Received: 23 September 2021 | Accepted: 2 January 2022

DOI: 10.1111/1365-2435.14014

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

REVIEW

Emerging relationships among microbes, soil carbon storage and climate change

Deconstructing the microbial necromass continuum to inform soil carbon sequestration

Kate M. Buckeridge[1] | Courtney Creamer[2] | Jeanette Whitaker[3]

[1]Luxembourg Institute of Science and Technology, Belvaux, Luxembourg

[2]U.S. Geological Survey, Menlo Park, CA, USA

[3]UK Centre for Ecology & Hydrology, Lancaster, UK

Correspondence
Kate Buckeridge
Email: kate.buckeridge@list.lu

Funding information
Natural Environment Research Council, Grant/Award Number: NE/R016429/1 and NE/S005137/1; U.S. Geological Survey Climate R&D Program, Grant/Award Number: ZT00U4U30

Handling Editor: Ji Chen

Abstract

1. Microbial necromass is a large, dynamic and persistent component of soil organic carbon, the dominant terrestrial carbon pool. Quantification of necromass carbon stocks and its susceptibility to global change is becoming standard practice in soil carbon research. However, the typical proxies used for necromass carbon do not reveal the dynamic nature of necromass carbon flows and transformations within soil that ultimately determine necromass persistence. In this review, we define and deconstruct four stages of the necromass continuum: production, recycling, stabilization and destabilization.
2. Current understanding of necromass dynamics is described for each continuum stage. We highlight recent advances, methodological limitations and knowledge gaps which need to be addressed to determine necromass pool sizes and transformations. We discuss the dominant controls on necromass process rates and aspects of soil microscale structure including biofilms and food web interactions. The relative importance of each stage of the continuum is then compared in contrasting ecosystems and for climate change drivers.
3. From the perspective of the continuum, we draw three conclusions to inform future research. First, controls on necromass persistence are more clearly defined when viewed through the lens of the continuum; second, destabilization is the least understood stage of the continuum with recycling also poorly evidenced outside of a few ecosystems; and third, the response of necromass process rates to climate change is unresolved for most continuum stages and ecosystems.
4. Future mechanistic research focused on the role of biotic and abiotic soil microscale structure in determining necromass process rates and the relative importance of organo–mineral and organo–organo interactions can inform necromass persistence in different climate change scenarios. Our review demonstrates that deconstructing the necromass continuum is key to predicting the vulnerability and persistence of necromass carbon in a changing world.

KEYWORDS
amino sugars, destabilization, microbial necromass continuum, necromass recycling, persistence, soil carbon sequestration, stabilization

1 | INTRODUCTION

Soil microbial products and residues (hereafter 'necromass') contribute, sometimes substantially (15%–80%), to soil organic matter (Angst et al., 2021; Hall et al., 2020; Liang et al., 2019). Microbial necromass accumulates in soil as microbially exuded extracellular compounds or the remains of dead microbial cells and cell fragments. Necromass persists in soil due to protection from microbial decomposition and through efficient recycling, in which necromass decomposition contributes towards microbial biomass growth (Buckeridge, Mason, et al., 2020; Creamer et al., 2019; Liang et al., 2019). Land management can increase soil carbon by optimizing necromass formation (sensu Kallenbach et al., 2015), making necromass a critical component of efforts to mitigate climate change through soil carbon sequestration. Conversely, necromass formation is climate sensitive: higher temperatures increase microbial turnover (death) and increase necromass production (Hagerty et al., 2014; Wang et al., 2020b). But to quantify how necromass responds to climatic changes, we need to understand some key fundamentals about *how, when and where* necromass is formed, transformed and lost in soil.

A new paradigm for soil organic carbon accumulation has developed (Cotrufo et al., 2013), moving away from a traditional focus on the chemical recalcitrance of plant carbon inputs influencing rates of decomposition. Current research emphasizes the efficiency of microbial incorporation of plant carbon into microbial biomass, and adsorption of necromass to mineral surfaces as mechanisms to promote carbon accrual and persistence (Liang et al., 2019). However, an assumption that microbial biomass will form stable (i.e. fixed, unvarying) necromass is not always correct. The high proportion of soil carbon that has a microbial signal supports the concept that most organic matter in aerobic, mineral soils must pass through a microbial filter, although this varies by ecosystem type (Angst et al., 2021). However, microbial turnover (i.e. death and necromass formation) and necromass reuse through recycling and destabilization are ecosystem specific and climate sensitive. For example, there is evidence that dead microbes are recycled by a broad number of microbial groups (Buckeridge, Mason, et al., 2020; Donhauser et al., 2020), and indirect evidence that microbial necromass on mineral surfaces is likely to be destabilized through microbial and plant root mining (Keiluweit et al., 2015). These findings suggest that microbial necromass is not always persistent, even after adsorption on mineral surfaces.

The concept of a soil organic matter continuum from production to stabilization on mineral surfaces has been expressed previously (Lehmann & Kleber, 2015). Soil organic matter persistence—or the likelihood it will remain in soil—reflects the combined processes of not just production to stabilization but also destabilization and recycling. Similarly, the microbial necromass continuum described in this review encompasses necromass production, recycling, stabilization and destabilization (Figure 1). For each stage of the continuum, we discuss current understanding; methods to quantify pools or process rates; biotic and abiotic properties that influence pool sizes and flows; and the major challenges in understanding how each stage influences necromass persistence. We then consider how the abiotic and biotic controls for each stage may differ, depending on the ecosystem and global change context.

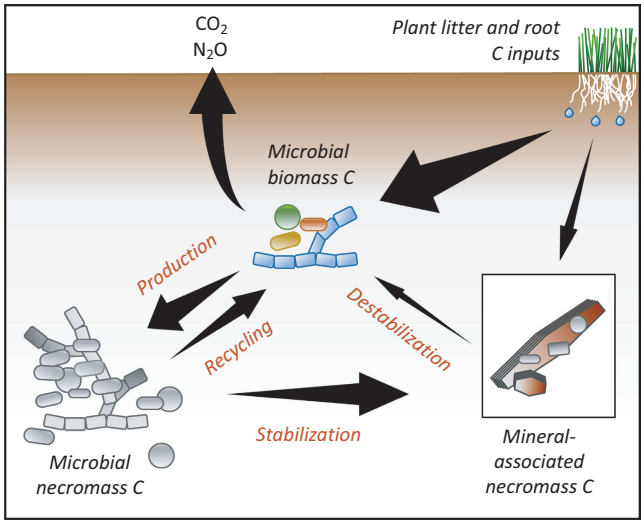

FIGURE 1 Microbial necromass persistence in soil is defined by the necromass continuum. Plant litter and root carbon (C) inputs may be directly stabilized on soil minerals, but much of this plant C will be immobilized or respired by soil microorganisms through the production of microbial biomass or other microbial products. When microorganisms die, they become microbial necromass (dead intact cells, cell parts, extracellular DNA, enzymes and other proteins, extracellular polymeric substances). Necromass may be recycled within or outside biofilms by live microorganisms or may be stabilized on a matrix of soil minerals and organics where it may persist for minutes to millennia. Once stabilized, necromass may be destabilized by chemical or biotic (plant or microbial) processes. The size of the arrows illustrates hypothetical differences in flow rates between pools. Many of these rates have not been verified or may differ strongly depending on the environmental context

2 | NECROMASS PRODUCTION

Microbial necromass 'production' (Figure 1) is the creation of residues derived from the extracellular release of microbial biopolymers, and from microbial turnover (death). Necromass residues or products include intact or burst cells or hyphae, fragments of cell walls and hyphae and monomers or polymers that were in the cytoplasm, biofilm or hyphal mucilage (polysaccharides, proteins [including enzymes] and DNA). The current favoured method of quantifying microbial necromass carbon is based on amino sugars (Table 1), polymers that are found in bacterial and fungal cell walls, but not in archaeal, plant or animal cells (Liang et al., 2019). Amino sugar carbon is ~7% of soil organic carbon (SOC; Ni et al., 2020; ~2× the soil microbial biomass carbon pool) but a negligible component of the live biomass (Glaser et al., 2004), making it an excellent proxy for quantifying necromass stocks (using conversion factors to upscale, reviewed in Liang et al., 2019). However, amino sugars and other proxies do not illuminate necromass carbon transformations

TABLE 1 Established methods to quantify or identify microbial necromass pools: advantages and limitations. Necromass is quantified either from its chemical constituents (biopolymers, functional groups) or through visual identification (biofilms, cell wall fragments). All biomarker approaches only quantify a portion of microbial necromass and must be upscaled to estimate all necromass contributions. Methods that quantify functional groups cannot definitively separate plant, live microbial biomass, and necromass components unless there is a diagnostic component that can be identified. Spatially resolved methods often require visual identification of microbial necromass and distinguishing live biomass versus dead necromass can be challenging. All spatial methods suffer from issues in upscaling. In many instances visual identification can be combined with spatially resolved functional group classification (like spectroscopy) to improve confidence in necromass identification. Without time-resolved sampling, these methods only provide a snapshot of necromass pool size and therefore do not directly inform rates for the stages of the necromass continuum (production, recycling, stabilization, or destabilization). Many methods not included here (like NanoSIMS) do not explicitly identify necromass but have been used for necromass quantification using appropriately designed experiments

Method	Appx scale	Necromass identification	Major advantages	Major limitations	Example citations
Biomarkers: Quantify components specific to necromass					
Amino sugars	Bulk	Fungal (glucosamine) and bacterial (muramic acid) amino sugars	Established necromass biomarker	Cell wall components only	Amelung (2000); Liang and Balser (2008)
Polysaccharides	Bulk	Microbial carbohydrates (mannose, galactose)	Established microbial biomarker	Not exclusive to necromass	Kiem and Kögel-Knabner (2003)
Glycerol dialkyl glycerol tetraethers (GDGTs)	Bulk	Isoprenoid (archaea) and branched (bacteria) membrane lipids	Persistent membrane lipid biomarker; measured archaeal necromass	Production and turnover rates not well established	Gies et al. (2021); Weijers et al. (2006)
-omics methods	Bulk	Diagnostic fungal or bacterial compounds	High resolution and may ID microbial groups (fungi v bacteria)	Non-trivial analysis and interpretation; includes biomass and necromass	Neurath et al. (2021); Malik et al. (2016)
EPS extractions	Bulk	Extracted pool	Quantifies extracellular necromass	Variety in EPS and methodology causes under- or over-extraction	Redmile-Gordon et al. (2014)
Extracellular DNA	Bulk	DNA from compromised cells or free in soil	Can ID source taxa	Degraded DNA not attributable	Carini et al. (2016)
Functional groups: Quantify compound classes assumed to be more abundant in necromass					
Solid-state ^{13}C NMR	Bulk	Mixing models place functional groups into compound classes	Measures all components of soil carbon with minimal sample prep	Specialized equipment; issues of carbon observability (Fe interference, low OM)	Simpson et al., (2007); Baldock et al. (1990)
Infrared (IR) spectroscopy (e.g., FTIR, MIR)	Bulk	ID of functional groups	Measures all components of soil carbon and minerals with minimal prep	Possible interferences (e.g., water, minerals); weak response from some functional groups	Certano et al. (2018)
Raman spectroscopy	Bulk	ID of functional groups or chemical fingerprints	Mapping possible with Raman microscopes; IDs organics and minerals; wet and unground OK	Fluorescence; calibration needed for molecular fingerprinting; weak response from some functional groups	Creamer et al. (2019)
FTICR-MS	Bulk	Places compounds into likely classes based on elemental ratios	Depth of information: can provide metabolite profiles; extractions of varying 'stability' can be analysed	No direct ID: van Krevlen diagrams group compounds	Tfaily et al. (2015); Coward et al. (2018)
Pyrolysis GC-MS	Bulk	Places fragments into most likely compound classes, then attributes class to source	Minimal sample prep	Many pyrolyzed fragments cannot be classified; classification is non-trivial	Kallenbach et al. (2016)

