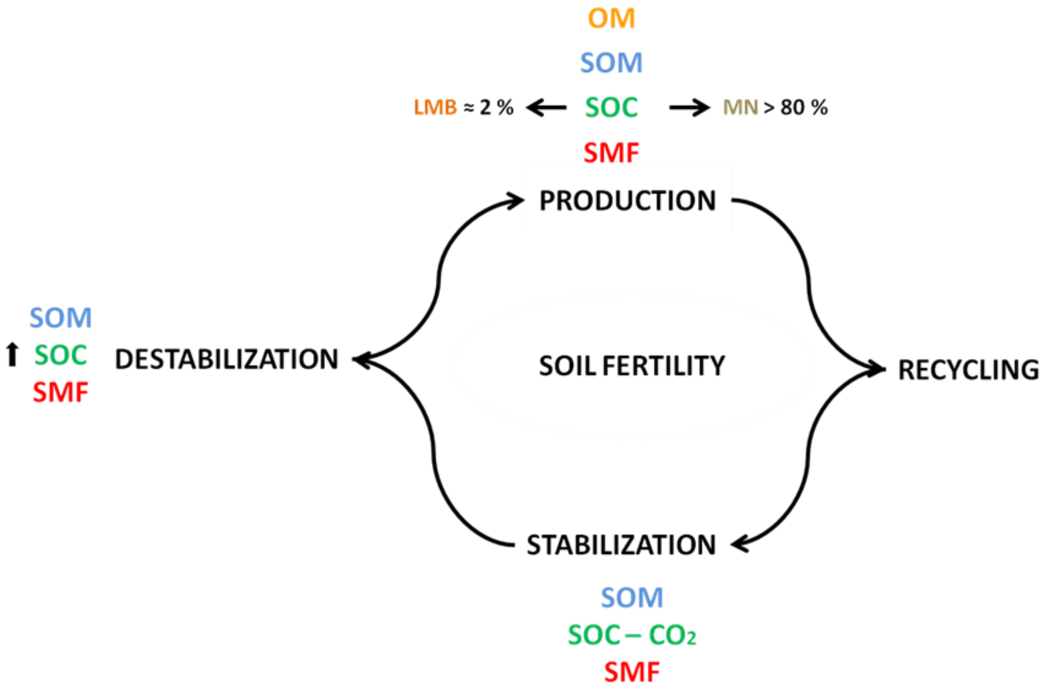

Figure 1. The four stages of Necromass continuum. Legend: OM – organic matter, SOM – soil organic matter, SOC – soil organic carbon, CO_2 – Carbon dioxide, SMF – soil microflora, C/N – carbon/nitrogen ratio, LMB – living microbial biomass, MN – microbial necromass. The model was synthesized based on a number of scientific papers by Buckeridge et al., 2020; Buckeridge et al., 2022a; Buckeridge et al., 2022b.

This process is dynamic and interrelated, playing a crucial role in recycling nutrients, maintaining soil fertility and impacting the global C cycle (Prasad et al., 2021). Microbial necromass cycles involve the continuous production, recycling, stabilization and destabilization of OM contributing to the functioning and sustainability of ecosystems (Kästner et al., 2021). All of these phenomena are intricately associated with the biotic and abiotic factors that exist within the soil environment (Kennedy and Maillard, 2023).

STAGE 1: THE PRODUCTION OF NECROMASS

Soil and sediment of organic matter (OM) comes from the remains of plants, animals, and microbes (Horwath and Paul, 2015). This OM formation and decomposition process is essential for regulating atmospheric trace gases, such as CO_2, N_2O, and CH_4. Soil OM includes partially decayed plant matter, microorganisms, soil fauna, decomposed by-products, and humic substances. The activities of microorganisms and fauna are crucial for balancing C absorption during photosynthesis and its release during decomposition. Microbial residue accumulation and decomposition are shaped by both living and non-living factors, including vegetation, OM inputs, soil properties, and climatic trends (Zhang et al., 2023). Changes in land use can alter these factors, influencing soil conditions and nutrient levels, and thus impacting microbial residue formation and accumulation.

The decomposition and formation of SOM are influenced significantly by plant inputs, acting as a key force in the C cycle (Paul, 2016). Evidence suggests that native organisms, adapted to specific environments, break down litter more efficiently within their home territory compared to foreign sites, demonstrating a distinct advantage in decomposition rates. Soil microorganisms play a key role in regulating the decomposition and formation of SOC. Research indicates that microbial-derived necromass C, including various cellular components, can constitute a substantial portion, from 50% to 80%, of SOC (Lehmann et al., 2015). The main source of SOC originates from the process of photosynthetic primary production carried out by plants, while soil microorganisms serve as the primary drivers of C mineralization (Wang, C., et al., 2021). They are responsible for both the depletion of organic C from the soil through decomposition and the addition of different biochemical carbon forms through their remains.

