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Substrate quality drives fungal necromass decay and decomposer community structure under contrasting vegetation types

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Abstract

1. Fungal mycelium is increasingly recognized as a central component of soil biogeochemical cycling, yet our current understanding of the ecological controls on fungal necromass decomposition is limited to single sites and vegetation types.
2. By deploying common fungal necromass substrates in a temperate oak savanna and hardwood forest in the midwestern USA, we assessed the generality of the rate at which high- and low-quality fungal necromass decomposes; further, we investigated how the decomposer 'necrobiome' varies both across and within sites under vegetation types dominated by either arbuscular or ectomycorrhizal plants.
3. The effects of necromass quality on decay rate were robust to site and vegetation type differences, with high-quality fungal necromass decomposing, on average, 2.5 times faster during the initial stages of decay. Across vegetation types, bacterial and fungal communities present on decaying necromass differed from bulk soil microbial communities and were influenced by necromass quality. Moulds, yeasts and copiotrophic bacteria consistently dominated the necrobiome of high-quality fungal substrates.
4. *Synthesis.* We show that regardless of differences in decay environments, high-quality fungal substrates decompose faster and support different types of decomposer micro-organisms when compared with low-quality fungal tissues. These findings help to refine our theoretical understanding of the dominant factors affecting fast cycling components of soil organic matter and the microbial communities associated with rapid decay.

KEYWORDS

fungal hyphae, fungal mycelium, melanin, mycorrhizal type, necrobiome, oak savanna, temperate forest

1 | INTRODUCTION

The amount of carbon (C) stored in soils is dependent upon the balance between soil organic matter (SOM) inputs and their subsequent

rates of decomposition and C loss (Chapin, Matson, & Vitousek, 2012). While plant-derived inputs and losses have received decades of study (Berg & McClaugherty, 2003), there is growing evidence that fungal mycelium is also a major determinant of soil C stocks (Clemmensen et al., 2013; Ekblad et al., 2013; Godbold et al., 2006; Zhang et al., 2019). Conservative estimates of fungal mycelial

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biomass range from 20 to 250 g/m², with turnover times ranging from 9 to 48 days (Allen & Kitajima, 2014; Godbold et al., 2006; Soudzilovskaia et al., 2015). Moreover, once fungal biomass dies (i.e. becomes necromass), it decays rapidly (decay rate: 6.76–15.6/year; Brabcová, Štursová, & Baldrian, 2018; Zhang, Hui, Luo, & Zhou, 2008) and is rapidly assimilated into living microbial biomass (Drigo, Anderson, Kannangara, Cairney, & Johnson, 2012; López-Mondéjar et al., 2018; Miltner, Bombach, Schmidt-Brücken, & Kästner, 2012). The high nutrient content of fungal necromass compared to other organic matter (OM) inputs also makes it an important resource for a variety of decomposers (Brabcová et al., 2018; Finlay & Clemmensen, 2016). Recent studies indicate that the presence of fungal necromass significantly increases microbial enzyme activity (Brabcová, Nováková, Davidová, & Baldrian, 2016; Zeglin & Myrold, 2013) and is responsible for up to 80% of nitrogen (N) cycling associated with the decomposition of below-ground OM inputs (Zhang et al., 2019).

Given the importance of soil fungi to C and nutrient cycling, there is a pressing need to understand the factors that control the fate of fungal necromass across diverse environments (Baskaran et al., 2017; Fernandez, Langley, Chapman, McCormack, & Koide, 2016; Smith & Wan, 2019; Zhang et al., 2019). Current knowledge of the controls on decomposition are largely derived from assessments of plant litter decay, which identify the following interrelated factors: (a) climate; (b) biochemical traits (which typically indicate resource quality for decomposers); (c) soil properties (e.g. moisture, pH, and nutrient availability); and (d) decomposer community composition (Berg & McClaugherty, 2003; Prescott, 2010; Waksman & Tenney, 1926). Although there are no studies comparing fungal necromass decomposition along climatic gradients, fungal necromass has been shown to decompose faster when exposed to experimentally elevated temperatures (Fernandez, Heckman, Kolka, & Kennedy, 2019), suggesting altered climatic conditions can influence the decomposition dynamics of this OM pool. At local scales, biochemical traits have been shown to be important predictors of fungal necromass decay and correspond with metrics of plant litter quality (Cleveland et al., 2014; Ekblad, Wallander, & Näsholm, 1998; Fernandez et al., 2016; Hurst & Wagner, 1969). Specifically, both N and cell wall melanin content have been identified as key biochemical traits driving rates of fungal necromass decomposition (Brabcová et al., 2018; Fernandez & Koide, 2012, 2014; Koide & Malcolm, 2009; Lenaers et al., 2018). Fungal tissues with a high melanin and low N content (i.e. low-quality substrates) tend to decay more slowly, when compared with fungal tissues with low melanin and high N content (high-quality substrates). In this way, melanin:N ratios in fungal necromass parallel lignin:N ratios in plant litter, which can be broadly predictive of decay rate (Fernandez et al., 2016; Melillo, Aber, & Muratore, 1982; Strickland, Osburn, Lauber, Fierer, & Bradford, 2009). Unlike plant litter decay, however, it is not yet understood how site environmental conditions interact with initial substrate quality to control the rate at which fungal necromass decomposes.

In addition to climate and substrate quality, it is well-established that litter decay is also influenced by the biotic and abiotic properties of the soil, which are controlled in large part, by the dominant

vegetation (Eviner & Chapin, 2003; Hooper & Vitousek, 1997; McLaren & Turkington, 2010). Plant communities influence decomposition processes directly through litter inputs (Cornwell et al., 2008) and indirectly via their alteration of soil moisture, pH and microbial community composition (Finzi, Canham, & Breemen, 1998; Vivanco & Austin, 2008). Broadly, rates of decay differ among plant functional types (Zhang et al., 2008), with some evidence to support faster rates of plant litter decay in grasslands when compared with forest ecosystems (Portillo-Estrada et al., 2016; Solly et al., 2014). Additionally, decay dynamics can vary within ecosystems depending on the dominant type of mycorrhizal symbiosis that is present. Trees that associate with arbuscular mycorrhizal (AM) fungi often promote soils that have properties distinct from trees that associate with ectomycorrhizal (EM) fungi (Phillips, Brzostek, & Midgley, 2013), and such differences can lead to divergent rates of litter decay of the same litters (Keller & Phillips, 2019; Midgley, Brzostek, & Phillips, 2015). Furthermore, differences in the dominant mycorrhizal symbioses across the landscape often reflect strong gradients in soil pH and nutrient availability (Jo, Fei, Oswalt, Domke, & Phillips, 2019; Lin, McCormack, Ma, & Guo, 2017; Phillips et al., 2013; Read & Perez-Moreno, 2003). There is evidence to support that these differences in soil properties may lead to functional variation among decomposer organisms within AM and EM communities (Cheeke et al., 2016; Mushinski et al., 2019), creating an ideal testbed for exploring how substrate quality and differences in abiotic and biotic environmental conditions interact to control fungal necromass decay.

Molecular-based identification techniques have led to a rapid increase in the characterization of necromass-associated microbial communities or the 'necrobiome' (Brabcová et al., 2016, 2018; Drigo et al., 2012; Fernandez & Kennedy, 2018; López-Mondéjar et al., 2018). Importantly, the composition of the fungal 'necrobiome' has been shown to be distinct from that of the surrounding soil environment, suggesting that fungal necromass has unique qualities relative to the bulk soil (Brabcová et al., 2016, 2018; Fernandez & Kennedy, 2018). Fungal decomposer communities of necromass are frequently dominated by fast-growing moulds in the order Eurotiales, but also show considerable changes in composition over time (Brabcová et al., 2016, 2018), including significant colonization by EM fungi (Fernandez & Kennedy, 2018). Similarly, bacterial decomposers of fungal necromass appear to be dominated by generalist Proteobacteria, at least initially (Brabcová et al., 2018; López-Mondéjar et al., 2018), but also include more specialized taxa such as *Chitinophaga*, which have high chitin degradation abilities (Sangkholobol & Skerman, 1981). Additionally, it appears that necromass quality can significantly influence bacterial and fungal decomposer community composition, either through variation in C:N ratio (Brabcová et al., 2018) or melanin content (Fernandez & Kennedy, 2018).

