

Review

Knowns and unknowns of the soil fungal necrobiome

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Dead microbial cells, commonly referred to as necromass, are increasingly recognized as an important source of both persistent carbon as well as nutrient availability in soils. Studies of the microbial communities associated with decomposing fungal necromass have accumulated rapidly in recent years across a range of different terrestrial ecosystems. Here we identify the primary ecological patterns regarding the structure and dynamics of the fungal necrobiome as well as highlight new research frontiers that will likely be key to gaining a full understanding of fungal necrobiome composition and its associated role in soil biogeochemical cycling. Because many members of the fungal necrobiome are culturable, combining laboratory functional assays with field-based surveys and experiments will allow ongoing studies of the fungal necrobiome to move from largely descriptive to increasingly predictive.

The importance of dead microbial cells as a primary source of soil organic matter has become increasingly appreciated in recent years [1,2]. These cells, collectively referred to as microbial **necromass** (see [Glossary](#)), are now recognized to be a substantial component of the carbon that is stored long-term in soils [3,4]. Microbial necromass has also been shown to play a significant role in soil nutrient availability, particularly in terms of the nitrogen available for plant and microbial uptake [5,6]. Among the different types of microbial necromass, those of fungal origin are more abundant than those deriving from bacteria as components of stabilized organic matter [3,4]. As such, a better understanding of the microbial communities involved in fungal necromass decomposition can improve knowledge of how carbon and nutrients move from decaying fungal necromass into ecosystem pools, both below and above ground [5,6]. In addition, characterizing how different microbial **functional groups** interact during fungal necromass decomposition will likely be key to accurately incorporating these interactions into ecosystem process-based models of soil biogeochemical cycling [7,8].

This review does not focus on the ecological factors driving rates of fungal necromass decomposition, which are concisely detailed elsewhere [9]. Instead, we focus on synthesizing the growing ‘knowns’ about the structure and dynamics of the microbial communities associated with decomposing fungal necromass (a.k.a. the **fungal necrobiome**). Additionally, we identify multiple ‘unknowns’ as important research frontiers about fungal necromass decomposition ([Box 1](#)), which we believe hold promise in more clearly linking necrobiome composition to interactions among microorganisms.

Known #1: fungal necromass is colonized very quickly

The colonization of fungal necromass by both bacteria and fungi appears to occur very rapidly. Sampling of fungal necromass after 7–8 days of incubation in soil has found a highly divergent microbial community structure compared to that in the surrounding environments [10–12],

Highlights

Fungal necromass is a dominant component of the dead microbial cells associated with persistent carbon in soils as well as a significant source of nutrient availability for plant and microbial uptake.

Recent molecular-based analyses of decomposing fungal necromass in a range of ecosystems have found a selective but dynamic microbial community that is codominated by bacteria and fungi.

Despite considerable taxonomic and functional variation in the fungal necrobiome over time, there appears to be a consistent set of bacteria and fungi encountered on decomposing fungal necromass across geographically and vegetatively diverse ecosystems.

The most abundant microbial taxa found in molecular surveys of decomposing fungal necromass are culturable, so both laboratory assays and manipulative ecological experiments should be conducted to better understand the processes underlying fungal necrobiome assembly.

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Box 1. Distinguishing fungal necromass decomposition and recycling

Although decomposition and recycling have both been used to refer to the degradation of microbial necromass [47], the two terms may not be equally well suited to describing fungal necromass degradation. We use decomposition to refer to the breakdown of fungal necromass by abiotic and biotic mechanisms. While we suspect the soil microbial communities to be the primary actors in fungal necromass decomposition, abiotic factors such as leaching might also be involved [10]. Recycling relates to microbial decomposition (i.e., catabolism) and biomass formation (i.e., anabolism) from necromass, as defined in Buckeridge *et al.* [47]. However, because many filamentous fungi actively recycle large parts of their mycelia as they grow, in association with likely being primary decomposers of fungal necromass, it remains critical to distinguish between fungal self-recycling and necromass recycling by exogenous microbial decomposers [48–50].

