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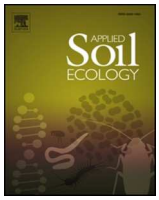

Short Communication

A cryptically diverse microbial community drives organic matter decomposition in forests

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ABSTRACT

Despite the critical role of microorganisms in plant and fungal residue decomposition, our understanding of their full diversity remains limited. This is due largely to the rapid microbial succession during decomposition, a scarcity of studies including multiple sampling times, and the omission of a species richness index encompassing all decay stages. To address these gaps, we conducted a meta-analysis of 12 studies, each examining bacterial and fungal communities at multiple time points during decomposition. We aimed to determine the overall microbial diversity involved in decomposition processes by aggregating microbial richness at different time points. By comparing cumulative microbial OTU (operational taxonomic unit) richness with single time point microbial richness, we show that the cumulative richness was 2–5 times greater, indicating that a high yet frequently overlooked diversity of microorganisms is involved in the decomposition process. This pattern was consistent across different organic matter types (plant and fungal residues) for both major microbial domains (bacteria and fungi). Moreover, the appearance rate of novel OTUs generally decreased over time for most organic matter types, except for dead wood, which accumulated new fungal OTUs at a notable pace. Our results collectively emphasize the importance of considering various microbial domains, organic matter types, and time points to successfully characterize the diversity of microorganisms involved in decomposition. Further, given the hidden cumulative number of bacterial and fungal species held within plant and fungal residues across decay stages, we propose that these substrates are crucial microbial reservoirs to include to accurately assess global terrestrial microbial diversity.

1. Introduction

Forest ecosystems represent one of the largest terrestrial carbon sinks and serve as vital habitats for biodiversity (Bonan, 2008; Brockerhoff et al., 2017; Lal, 2004). Decomposers, a central component of forest food webs, are crucial in recycling carbon (C) and nutrients (López-Mondéjar et al., 2018; Scheu, 2002). The main microbial decomposers are bacteria and fungi, which catalyze the breakdown of organic matter and thus influence soil organic C stocks and fertility (Baldrian, 2017; Uroz et al., 2016). Consequently, soil organic C and nutrients primarily originate from the decomposition of residues from primary producers, such as trees, as well as decomposers themselves (microbial residues or necromass) (Liang et al., 2019). Therefore, a better understanding of the bacterial and fungal diversity engaged in plant and microbial residue decomposition could contribute to the improvement of forest biogeochemical models, leading to potential increases in forest soil C sequestration and nutrient availability through adapted forest management practices, restoration, and protection policies (Baldrian et al., 2023;

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Gessner et al., 2010).

Several studies have shown a positive link between microbial richness and organic matter decomposition rates, especially in plant residues (Chiba et al., 2021; Maron et al., 2018; Wagg et al., 2021; Xu et al., 2021). However, these studies primarily focused on bacterial and fungal richness in soil—considered the primary reservoir of microbial diversity in terrestrial ecosystems—instead of the residues themselves (Delgado-Baquerizo et al., 2016). While soil bacterial and fungal richness is consistently higher compared to plant and fungal residues, the microbial communities inhabiting decomposing organic matter differ significantly from those in soils (Beidler et al., 2020; Herzog et al., 2019; Mäkipää et al., 2017). Notably, bacterial communities decomposing plant and fungal residues are often enriched in copiotrophic taxa, unlike soil populations dominated by oligotropic taxa (Beidler et al., 2020; Martinović et al., 2022; Viotti et al., 2021). Regarding fungi, soil communities primarily include mycorrhizal and early-diverging saprotrophic fungi, whereas organic residues are generally colonized by specialized fungal decomposers. Specifically, plant residues are colonized by lignolytic-basidiomycota (Brabcová et al., 2022; Herzog et al., 2019; Maillard et al., 2023a), and fungal residues by mycoparasitic fungi, likely acting as facultative saprotrophs (Beidler et al., 2020; Maillard et al., 2020, 2023b). Further, while soil microbial communities tend to be relatively stable concerning richness and composition over time at a local scale (Martinović et al., 2021; Santalahti et al., 2016; Shigyo et al., 2019), recent studies have consistently demonstrated rapid changes in both metrics of microbial communities during the decomposition of plant and fungal residues for dead wood (Brabcová et al., 2022; Viotti et al., 2021), leaf and needle litter (Maillard et al., 2023a; Šťursová et al., 2020; Tláskal et al., 2016), fine root litter (Herzog et al., 2019; Kohout et al., 2018, 2021; Martinović et al., 2022), and fungal residues (Beidler et al., 2020; Brabcová et al., 2016; Maillard et al., 2020). The rapid succession of bacteria and fungi, likely due to changing substrate physicochemical properties, might imply that a more extensive set of decomposers is involved in forest ecosystem decomposition processes than previously assumed (Maillard et al., 2023a; Šnajdr et al., 2011). Nevertheless, many studies on organic matter decomposition often include a limited number of time points and cumulative microbial richness (i.e., the total number of bacterial and fungal species participating in the decomposition processes) is rarely quantified. As a result, aggregating microbial richness across time points to assess the full extent of microbial diversity involved in decomposition processes has substantial implications. Specifically, this cumulative view is important from the perspective of microbial conservation strategies and holds substantial significance for ecosystem sciences, given that many soil processes are tightly linked with microbial diversity (Delgado-Baquerizo et al., 2016; Maron et al., 2018).