While there has been notable recent progress in characterizing the effects of abiotic and biotic factors on fungal necromass decomposition and necromass-associated decomposer communities, the generality of the aforementioned patterns remains unclear. This is because all studies of this topic to date have been conducted at single sites. Here, by deploying common fungal necromass substrates

in a temperate oak savanna and hardwood forest, we sought to address two key gaps in current knowledge: (a) to determine whether high- and low-quality fungal necromass would decompose differently between the two sites and (b) to characterize the structure of the fungal necromass 'necrobiome' within and across sites under differing vegetation types. We hypothesized that similar to plant litter, high-quality fungal necromass (i.e. low melanin, high N) would decompose more rapidly than low-quality necromass (i.e. high melanin, low N). However, we also predicted that the effects of necromass quality would depend on the dominant vegetation under which it decayed, with the expectation that plant litter inputs can lead to functional differences in decomposer communities between vegetation types (Lambers, Chapin, & Pons, 1998; Strickland et al., 2009). We further hypothesized that both necromass quality and vegetation type would significantly influence the taxonomic and functional guild composition of microbial communities present on decomposing necromass, with fast-growing moulds, yeasts, and copiotrophic bacteria being the dominant decomposers of high-quality necromass and low-quality necromass being more heavily colonized by oligotrophic bacteria as well as saprotrophic and/or EM fungi depending on vegetation type.

2 | MATERIALS AND METHODS

2.1 | Study sites

Parallel necromass decomposition experiments were conducted at two sites and under two different vegetation types at each site: a temperate savanna containing EM-associated trees and AM-associated grasses and a temperate hardwood forest containing adjacent EM- and AM-dominated stands. The savanna site was located at Cedar Creek Ecosystem Science Reserve in central Minnesota, USA (45.42577N 093.20852W). Cedar Creek is a 2,266 ha reserve affiliated with the University of Minnesota, which contains a mix

of prairie and forest ecosystems. The mean annual temperature at Cedar Creek is 6.7°C and the mean annual precipitation is 801 mm. The forest site was located at Moores Creek in south-central Indiana, USA (39.08333N 086.46666W). Moores Creek, which is part of the Indiana University Research and Teaching Preserve system, is comprised of 105 ha of mixed deciduous hardwood forest (~80 years in age). The mean annual temperature at Moores Creek is 11.6°C and the mean annual precipitation is 1,200 mm. Within both sites, vegetation communities differed in their AM- and EM-associated plant species and edaphic characteristics (Table 1).

Plot locations at each site were chosen based on dominant vegetation type and mycorrhizal association. Three replicate plots were established at two locations in the savanna site; 10 m into EM-dominated *Quercus* forest and 20 m into the adjacent AM-dominated grassland. These distances were chosen based on previous work at the same site by Dickie and Reich (2005), which found little to no EM colonization of *Quercus* seedlings at 20 m away from the forest edge. At the forest site, seven replicate plots were established based on known mycorrhizal associations of dominant tree species. In all plots, trees from the dominant mycorrhizal type (AM or EM) represented >85% of the basal area of the plot and AM and EM plots were paired according to geographic proximity. Additional details about the layout of the plots in the forest site are available in Midgley and Phillips (2016).

2.2 | Fungal necromass generation and incubation

Two fungal species, *Mortierella elongata* and *Meliniomyces bicolor*, which have previously been demonstrated to differ in multiple chemical traits (Maillard, Schilling, Andrews, Schreiner, & Kennedy, 2020; Table 2), were chosen to represent high- and low-quality necromass. *M. elongata* is a fast-growing saprotrophic fungus in the phylum Mucromycota, which is frequently found in both forest and agricultural soils (Li et al., 2018). *M. bicolor* is an EM and ericoid

TABLE 1 Site characteristics. Climate decomposition index (CDI) is a multiplicative function developed by Adair et al. (2008) that describes the effect of monthly variation in temperature and water on decomposition, values range from 0 to 1, with higher values being indicative of faster rates of decay. See Supplementary Note 2 for more details on site CDI calculations

Site	Latitude (°N)	Longitude (°W)	Climate decomposition index	Soil description	Dominant plant species	Mycorrhizal type	pH
Oak savanna	45.425770	093.208520	0.2698	Outwash derived entisols with a fine sand texture	<i>Poa</i> sp., <i>Ambrosia</i> sp. and <i>Agropyron</i> sp.	AM	5.3 ± 0.03
					<i>Quercus ellipsoidalis</i> and <i>Quercus macrocarpa</i>	EM	4.3 ± 0.04
Temperate forest	39.083333	086.466667	0.3482	Sandstone-derived inceptisols with a silty loam texture	<i>Acer saccharum</i> , <i>Liriodendron tulipifera</i> , <i>Prunus serotina</i> and <i>Sassafras albidu</i>	AM	4.7 ± 0.1
					<i>Quercus rubra</i> , <i>Quercus velutina</i> , <i>Quercus alba</i> , <i>Carya glabra</i> and <i>Fagus grandifolia</i>	EM	3.4 ± 0.02

TABLE 2 Analyses of initial fungal necromass quality. Three independent replicates were analysed where standard errors are reported, otherwise values are based on a single replicate

	High quality <i>Mortierella elongata</i>	Low quality <i>Meliniumyces bicolor</i>
Elemental analysis		
C(%)	49.4 ± 2.2	51.4 ± 0.3
N(%)	7.0 ± 1.5	3.8 ± 0.03
C/N	7.5 ± 1.6	13.7 ± 0.2
GC/MS analysis (%)		
Aromatic	6.2 ± 0.3	17.6
Lipid	44.7 ± 3.1	57.8
N-containing	10.3 ± 2.5	1.1
Sterol	0.0 ± 0.0	0.3
Sugar	29.3 ± 1.8	22.0
Unspecified	9.5 ± 0.3	1.3
Melanin analysis (%)		
Melanin	4.3	17.5

mycorrhizal (ErM) Ascomycotan fungus frequently found in temperate and boreal forest soils (Grelet, Meharg, Duff, Anderson, & Alexander, 2009; see Fehrer, Réblová, Bambasová, & Vohník, 2019 for an update on the taxonomic status of this genus). These two species have contrasting melanin and nitrogen levels, with *M. elongata* representing a high-quality substrate and *M. bicolor* representing a low-quality substrate (Table 2). Complete details on the methods used for the chemical characterization of both species are provided in the online Supporting Information.

Fungal biomass for both species was produced in liquid cultures by individually inoculating 50 ml flasks containing half-strength potato dextrose broth with 3 mm diameter mycelial plugs (one plug per flask). Following inoculation, cultures were transferred to an orbital shaker and left to shake at 80 rpm for at least 30 days or until growth stopped. To produce fungal necromass, cultures were rinsed with distilled water and dried at 26°C for 24 hr. Dried fungal necromass (~25 mg) was then placed into nylon mesh litter bags constructed from 53-micron mesh (Elko) and heat-sealed. The 53-micron mesh size excluded both tree and grass root in-growth.

Separate litter bags were constructed for replicates of each fungal species. During deployment, litter bags were buried at organic–mineral soil interface (0–5 cm depth). To determine if there was any mass loss due to transport and handling, an additional set of litter bags was carried into the field ($n = 3$). Necromass recovery was greater than 98% and did not differ between fungal species, so masses were not corrected for any loss during transport. At each harvest, litter bags were individually bagged, placed on ice, and taken directly to the laboratory for processing. For each sample, necromass was carefully removed from the litterbag and dried at 30°C to a constant mass to determine mass remaining (this temperature was chosen to limit DNA degradation ahead of molecular analyses). Following mass measurements, the remaining necromass was stored at –80°C for molecular analyses.