TABLE 1 (Continued)

Method	Appx scale	Necromass identification	Major advantages	Major limitations	Example citations
Spatially resolved: Identify necromass through visual appearance or functional groups					
Transmission electron microscopy (TEM)	nm	Visual ID of cell wall fragments or EPS	High resolution at small scales	Not quantitative	Foster (1988)
X-ray microscopy (e.g., STXM-NEXAFS; XPS)	50 nm	Chemical mapping of functional groups	Can maps both organics and metals (beamline dependent)	Specific beamlines at synchrotron user facilities required for light elements; samples should be flat	Keiluweit et al. (2012)
Laser ablation with mass spectrometry (e.g. LAESI)	20 µm	Places fragments into compound classes (fragment size depends on ionization method)	High depth of information: can provide metabolite profiles	Classification and interpretation of fragments is non-trivial	Stopka et al. (2017)
Scanning electron microscopy (SEM)	µm	Visual ID of cell wall fragments or EPS	Minimal prep; with energy Dispersive X-Ray (EDX) analysis, provides elemental distributions	Vacuum artifacts possible; image only without time-intensive elemental mapping	Miltner et al. (2012)
Fluorescence microscopy	mm - µm	Visual ID of cells and EPS or by fluorescence of organics	High throughput using common lab equipment	Samples are optimally flat (thin sections); not a definitive ID	DeLeo et al. (1997); Nunan et al. (2001)

(Figure 1) or the sensitivity of each stage of the continuum to climate change. Amino sugar quantification also misses extracellular biopolymers, the primary matrix of biofilms, which may be recycled or stabilized differently than amino sugars.

Several microbial biopolymers or functional groups are distinct from plant litter carbon or at least more likely to be sourced from microbial necromass carbon, providing an opportunity to better quantify microbial necromass. Operationally, necromass persistence is recorded not only as amino sugars but also carbohydrates, lipids and proteins (Hall et al., 2020; Kallenbach et al., 2016) or extracellular polysaccharides (EPS; Redmile-Gordon et al., 2014). Given the variable residence times of these compounds, quantification does not equate with an estimate of production, instead, methods that measure carbon flows or turnover provide better estimates of production and other stages of the continuum. For instance, isotopic methods have been used to quantify necromass production rates, inferred from the carbon turnover time in the biomass (Hagerty et al., 2014) or through isotope pool dilution of amino sugars (Hu et al., 2018). These isotopic methods are the best current practice for measuring gross necromass production rates.

Necromass production is difficult to quantify in soils because it is diffuse. It is estimated that 100% of soil microbial life exists in biofilms, which are composed of microbial cells and EPS (Flemming & Wuertz, 2019). Biofilm EPS comprises 10% of the live microbial biomass carbon, meaning that this EPS carbon is only ~0.2%–0.3% of SOC (Chenu, 1995). However, this low carbon value does not include EPS that persists after individual cell death, other carbon in soil biofilms or any stabilized EPS carbon, so total extracellular carbon production may be much higher if other microbial products (such as extracellular DNA (Carini et al., 2016) or extracellular enzymes (Burns et al., 2013)) and their turnover times are considered (Or, Smets, et al., 2007). Therefore, although we can estimate necromass persistence with established methods, the many small carbon pools constantly produced by microbes are difficult to quantify. As a result, most estimates of necromass production are based on microbial cell residues and are missing these other carbon pools. Model or built soils (without SOM) are an ideal method to quantify new production of these small pools (e.g. Kallenbach et al., 2016).

Biotic properties or traits that control rates of necromass production are those that influence microbial biomass creation, such as the efficiency of biomass growth on a substrate ('growth efficiency', 'carbon use efficiency', 'substrate use efficiency'; reviewed in Manzoni et al., 2012). Other biotic controls on production include microbial community interactions (competition, facilitation, dispersal; reviewed in Anthony et al. (2020)) and food web interactions, such as macrofaunal (Angst et al., 2019), bacterial (Lueders et al., 2006) or viral predation (Emerson et al., 2018). Stress tolerance (Anthony et al., 2020) may promote biofilm production (Redmile-Gordon et al., 2014), possibly increasing SOC, although stress has also been negatively associated with fungal necromass persistence (Crowther et al., 2015).

The microscale spatial strategy of microbes and their biofilms in soil pores is an important link between production and the rest

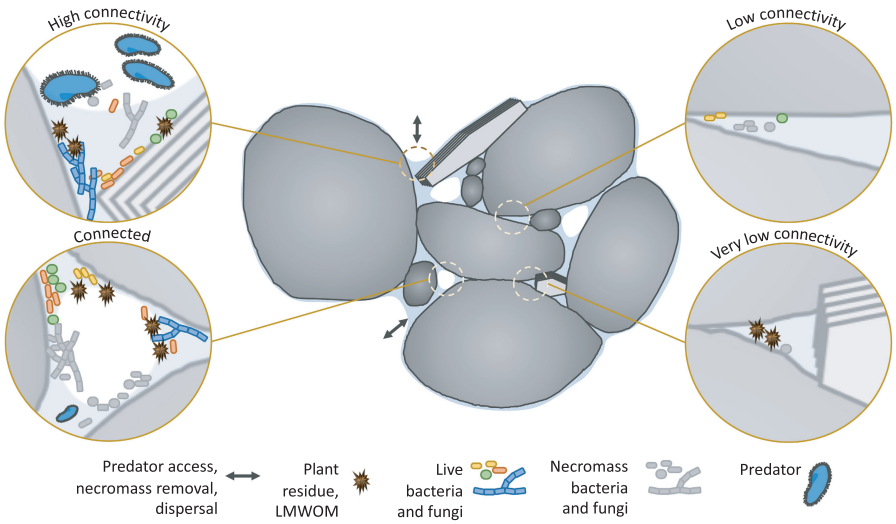

FIGURE 2 Influence of soil pore neck size on necromass production, recycling and destabilization through effects on resource availability and physical protection. The matrix controlling pore connectivity is comprised of both particulate organic matter (OM) and soil minerals. Pores with very low connectivity (<1 μm pore necks) trap plant residues or low molecular weight organic matter (LMWOM), with low O_2 and microbial abundance and restricted OM decomposition. Pores with low connectivity (1–6 μm sized pore necks) may host live microbial biomass, but reduced diffusion will result in energy constraints, slower biomass turnover and higher dependency on necromass recycling. These restricted access pores will be more buffered against hydrologic changes in the environment. Connected soil pores with wider pore necks (30–100 μm) will offer faster diffusion, and more nutrient, biological and metabolic diversity; air bubbles will decrease wet–dry buffering. The size of the pore neck (or biofilm constriction of the pore neck) may restrict some fungal or predator access, although smaller predators (nematodes) are common with 30–100 μm access. Here, necromass may be rapidly produced but may also be rejected (dispersed) as a less-favourable substrate. Biofilms in macropores, on external surfaces or as aggregates in solution may offer the same or stronger benefits of connected pores with regard to nutrients and diversity, but without the protection from predators, resulting in more frequent disturbances. In these high connectivity biofilms, necromass may be dispersed or consumed by predators together with live cells

of the continuum. It defines where necromass is produced, in turn defining the potential for recycling versus stabilization and the likelihood of destabilization. Necromass production is spatially heterogenous, because microbial biofilms preferentially establish on rough surfaces and in soil cracks (Lehmann et al., 2008; Nunan et al., 2001). Necromass production is also influenced by soil pore size because pore size and accessibility determine whether the necromass is likely to be recycled within the pore or released from the pore and biofilm. For instance (Figure 2), small pores with restricted hydrologic connectivity have slower organic matter decomposition; slower oxygen, organic matter and nutrient diffusion; and higher proportions of plant-derived organic matter (Bailey et al., 2017; Strong et al., 2004) implying less microbial growth and necromass production. Bacterial necromass is likely more important in pores with restricted connectivity, whereas flow-permitting macropores (>100 μm neck) and biofilms that have very high connectivity are more likely to include fungal necromass (Otten et al., 2001). Macropores are more accessible and may produce and disperse more necromass to the soil environment and are presumably recycled or stabilized depending on multiple factors as discussed in the sections to follow. This propensity for necromass to disperse in soil, as opposed to stabilizing in situ and creating 'hotspots', is critical for both our experimental designs (e.g. adding isotopically labelled necromass vs. growing biomass [then necromass] from isotopically labelled substrate), and our understanding of where necromass carbon accumulates and persists in soil.

3 | NECROMASS RECYCLING

Necromass recycling is the microbial decomposition of dead microbes, resulting in necromass carbon assimilation into biomass, and loss through respiration (Figure 1). Necromass recycling as defined here does not include predation and consumption of live microbial biomass, although operationally this may be difficult to separate, and in fact, the process of live and dead microphagy may overlap for some consumers (Ballhausen & de Boer, 2016).

Microbes consume microbial necromass as substrate, although it is unclear if this is universal, species-specific or facultative, for instance, induced by energy constraints (Bradley et al., 2018). It is also unknown if the necrobiome is a general organic saprotroph, or specific to necromass. There appears to be a subset of the microbial community that acts as the necrobiome, in both natural and managed systems (Apostel et al., 2018; Bai et al., 2016; Ballhausen & de Boer, 2016; Beidler et al., 2020; Buckeridge, Mason, et al., 2020; Crowther et al., 2015). For example, *Actinobacteria* consistently assimilate isotopically labelled carbon from *E. coli* necromass (Apostel et al., 2018; Buckeridge, Mason, et al., 2020); *Actinobacteria* have a diverse set of chitinase genes required for necropaghy (Bai et al., 2016); and the necrobiome community appears to be less diverse and more copiotrophic than the overall soil community (Beidler et al., 2020). The necrobiome community structure alters the efficiency of necromass recycling (Buckeridge, Mason, et al., 2020), and the broader SOC decomposer community structure impacts the final

quality and chemical composition of SOC (Kallenbach et al., 2016). This field of research is developing and has strong potential for manipulation (Gutierrez et al., 2020). For instance, a soil microbial community may be managed to have a lower necrobiome abundance or activity if the goal is to reduce necromass recycling and promote soil carbon stabilization.