suggesting active colonization begins shortly after fungal senescence. Because microbes are capable of extremely rapid growth, however, shorter time intervals of sampling (e.g., 1–6 days) are needed to determine how quickly fungal necromass becomes colonized. Microbial colonization can also be assessed using methods such as quantitative PCR, which provide a more accurate estimate of microbial abundance than **high-throughput sequencing (HTS)** alone. Interestingly, Brabcová *et al.* [10] found that, although significant bacterial abundances were measurable on fungal necromass after 7 days in forest soil, they were not detectable on the same type of necromass incubated in forest litter until 14 days after incubation. Given the high similarity in the microbial communities that subsequently developed on fungal necromass in both locations, environmental conditions (e.g., moisture availability) may play an important role in controlling the specific rate at which fungal necromass-associated microbial communities develop.

Known #2: fungal necromass hosts a select but dynamic community

The microbial communities associated with decaying fungal necromass have been shown to consistently differ from those present in surrounding environments. Relative to soil, lower species diversity has been demonstrated for both bacterial and fungal communities across a range of different ecosystems (grassland [12], savannah [12], deciduous forest, [12,13]). Changes in **alpha diversity** are most strongly associated with declines in species richness, although the species evenness can also decline on decaying fungal necromass [11]. While alpha diversity on decaying fungal necromass is typically lower than in the surrounding environments, there is a notable lack of decline in this metric over time. This pattern has been observed at the scale of both weeks and months [11,12] as well as over multiple years [14]. If resources were rapidly depleted from necromass due to abiotic factors, such as leaching or microbial consumption, it might be expected that alpha diversity would peak in the early stages of decomposition and then decline over time. In contrast, in studies from a range of different kinds of ecosystems, alpha diversity stays consistently similar (sometimes even increasing, [12,14]), even when the original fungal necromass is no longer changing in mass remaining. Given that microbial species composition shifts over this time period (see subsequent text), apparent substitutions in community membership between the earlier and later stages of decay seem to buffer alpha diversity. The community shifts may parallel differences in resource availability, as has been observed on other decomposing organic types [15,16], but may also reflect the fact that the decomposing microbes may themselves be the targets of parasitism and predation by other microbes [17,18]. For example, Maillard *et al.* [11] found a notable increase in fungal mycoparasite abundance over the course of necromass decomposition, suggesting that the originally colonizing microbes were subject to greater parasitism over time.

Along with reduced alpha diversity, the microbial communities present on decaying fungal necromass differ from their surrounding environments in species composition (a.k.a. **beta diversity**). Soils harbor highly diverse microbial communities, both taxonomically and functionally, and colonization of decaying fungal necromass typically involves different subsets of microbial taxa being present at

Glossary

Alpha diversity: a metric of community structure that quantifies species richness or evenness. Those measures can also be combined into a single diversity metric, such as the Shannon or Simpson Index [45].

Beta diversity: a metric of community structure that quantifies species composition and particularly how much composition changes across samples spatially or temporally. High beta diversity would correspond with a set of samples that shared very few species in common.

Congeneric colonization pattern (CCP): a pattern emerging in some fungal necrobiome datasets of preferential colonization of fungal necromass by congeneric taxa. For example, Maillard *et al.* [19] observed that other members of the genus *Meliniomyces* were disproportionately abundant on *Meliniomyces bicolor* necromass compared to other types of fungal necromass.

Functional group: classification of an organism not based on its taxonomy but rather its nutritional or trophic mode. For example, a copiotrophic bacterium is one that is typically faster growing regardless of its taxonomic identity.

Fungal necrobiome: the biotic communities that assemble on decaying fungal necromass. The necrobiome includes multiple domains of life as well as multiple trophic levels.

High-throughput sequencing (HTS): the most widely used method for characterizing the structure of the fungal necrobiome. Currently, this is most frequently done using short-read sequencing platforms, such as Illumina MiSeq.

Necromass: the cells remaining after an organism has died or senesced. Sometimes also referred to as residue or litter, although the latter is largely used to describe dead plant material.