While the preparation and processing of fungal necromass were standardized across the two sites, the specific incubation times varied slightly between studies due to logistical constraints. At the savanna site, fungal necromass was incubated for 14, 28, 42 and 56 days beginning in July 2017 ($n = 3$ litter bags of each fungal species for each vegetation type for each sampling date). At the forest site, fungal necromass was incubated for 14, 31 and 92 days beginning in July 2017 ($n = 7$ litter bags of each fungal species for each vegetation type for each sampling date). Soil moisture measurements at both sites were taken at the time litter bags were harvested. Gravimetric soil moisture data were collected from the composite of two 5×10 cm soil cores per plot at the savanna site and three 6.35×10 cm soil cores per plot at the forest site. To determine pH, a subsample of soil collected at the time of the first litter bag harvest was air-dried and analysed in a 0.01 M CaCl_2 solution using a bench-top pH meter. An additional subsample of soil taken from the first litter bag harvest was stored at –80°C prior to molecular analyses.

2.3 | Molecular analyses

Total genomic DNA was isolated from soil and necromass samples using DNeasy PowerSoil Extraction Kits (QIAGEN). DNA extractions were done according to the manufacturer's instructions, with the addition of a 30 s bead-beating step prior to extraction to enhance sample homogenization (as in Fernandez & Kennedy, 2018). Positive and negative controls were included for both bacteria and fungi. Positive controls included the bacterial mock community from the Human Microbiome Project (<https://www.hmpdacc.org/HMMC/>) and the fungal synthetic mock community developed by Palmer, Jusino, Banik, and Lindner (2018). DNA extractions were also performed on necromass samples that were placed into litterbags but not incubated. Negative controls included lysis tubes lacking substrate and PCR reactions with no DNA template added.

Microbial communities in soil and on decomposing fungal necromass were identified using high-throughput sequencing (HTS). For bacteria, the 515F–806R primer pair was chosen to target the V4 region of the 16S rRNA gene. For fungi, the 5.8S–Fun and ITS4–Fun primer pair (Taylor et al., 2016) was used to target the ITS2 region of the fungal rRNA operon. Samples were first amplified in individual 20 µl reactions containing 10 µl of Phusion Hot Start II High-Fidelity PCR Master Mix (Thermo Scientific), 0.5 µl of each 20 mM primer, 1 µl of DNA template and 8 µl of PCR-grade water. Thermocycling conditions were as follows: (1) 98°C for 30 s, (2) 98°C for 10 s, (3) 55°C for 30 s, (4) 72°C for 30 s, repeat steps (2)–(4) 34 times, (5) 72°C for 10 min and (6) Infinite hold at 4°C. If initial PCRs were not successful, dilutions or increased cycle numbers (34×) were performed. For all samples with amplicons, a second PCR was run under thermocycling conditions to add unique Golay barcodes and sequencing adaptors. PCR products were then cleaned using the Charm Just-a-Plate Purification and Normalization Kit (Charm Biotech). Each sample was then pooled at equimolar concentration and sequenced on a full MiSeq lane (2 × 300 bp V3 Illumina chemistry) at the University of Minnesota Genomics Center.

Sequences were processed using the AMPtk pipeline v1.1 (Palmer et al., 2018). First, paired-end reads were merged using VSEARCH (Rognes, Flouri, Nichols, Quince, & Mahé, 2016) and then subjected to quality trimming. Following pre-processing, reads were denoised with UNOISE3 (Edgar, 2016), and clustered into unique OTUs at 97% similarity using USEARCH v10 (Edgar, 2010). A 0.0005 abundance cut-off was applied to the bacterial data to eliminate low abundance OTUs thought to be spurious. For the fungal data, SynMock abundances were used to determine a similar filtering threshold. Read counts for any OTUs present in PCR and DNA negative controls were also subtracted from all samples. A small number of samples contained OTUs that matched the decomposing necromass (i.e. *M. elongata* and *M. bicolor* necromass). This signal could be residual DNA from the fungal necromass itself or from colonization by closely related species present in the soil. Because we encountered these OTUs in the soils at our sites and previous studies have demonstrated that the DNA associated with necromass decomposes rapidly (~7–14 days; Drigo et al., 2012; Schweigert, Herrmann, Miltner, Fester, & Kästner, 2015), they were retained in our analyses. However, any bacterial OTUs assigned as chloroplast without genus identification were removed.

Bacterial OTUs were assigned to copiotrophic and oligotrophic trophic modes based on Trivedi et al. (2017). Specifically, all bacterial OTUs belonging to the phylum Bacteroidetes and classes alpha-Proteobacteria, beta-Proteobacteria and gamma-Proteobacteria were defined as copiotrophs, while bacterial OTUs belonging to phylum Acidobacteria and class delta-Proteobacteria were defined as oligotrophs. Trophic mode assignments for fungi were made with FUNGuild (Nguyen et al., 2016). Fungi that could not be assigned to a functional guild were classified as 'unidentified'. Symbiotrophic fungi were parsed between ectomycorrhizal fungi and arbuscular mycorrhizal fungi. Remaining fungal OTUs belonging to Eurotiales, Hypocreales, Mortieriales, Mucorales, Saccharomycetales, Tremellales and Sporidiales as well as fungal OTUs defined by FUNGuild as microfungi, yeast and facultative yeast were classified as moulds and yeasts, following Sterkenburg, Bahr, Brandström Durling, Clemmensen, and Lindahl (2015).

2.4 | Statistical analyses

Statistical analyses and data visualization were conducted in R version 3.5.1 (R Core Team, 2018). ANOVA was used to test for differences in soil pH between sites and vegetation types within sites. To test for differences in soil moisture, ANOVAs were run with vegetation type (AM- vs. EM-associated vegetation) and sampling date as the predictor variables for each site. Prior to running the ANOVAs, soil moisture data were log-transformed to meet the assumptions of normality. Linear mixed-effect (LME) models were used to analyse the amount of fungal necromass remaining within each site (Bradford, Berg, Maynard, Wieder, & Wood, 2016). Fixed predictor factors included vegetation type (AM- vs. EM-associated vegetation), necromass type (high- vs. low-quality), incubation period, and soil moisture. Replicate sampling locations (either plots or plot

pairs) were designated as a random factor. Because pH was only measured during one harvest at each site, it was not included in this analysis. Mass remaining data were log logit-transformed to meet statistical assumptions (Power, Sokal, Rohlf, Rohlf, & Sokal, 1970; Warton & Hui, 2011). To evaluate the significance of linear mixed-effects models the Kenward–Roger approximation was used to estimate *F* statistics and denominator degrees of freedom (Halekoh & Højsgaard, 2014). Least square means were computed for each fixed effect and post-hoc comparisons were carried out on pairs of the least-squares means using the Tukey's adjustment for multiple comparisons.

Given the well-established nonlinear nature of OM decomposition (Berg, 2014), decay constants were calculated separately for each necromass type at each site. To calculate decay constants, we fit the proportion of remaining necromass against incubation time (days) using single- and double-exponential decay models. The best fitting model was selected using Akaike's information criteria (AIC). According to AIC values, a double-exponential decay model (Equation 1) produced the best fit.

$$[\text{mass}]_t = ae^{-k_1 t} + (1 - a)e^{-k_2 t}. \quad (1)$$

The proportional mass remaining ($[\text{mass}]_t$) was calculated by dividing the mass remaining at time (*t*) by the initial mass for each litterbag. In Equation 1, *a* refers to the initial proportion of fast decomposing or labile material, $1 - a$ is the initial proportion of slow decomposing or recalcitrant material. k_1 and k_2 are the degradation rate constants of the labile (fast-decomposing) and recalcitrant (slow-decomposing pool), respectively. The nonlinear least-squares Levenberg–Marquardt algorithm used to estimate model parameters, *a*, k_1 and k_2 , using the MINPAK.LM package (Elzhov, Mullen, Spiess, & Bolker, 2016). Like the mass remaining analyses, due to differences in the fungal necromass incubation times at the two sites, the following microbial community analyses were analysed for each site separately. Sample-OTU accumulation curves indicated that most samples achieved sequencing depths with high levels of OTU saturation (Figure S1). To account for differences in sequence read totals among samples, rarefaction was applied to 4,000 and 1,000 reads/sample for bacteria and fungi, respectively. OTU richness (N0) and diversity (H) were calculated using the VEGAN package (Oksanen et al., 2013). The effect of vegetation type, necromass quality, and incubation period on each of these metrics was assessed using a series of three-way ANOVAs for each decomposer group (bacteria or fungi) separately. Due to successful sequencing of only one 56-day sample at the savanna site, that harvest date was not included in the ANOVAs. Additionally, to balance the sampling design between sites (i.e. each site having an equal number samples from AM and EM vegetation types), all of the samples from the 5m grassland plots in the savanna site were not included in the ANOVAs, as preliminary analyses revealed very similar patterns of richness and diversity between the two AM grass-dominated plots (data not shown). Prior to running each ANOVA, variance homoscedasticity was tested using Cochran's test and data were log-transformed if necessary.