In addition to necrobiome community structure, biotic properties that control microbial necromass production (such as growth efficiency, community and food web interactions) should influence necromass recycling by altering the quantity and chemical composition of necromass available for recycling. However, necromass carbon (Throckmorton et al., 2012) and nitrogen (Wang et al., 2020b) recycling rates appear in some studies to be independent of the necromass taxa being decomposed. In contrast, decomposition rates of fungal necromass are slowed by necromass chemistry (i.e. high melanin or low nitrogen (Fernandez et al., 2019)) and fungal morphology (i.e. rhizomorphs decompose slower than diffuse mycelia (Certano et al., 2018)). Two-pool models of necromass decomposition (Beidler et al., 2020) also suggest that necromass recycling rates are determined by its molecular structure (e.g. chitin, melanin, peptidoglycan, amino sugars).

Necromass recycling may interfere with soil carbon stabilization if there is competition between mineral surfaces and microbial mineralization of necromass carbon. Microbial immobilization of soluble substrates can occur within 30 min and controls carbon retention in some soils (Fischer et al., 2010). Stabilization through sorption depends on an equilibrium between sorbed and unsorbed necromass, but nonetheless can be quick and substantial, and may dominate in other soils (Buckeridge, La Rosa, et al., 2020). It appears that sorption will dominate in soils with highly reactive minerals, whereas immobilization will be more important in more coarsely textured soils with more crystalline/primary minerals (Creamer et al., 2019). Furthermore, the amount of necromass carbon immobilized by microbes could influence carbon sorption and desorption from mineral surfaces, by changing the native pool of dissolved organic carbon (DOC). This balance between recycling and stabilization is determined by interactions between soil nutrient availability, soil mineralogy, necromass chemistry and the necrobiome community structure.

Current characterization of necromass recycling is dominated by ex situ production of necromass (often isotopically labelled) that is added to soil. For instance, isotopically labelled necromass has been tracked into microbial biomass (Buckeridge, Mason, et al., 2020; Wang et al., 2020a); into CO_2 (Crowther et al., 2015; Throckmorton et al., 2012); and into phospholipid fatty acids (PLFAs; Buckeridge, Mason, et al., 2020). Litter bags are also commonly used to estimate fungal necromass decomposition rates (Beidler et al., 2020; Fernandez et al., 2019). Similar to plant litter bags, fungal necromass follows an exponential decay curve of net mass loss to ~20% mass remaining, suggesting new necromass is accumulating at the same time as necromass is decomposing to CO_2 (Prescott & Vesterdal, 2021). These methods all assume that necromass produced ex situ, effectively represents native necromass, which may or may not be true, given the contrasting results on the importance of cell identity or chemistry for recycling. Time course tracking of stable isotope-labelled substrate into PLFAs overcomes this issue and provides indirect evidence for controls on recycling (Apostel et al., 2018). Similarly, amino sugar and amino acid isotope pool dilution was used to measure gross rates of amino sugar production and consumption, and suggests that fungal necromass was produced and consumed at the same rate, and much faster than bacterial necromass, which is consumed much faster than it was produced (Hu et al., 2018). Less common methods to infer recycling include characterizing the gene profile of chitinases that show *Actinobacteria* have the widest diversity of enzyme genes to degrade fungal cell walls (Bai et al., 2016), the development of energy constraint models that imply that necromass in ocean sediments can only provide maintenance power for non-growing cells or a tiny proportion of living biomass (Bradley et al., 2018), and D:L-amino acid racemization models to estimate very slow necromass and biomass turnover time in ocean sediments (Lomstein et al., 2012).

Necromass recycling is an important unknown in determining soil carbon sequestration. As with necromass production, we are missing insight into how soil microscale structure influences recycling (Figure 2). We hypothesize that necromass recycling is influenced both by pore size and biofilms, as these conditions will control necromass dispersal versus within-pore decomposition, for instance, via water retention in biofilms (Or, Phutane, et al., 2007), as well as access for predators (Erktan et al., 2020). Induction of cell death and lysis by viruses and bacterial predators promotes recycling of necromass by releasing it into solution (Kuzyakov & Mason-Jones, 2018)—a step that is required for biotic decomposition of mineral-associated necromass. Soil microaggregate structures will also influence microbial distribution (Voltolini et al., 2017), and therefore necromass recycling hotspots. Microbial biofilms typically form in cracks and at soil pore necks (Lehmann et al., 2008). These are the optimal spots for microorganisms to grow, due to substrate accessibility and ease of attachment, but microbial growth can clog, fill or reduce the size of these pits and pores (Mccarthy et al., 2008), further increasing the physical isolation of necromass. This process could promote stable, hydrologically disconnected microhabitats for microorganisms with unique ecological niches and lowered inputs of organic matter (Lehmann et al., 2020; Or, Smets, et al., 2007) that are buffered against environmental changes (like drying and rewetting) due to their isolation (Or, Phutane, et al., 2007). This metabolic diversity and potential for nutrient limitations may in turn influence within-pore necromass recycling versus necromass dispersal.

4 | NECROMASS STABILIZATION

Stabilization is the protection of microbial necromass from biotic and abiotic transformation or physical transport. Necromass, like all soil organic matter, is protected from decomposition when it is physically isolated from decomposers and enzymes (Dungait et al., 2012; Figure 1). General principles dictating the stabilization of soil organic

matter and necromass must be the same: A proportion of what we measure as soil organic matter and mineral-associated organic matter is necromass (Miltner et al., 2012). However, differences in the relative importance of necromass stabilization mechanisms—controlled by the chemical composition, organo–mineral association and spatial location of necromass—will influence the probability that necromass carbon persists in soil.

The sorptive stabilization of necromass is influenced by its chemical composition. Compared to plant tissues, microbial necromass generally has greater proportions of lipids and proteins and fewer aromatics (Kögel-Knabner, 2002). Even so, there is incredible—yet poorly characterized—diversity in the composition of necromass that is directly controlled by the soil microbiome (Fernandez et al., 2016). This diversity will change necromass adsorption in ways that reflect our understanding of organic matter absorption (as reviewed in Kleber et al. (2021)). For example, like other organics, chemical fractionation of necromass occurs during sorption, with preferential association of specific compound classes with certain minerals (Liu et al., 2013; Omoike & Chorover, 2006). Although the mechanisms of sorption do not differ between necromass and plant organic matter, the relative distribution of compound classes in necromass (e.g. fewer aromatics) will change both the quantity and stability of necromass–mineral associations based on soil mineralogy (sensu Sanderman et al., 2014).

Compared to plant tissues, the high nutrient content of necromass may be disproportionately important to its stabilization (Kopittke et al., 2017). Phosphorus and sulphur components (or functional groups) of necromass can be preferentially sorbed or coprecipitated relative to necromass carbon, potentially resulting in stronger mineral associations and greater stabilization (Mikutta et al., 2011; Omoike & Chorover, 2006). The dominance of necromass-nitrogen over total soil nitrogen (about 80% on average; (Liu et al., 2021)) may arise from the decoupling of necromass-nitrogen and necromass-carbon persistence (Miltner et al., 2009). Necromass–mineral associations can be irreversible if proteins undergo conformational changes like unfolding and racemization during adsorption (Quiquampoix et al., 1995), or during biofilm attachment as bacteria produce strong extracellular anchors (like adhesion proteins) and physically rearrange themselves to increase surface contact (Berne et al., 2018). However, whether the diversity of taxa initiating and developing biofilms affects the adhesion and subsequent persistence of biofilm necromass—and how this compares to necromass sorption—is unknown.

Microorganisms both modify and are modified by their environment. The formation of microbial necromass is a dynamic process with positive feedbacks between microbial growth and necromass stabilization, and is thus self-organizing (Young & Crawford, 2004). Microbial activity facilitates mineral protection via two dominant processes: by chemically and biotically driven dissolution and precipitation of minerals (Banfield et al., 1999) that can encrust microorganisms and biofilms with clay minerals (Lünsdorf et al., 2000), and by the physical entanglement and crosslinking of clay particles by EPS and fungal hyphae (Chenu, 1995). This 'entombment' of necromass within clays and aggregates, through microbially catalysed micro- and macroaggregation, stabilizes necromass by physically isolating it from decomposers (Liang et al., 2017). Microbially mediated filling, plugging or clogging of soil pores (Mccarthy et al., 2008) will reduce the diffusion of nutrients and oxygen into smaller pores, turning these smaller pores into anaerobic microsites with slow decomposition of reduced microbial compounds (like lipids) (Keiluweit et al., 2017). The composition of the microbial community has a similar feedback, where increasing fungal dominance increases soil porosity and pore connectivity, thereby enhancing hydrologic connectivity and enhancing microbial growth (Crawford et al., 2012). Thus, the hydrologic connectivity between soil pores should be a major determinant of necromass stabilization (Figure 2).

Soil minerals are not the only matrix where microorganisms adhere, die and form necromass—organic plant litter is an important catalyst for microbial growth, aggregate formation and mineral associations (Witzgall et al., 2021). Necromass associated with root and leaf litter will have minimal physical protection unless it is occluded within aggregates or transported away from hotspots of microbial activity by fungi (Vidal et al., 2021), macrofauna (Angst et al., 2019) or environmental physical transfer processes (e.g. cryoturbation (Kaiser et al., 2007)). Soils with high litter inputs or low mineral content, and high activities of litter translocation or aggregation (like forests with earthworms) may therefore effectively stabilize necromass with organic material (Kögel-Knabner & Amelung, 2021). Necromass stabilization through organo–organo layering on minerals is also likely to be important: Nitrogen-containing organics, like those found in higher abundance in microbial necromass, can initiate organo–organo layering on minerals (Possinger et al., 2020) and new organics preferentially associate with existing organics on minerals (Vogel et al., 2014). However, it is unclear that the role necromass may (or may not) play in promoting organo–organo layering by establishing an initial attachment of organics and cell wall fragments on mineral surfaces (Gao et al., 2020). Necromass-organo interactions are clearly important in soil carbon stabilization and persistence. However, the relative importance of necromass–mineral and necromass-organic associations is unknown and likely to differ strongly between ecosystems.