Stable isotope probing (SIP): this method utilizes isotopic enrichment to track specific elements or compounds from substrates into organisms. One version of SIP, known as DNA-SIP, involves obtaining DNA from all organisms that are present on the substrate and, using centrifugation, separating organisms that have incorporated resources from the isotopically enriched substrate due to their heavier DNA. That heavier DNA is then sequenced using HTS to identify

different times. During initial colonization (i.e., in the first days to few weeks), bacterial communities tend to be dominated by taxa in the classes *deltaproteobacteria* and *betaproteobacteria* [12,13]. Early-colonizing fungal communities are enriched in taxa in the orders *Mortierellales* and *Eurotiales*, which are typically classified as fast-growing molds in the phyla *Mucoromycota* and *Ascomycota*, respectively [10,11]. In the later stages of necromass decomposition (i.e., months to years), bacterial communities have increased representation by taxa in the phylum *Bacteroidota* as well as classes *Alphaproteobacteria* and *Bacilli* [12,14]. For fungi, later colonizers include members of the orders *Agaricales*, *Cystofillobasidiales*, and *Saccharomycetales* [14,19], which span multiple phyla (*Ascomycota* and *Basidiomycota*) and have multiple growth morphologies (hyphae and yeast).

which microbes are obtaining resources from the substrate. In isotope-based studies of fungal necromass, carbon and nitrogen are the two most commonly enriched elements, although SIP tracking of phosphorus is also possible [46].

From a functional perspective, the composition of bacterial communities on decaying fungal necromass has been consistently documented to shift from a dominance of copiotrophic taxa to increasing proportions of oligotrophic taxa over time [12,13]. Similarly, fungal community composition often changes over time to taxa with greater enzymatic capacity to degrade recalcitrant compounds (e.g., increases in *basidiomycete* fungi [11,13]). These compositional shifts broadly parallel changes in fungal necromass chemistry during decomposition, which declines in nitrogen and increases in aromatic compound content over time [20]. That said, it appears that fungal functional community development may be influenced by initial fungal necromass chemistry, as Brabcová *et al.* [13] and Fernandez and Kennedy [21] found that the initial carbon:nitrogen ratio and melanization level, respectively, strongly influenced necromass-associated microbial composition. More recently, Maillard *et al.* [19] found that the lipid content of remaining fungal necromass was a strong predictor of both fungal and bacterial composition. This latter finding suggests that aliphatic compounds, which make up a larger fraction of fungal necromass than aromatic compounds such as melanin [20], may play a particularly crucial role in determining decomposer community composition, especially since they are much more likely an active resource target for microbial catabolism than melanin [22].

A related ecological question is the extent to which the microbes associated with decaying fungal necromass also occur on other types of organic matter. This question was most directly addressed by Brabcová *et al.* [10], who compared the microbial communities in soil, in the litter layer, and on fungal necromass incubated in both locations. They found that regardless of whether fungal necromass was incubated in soil or litter, the microbial communities that developed on it were significantly different from either surrounding community. Additionally, they showed that this compositional distinction remained present through both the early and late stages of fungal necromass decay, suggesting that the communities of bacteria and fungi present on fungal necromass are largely specific to this substrate. Comparing across studies done at the same field location, however, Fernandez and Kennedy [21] and Fernandez *et al.* [23] found a high abundance of the ectomycorrhizal fungal genus *Tomentella* colonizing fungal necromass and plant litter, respectively. Working in a laboratory setting, López-Mondéjar *et al.* [24] examined the extent to which fungal necromass-associated bacteria and fungi could also degrade other organic matter types. Using isotopic tracking of carbon from different substrates, they found that the majority of both the bacteria and fungi that efficiently grew on fungal necromass could also develop on plant litter. Collectively, these results suggest that there is reasonable potential for microbial decomposers to co-occur on fungal necromass as well as other organic matter types, but that community differentiation may occur *in situ* likely due to ecological factors such as resource competition.