For analyses of microbial community composition, quality-filtered sequence read counts were transformed to proportional data per sample for all bacterial and fungal OTUs. Differences in bacterial and fungal OTU composition were visualized with non-metric multi-dimensional scaling (NMDS) plots using the 'metaMDS' function. The NMDS plots were generated based on Bray-Curtis OTU dissimilarity matrices. Permutational multivariate analyses of variance (PERMANOVA) were applied to assess the effect of vegetation type, necromass quality and incubation period on microbial community composition. Effects of the same three predictor variables were also assessed for each microbial guild using three-way ANOVAs. Finally, Wilcoxon signed-rank tests were used to identify specific bacterial and fungal genera that had significantly differential relative abundance depending on necromass quality. Similar to the analyses of richness and diversity, preliminary analyses of two AM grass-dominated plots at the savanna site revealed very high similarity in OTU and guild composition, so all samples from the 5 m grassland plots were not included in any of the community composition analyses. All tests were considered significant using a threshold of $p \leq 0.05$.

3 | RESULTS

Soil pH did not differ between sites ($F_{1,19} = 1.20, p = 0.291$), but did differ between vegetation types within sites ($F_{1,19} = 5.17, p = 0.038$),

being ~1 pH unit lower under EM vegetation compared to soils under AM vegetation (Table 1). In contrast to pH, soil moisture did not differ between vegetation types ($F_{1,57} = 0.010, p = 0.921$), but there was a modest difference between sites ($F_{1,57} = 3.96, p = 0.051$). On average, the savanna site soils were ~65% wetter ($10.6 \pm 0.5\%$) ($M \pm 1 SE$) during the necromass decay period than those at the forest site ($6.8 \pm 0.4\%$) over the duration of the incubations.

At each site, the amount of mass remaining in fungal necromass was significantly influenced by both necromass quality ($F_{1,37} = 20.24$, and $F_{1,66} = 100.22$ for the savanna and forest sites respectively; $p < 0.001$) and incubation period (savanna, $F_{1,37} = 74.29$; forest, $F_{1,66} = 66.76$; $p < 0.001$), but not vegetation type (savanna, $F_{1,37} = 0.24, p = 0.627$; forest, $F_{1,66} = 0.26, p = 0.609$). On average, the high-quality fungal necromass decomposed 2–3 times faster than low-quality fungal necromass. However, the effect of necromass quality was mediated by incubation time (see quality by time interaction terms in Table S1), with the greatest differences between quality types occurring at 14 days (Figure 1). After 14 days, 60% and 80% more low-quality necromass remained at the savanna and forest sites respectively, but after 56 and 92 days, the mass remaining of both necromass types reached a similarly stable value (~80% mass loss; Figure 1). No other higher order interactions were significant (Table S1). The nonlinear decay models showed similar trends, with k_1 values being much higher at both sites for high-quality fungal necromass, and the k_2 values being largely equivalent across sites and necromass types (Figure 1; Figure S1).

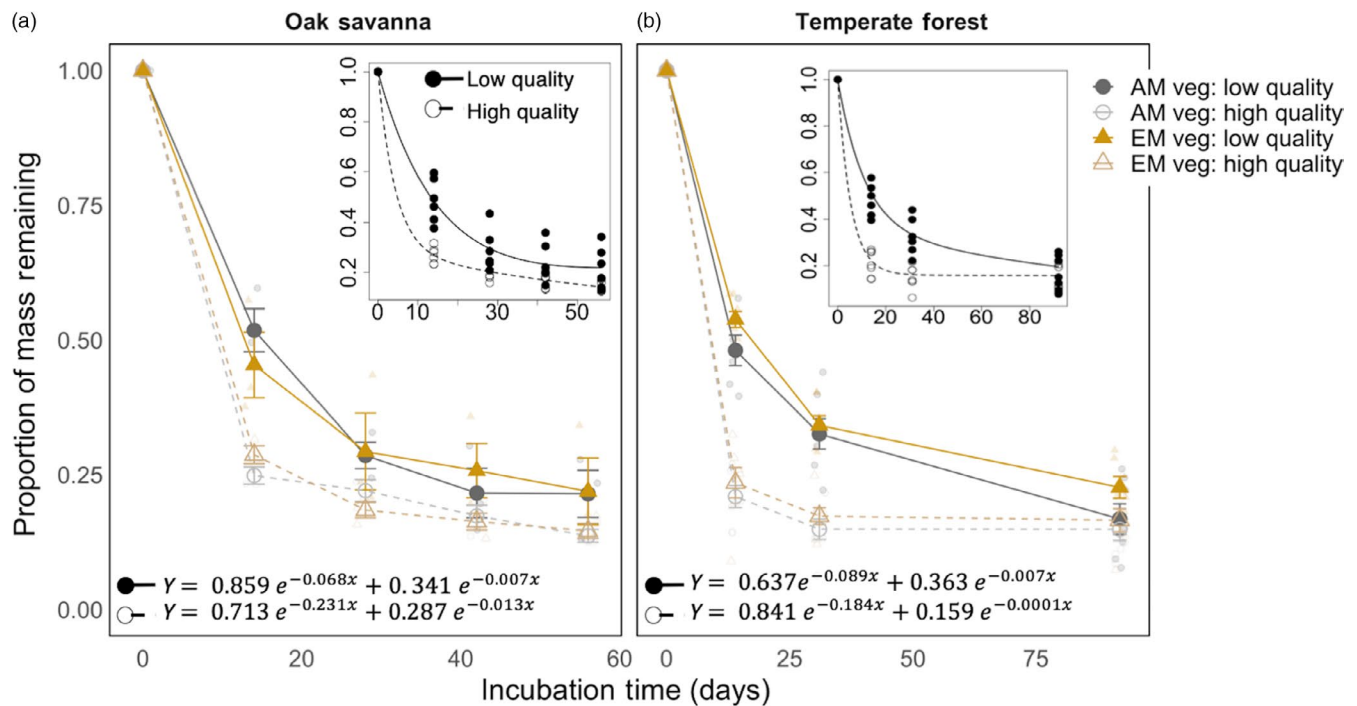
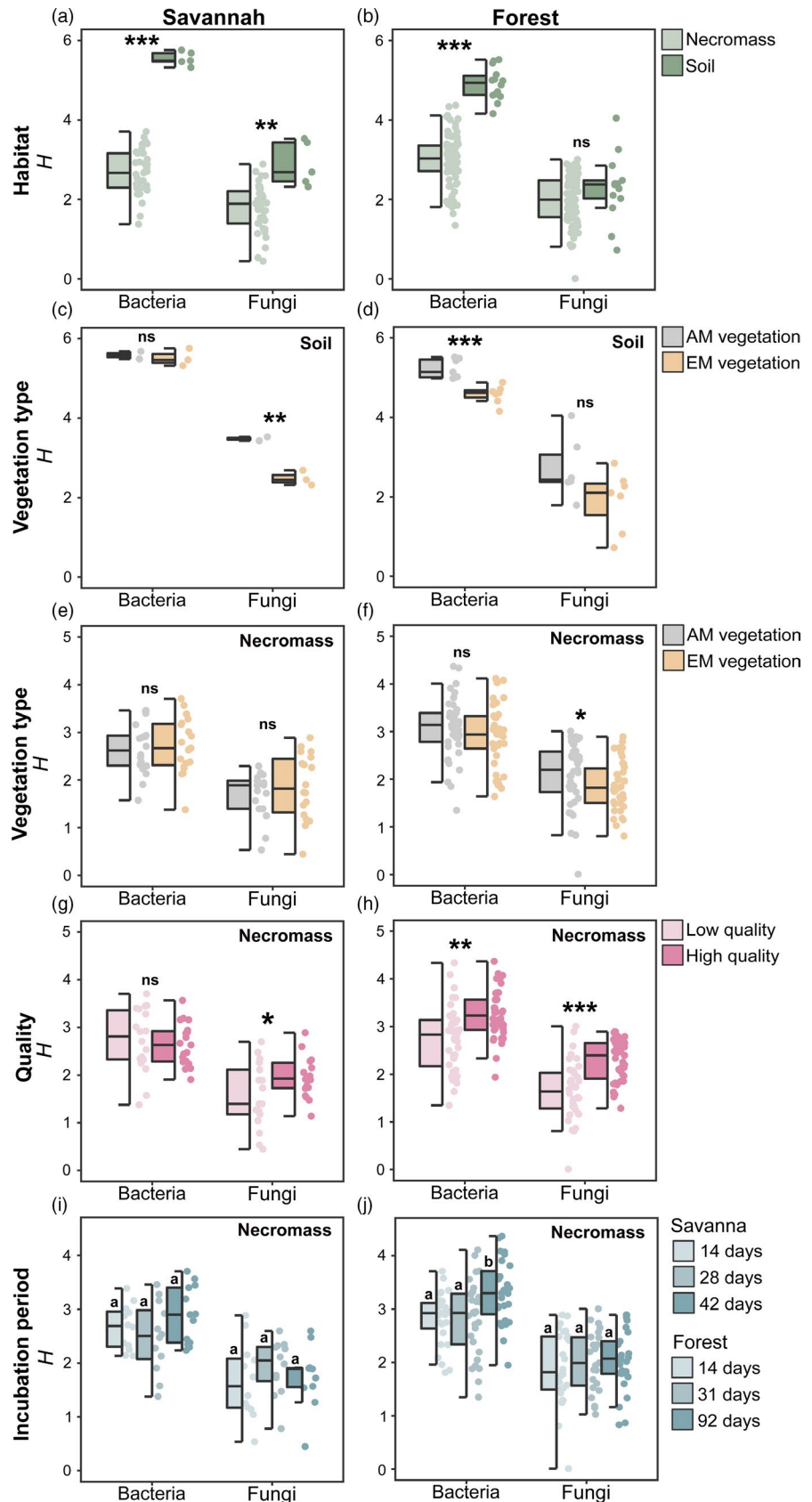