5 | NECROMASS DESTABILIZATION

Destabilization releases necromass from physiochemical protection (Figure 1), enabling abiotic and biotic transformation and transport. Importantly, destabilization does not occur at the same rate or extent as stabilization. For example, organic matter adsorption onto mineral surfaces can be irreversible (Gu et al., 1994), organic matter can become available by abrupt disruption of soil microhabitats and aggregates that were progressively formed (Dungait et al., 2012) and microbial biofilms in soil pores can be lost more slowly than they were formed (Seifert & Engesgaard, 2012). Compared to the other processes in the continuum, we know comparatively little about necromass destabilization and soil organic matter destabilization in general.

Much of what we do know about necromass destabilization is related to direct or inferred evidence from three high-level controls on SOC destabilization (as conceptualized by Bailey et al. (2019)): the destruction of microbial habitats, the desorption of mineral-associated necromass and the biotically mediated mining of necromass for nutrients. Destabilization of necromass through the physical destruction of microbial habitats in soil aggregates may cause selective loss of fungal necromass (Simpson et al., 2004), since it contributes more to micro- and macroaggregate fractions than bacterial necromass (which dominates the clay-sized fraction (Angst et al., 2021)). There are remarkably few studies that directly examine the destabilization of necromass via desorption, but they generally show that all adsorbed necromass does not desorb, and that the extent of desorption is related to the mechanism of adsorption. For example, EPS is more readily desorbed if co-precipitated with Al than if it is associated with amorphous Al via inner sphere complexation (Mikutta et al., 2011). Plants and microorganisms produce exudates, like organic acids, that destabilize mineral-associated organic matter (and presumably necromass) through direct (e.g. mineral weathering) and indirect means (e.g. local disequilibria; Keiluweit et al., 2015). The extent of destabilization via mineral weathering varies with extent of microbial activity; groups of microbes living in a biofilm weather minerals more than cells in isolation (Barker et al., 1998).

Living microbes can also directly destabilize microbial necromass by mining it for nutrients. Microbial necromass has lower carbon: nutrient ratios than plant organic matter, so under conditions of nutrient limitation, the destabilization and subsequent mining of necromass for nutrients are enhanced (Cui et al., 2020). Necromass-nitrogen mining can also occur via destabilization of necromass from mineral surfaces through enhanced biotic desorption (like the production of organic acids) and/or higher proximal production of nitrogen-acquiring enzymes (Jilling et al., 2018). Therefore, hotspots of biotic activity should have more extensive and faster rates of necromass destabilization. However, these hotspots will also have greater necromass formation, so whether this enhanced destabilization translates to lower necromass persistence will depend on the balance between production and loss pathways (Ahrens et al., 2015). If destabilization is enhanced over production, it could result in lower relative necromass contributions in hotspots of activity like the rhizosphere (Neurath et al., 2021) and topsoil (Ni et al., 2020).

6 | NECROMASS PERSISTENCE, THE NET EFFECT OF THE CONTINUUM

Persistence indicates how long necromass is retained in soil, representing the combined outcome of all stages in the continuum (Figure 1). Most necromass research quantifies the amount of necromass, and so proxies necromass persistence (Table 1). The paucity of data on the processes of the necromass continuum is largely a methodological issue. Specifically, the age of microbial carbon is decoupled from its turnover because necromass can persist in soil by continuous and efficient recycling, or by stabilization without decomposition (Gleixner, 2013). While this is true for all soil organic matter, the difficulty for necromass is that the compounds formed during decomposition are often the same as the ones being decomposed (e.g. amino sugars are both lost and formed during decomposition). The challenge of determining whether a necromass biopolymer is stable or recycled is further compounded by the fact that some components of microbial necromass can be re-incorporated into living microorganisms either 'as-is' or without significant depolymerization (Hu et al., 2020). This contrasts with plant-derived biomarkers that are chemically changed upon decomposition (e.g. lignin demethylation) so that the loss of the biomarker provides direct estimates of its turnover. Our best methods to study necromass processes in the continuum therefore rely on using labelled substrates (such as ^{13}C or ^{15}N) in ways that reveal metabolic pathways (i.e. position-specific labelling), utilize techniques that differentiate necromass from living microorganisms (Creamer et al., 2019) or rely on temporal harvesting to capture processes through time (Apostel et al., 2018). Perhaps then, a better approach is to describe necromass persistence through integrated metrics that include formation, recycling and stabilization processes, and can incorporate ecosystem properties (sensu Ernakovich et al., 2021). However, knowing the size of the necromass pool, or even using an integrated ecosystem-specific metric of persistence, provides only indirect information on which processes in the continuum are the rate-limiting steps for necromass retention in soil. Determining how the necromass continuum stages interact to form persistent—and sometimes very old necromass (e.g. >1,000 years, Gies et al., 2021)—is necessary for understanding the potential responses of necromass across ecosystems and in response to climate change.

7 | THE NECROMASS CONTINUUM ACROSS ECOSYSTEMS AND UNDER A CHANGING CLIMATE

Microbial necromass stocks vary across ecosystems and climate change scenarios, with roughly two to three times more necromass in arable, pasture and rangeland systems compared to forests (Angst et al., 2021; Liang et al., 2019). Hydrologically extreme ecosystems such as wetlands and deserts; and non-temperate climates such as arctic, alpine and tropical regions tend to be understudied. Preliminary work in these regions indicates that necromass contributions to soil organic matter, and the relative importance of fungal versus bacterial necromass, reflect general patterns in microbial activity and biogeography that arise from prevailing environmental conditions. For example, cold temperatures, low oxygen or low N reduce proportional microbial necromass contributions to soil organic matter (Chen et al., 2020; Zhang et al., 2021). Warmer temperatures may increase necromass production by increasing the turnover of biomass and accumulation of amino sugars (Hagerty et al., 2014; Wang et al., 2020b). Both production and recycling of fungal necromass have a high temperature sensitivity (Hu et al., 2018), and in alpine soil incubations,

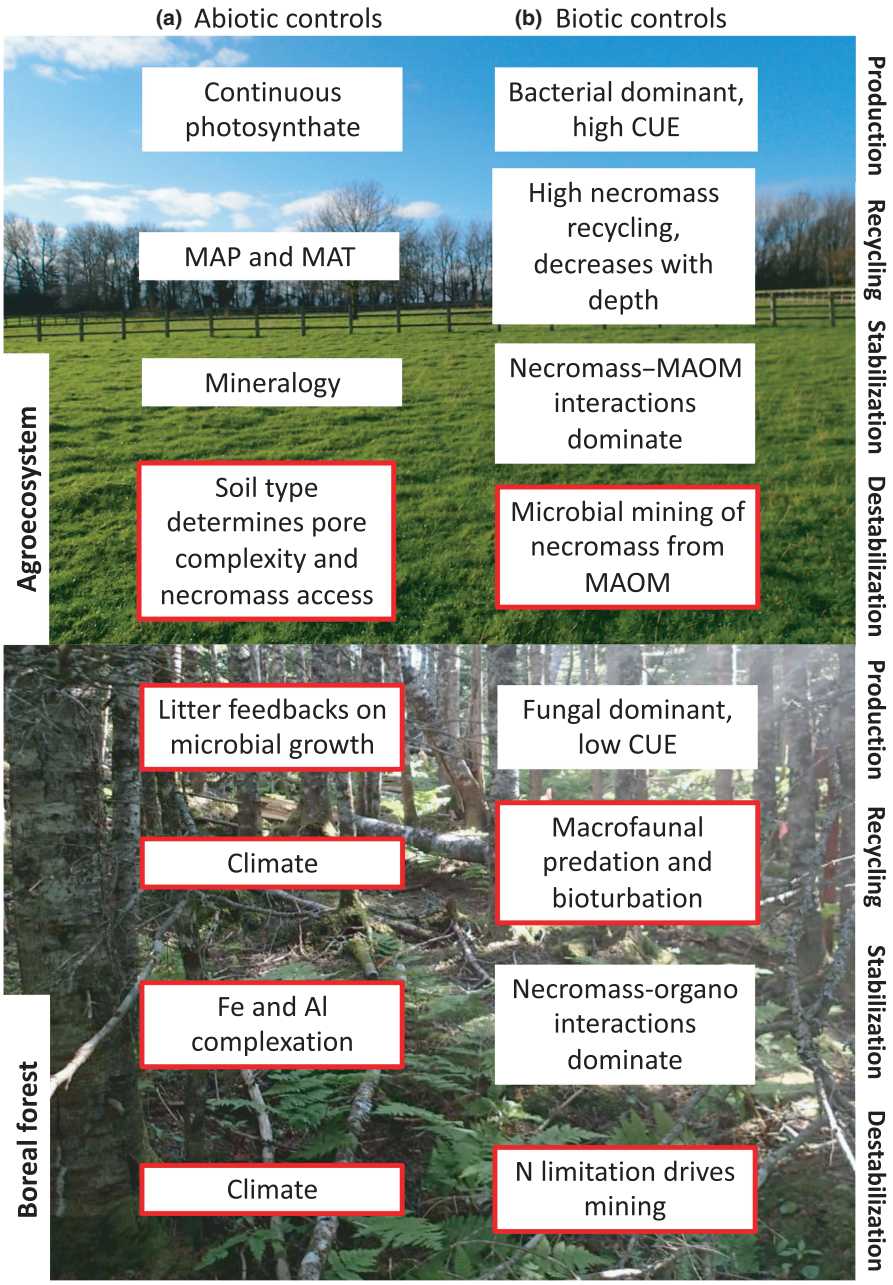

FIGURE 3 Abiotic (a) and biotic (b) controls hypothesized as important for each necromass continuum stage (production–recycling–stabilization–destabilization) in two representative ecosystems (agroecosystem and boreal forest). The red borders highlight when a specific hypothesis is based on indirect evidence. CUE, carbon use efficiency; MAP, mean annual precipitation; MAT, mean annual temperature; MAOM, mineral-associated organic matter

TABLE 2 Key knowledge gaps for each stage of the necromass continuum

Necromass continuum stage	Process uncertainties	Spatial uncertainties	Microbial community and trophic uncertainties
Production	Turnover rates and controls	Biofilm necromass management	Predation and viral lysis
Recycling	Recycling efficiency across ecosystems	Isolation, metabolic diversity, necrophagy	Necrobiome metabolism
Stabilization	Necromass-organo controls	Dynamic soil-microbe self-organization	Biofilm initiator persistence
Destabilization	Rates and controls	Location and mechanisms	Predation

temperature increased the rate of necromass recycling (Donhauser et al., 2020). In the Tibetan Plateau, an increase in bacterial necromass with winter warming was associated with reduction in fungal abundance and fungal genes required for necromass decomposition (Tian et al., 2021). Historical precipitation was a dominant control on the recycling efficiency of *E.coli* necromass in agricultural grasslands, and was correlated with the necrobiome community structure (Buckeridge, Mason, et al., 2020). Historical precipitation is also a strong control on amino sugar persistence, with more fungal and less bacterial biomarkers in cooler, wetter soils along a climate gradient; Amelung et al. (1999) suggest that this is driven by cold winters limiting production in higher latitudes, and warm

winters favouring destabilization or recycling in lower latitudes. The growing number of studies that isolate individual climate or land use effects on necromass persistence support our emerging understanding that microbial physiology is a strong control on soil organic carbon storage, but also highlight the lack of understanding we have for certain stages of the continuum in a changing world.