Known #3: the fungal necrobiome is environmentally sensitive yet consistently similar

Among the growing number of studies profiling the structure of microbial communities on decaying fungal necromass, multiple have documented sensitivity to altered environmental

conditions. For example, Maillard *et al.* [11] found that the alpha diversity of fungal necromass-associated communities was notably lower in wood than in soil, which are habitats that differ in many ways biotically and abiotically. Similarly, sizable differences in fungal necromass-associated microbial community beta diversity were demonstrated across natural vegetation gradients (i.e., forests versus grasslands [12]), which also have contrasting biotic and abiotic conditions. While these examples suggest that environmental variation may be important, multicollinear variables make it difficult to determine to what specifically the fungal necromass-associated microbial communities are responding. Working in a field experiment incorporating both above- and below-ground warming up to 9° Celsius, Maillard *et al.* [19] demonstrated that fungal necromass-associated communities in peatland soils were significantly altered by increased temperature. Specifically, the authors showed that, as warming reduced peatland water depth, the fungal necromass-associated microbial communities normally present at lower locations became compositionally similar to those of the communities from higher locations. While this is the only study to our knowledge that has directly examined the response of fungal necromass-associated microbial communities to experimentally altered conditions, there are many environmental gradients (e.g., water availability, nutrient addition, soil disturbance, land management) that would be beneficial to test to better determine which factors primarily drive changes in fungal necromass community structure.

Despite the aforementioned environmental effects on fungal necromass-associated community structure, a growing number of studies have found striking genus-level resemblance in community composition. This is true for both bacteria and fungi, suggesting that there may be a repeatable set of core taxa that dominate the fungal necrobiome ([12], Box 2). For example, *Mucilaginibacter*, *Pseudomonas*, *Dyella*, and *Chitinophaga* have been consistently observed among the more abundant genera in studies ranging geographically across Europe and North America as well as across temperate and boreal biomes [10,12–14,19,21]. Likewise, *Mortierella*, *Trichoderma*, *Umbelopsis*, and *Tomentella* were also consistently among the most common fungal genera sampled in the same studies. While interesting exceptions exist (e.g., the fungal genus *Mucor* seems to dominate the fungal necromass-associated fungal communities in boreal but not temperate forests [14,19]), the high redundancy across studies suggests that these microbial genera may be particularly efficient at utilizing resources in fungal necromass. This taxonomic pattern does show some general alignment with known physiological abilities (e.g., chitin degradation) among both bacteria and fungi [25,26], but we suspect that additional studies may also reveal affinities for particular polysaccharides (e.g., glucans) or lipids (e.g., ergosterol) that are largely present only in fungal cells [27]. Importantly, the majority of the aforementioned bacterial and fungal genera are known to grow well in laboratory culture [25,28,29], which will greatly facilitate more detailed physiological profiling.

Box 2. Designating a core fungal necrobiome

Given the high diversity in most microbial communities, including the soil fungal necrobiome, there has been growing interest among microbial ecologists in determining whether a core set of taxa can be identified in different study systems. A core microbiome has been proposed to include 'the members common to two or more microbial assemblages associated with a habitat' [51]. While conceptually appealing, the specific details of calculating core membership have been surprisingly inconsistent across studies. For example, some emphasize taxon frequency as a key metric of membership (e.g., [52]), while others focus only on taxon abundance (e.g., [53]). Given that these metrics are often positively correlated but can have different ecological consequences [54], a consensus is now growing around using both metrics at the same time. Known as abundance-occupancy distributions [55], these plots help to identify taxa that are both common and abundant, which is one way to prioritize which taxa might belong to the core. Interestingly, this method can also be combined with null modeling to determine which taxa fall outside the expected bounds of this relationship, which may reflect a particular ecological strategy that differs from other core members.

Known #4: some fungal decomposers preferentially colonize closely related necromass