FIGURE 1 Proportional mass remaining ($M \pm 1 SE$) for high-quality *Mortierella elongata* (light shading) and low-quality *Meliniomyces bicolor* (dark shading) fungal necromass in AM-associated vegetation (grey circles) and EM-associated vegetation (tan triangles) at the oak savanna (a) and temperate forest (b) sites. At the oak savanna site, mass remaining was measured at four time periods, 14, 28, 42 and 56 days ($n = 3$ litter bags of each fungal species for each mycorrhizal association treatment for each sampling date). At the temperate forest site, mass remaining was measured at three time periods, 14, 31 and 92 days ($n = 7$ litter bags of each fungal species for each mycorrhizal association treatment for each sampling date). Inset graphs show double exponential decay curves for high- and low-quality necromass, as decomposition did not differ between vegetation-mycorrhizal types. For measures of error around model parameter estimates see Figure S1

FIGURE 2 Diversity indices (H) for bacterial and fungal communities in different habitats (in the surrounding soil or on fungal necromass) at the oak savanna (a) and temperate forest (b) sites. H values are also presented for bacterial and fungal communities under AM- and EM-associated vegetation for soil and necromass habitats in the oak savanna (c and e) and temperate forest sites (d and f). Differences in H values between microbial communities on high- and low quality necromass and for the different fungal necromass periods are shown for the oak savanna (g and i) and temperate forest sites (h and j). The high-quality necromass species was *Mortierella elongata* and the low-quality necromass species was *Meliniomyces bicolor*. ns refers to non-significant results; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; boxes that do not share similar letters denote statistical significance, $p < 0.05$



Microbial OTU diversity was significantly higher under AM- than EM-dominated vegetation soils, particularly fungal communities at the savanna site and bacterial communities at the forest site

(Figure 2a,b; Table S2). Bacterial OTU diversity was ~50% lower on necromass than in the surrounding soil at both sites (Figure 2c) and fungal OTU diversity was also decreased on necromass relative

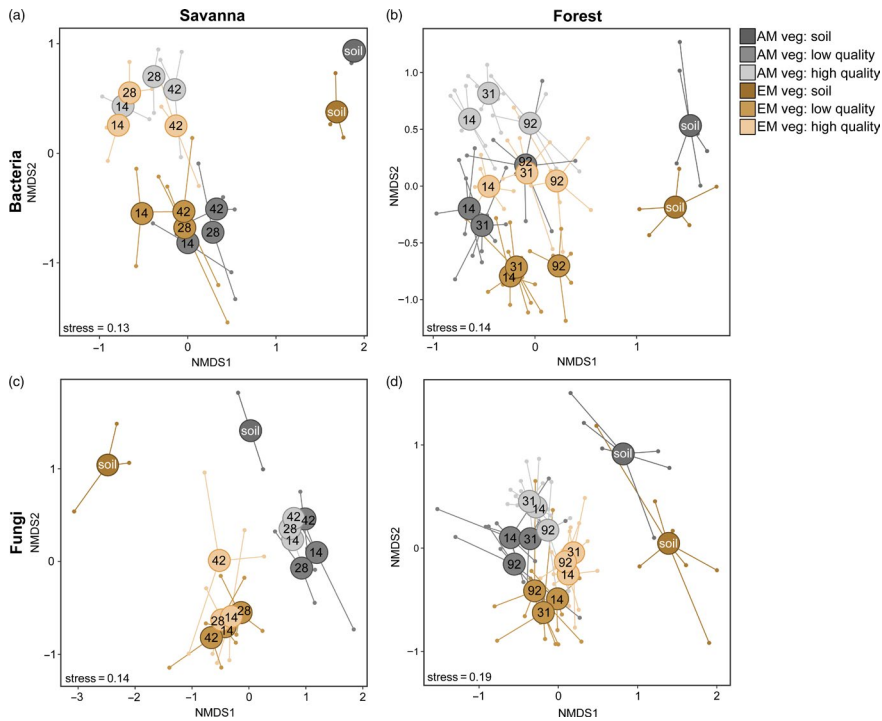


FIGURE 3 Non-metric multidimensional scaling (NMDS) analysis of bacterial (a and b) and fungal (c and d) communities colonizing high- and low-quality necromass, as well as, in the soil under AM- and EM-associated vegetation at the oak savanna (a and c) and temperate forest (b and d) sites. Small circles represent individual samples and large circles represent the centroids