Climate and climate change drivers of ecosystem processes, such as precipitation variability and increasing temperatures, may all have impacts on different stages of the continuum, depending on the ecosystem and their dominant abiotic and biotic controls (Figure 3). Each continuum stage has testable specific controls, which will determine their relative importance in different ecosystems. In Figure 3, we illustrate the abiotic and biotic controls likely to be important for different stages of the necromass continuum in two contrasting ecosystems, agroecosystems and boreal forests. We hypothesize that in temperate, loamy, nutrient-rich and bacterially dominated soils—like agroecosystems—necromass production may be a primary controller of necromass stocks. Here, improved microbial growth and carbon use efficiency can increase mineral-associated necromass and soil carbon (Kallenbach et al., 2015). Recycling of necromass, rather than stabilization without turnover, will presumably be more important for necromass persistence and will be highest in the rhizosphere (Liang et al., 2016) and decrease sharply with depth, following patterns in microbial abundance and activity (Figure 3). Conversely, in cold, wet, nutrient-poor, high-organic ecosystems—like boreal forests—we hypothesize that necromass production and recycling will be limited by environmental constraints on microbial growth, resulting in lower proportional contributions of necromass to soil organic matter (Chen et al., 2020). Necromass–mineral associations here will likely occur via complexation with Fe and Al (Kramer & Chadwick, 2018). Fungal necromass will dominate (Fernandez et al., 2019) and so necromass-organo interactions (Adamczyk et al., 2019) and the production of extracellular enzymes needed to depolymerize fungal necromass (Fernandez et al., 2016) will be critical for its persistence (Figure 3). These ecosystem-specific examples provide hypothetical scenarios with a great deal of uncertainty, because we do not fully understand how so much microbial carbon becomes mineral-associated, or the relative importance of production, recycling, stabilization and destabilization processes that lead to necromass persistence in different contexts.

8 | KEY KNOWLEDGE GAPS AND THE WAY FORWARD

8.1 | Knowledge gaps

A large amount of research is now dedicated to quantifying the relative importance of microbial necromass to soil organic matter. The quantification of amino sugars has thus far been our most reliable and consistently used tool to identify microbial necromass, but it measures only a portion of necromass (cell wall components), contains no spatially resolved information and cannot directly inform the necromass continuum stages that ultimately control persistence. Microorganisms live and die in aqueous films within spatially discrete, metabolically diverse and trophically complex microhabitats, creating hotspots of microbial activity for each stage of the necromass continuum. The feedbacks between these spatially and temporally fluctuating environments and the processes that control necromass persistence are not known. Necromass recycling and destabilization are particularly understudied yet are major determinants on the availability and microbial transformation of necromass. Our understanding of how, when and where necromass is formed and stabilized in soil comes predominantly from agro-ecosystems and temperate climates. From these ecosystems, we know that microbial necromass broadly reflects the quantities and locations of living microbial biomass and community structure. Yet ecosystems at climatic and hydrologic extremes are disproportionately experiencing global change, but also have the greatest uncertainties and the fewest observations and measurements of necromass (Figure 3). Even our most extensively studied systems have major knowledge gaps (Table 2), especially in the context of global change. The potential decoupling of necromass carbon from necromass nitrogen (and potentially necromass phosphorus) warrants further investigation, since ongoing or future nutrient limitations (Wieder et al., 2015) may exacerbate necromass losses via nutrient mining. Climatic changes that alter the pore-scale distribution of specific microbial taxa, pore or profile-scale hydrologic connectivity or substantially alter microbial activity will affect the necromass continuum and diminish or enhance the potential of microbial necromass to increase soil organic matter.

8.2 | The way forward

Necromass production (Figure 1) may be a rate-limiting step for soil carbon stabilization (Hagerty et al., 2014), so a better understanding is needed of what controls microbial biomass turnover rates. More studies using isotope pool dilution to trace amino sugar production would be informative. Similarly, greater insight is needed into the many, diffuse carbon products made by microbes, and their persistence in soil. Advances in in situ soil imaging combined with chemical mapping and stable isotope techniques (Raman, nanoSIMS, confocal reflection microscopy; Table 1) could be harnessed to gain insight into the spatial aspects of necromass production, including how biofilm and pore communities deal with their dead and the impact of predation on necromass production (Figure 2).

Future research goals in necromass recycling include understanding how climate influences recycling efficiency of both labile and recalcitrant, free and attached necromass carbon. Most of our work so far has focused on the decomposition of ex situ necromass, which may or may not reflect in situ process rates. Greater insight is needed into how the spatial isolation and organization of necromass,

and the efficiency of necrobiome taxa, influence decomposition, as this can contribute to our ability to protect microbial necromass carbon in soil. We do not understand how taxa-specific necromass chemistries, such as necromass nitrogen and recalcitrant components, interact with soil spatial properties and respond to climate to influence recycling. Finally, linking community structure to function is needed to understand how the composition of the necrobiome and their activity is influenced by ecosystem and climate-induced nutrient limitations.

Future research goals for necromass stabilization should focus on understanding the in situ feedbacks between necromass formation and its protection, for both necromass–mineral and necromass-organo associations. Most of our work on necromass has focused on bacterial necromass associating with minerals in agricultural or grassland ecosystems in temperate soils (Angst et al., 2021). While these ecosystems and processes are undoubtedly important, general mechanisms of carbon stabilization are often distinct in ecosystems most sensitive to climatic changes, like in dryland or high-latitude ecosystems, which causes uncertain projections of soil carbon stocks in these regions (Todd-Brown et al., 2013). Understanding which necromass stabilization processes dominate across soil types and ecosystems is important for understanding its sensitivity to change (Figure 3).

Despite the vulnerability of soil carbon to current land management and future climate change, there are few studies that directly address the process of necromass destabilization in soils. The destabilization of living and dead microbial biomass can be indirectly assessed by tracking the transformation of traceable carbon substrates and assuming that any added carbon not respired, sorbed or in living microbial biomass is in necromass and associated residues (Creamer et al., 2016; Geyer et al., 2020). In this way, subsequent respiratory or aqueous losses can be attributed to necromass decomposition resulting from destabilization. However, these studies do not address differences between living biomass and necromass, are selecting initially for faster growing microbial populations and only proxy destabilization process by losses into solution or gaseous phases. We need to understand the mechanisms of microbial necromass destabilization, and whether it will accelerate with climate change. Creative experimental ideas are beneficial, for example, using synthesized organo–mineral complexes in the lab, short- and long-term tracing of isotopically labelled substrates in the field and nano- and microscale visualization of microbial necromass accumulation and loss.

This litany of knowledge gaps is both daunting and refreshing. Despite numerous unknowns, it is exciting to consider that necromass research, which embraces biofilm ecology, soil-microbial self-organization and microbial nutrient limitations, can help us to mitigate global challenges. Researchers need to disentangle the necromass continuum to explore *how*, *when and where* necromass is formed, transformed and lost in soil. This can deliver an enhanced understanding of the persistence and vulnerability of necromass to future climate change and inform land-based climate mitigation strategies in a changing environment.

ACKNOWLEDGEMENTS

C.C. was supported by the US Geological Survey Ecosystems Climate R&D Program (ZT00U4U30). J.W. was supported by the Natural Environment Research Council award NE/S005137/1, The role of biotic and abiotic interactions in the stabilisation and persistence of soil organic carbon (LOCKED UP) and the Natural Environment Research Council award NE/R016429/1 as part of the UK-SCAPE programme delivering National Capability.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

K.M.B., C.C., and J.W. conceived the ideas and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

We present no new data in this manuscript.

ORCID

Kate M. Buckeridge https://orcid.org/0000-0002-3267-4216
Courtney Creamer https://orcid.org/0000-0001-8270-9387
Jeanette Whitaker https://orcid.org/0000-0001-8824-471X

REFERENCES

Adamczyk, B., Sietiö, O.-M., Straková, P., Prommer, J., Wild, B., Hagner, M., Pihlatie, M., Fritze, H., Richter, A., & Heinonsalo, J. (2019). Plant roots increase both decomposition and stable organic matter formation in boreal forest soil. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-11993-1

Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schrumpf, M., & Reichstein, M. (2015). Contribution of sorption, DOC transport and microbial interactions to the ^{14}C age of a soil organic carbon profile: Insights from a calibrated process model. *Soil Biology & Biochemistry*, *88*, 390–402. https://doi.org/10.1016/j.soilbio.2015.06.008

Amelung, W. (2000). Methods using amino sugars as markers for microbial residues in soil. In J. M. Kimble, R. F. Follett, & B. A. Stewart (Eds.), *Assessment methods for soil carbon* (pp. 251–290). CRC Press.

Amelung, W., Zhang, X., Flach, K. W., & Zech, W. (1999). Amino sugars in native grassland soils along a climosequence in North America. *Soil Science Society of America Journal*, *63*, 86–92. https://doi.org/10.2136/sssaj1999.03615995006300010014x

Angst, G., Mueller, C. W., Prater, I., Angst, Š., Frouz, J., Jílková, V., Peterse, F., & Nierop, K. G. J. (2019). Earthworms act as biochemical reactors to convert labile plant compounds into stabilized soil microbial necromass. *Communications Biology*, *2*, 441. https://doi.org/10.1038/s42003-019-0684-z

Angst, G., Mueller, K. E., Nierop, K. G. J., & Simpson, M. J. (2021). Plant- or microbial-derived? A review on the molecular composition of stabilized soil organic matter. *Soil Biology & Biochemistry*, *156*, 108189. https://doi.org/10.1016/j.soilbio.2021.108189

Anthony, M. A., Crowther, T. W., Maynard, D. S., van den Hoogen, J., & Averill, C. (2020). Distinct assembly processes and microbial communities constrain soil organic carbon formation. *One Earth*, *2*, 349–360. https://doi.org/10.1016/j.oneear.2020.03.006

Apostel, C., Herschbach, J., Bore, E. K., Spielvogel, S., Kuzyakov, Y., & Dippold, M. A. (2018). Food for microorganisms: Position-specific ^{13}C labeling and ^{13}C-PLFA analysis reveals preferences for sorbed

or necromass C. *Geoderma*, *312*, 86–94. https://doi.org/10.1016/j.geoderma.2017.09.042

Bai, Y., Eijsink, V. G. H., Kielak, A. M., van Veen, J. A., & de Boer, W. (2016). Genomic comparison of chitinolytic enzyme systems from terrestrial and aquatic bacteria. *Environmental Microbiology*, *18*, 38–49. https://doi.org/10.1111/1462-2920.12545

Bailey, V. L., Pries, C. H., & Lajtha, K. (2019). What do we know about soil carbon destabilization? *Environmental Research Letters*, *14*, 083004.