A final emerging trend regarding the composition of fungal necromass-associated fungal communities is the observation of high colonization by certain congeneric taxa. This was most clearly observed in the recent study of Maillard *et al.* [19] who found that the necromass of both *Meliniomyces bicolor* and *Oidiodendron griseum* were significantly enriched in fungi from the same genus in their decomposer communities. The common distinguishing ecological feature of these two necromass types was that both *Meliniomyces* and *Oidiodendron* are ericoid mycorrhizal fungi, which have particularly efficient nitrogen-acquisition capacities due to their growth in low-nitrogen ecosystems [30]. Since that study was conducted in an ombotrophic forested peatland with high ericoid shrub presence, it is perhaps not surprising that congeneric colonization was observed. However, reinspection of the results of Beidler *et al.* [12] shows a similar pattern on the fungal necromass of *Mortierella elongata*. Specifically, members of the genus *Mortierella* were significantly more abundant on *M. elongata* dead mycelium than the other fungal necromass type in all the four study sites of that study, suggesting that this **congeneric colonization pattern (CCP)** does not just occur in a single type of ecosystem. The mechanisms responsible for a CCP, however, are far from understood. It is possible that congeneric taxa have efficient chemotaxis abilities for congeneric fungal necromass and/or that their enzymatic capacities are particularly well suited to decomposing similarly built cells. Both chemotaxis assays to better determine recognition cues as well as degradation analyses of congeneric and noncongeneric fungal necromass will be helpful in assessing the generality and mechanics of this phenomenon.

Unknown #1: do microbial interactions shape the composition of the fungal necrobiome?

Although bacteria and fungi are clearly both integral members of the fungal necrobiome, there has been very little work on their interactions, either as they relate to colonization dynamics or to mass loss and chemical modifications of the fungal necromass itself. Based on evidence from other decomposing organic matter types (e.g., [31]), it seems highly likely that interactions among these different groups of microbes may have dramatic effects on necrobiome community dynamics. For example, it seems likely that fungi may play a substantial role in bacterial community dynamics through the production of diverse metabolites, which can influence bacterial population density, species composition, or both [32]. Similarly, while it is likely that bacteria and fungi compete for the most labile resources in fungal necromass, the capacity of fungi to enzymatically modify more recalcitrant compounds may be key to ‘unlocking’ resources not immediately available to most bacteria. Additionally, there is growing evidence that fungal hyphae serve as physical ‘highways’ for bacterial movement [33]. As such, fungal ingrowth into fungal necromass may be an important facilitator of bacterial colonization. The aforementioned patterns may also work in the other direction, with bacteria facilitating fungal exploitation of fungal necromass. For example, arbuscular fungi are reliant on the degradation capacities of bacteria to solubilize phosphorus (P) from organic substrates that they cannot obtain independently [34].

Unknown #2: which necromass resources are used by which microbes, and when?

Unlike for other soil organic matter types such as leaf litter, in which the relative contributions of different microbial groups to the decomposition process have been largely defined [15], which resources in fungal necromass are targeted by which groups of microbes is poorly known. Most work to date has inferred physiological functioning based on molecular identification, but the use of isotopic tracing provides a much more direct way to assess which microbes are responsible for the utilization of specific resources [35]. The use of nonradioactive isotopically

enriched substrates, broadly known as **stable isotope probing (SIP)**, has been applied in two studies examining carbon assimilation from fungal necromass. Zeglin *et al.* [36] incubated ^{13}C -enriched fungal necromass in a temperate coniferous forest and after 7 days determined carbon uptake by specific microbial groups using phospholipid fatty acid analysis (PLFA-SIP). They found that fungi were the most carbon-enriched group of microbes, followed by Gram-negative bacteria (Gram-positive bacteria, by contrast, did not show significant enrichment). Using a field-collected forest soil, but working under laboratory conditions, López-Mondéjar *et al.* [2018] incubated ^{13}C -enriched fungal necromass over a 21-day period and assessed carbon movement into bacteria and fungi using DNA-SIP. Unlike the Zeglin *et al.* [24] study, those authors showed that carbon from fungal necromass was much more frequently present in bacteria than fungi, although both types of microbes showed enrichment across a diverse range of taxa.

Given differences in results, additional isotopic-based studies are clearly needed to better define the functional roles of fungi and bacteria that co-occur on decaying fungal necromass. We advocate that these studies be field- or mesocosm-based (to include plant-symbiotic microbial guilds) and also multiresource focused. For example, the independent isotopic labeling of both carbon and nitrogen would allow for better discrimination in exactly which resource is targeted by which microbial group at which time in decomposition. Complementarily, more studies that quantify the abundances of each group using methods beyond HTS will help in validating how bacterial and fungal populations co-fluctuate on necromass over time. This can be accomplished with either molecular analyses (e.g., qPCR) or chemical analyses (e.g., PLFA), but also with more classic microbiological approaches (e.g., plating with differential antibiotics, [37]). The latter has the advantage of isolating representatives of each group, which can then be more specifically assayed for their growth capacities on different components of fungal necromass.