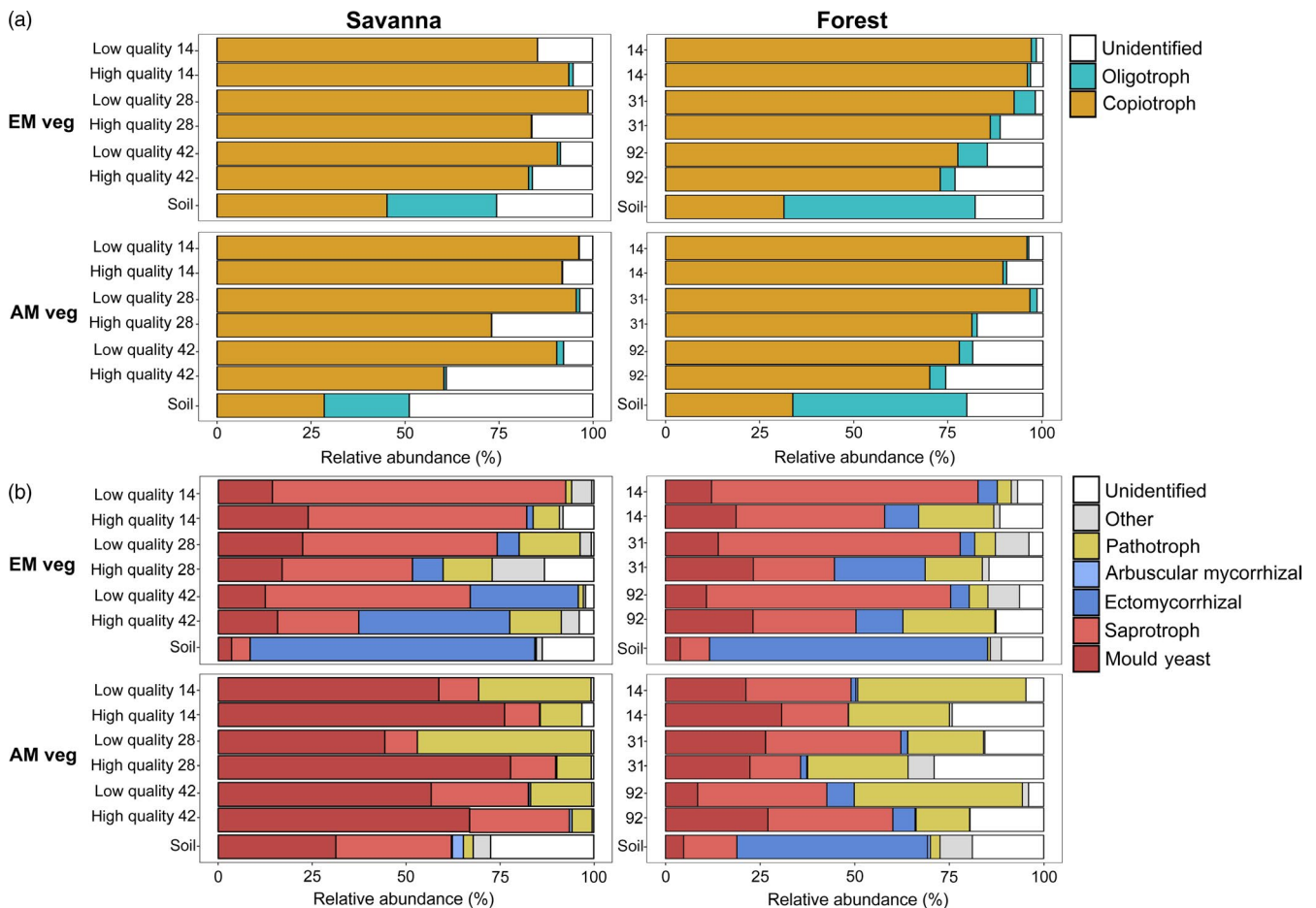


FIGURE 4 Relative abundances of necromass-associated bacterial (a) and fungal (b) guilds for the different vegetation types (AM- and EM-dominated vegetation), necromass qualities (high and low) and fungal necromass incubation periods (14, 28 and 42 days) in the oak savanna and temperate forest sites

TABLE 3 Results from permutational multivariate analysis of variance (PERMANOVA) statistical tests showing the effects of incubation time, vegetation type, necromass quality and their interactions on Bray–Curtis and Euclidean dissimilarity matrices for both fungal and bacterial communities at the oak savanna and temperate forest sites (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$)

Oak savannah					Temperate forest				
Fungi	df	F	R ²	p	Fungi	df	F	R ²	p
Incubation time	2	1.0855	0.02278	0.296	Incubation time	2	1.4466	0.03384	0.062
Vegetation type	1	14.1972	0.29800	0.001***	Vegetation type	1	6.1621	0.07207	0.001***
Necromass quality	1	1.6946	0.03557	0.086	Necromass quality	1	5.4378	0.06360	0.001***
Vegetation type × Incubation time	2	0.8846	0.01857	0.471	Vegetation type × Incubation time	2	1.2012	0.02810	0.178
Necromass quality × Incubation time	2	0.5539	0.01163	0.851	Necromass quality × Incubation time	2	1.1063	0.02588	0.293
Necromass quality × Vegetation type	1	1.5594	0.03273	0.136	Necromass quality × Vegetation type	1	2.1526	0.02518	0.014*
Necromass quality × Vegetation type × Incubation time	2	0.6666	0.01399	0.737	Necromass quality × Vegetation type × Incubation time	2	0.6224	0.01456	0.964
Bacteria	df	F	R ²	p	Bacteria	df	F	R ²	p
Incubation time	2	2.9100	0.05658	0.005**	Incubation time	2	4.4864	0.07647	0.001***
Vegetation type	1	4.0124	0.29800	0.002**	Vegetation type	1	10.0354	0.08553	0.001***
Necromass quality	1	10.4038	0.03557	0.001***	Necromass quality	1	15.3718	0.13101	0.001***
Vegetation type × Incubation time	2	1.3648	0.01857	0.159	Vegetation type × Incubation time	2	1.3491	0.02300	0.110
Necromass quality × Incubation time	2	1.1701	0.01163	0.265	Necromass quality × Incubation time	2	1.9833	0.03381	0.011*
Necromass quality × Vegetation type	1	1.6475	0.03204	0.092	Necromass quality × Vegetation type	1	4.6002	0.03921	0.001***
Necromass quality × Vegetation type × Incubation time	2	0.9183	0.01786	0.479	Necromass quality × Vegetation type × Incubation time	2	0.8444	0.01439	0.675

to soil, although only significantly at the savanna site (Figure 2d). Microbial diversity was 20% higher, on average, on high than low quality necromass, being significant at the forest site for bacteria and both sites for fungi (Figure 2e,f). The effect of vegetation type on microbial OTU diversity was generally low, only being significantly higher for fungi in AM vegetation at the forest site (Figure 2g,h). Similarly, incubation period had a limited impact on microbial OTU diversity, only being significantly higher for bacteria after 92 days of incubation at the forest site (Figure 2i,j).

Like OTU diversity, the composition of bacterial and fungal communities in soil and on necromass was significantly different at both sites (Figure 3; Table S4). Soils under EM vegetation were dominated by EM fungi and oligotrophic bacteria, whereas soils under AM vegetation had some AM fungi, but a greater proportion of saprotrophic fungi along with oligotrophic bacteria (Figure 4; Figure S6). By contrast, yeasts, moulds, and copiotrophic bacteria were much more common on necromass at both sites (Figure 4). Necromass quality significantly influenced bacterial composition at both sites and fungal community composition at the forest site (Table 3; Table S5). In general, high-quality fungal necromass had greater relative abundances of copiotrophic bacteria, moulds,

yeasts, and less saprotrophic fungi (Figure S7). Microbial community composition was also significantly influenced by vegetation type (Table 3; Table S5), with fungal pathotrophs being more abundant on fungal necromass in AM-dominated vegetation and EM and AM fungi being more abundant on fungal necromass in their matching vegetation types, respectively (Figure 4). Additionally, incubation time significantly affected bacterial but not fungal community composition on fungal necromass at both sites (Table 3; Table S5), with oligotrophic bacteria increasing in abundance over time at both sites, particularly on low-quality fungal necromass at the forest site (Figure 4; Table S5).