Bailey, V. L., Smith, A. P., Tfaily, M., Fansler, S. J., & Bond-Lamberty, B. (2017). Differences in soluble organic carbon chemistry in pore waters sampled from different pore size domains. *Soil Biology & Biochemistry*, *107*, 133–143. https://doi.org/10.1016/j.soilbio.2016.11.025

Baldock, J. A., Oades, J. M., Vassallo, A. M., & Wilson, M. A. (1990). Solid-state CP/MAS ^{13}C NMR analysis of bacterial and fungal cultures isolated from a soil incubated with glucose. *Australian Journal of Soil Research*, *28*, 213–225.

Ballhausen, M. B., & de Boer, W. (2016). The sapro-rhizosphere: Carbon flow from saprotrophic fungi into fungus-feeding bacteria. *Soil Biology & Biochemistry*, *102*, 14–17. https://doi.org/10.1016/j.soilbio.2016.06.014

Banfield, J. F., Barker, W. W., Welch, S. A., & Taunton, A. (1999). Biological impact on mineral dissolution: Application of the lichen model to understanding mineral weathering in the rhizosphere. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 3404–3411. https://doi.org/10.1073/pnas.96.7.3404

Barker, W. W., Welch, S. A., Chu, S., & Banfield, J. F. (1998). Experimental observations of the effects of bacteria on aluminosilicate weathering. *American Mineralogist*, *83*, 1551–1563. https://doi.org/10.2138/am-1998-11-1243

Beidler, K. V., Phillips, R. P., Andrews, E., Maillard, F., Mushinski, R. M., & Kennedy, P. G. (2020). Substrate quality drives fungal necromass decay and decomposer community structure under contrasting vegetation types. *Journal of Ecology*, *108*, 1845–1859. https://doi.org/10.1111/1365-2745.13385

Berne, C., Ellison, C. K., Ducret, A., & Brun, Y. V. (2018). Bacterial adhesion at the single-cell level. *Nature Reviews Microbiology*, *16*, 616–627. https://doi.org/10.1038/s41579-018-0057-5

Bradley, J. A., Amend, J. P., & LaRowe, D. E. (2018). Necromass as a limited source of energy for microorganisms in marine sediments. *Journal of Geophysical Research: Biogeosciences*, *123*, 577–590. https://doi.org/10.1002/2017JG004186

Buckeridge, K. M., La Rosa, A. F., Mason, K. E., Whitaker, J., McNamara, N. P., Grant, H. K., & Ostle, N. J. (2020). Sticky dead microbes: Rapid abiotic retention of microbial necromass in soil. *Soil Biology & Biochemistry*, *149*, 107929. https://doi.org/10.1016/j.soilbio.2020.107929

Buckeridge, K. M., Mason, K. E., McNamara, N. P., Ostle, N., Puissant, J., Goodall, T., Griffiths, R. I., Stott, A. W., & Whitaker, J. (2020). Environmental and microbial controls on microbial necromass recycling, an important precursor for soil carbon stabilization. *Communications Earth & Environment*, *1*, 1–9. https://doi.org/10.1038/s43247-020-00031-4

Burns, R. G., DeForest, J. L., Marxsen, J., Sinsabaugh, R. L., Stromberger, M. E., Wallenstein, M. D., Weintraub, M. N., & Zoppini, A. (2013). Soil enzymes in a changing environment: Current knowledge and future directions. *Soil Biology & Biochemistry*, *58*, 216–234. https://doi.org/10.1016/j.soilbio.2012.11.009

Carini, P., Marsden, P. J., Leff, J. W., Morgan, E. E., Strickland, M. S., & Fierer, N. (2016). Relic DNA is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology*, *2*, 16242.

Certano, A. K., Fernandez, C. W., Heckman, K. A., & Kennedy, P. G. (2018). The afterlife effects of fungal morphology: Contrasting decomposition rates between diffuse and rhizomorphic necromass. *Soil Biology & Biochemistry*, *126*, 76–81. https://doi.org/10.1016/j.soilbio.2018.08.002

Chen, G., Ma, S., Tian, D. I., Xiao, W., Jiang, L., Xing, A., Zou, A., Zhou, L., Shen, H., Zheng, C., Ji, C., He, H., Zhu, B., Liu, L., & Fang, J. (2020). Patterns and determinants of soil microbial residues from tropical to boreal forests. *Soil Biology & Biochemistry*, *151*, 108059. https://doi.org/10.1016/j.soilbio.2020.108059

Chenu, C. (1995). Extracellular polysaccharides: An interface between microorganisms and soil constituents. In P. M. Huang, J. Berthelin, J.-M. Bollag, W. B. McGill, & A. L. Page, *Environmental impact of soil component interactions* (pp. 217–233). CRC Lewis Publishers. Retrieved from https://books.google.lu/books?hl=en&lr=&id=qfTrg6iPwoEC&oi=fnd&pg=PA217&dq=Extracellular+polysaccharides:+An+interface+between+microorganisms+and+soil+-constituents&ots=s_BRJFGCxb&sig=2W501XFHPUe3O9kjA4EIVHGoJr8&redir_esc=y#v=onepage&q=Extracellular%20polysaccharides%3A%20An%20interface%20between%20microorganisms%20and%20soil%20constituents&f=false

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*, 988–995. https://doi.org/10.1111/gcb.12113

Coward, E. K., Ohno, T., & Plante, A. F. (2018). Adsorption and molecular fractionation of dissolved organic matter on iron-bearing mineral matrices of varying crystallinity. *Environmental Science and Technology*, *52*, 1036–1044. https://doi.org/10.1021/acs.est.7b04953

Crawford, J. W., Deacon, L., Grinev, D., Harris, J. A., Ritz, K., Singh, B. K., & Young, I. (2012). Microbial diversity affects self-organization of the soil – Microbe system with consequences for function. *Journal of the Royal Society, Interface*, *9*, 1302–1310. https://doi.org/10.1098/rsif.2011.0679

Creamer, C. A., Foster, A. L., Lawrence, C., McFarland, J., Schulz, M., & Waldrop, M. P. (2019). Mineralogy dictates the initial mechanism of microbial necromass association. *Geochimica et Cosmochimica Acta*, *260*, 161–176. https://doi.org/10.1016/j.gca.2019.06.028

Creamer, C. A., Jones, D. L., Baldock, J. A., Rui, Y., Murphy, D. V., Hoyle, F. C. et al. (2016). Is the fate of glucose-derived carbon more strongly driven by nutrient availability, soil texture, or microbial biomass size? *Soil Biology & Biochemistry*, *103*, 201–212.

Crowther, T. W., Sokol, N. W., Oldfield, E. E., Maynard, D. S., Thomas, S. M., & Bradford, M. A. (2015). Environmental stress response limits microbial necromass contributions to soil organic carbon. *Soil Biology & Biochemistry*, *85*, 153–161. https://doi.org/10.1016/j.soilbio.2015.03.002

Cui, J., Zhu, Z., Xu, X., Liu, S., Jones, D. L., Kuzyakov, Y., Shibistova, O., Wu, J., & Ge, T. (2020). Carbon and nitrogen recycling from microbial necromass to cope with C:N stoichiometric imbalance by priming. *Soil Biology & Biochemistry*, *142*, 107720. https://doi.org/10.1016/j.soilbio.2020.107720

DeLeo, P. C., Baveye, P., & Ghiorse, W. C. (1997). Use of confocal laser scanning microscopy on soil thin-sections for improved characterization of microbial growth in unconsolidated soils and aquifer materials. *Journal of Microbiol Methods*, *30*, 193–203. https://doi.org/10.1016/S0167-7012(97)00065-1

Donhauser, J., Qi, W., Bergk-Pinto, B., & Frey, B. (2020). High temperatures enhance the microbial genetic potential to recycle C and N from necromass in high-mountain soils. *Global Change Biology*, 1–22.

Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012). Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*, *18*, 1781–1796. https://doi.org/10.1111/j.1365-2486.2012.02665.x

Emerson, J. B., Roux, S., Brum, J. R., Bolduc, B., Woodcroft, B. J., Jang, H. B., Singleton, C. M., Solden, L. M., Naas, A. E., Boyd, J. A., Hodgkins, S. B., Wilson, R. M., Trubl, G., Li, C., Frolking, S., Pope, P. B., Wrighton, K. C., Crill, P. M., Chanton, J. P., … Sullivan, M. B.

(2018). Host-linked soil viral ecology along a permafrost thaw gradient. *Nat. Microbiol*, *3*, 870–880. https://doi.org/10.1038/s41564-018-0190-y

Erktan, A., Or, D., & Scheu, S. (2020). The physical structure of soil: Determinant and consequence of trophic interactions. *Soil Biology & Biochemistry*, *148*, 107876.

Ernakovich, J. G., Baldock, J., Creamer, C., Sanderman, J., Kalbitz, K., & Farrell, M. (2021). A combined microbial and ecosystem metric of carbon retention efficiency explains land cover-dependent soil microbial biodiversity–ecosystem function relationships. *Biogeochemistry*, *153*, 1–15. https://doi.org/10.1007/s10533-020-00736-w

Fernandez, C. W., Heckman, K., Kolka, R., & Kennedy, P. G. (2019). Melanin mitigates the accelerated decay of mycorrhizal necromass with peatland warming. *Ecology Letters*, *22*, 498–505. https://doi.org/10.1111/ele.13209

Fernandez, C. W., Langley, J. A., Chapman, S., McCormack, M. L., & Koide, R. T. (2016). The decomposition of ectomycorrhizal fungal necromass. *Soil Biology & Biochemistry*, *93*, 38–49. https://doi.org/10.1016/j.soilbio.2015.10.017

Fischer, H., Ingwersen, J., & Kuzyakov, Y. (2010). Microbial uptake of low-molecular-weight organic substances out-competes sorption in soil. *European Journal of Soil Science*, *61*, 504–513. https://doi.org/10.1111/j.1365-2389.2010.01244.x

Flemming, H. C., & Wuertz, S. (2019). Bacteria and archaea on Earth and their abundance in biofilms. *Nature Reviews Microbiology*, *17*, 247–260. https://doi.org/10.1038/s41579-019-0158-9

Foster, R. C. (1988). Microenvironments of soil microorganisms. *Biology and Fertility of Soils*, *6*, 189–203. https://doi.org/10.1007/BF00260816

Gao, J., Mikutta, R., Jansen, B., Guggenberger, G., Vogel, C., & Kalbitz, K. (2020). The multilayer model of soil mineral–organic interfaces – A review. *Journal of Plant Nutrition and Soil Science*, *183*, 27–41. https://doi.org/10.1002/jpln.201900530

Geyer, K., Schnecker, J., Grandy, A. S., Richter, A., & Frey, S. (2020). Assessing microbial residues in soil as a potential carbon sink and moderator of carbon use efficiency. *Biogeochemistry*, *151*, 237–249. https://doi.org/10.1007/s10533-020-00720-4

Gies, H., Hagedorn, F., Lupker, M., Montluçon, D., Haghipour, N., Sophia Van Der Voort, T. et al. (2021). Millennial-age glycerol dialkyl glycerol tetraethers (GDGTs) in forested mineral soils: ^{14}C-based evidence for stabilization of microbial necromass. *Biogeosciences*, *18*, 189–205.