Microbial necromass is an important element of SOM and can play a vital role in addressing atmospheric CO_2 levels and mitigating climate change through effective management (Angst et al., 2022). It primarily consists of particulate organic material originating from cell envelope remnants, along with certain colloidal components like enzymes, ribosomes, and small biopolymers that have managed to avoid being reutilized by subsequent microbial generations (Liang et al., 2019). The balance between microbial necromass formation and decomposition greatly affects its contribution to SOC accumulation (Wang et al., 2021). Living microbial biomass accounts for approximately 2% of SOC, whereas microbial necromass can contribute up to 80% of organic C in soil (Luo et al., 2022). Soil depth plays a crucial role in the accumulation of microbial necromass and its impact on soil on SOC due to variations in nutrient and OM distribution vertically, affecting microbial growth and biomass production (Li et al., 2022). SOC is a major indicator of soil quality, playing essential roles in nutrient provision, the preservation of biodiversity, and the mitigation of climate change (Zhou et al., 2023).

STAGE 2: THE RECYCLING OF NECROMASS

The process of necromass recycling is significantly impacted by environmental conditions and microbial nutrient requirements (Wang et al., 2021). Recycling of microbial necromass carbon (C) and nitrogen (N) linked to mineral surfaces might decrease due to necromass recycling (Buckeridge et al., 2022a). The process of recycling refers to the microbial decomposition of dead microorganisms and their byproducts, which can result in the conversion of C and N from necromass into living biomass or their release through mineralization processes before becoming part of mineral structures. This process is separate from removing microbial necromass from mineral surfaces (destabilization or mining). Soil microorganisms utilize microbial necromass as a substrate for their growth. In the initial stages of microorganism-driven SOM recycling, certain plants and microbial necromass elements are preserved due to their resistance to decomposition (Liu et al., 2023). In the middle and late stages of SOM breakdown, protection within aggregates becomes vital for stabilizing C from plant and microbial necromass.

High N availability can accelerate microbial necromass accumulation, especially when sufficient C is present (Wang et al., 2022). In nutrient-rich environments, microbial growth and microbial necromass accumulation increase. Low precipitation enhances microbial necromass recycling efficiency due to limited nutrients and water availability, with drying-rewetting cycles contributing to mineral-associated SOM formation.

STAGE 3: THE STABILIZATION OF NECROMASS

Soils contain a vast amount of C, which can be released into the atmosphere or stored in the ground (Trivedi et al., 2013). They serve as a natural barrier against rising atmospheric CO_2 levels and can absorb more C depending on the interplay between plant photosynthesis, decomposer organisms' respiration, and C stabilization processes within the soil. Microorganisms are essential for both reducing SOC stocks by converting OM to CO_2 and increasing SOC stocks through microbial biomass formation and its stabilization in soil structures or minerals (Liang et al., 2019). Enhancing the storage and stabilization of SOC offers dual benefits: it not only helps mitigate climate change but also enhances soil fertility, structural stability, and agricultural productivity, which is a strategy that brings advantages on multiple ecosystem services (Poirier et al., 2018).

Plant litter is the main origin of SOM, yet the processes of litter decomposition and SOM stabilization are typically studied independently, with decomposition focusing on short-term effects, and stabilization emphasizing organo-mineral interactions that slow SOM turnover (Castellano et al., 2015). However, it is generally acknowledged that litter quality can impact SOM stabilization, with varying effects based on the source of OM and stabilization mechanisms in different stable SOM pools. The decomposition of litter and the stabilization of SOM are influenced by the types of soil organisms involved in decomposition (Frouz et al., 2018). While soil microorganisms play a major role in organic matter breakdown, research indicates that soil fauna also significantly impacts decomposition rates, often by affecting microbial activity. Variations in soil composition, specifically the proportion of fungal and bacterial necromass, are influenced by the type of land use, such as agroecosystems, grasslands, or forests (Wang et al., 2021). These differences can be attributed to the impact of ecosystem type on three key factors:

- The ratio between fungi and bacteria: ecosystem type affects the balance of living fungi to bacteria present in the soil.
- Decomposition and stabilization rates of microbial necromass: different ecosystems influence how quickly necromass (dead organic matter) decomposes and stabilizes within the soil.
- Accumulation of microbial biomass and necromass residues: these variations lead to differences in the accumulation of both living microbial biomass and necromass residues in the soil.