A number of bacterial and fungal genera displayed significant differential abundances depending on necromass quality. Both across sites (i.e. savanna vs. forest) and between vegetation types (AM vs. EM vegetation), the bacterial genera most commonly detected in greater abundance on high-quality fungal necromass included *Nocardia*, *Mesorhizobium*, *Orchobacterium*, and *Chitinophaga* (Figure 5). In contrast, the bacterial genera most commonly found in greater abundance on low-quality fungal necromass included *Burkholderia* and *Mucilaginibacter*. Of the fungal genera that had significant differential abundance by necromass quality, *Mortierella* was the lone

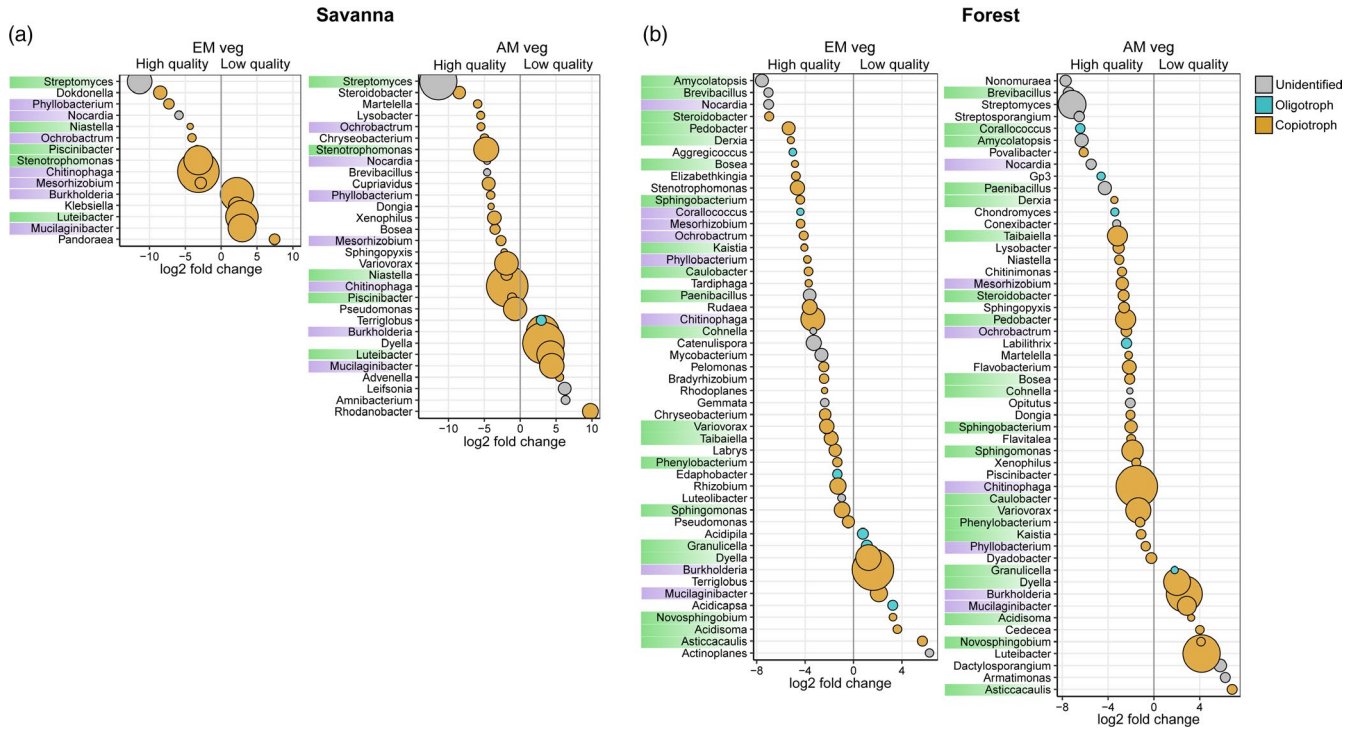


FIGURE 5 Fungal genera significantly impacted by the necromass quality type (high and low) depending of vegetation type (AM- and EM-dominated vegetation) in the oak savanna and temperate forest sites. Circles are coloured based on guild assignment and circle size is proportional to the relative abundance. Green highlights indicate fungal genera responding in the same way to the necromass species (high and low) within each site. Purple highlights indicate fungal genera responding in the same way to the necromass quality type (high and low) within and between sites

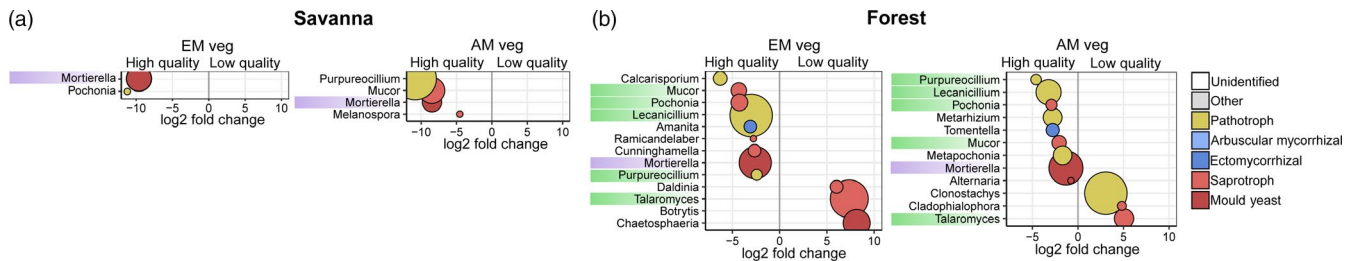


FIGURE 6 Bacterial genera significantly impacted by the necromass quality type (high and low) depending on vegetation type (AM- and EM-dominated vegetation) in the oak savanna and temperate forest sites. Circles are coloured based on guild assignment and circle size is proportional to the relative abundance. Green highlights indicate bacterial genera responding in the same way to the necromass species (high and low) within each site. Purple highlights indicate bacterial genera responding in the same way to the necromass species (high and low) within and between sites

genus consistently found on high-quality fungal necromass within and across both sites, although *Mucor* and *Pochonia* showed similar preferences for high-quality fungal necromass (Figure 6). Fungal genera most positively associated with low-quality fungal necromass included *Talaromyces* at both sites, *Clonostachys* at the forest site, and *Chaetosphaeria* at the savanna site.

4 | DISCUSSION

In this study, we utilized differences between study systems and vegetation types to explore the relative importance of necromass

quality and edaphic characteristics in controlling fungal necromass decay and microbial decomposer community structure. We found that the effects of necromass quality on decay were robust to vegetation type as well as differences in site edaphic characteristics. High-quality fungal necromass decomposed, on average, 2.5 times faster during the initial stages of decay regardless of site-level variation in soil moisture, pH, or CDI. This result is consistent with recent studies that have found substrate quality to be a key local predictor of fungal necromass decay. Brabcová et al. (2018) demonstrated that decreasing C:N ratio was positively associated with increasing mass loss rates from dead mycelium of 12 fungal species. Likewise, Fernandez and Kennedy (2018) showed that differences in substrate

quality, particularly increased melanin content, were strongly associated with decreases in mass loss rates. Collectively, these results indicate that, like plant litter decay, substrate quality is a key driver of fungal decay at both local and regional scales.

We did not find support for our hypothesis that necromass quality would interact with vegetation type to determine decay rate. This was somewhat surprising, particularly at the temperate forest site, given that the mycorrhizal associations of dominant tree species at this site have been shown to have distinct effects on soil biogeochemistry via their selection of microbial groups (including mycorrhizal fungi) with differing enzyme function (Brzostek, Dragoni, Brown, & Phillips, 2015; Cheeke et al., 2016; Lin et al., 2017; Midgley et al., 2015; Rosling et al., 2016). We speculate that the difference between our results and those of previous studies may be due to the fact that fungal necromass used in this study had chemical qualities that would be considered high compared to plant litter. Specifically, the C:N ratios for the two necromass types were 7 and 13 respectively, which are much lower than C:N ratios typically reported for leaf litter which can range from 20 to 100 (Brabcová et al., 2018; Ferlian, Wirth, & Eisenhauer, 2017; Zhang et al., 2008). In this case, the higher nutrient content of fungal necromass may not demand the same selective enzymatic activity to facilitate decomposition, particularly if initial rates of mass loss are influenced by differences in leaching capacity rather than direct microbial degradation (Maillard et al., 2020). It is certainly possible that with more time, differences in the decomposition of the more recalcitrant fraction of the remaining fungal necromass would develop between vegetation types, though the rapid mass loss from our high-quality necromass is consistent with a similarly fast rate of mass loss recently observed for AM necromass in temperate AM-dominated forests in Japan (Schäfer, Dannoura, Ataka, & Osawa, 2019). Moreover, given that hyphal production can be 2–3-fold greater in EM-dominated plots relative to AM-dominated plots (Cheeke, Phillips, Kuhn, Rosling, & Fransson, 2019), total inputs of C and N from necromass may depend on vegetation types.