Unknown #3: are other trophic levels important effectors of the fungal necrobiome?

A third area ripe for further investigation is the possible contributions of other trophic levels to fungal necrobiome community dynamics. Particularly in soils, it is well known that bacteria and fungi interact with all kinds of different organisms, particularly as targets of consumption by higher trophic levels [38]. For example, Crowther *et al.* [39] demonstrated that fungus–fungus interactions had dramatically different outcomes in the presence of fungal-feeding mites. Nematodes are well classified into bacterivorous and fungivorous trophic modes [40], and given their abundance in soils, may act as key mediators of fungal and bacterial community dynamics. Alternatively, the presence and activities of additional microbes may be key to fully using resources present in necromass. Protists (i.e., single-celled microeukaryotes) are one possibility, as demonstrated by the recent study of Rozmoš *et al.* [41], which found that protist presence increased fungal utilization of nitrogen in chitin by up to 65% compared to samples that contained just bacteria and fungi. While predictions about changes in fungal necrobiome composition are likely to be system-specific, we suspect that fungal necromass turnover is likely generally facilitated by higher trophic levels, both by mediating microbe–microbe competition and affecting the quality and quantity of the necromass itself. For the latter, it is known that soil mesofauna, such as collembolans, directly feed on fungal necromass [42]. To date, the evaluation of mesofauna in fungal necromass degradation has likely been underestimated due to the use of nylon mesh bags in most studies, which restrict the access of larger fungivorous animals. This direct physical limitation of the role of the soil mesofauna in fungal necromass degradation is also associated with the fact that it has been shown that organic matter conversion into feces accelerates decomposition rates [43]. Consequently, developing experimental set-ups that allow the free colonization of fungal necromass by soil animals is critical for better incorporating the nonmicrobial trophic levels, and their direct and indirect effects on necromass-associated microbial communities, into decomposition processes of fungal necromass.

Concluding remarks and future perspectives

On the spectrum of pattern to process to mechanism [44], knowledge regarding the structure (i.e., the pattern) of the fungal necrobiome is now largely available. This is exciting because the general taxonomic boundaries are established for bacteria and fungi, but we remain a long way from any well-developed understanding of either process or mechanism underpinning these communities (see [Outstanding questions](#)). Moving forward, research on the fungal necrobiome will surely benefit from the application of diverse ‘omics-based methods, but also can be tractably addressed with classic microbiology techniques since many of the dominant microorganisms on fungal necromass can be readily cultured. In addition, having greater collaboration across research groups with different expertise will help to move the study of the fungal necrobiome from one that has been primarily descriptive to one that will be increasingly predictive.

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Declaration of interests

There are no interests to declare.

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Outstanding questions

What resources are used by bacteria or fungi during the degradation of fungal necromass? Determining the simultaneous contributions of these two microbial domains to fungal necromass degradation, particularly under field conditions, would greatly enhance our ability to predict not only decomposition rates but also long-term chemical fates of necromass based on surveys of fungal necrobiome composition.

How do microbial interactions shape the composition of the fungal necrobiome? The extent to which bacteria and fungi help or harm each other during the process of fungal necromass decomposition is largely unclear. If, for example, there are certain obligate cross-feeding relationships, or a particular ordering of fungal and bacteria taxa based on remaining fungal necromass chemistry, this would help in determining the trajectory of decomposition over time.

How do higher trophic levels affect the fungal necrobiome and contribute to fungal necromass decomposition? Fungal necromass is widely considered a decomposition hotspot based on the high abundance of bacteria and fungi during its degradation. Both of these microbial groups are the base of the ‘brown food web’, and aggregations of dead mycelium in particular likely are prime hunting grounds for higher trophic level fungivores and bacterivores (e.g., protists, nematodes, and collembola).

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