Glaser, B., Turrión, M. B., & Alef, K. (2004). Amino sugars and muramic acid – Biomarkers for soil microbial community structure analysis. *Soil Biology & Biochemistry*, *36*, 399–407. https://doi.org/10.1016/j.soilbio.2003.10.013

Gleixner, G. (2013). Soil organic matter dynamics: A biological perspective derived from the use of compound-specific isotopes studies. *Ecological Research*, *28*, 683–695. https://doi.org/10.1007/s11284-012-1022-9

Gu, B., Schmitt, J., Chen, Z., Liang, L., & McCarthy, J. F. (1994). Adsorption and desorption of natural organic matter on iron oxide: Mechanisms and models. *Environmental Science and Technology*, *28*, 38–46. https://doi.org/10.1021/es00050a007

Gutierrez, C. F., Sanabria, J., Raaijmakers, J. M., & Oyserman, B. O. (2020). Restoring degraded microbiome function with self-assembled communities. *FEMS Microbiology Ecology*, *96*, 1–9. https://doi.org/10.1093/femsec/fiaa225

Hagerty, S. B., van Groenigen, K. J., Allison, S. D., Hungate, B. A., Schwartz, E., Koch, G. W., Kolka, R. K., & Dijkstra, P. (2014). Accelerated microbial turnover but constant growth efficiency with warming in soil. *Nature Climate Change*, *4*, 903–906. https://doi.org/10.1038/nclimate2361

Hall, S. J., Ye, C., Weintraub, S. R., & Hockaday, W. C. (2020). Molecular trade-offs in soil organic carbon composition at continental scale. *Nature Geoscience*, *13*, 687–692. https://doi.org/10.1038/s41561-020-0634-x

Hu, Y., Zheng, Q., Noll, L., Zhang, S., & Wanek, W. (2020). Direct measurement of the in situ decomposition of microbial-derived soil organic matter. *Soil Biology & Biochemistry*, *141*, 107660. https://doi.org/10.1016/j.soilbio.2019.107660

Hu, Y., Zheng, Q., Zhang, S., Noll, L., & Wanek, W. (2018). Significant release and microbial utilization of amino sugars and D-amino acid enantiomers from microbial cell wall decomposition in soils. *Soil Biology & Biochemistry*, *123*, 115–125. https://doi.org/10.1016/j.soilbio.2018.04.024

Jilling, A., Keiluweit, M., Contosta, A. R., Frey, S., Schimel, J., Schnecker, J., Smith, R. G., Tiemann, L., & Grandy, A. S. (2018). Minerals in the rhizosphere: Overlooked mediators of soil nitrogen availability to plants and microbes. *Biogeochemistry*, *139*, 103–122. https://doi.org/10.1007/s10533-018-0459-5

Kaiser, C., Meyer, H., Biasi, C., Rusalimova, O., Barsukov, P., & Richter, A. (2007). Conservation of soil organic matter through cryoturbation in arctic soils in Siberia. *Journal of Geophysical Research*, *112*, 1–8. https://doi.org/10.1029/2006JG000258

Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications*, *7*, 13630. https://doi.org/10.1038/ncomms13630

Kallenbach, C. M., Grandy, A. S., Frey, S. D., & Diefendorf, A. F. (2015). Microbial physiology and necromass regulate agricultural soil carbon accumulation. *Soil Biology & Biochemistry*, *91*, 279–290. https://doi.org/10.1016/j.soilbio.2015.09.005

Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., & Kleber, M. (2015). Mineral protection of soil carbon counteracted by root exudates. *Nature Climate Change*, *5*, 588–595. https://doi.org/10.1038/nclimate2580

Keiluweit, M., Wanzek, T., Kleber, M., Nico, P., & Fendorf, S. (2017). Anaerobic microsites have an unaccounted role in soil carbon stabilization. *Nature Communications*, *8*, 1771. https://doi.org/10.1038/s41467-017-01406-6

Kiem, R., & Kögel-Knabner, I. (2003). Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. *Soil Biology & Biochemistry*, *35*, 101–118. https://doi.org/10.1016/S0038-0717(02)00242-0

Kleber, M., Bourg, I. C., Coward, E. K., Hansel, C. M., Myneni, S. C. B., & Nunan, N. (2021). Dynamic interactions at the mineral–organic matter interface. *Nature Reviews Earth & Environment*, *2*, 402–421. https://doi.org/10.1038/s43017-021-00162-y

Kögel-Knabner, I. (2002). The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biology & Biochemistry*, *34*, 139–162. https://doi.org/10.1016/S0038-0717(01)00158-4

Kögel-Knabner, I., & Amelung, W. (2021). Soil organic matter in major pedogenic soil groups. *Geoderma*, *384*, 114785. https://doi.org/10.1016/j.geoderma.2020.114785

Kopittke, P. M., Hernandez-Soriano, M. C., Dalal, R. C., Finn, D., Menzies, N. W., Hoeschen, C. et al. (2017). Nitrogen-rich microbial products provide new organo-mineral associations for the stabilization of soil organic matter. *Global Change Biology*, *12*, 3218–3221.

Kramer, M. G., & Chadwick, O. A. (2018). Climate-driven thresholds in reactive mineral retention of soil carbon at the global scale. *Nature Climate Change*, *8*, 1104–1108. https://doi.org/10.1038/s41558-018-0341-4

Kuzyakov, Y., & Mason-Jones, K. (2018). Viruses in soil: Nano-scale undead drivers of microbial life, biogeochemical turnover and ecosystem functions. *Soil Biology & Biochemistry*, *127*, 305–317. https://doi.org/10.1016/j.soilbio.2018.09.032

Lehmann, J., Hansel, C. M., Kaiser, C., Kleber, M., Maher, K., Manzoni, S., Nunan, N., Reichstein, M., Schimel, J. P., Torn, M. S., Wieder, W.

R., & Kögel-Knabner, I. (2020). Persistence of soil organic carbon caused by functional complexity. *Nature Geoscience*, *13*, 529–534. https://doi.org/10.1038/s41561-020-0612-3

Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, *528*, 60–68. https://doi.org/10.1038/nature16069

Lehmann, J., Solomon, D., Kinyangi, J., Dathe, L., Wirick, S., & Jacobsen, C. (2008). Spatial complexity of soil organic matter forms at nanometre scales. *Nature Geoscience*, *1*, 238–242. https://doi.org/10.1038/ngeo155

Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology*, *25*, 3578–3590. https://doi.org/10.1111/gcb.14781

Liang, C., & Balser, T. C. (2008). Preferential sequestration of microbial carbon in subsoils of a glacial-landscape toposequence, Dane County, WI, USA. *Geoderma*, *148*, 113–119. https://doi.org/10.1016/j.geoderma.2008.09.012

Liang, C., Jesus, E. D. C., Duncan, D. S., Quensen, J. F., Jackson, R. D., Balser, T. C., & Tiedje, J. M. (2016). Switchgrass rhizospheres stimulate microbial biomass but deplete microbial necromass in agricultural soils of the upper Midwest, USA. *Soil Biology & Biochemistry*, *94*, 173–180. https://doi.org/10.1016/j.soilbio.2015.11.020

Liang, C., Schimel, J. P., & Jastrow, J. D. (2017). The importance of anabolism in microbial control over soil carbon storage. *Nature Microbiology*, *2*, 1–6. https://doi.org/10.1038/nmicrobiol.2017.105

Liu, X., Eusterhues, K., Thieme, J., Ciobota, V., Höschen, C., Mueller, C. W., Küsel, K., Kögel-Knabner, I., Rösch, P., Popp, J., & Totsche, K. U. (2013). STXM and NanoSIMS investigations on EPS fractions before and after adsorption to goethite. *Environmental Science and Technology*, *47*, 3158–3166. https://doi.org/10.1021/es3039505

Liu, Z., Liu, X., Wu, X., Bian, R., Liu, X., Zheng, J., Zhang, X., Cheng, K., Li, L., & Pan, G. (2021). Long-term elevated CO_2 and warming enhance microbial necromass carbon accumulation in a paddy soil. *Biology and Fertility of Soils*, *57*(5), 673–684. https://doi.org/10.1007/s00374-021-01557-1

Lomstein, B. A., Langerhuus, A. T., D'Hondt, S., Jørgensen, B. B., & Spivack, A. J. (2012). Endospore abundance, microbial growth and necromass turnover in deep sub-seafloor sediment. *Nature*, *484*, 101–104. https://doi.org/10.1038/nature10905

Lueders, T., Kindler, R., Miltner, A., Friedrich, M. W., & Kaestner, M. (2006). Identification of bacterial micropredators distinctively active in a soil microbial food web. *Applied and Environment Microbiology*, *72*, 5342–5348. https://doi.org/10.1128/AEM.00400-06

Lünsdorf, H., Erb, R. W., Abraham, W. R., & Timmis, K. N. (2000). "Clay hutches": A novel interaction between bacteria and clay minerals. *Environmental Microbiology*, *2*, 161–168. https://doi.org/10.1046/j.1462-2920.2000.00086.x

Malik, A. A., Chowdhury, S., Schlager, V., Oliver, A., Puissant, J., Vazquez, P. G. M., Jehmlich, N., von Bergen, M., Griffiths, R. I., & Gleixner, G. (2016). Soil fungal: Bacterial ratios are linked to altered carbon cycling. *Frontiers in Microbiology*, *7*, 1–11. https://doi.org/10.3389/fmicb.2016.01247

Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, *196*, 79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x

Mccarthy, J. F., Ilavsky, J., Jastrow, J. D., Mayer, L. M., Perfect, E., & Zhuang, J. (2008). Protection of organic carbon in soil microaggregates via restructuring of aggregate porosity and filling of pores with accumulating organic matter. *Geochimica et Cosmochimica Acta*, *72*, 4725–4744. https://doi.org/10.1016/j.gca.2008.06.015