Stabilization is the ability to protect microbial necromass from decomposition by natural and chemical processes. Necromass is protected from decomposition if it is isolated from organisms that can degrade it and from enzymes, just like any other OM in the soil (Buckeridge et al., 2022b).

SOM is mainly stabilized through two mechanisms: the creation of mineral-bound OM and the development of soil aggregates (Angst et al., 2021). The interplay between mineralization and stabilization of OM plays an important role in shaping the creation and breakdown of microbial necromass and its impact on the accumulation of SOC (Wang et al., 2022).

Improving the knowledge of SOM stabilization and destabilization can lead to more efficient soil management (Dignac, and Rumpel, 2013). This, in effect, can optimize ecosystem benefits such as C storage, greenhouse gas control, enhanced soil structure, erosion prevention, and the sustained fertility of soils.

STAGE 4: THE DESTABILIZATION OF NECROMASS

In the late 1990s, SOM destabilization was defined as an escalation in the potential for organic C liberation, encompassing respiration, erosion, or leaching, while at 2016 Boulder workshop it was postulated the SOM vulnerability with destabilization (Jeanneau et al., 2019). They explained that SOM vulnerability increases when various factors like soil properties (Weiglein et al., 2022), environmental conditions, and disturbances reduce stable aggregates, soil microbes, and different forms of C, leading to higher proportions of leached C and greenhouse gas emissions (Smith et al., 2008). Understanding C destabilization mechanisms is complicated due to the various ways we categorize soil C based on factors like density, decomposition rate and chemical composition (Bailey et al., 2019). To make sense of these mechanisms, it's important to focus on the C most vulnerable to destabilization, often involving the conversion of soil organic C into a soluble form that microbes can readily metabolize.

Three primary mechanisms in soil that can disrupt C stability, making it available for microbial transformation, are driven by physical, chemical, and biological factors (Bailey et al., 2019):

- Release from physical enclosures: C that is physically shielded (within pores and aggregates) can be made accessible for microbial transformation through processes like soil mixing (e.g. bioturbation), freeze-thaw cycles, wetting-drying cycles, and aggregate turnover (Krull et al., 2003)
- C Desorption: Local chemical conditions, like changes in redox potential and pH, influence the forms of SOC that are released from soil solids and colloids (Bailey et al., 2019). The desorbed SOC forms have varying transport capabilities.
- Increased metabolism: In essence, the release and transport of C in soil make it available for microbial activity (Vaughan & Malcolm, 2012). The rates and extent of microbial transformations depend on the overall input of C into the soil and are sensitive to variations in temperature and moisture.

The realistic assessment of the processes and interactions involved in C stabilization/destabilization within SOC is essential for forecasting its fluctuation amidst climate shifts, management practices, and disturbances (Harden et al., 2018). Incorporating these complex mechanisms into models is challenging due to data limitations and local-scale interactions, yet essential for precise SOC dynamic predictions under varied conditions.

CONCLUSIONS

SOM refers to all organic materials present in soil, originating from or having been part of living organisms. It encompasses a range of biological materials undergoing transformations due to both abiotic and biotic processes. The first phase of the necromass cycle involves the production of OM from the remains of plants, animals and microbes. This process is important for maintaining soil health. Biotic and ecosystem functions influenced by factors such as vegetation, organic matter, soil type and climate determine the accumulation and decomposition of OM residues. Moving on to the second phase of the necromass cycle which focuses on recycling, environmental conditions and microbial nutrient requirements It was microbial decomposition of dead organisms, and C and N are converted into OM or released through mineralization. Different from stabilization, this process relies on microbial activity and soil structure to preserve and stabilize necromass elements. The third phase of the soil cycle focuses on the stability of soil ecosystems, affects soil microorganisms, and ecosystem characteristics. Soil organisms, including microorganisms and animals, have an important role in decay rate and SOM stability. Specific ecological factors, such as the balance of fungal and bacterial, influence the rate of decomposition and stability, ultimately affecting C accumulation in soil. The final phase of the necromass cycle is the destabilization of soil ecosystems, where factors such as soil type, environment, and disturbance facilitate the release of C. This stage involves physical, chemical and biological processes that release C for microbial transformation. The dynamic and interconnected nature of this process is essential for nutrient recycling, soil fertility maintenance, and its impact on the global C cycle. The continuous production, recycling, stabilization, and destabilization of OM in microbial necromass cycles significantly contribute to ecosystem functioning and sustainability. The highly dynamic C cycling in soil microbes provides the basis for understanding how soil C persists over time, which has implications for controlling atmospheric CO_2 and managing agricultural productivity.

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Conflicts of Interest

The authors declare that they do not have any conflict of interest.

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