The overall patterns of microbial community diversity on decaying fungal necromass were notably similar between sites, necromass qualities, vegetation types, and incubation times. The lower richness of bacterial and fungal communities on fungal necromass relative to bulk soil likely reflects the active growth required to colonize new substrates, which unlike soil, may contain little 'relic' DNA (Carini et al., 2016). The greater microbial diversity on high-quality necromass relative to low-quality necromass suggests that this resource is utilized by a wider variety of microbes like fungi, which had elevated diversity on high-quality necromass at both sites. While the diversity of microbial communities was higher under AM- than EM-dominated vegetation, diversity on necromass was equivalent between vegetation types. The commonality of this finding suggests that fungal necromass may foster a distinct community of decomposers, likely due to its unique chemical composition (Brabcová et al., 2018; López-Mondéjar et al., 2018). Further, the general absence of an incubation time effect on microbial diversity indicates that fungal necromass likely represents a sustained 'hotspot' of decomposition (sensu Brabcová et al., 2016), even after the rapid mass loss observed during the first weeks of incubation. The general

equivalency in microbial community diversity over time appears to be due to substitutions rather than gains or losses in local OTU dominance, likely reflecting shifts in substrate chemistry and the availability of resources during the course of necromass decomposition (Certano, Fernandez, Heckman, & Kennedy, 2018; Drigo et al., 2012; Fernandez, Heckman, et al., 2019; Ryan, Schreiner, Swenson, Gagne, & Kennedy, in press; Tláskal, Voříšková, & Baldrian, 2016).

Analyses of the microbial guilds colonizing the different types of fungal necromass were also notably similar across sites. At both the savanna and forest sites, fast-growing moulds and copiotrophic bacteria dominated the necrobiome, particularly during early stages of decay. Generalist fungal saprotrophs were also a common part of the necrobiome, although their relative abundances were frequently negatively correlated with fungal pathotroph relative abundance. We suggest the latter guild-level pattern may be the direct result of mycoparasitism rather than generalist fungal pathogen accumulation. Specifically, the high relative abundance of the fungal genus *Clonostachys*, which has been demonstrated to be an effective fungal biocontrol agent (Cota, Maffia, Mizubuti, & Macedo, 2009), indicates that the rapid increase in living fungi on decomposing mycelium, may itself be a target for resource exploitation. Furthermore, when grouped at the genus level, differences in relative abundances of many bacteria and fungi between the two necromass types aligned with their putative decomposition preferences and abilities. For example, many chitinolytic bacteria (e.g. *Chitinophaga* (Sangkhobol & Skerman, 1981), *Streptrophonas* (Yoon, Kang, Oh, & Oh, 2006), *Variovax* (Bers et al., 2011)) and fungi (*Mortierella*: De Boer, Gerards, Klein Gunnewiek, & Modderman, 1999) had significantly higher abundance on the high-quality fungal necromass, which may reflect easier access to chitin not imbedded in a melanized cell wall matrix (Bull, 1970). Conversely, the higher abundance of bacterial genera such as *Mucilinicoccus* and *Granulicella* as well as fungal genera such as *Chaetosphaeria* and *Talaromyces* on low-quality necromass is consistent with their common association with decomposing leaf litter and wood (Huhndorf, Fernández, Taylor, & Hyded, 2001; López-Mondéjar et al., 2016; Pankratov, Ivanova, Dedysh, & Liesack, 2011; Yilmaz et al., 2016), which requires greater carbohydrate-active enzymes activity to initiate decomposition. Additionally, the high overlap in the dominant microbial genera detected on fungal necromass at both our study sites and those present on fungal necromass in other study systems (Brabcová et al., 2016, 2018; Fernandez & Kennedy, 2018; López-Mondéjar et al., 2018), suggests there may be core necrobiome (Shade & Handelsman, 2012) that is broadly associated with decomposing mycelium.

While our results provide novel insights into the dynamics of fungal necromass decomposition, there are some methodological caveats that warrant mentioning. In particular, our two necromass substrates differed in multiple aspects of their initial biochemistry, including both melanin and nitrogen. As noted above, it is likely that these two traits interact to determine the quality of fungal necromass for decomposers (Fernandez & Koide, 2014); as such, future tests should disentangle the relative importance of each to necromass decay rates. Given the recent documentation of fungal necromass C being disproportionately utilized by bacteria relative to fungi

(López-Mondéjar et al., 2018), but also the significant C and N mining from fungal necromass by EM fungi (Akroume et al., 2019), it will also be important to use isotopic labelling techniques to understand exactly which resources are utilized by which micro-organisms, particularly in field settings where symbiotic fungi are present (Fernandez & Kennedy, 2018; Maillard et al., 2020; Zeglin, Kluber, & Myrold, 2013). Additionally, like most studies of microbial communities, we relied on relative sequence read counts as proxies for microbial community abundances. There are known issues with this approach in terms of potential taxonomic biases (Lloyd-Macgilp et al., 1996, but see Lekberg & Helgason, 2018) as well as count differences being affected by variation in gene copy number (Lofgren et al., 2019). As such, the differential relative abundances we observed across our experimental treatments must be interpreted with some caution. However, the notable consistency in effects of necromass quality across study systems as well as differential responses of fungi to vegetation type and bacteria to incubation period suggests that our results did capture significant ecological signal. Lastly, we recognize the limitations of the litter-bag technique, which excludes potentially important decomposers including soil fauna, as well as roots and rhizosphere-associated microbes (Bradford, Tordoff, Eggers, Jones, & Newington, 2002; Brzostek et al., 2015; Crowther et al., 2013).

5 | CONCLUSIONS

In this study, we demonstrate the regional-scale importance of fungal necromass quality in influencing both decay rate and microbial community composition across sites differing in their edaphic characteristics and vegetation types. Our results contribute to a growing body of literature that recognizes the importance of fungal necromass as a fast cycling OM resource that supports a distinct assemblage of decomposers with consistent taxonomic and functional guild membership. Future studies analysing the community structure of fungal necromass-associated microbial communities in tropical ecosystems will be particularly valuable in gaining a global perspective on the consistency of the fungal 'necrobiome'. While our work emphasizes the link between substrate quality and decomposer community structure, additional studies are required to link specific characteristics of fungal necromass quality and the necrobiome to long-term soil C stabilization.

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AUTHORS' CONTRIBUTIONS

K.V.B. designed and performed the experiment at Moores Creek, collected data, analysed data and co-wrote the manuscript; R.P.P. contributed to experimental design and manuscript preparation; E.A. generated the necromass, performed the experiment at Cedar Creek, collected data and contributed to the final version of the manuscript; F.M. performed analyses of microbial community data and contributed to manuscript preparation; R.M.M. assisted with DNA extractions and contributed to manuscript preparation; P.G.K. conceived of and designed the study, supervised the research, and co-wrote the manuscript.

DATA AVAILABILITY STATEMENT

Raw.fastq files for all samples are available under the following NCBI BioProject Accessions: <https://www.ncbi.nlm.nih.gov/bioproject/> Moores Creek Bacteria (PRJNA607032), Moores Creek Fungi (PRJNA607029), Cedar Creek Bacteria (PRJNA607034), Cedar Creek Fungi (PRJNA607030). Fungal necromass remaining, pH, and soil moisture data for both sites can be accessed through the Dryad Digital Repository: <https://doi.org/10.5061/dryad.nk98sf7qj> (Beidler et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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