Mikutta, R., Zang, U., Chorover, J., Haumaier, L., & Kalbitz, K. (2011). Stabilization of extracellular polymeric substances (*Bacillus subtilis*) by adsorption to and coprecipitation with Al forms. *Geochimica et Cosmochimica Acta*, *75*, 3135–3154. https://doi.org/10.1016/j.gca.2011.03.006

Miltner, A., Bombach, P., Schmidt-Brucken, B., & Kastner, M. (2012). SOM genesis: Microbial biomass as a significant source. *Biogeochemistry*, *111*, 41–55. https://doi.org/10.1007/s10533-011-9658-z

Miltner, A., Kindler, R., Knicker, H., Richnow, H. H., & Kästner, M. (2009). Fate of microbial biomass-derived amino acids in soil and their contribution to soil organic matter. *Organic Geochemistry*, *40*, 978–985. https://doi.org/10.1016/j.orggeochem.2009.06.008

Neurath, R. A., Pett-Ridge, J., Chu-Jacoby, I., Herman, D., Whitman, T., Nico, P. S., Lipton, A. S., Kyle, J., Tfaily, M. M., Thompson, A., & Firestone, M. K. (2021). Root carbon interaction with soil minerals is dynamic, leaving a legacy of microbially derived residues. *Environmental Science & Technology*, 1–36. https://doi.org/10.1021/acs.est.1c00300

Ni, X., Liao, S., Tan, S., Peng, Y., Wang, D., Yue, K., Wu, F., & Yang, Y. (2020). The vertical distribution and control of microbial necromass carbon in forest soils. *Global Ecology and Biogeography*, *29*, 1829–1839. https://doi.org/10.1111/geb.13159

Nunan, N., Ritz, K., Crabb, D., Harris, K., Wu, K., Crawford, J. W., & Young, I. M. (2001). Quantification of the in situ distribution of soil bacteria by large-scale imaging of thin sections of undisturbed soil. *FEMS Microbiology Ecology*, *37*(1), 67–77. https://doi.org/10.1111/j.1574-6941.2001.tb00854.x

Omoike, A., & Chorover, J. (2006). Adsorption to goethite of extracellular polymeric substances from Bacillus subtilis. *Geochimica et Cosmochimica Acta*, *70*, 827–838. https://doi.org/10.1016/j.gca.2005.10.012

Or, D., Phutane, S., & Dechesne, A. (2007). Extracellular polymeric substances affecting pore-scale hydrologic conditions for bacterial activity in unsaturated soils. *Vadose Zone Journal*, *6*, 298–305. https://doi.org/10.2136/vzj2006.0080

Or, D., Smets, B. F., Wraith, J. M., Dechesne, A., & Friedman, S. P. (2007). Physical constraints affecting bacterial habitats and activity in unsaturated porous media – A review. *Advances in Water Resources*, *30*, 1505–1527. https://doi.org/10.1016/j.advwatres.2006.05.025

Otten, W., Hall, D., Harris, K., Ritz, K., Young, I. M., & Gilligan, C. A. (2001). Soil physics, fungal epidemiology and the spread of Rhizoctonia solani. *New Phytologist*, *151*, 459–468.

Possinger, A. R., Zachman, M. J., Enders, A., Levin, B. D. A., Muller, D. A., Kourkoutis, L. F., & Lehmann, J. (2020). Organo–organic and organo–mineral interfaces in soil at the nanometer scale. *Nature Communications*, *11*, 6103. https://doi.org/10.1038/s41467-020-19792-9

Prescott, C. E., & Vesterdal, L. (2021). Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. *Forest Ecology and Management*, *498*, 119522. https://doi.org/10.1016/j.foreco.2021.119522

Quiquampoix, H., Abadie, J., Baron, M. H., Leprince, F., Matumoto-Pintro, P. T., Ratcliffe, R. G., & Staunton, S. (1995). Mechanisms and consequences of protein adsorption on soil mineral surfaces. In *ACS Symposium series* (Vol. 602, pp. 321–333). American Chemical Society.

Redmile-Gordon, M. A., Brookes, P. C., Evershed, R. P., Goulding, K. W. T., & Hirsch, P. R. (2014). Measuring the soil-microbial interface: Extraction of extracellular polymeric substances (EPS) from soil biofilms. *Soil Biology & Biochemistry*, *72*, 163–171. https://doi.org/10.1016/j.soilbio.2014.01.025

Sanderman, J., Maddern, T., & Baldock, J. (2014). Similar composition but differential stability of mineral retained organic matter across four classes of clay minerals. *Biogeochemistry*, *121*, 409–424. https://doi.org/10.1007/s10533-014-0009-8

Seifert, D., & Engesgaard, P. (2012). Sand box experiments with bioclogging of porous media: Hydraulic conductivity reductions. *Journal of Contaminant Hydrology*, *136–137*, 1–9. https://doi.org/10.1016/j.jconhyd.2012.04.007

Simpson, A. J., Simpson, M. J., Smith, E., & Kelleher, B. P. (2007). Microbially derived inputs to soil organic matter: Are current

estimates too low? *Environmental Science and Technology*, *41*, 8070–8076. https://doi.org/10.1021/es071217x

Simpson, R. T., Frey, S. D., Six, J., & Thiet, R. K. (2004). Preferential accumulation of microbial carbon in aggregate structures of no-tillage soils. *Soil Science Society of America Journal*, *68*, 1249–1255. https://doi.org/10.2136/sssaj2004.1249

Stopka, S. A., Agtuca, B. J., Koppenaal, D. W., Paša-Tolić, L., Stacey, G., Vertes, A., & Anderton, C. R. (2017). Laser-ablation electrospray ionization mass spectrometry with ion mobility separation reveals metabolites in the symbiotic interactions of soybean roots and rhizobia. *The Plant Journal*, *91*, 340–354. https://doi.org/10.1111/tpj.13569

Strong, D. T., De Wever, H., Merckx, R., & Recous, S. (2004). Spatial location of carbon decomposition in the soil pore system. *European Journal of Soil Science*, *55*, 739–750. https://doi.org/10.1111/j.1365-2389.2004.00639.x

Tfaily, M. M., Chu, R. K., Tolić, N., Roscioli, K. M., Anderton, C. R., Paša-Tolić, L., Robinson, E. W., & Hess, N. J. (2015). Advanced solvent based methods for molecular characterization of soil organic matter by high-resolution mass spectrometry. *Analytical Chemistry*, *87*, 5206–5215. https://doi.org/10.1021/acs.analchem.5b00116

Throckmorton, H. M., Bird, J. A., Dane, L., Firestone, M. K., & Horwath, W. R. (2012). The source of microbial C has little impact on soil organic matter stabilisation in forest ecosystems. *Ecology Letters*, *15*, 1257–1265. https://doi.org/10.1111/j.1461-0248.2012.01848.x

Tian, J., Zong, N., Hartley, I. P., He, N., Zhang, J., Powlson, D., Zhou, J., Kuzyakov, Y., Zhang, F., Yu, G., & Dungait, J. A. J. (2021). Microbial metabolic response to winter warming stabilizes soil carbon. *Global Change Biology*, 1–18. https://doi.org/10.1111/gcb.15538

Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. A. G., & Allison, S. D. (2013). Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences*, *10*, 1717–1736. https://doi.org/10.5194/bg-10-1717-2013

Vidal, A., Klöffel, T., Guigue, J., Angst, G., Steffens, M., Hoeschen, C., & Mueller, C. W. (2021). Visualizing the transfer of organic matter from decaying plant residues to soil mineral surfaces controlled by microorganisms. *Soil Biology & Biochemistry*, *160*, 108347. https://doi.org/10.1016/j.soilbio.2021.108347

Vogel, C., Mueller, C. W., Höschen, C., Buegger, F., Heister, K., Schulz, S., Schloter, M., & Kögel-Knabner, I. (2014). Submicron structures provide preferential spots for carbon and nitrogen sequestration in soils. *Nature Communications*, *5*, 1–7. https://doi.org/10.1038/ncomms3947

Voltolini, M., Taş, N., Wang, S., Brodie, E. L., & Ajo-Franklin, J. B. (2017). Quantitative characterization of soil micro-aggregates: New opportunities from sub-micron resolution synchrotron X-ray microtomography. *Geoderma*, *305*, 382–393. https://doi.org/10.1016/j.geoderma.2017.06.005

Wang, C., Wang, X. U., Pei, G., Xia, Z., Peng, B. O., Sun, L., Wang, J., Gao, D., Chen, S., Liu, D., Dai, W., Jiang, P., Fang, Y., Liang, C., Wu, N., & Bai, E. (2020a). Stabilization of microbial residues in soil organic matter after two years of decomposition. *Soil Biology & Biochemistry*, *141*, 107687. https://doi.org/10.1016/j.soilbio.2019.107687

Wang, X. U., Wang, C., Cotrufo, M. F., Sun, L., Jiang, P., Liu, Z., & Bai, E. (2020b). Elevated temperature increases the accumulation of microbial necromass nitrogen in soil via increasing microbial turnover. *Global Change Biology*, *26*, 5277–5289. https://doi.org/10.1111/gcb.15206

Weijers, J. W. H., Schouten, S., Spaargaren, O. C., & Sinninghe Damsté, J. S. (2006). Occurrence and distribution of tetraether membrane lipids in soils: Implications for the use of the TEX86 proxy and the BIT index. *Organic Geochemistry*, *37*, 1680–1693. https://doi.org/10.1016/j.orggeochem.2006.07.018

Wieder, W. R., Cleveland, C. C., Smith, W. K., & Todd-Brown, K. (2015). Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience*, *8*, 441–444. https://doi.org/10.1038/ngeo2413

Witzgall, K., Vidal, A., Schubert, D. I., Höschen, C., Schweizer, S. A., Buegger, F., Pouteau, V., Chenu, C., & Mueller, C. W. (2021). Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nature Communications*, *12*, 4115. https://doi.org/10.1038/s41467-021-24192-8

Young, I. M., & Crawford, J. W. (2004). Interactions and self-organization in the soil-microbe complex. *Science*, *304*, 1634–1637. https://doi.org/10.1126/science.1097394

Zhang, X., Jia, J., Chen, L., Chu, H., He, J.-S., Zhang, Y., & Feng, X. (2021). Aridity and NPP constrain contribution of microbial necromass to soil organic carbon in the Qinghai-Tibet alpine grasslands. *Soil Biology & Biochemistry*, *156*, 108213. https://doi.org/10.1016/j.soilbio.2021.108213

How to cite this article: Buckeridge, K. M., Creamer, C., & Whitaker, J. (2022). Deconstructing the microbial necromass continuum to inform soil carbon sequestration. *Functional Ecology*, 36, 1396–1410. https://doi.org/10.1111/1365-2435.14014