Here, we conducted a meta-analysis of the recent literature characterizing bacterial and fungal community composition at multiple time points during the decomposition of a range of organic matter types. We aimed to estimate the cumulative microbial richness associated with plant and fungal residue decomposition and juxtapose it with time-point specific microbial richness (i.e., the microbial richness at any single time point during decomposition). Additionally, we determined how the appearance rate of novel bacterial and fungal species changes as decomposition advances.

2. Materials and methods

We collected data from 12 studies investigating bacterial or fungal richness during the decomposition of plant and fungal organic matter types based on high-throughput amplicon sequencing of 16S rRNA and ITS barcodes (Table 1). The literature search was conducted in Web of Science and Google Scholar using keywords such as “leaf litter,” “fine root litter,” “dead wood,” “fungal necromass,” “16S,” “ITS,” “bacterial communities,” and “fungal communities.” Given the relative recent development of high-throughput amplicon sequencing of 16S rRNA and ITS barcodes, we acknowledge that a completely comprehensive literature search has not been conducted. Our review primarily relied on the article authors' literature knowledge, and while we are confident that our review of available literature on the topic is broadly representative, some studies are absent, primarily due to author unwillingness to share data. Studies incorporated met two criteria: having at least four sampling times during the decomposition experiment and involving plant (leaf litter, fine root litter, dead wood) or fungal (necromass) residue

Table 1
Summary of the studies analyzed, including organic matter type, decomposition time, and sampling details.

Study	Domain	Location	Forest type	Organic matter type	Number of samplings and incubation time	Additional treatment	Individual time-series
Viotti et al., 2021. Environmental microbiology	Bacteria and fungi	France	Temperate oak forest	Dead wood	10 sampling times: 971 days of incubation	Wood types	2 (bacteria), 2 (fungi)
Brabcová et al., 2022. Frontiers in Microbiology	Fungi	Germany	Temperate forest	Dead wood	6 sampling times: 2190 days of incubation	Wood types	2
Kohout et al., 2021. Frontiers in Microbiology	Fungi	Czech Republic	Temperate spruce forest	Root litter	4 sampling times: 456 days of incubation	Incubation microhabitats	3
Kohout et al., 2018. ISME journal	Fungi	Czech Republic	Temperate spruce forest	Root litter	8 sampling times: 761 days of incubation		1
Herzog et al., 2019. ISME journal	Bacteria and fungi	Switzerland	Temperate forest	Root litter	5 sampling times: 730 days of incubation	Irrigation levels	2 (bacteria), 2 (fungi)
Martinović et al., 2022. FEMS Microbiology Ecology	Bacteria	Czech Republic	Temperate spruce forest	Root litter	8 sampling times: 761 days of incubation		1
Maillard et al., 2020. FEMS Microbiology Ecology	Fungi	USA	Boreal forest	Fungal necromass	4 sampling times: 56 days of incubation	Fungal necromass types and incubation microhabitats	4
Beidler et al., 2020. Journal of Ecology	Bacteria and fungi	USA	Temperate oak forest	Fungal necromass	4 sampling times: 56 days of incubation	Fungal necromass types	2 (bacteria), 2 (fungi)
Brabcová et al., 2016. New Phytologist	Bacteria and fungi	Czech Republic	Temperate oak forest	Fungal necromass	6 sampling times: 147 days of incubation	Incubation microhabitats	2 (bacteria), 2 (fungi)
Maillard et al., 2023a Plant and Soil	Fungi	France	Temperate oak forest	Leaf litter	9 sampling times: 768 days of incubation	Litter types	2
Tláskal et al., 2016. FEMS Microbiology Ecology	Bacteria	Czech Republic	Temperate oak forest	Leaf litter	8 sampling times: 730 days of incubation		1
Šťursová et al., 2020. Fungal Ecology	Fungi	Czech Republic	Temperate forest	Leaf litter	7 sampling times: 2080 days of incubation	Litter types	2

decomposition in forest ecosystems. We established a cutoff of at least four sampling times, enabling the observation of temporal trends that are more challenging to discern with fewer sampling times. Despite no geographic filters being applied, most studies in our meta-analysis were conducted in temperate forests. Time zero data were excluded, as it is uncertain that all microbial pre-colonizers participate in the decomposition process (Cline et al., 2018). When multiple treatments were tested (e.g., organic matter quality, incubation microhabitat, etc.), these were segregated into separate time series. Our meta-analysis encompassed 10 bacterial and 22 fungal time-series from 6 and 10 studies, respectively, averaging 5.9 sampling times per study, with decomposition periods ranging from 8 to 2190 days across all combined organic matter types (Table 1).

Bacterial and fungal OTU (operational taxonomic unit) tables were directly obtained from their respective studies without any new bioinformatics analysis. Statistical analysis and data visualization were conducted in R (R Core Team, 2021). To account for within-study read depth variations, we used the 'rarefy' function from the R *vegan* package (Oksanen et al., 2022) to rarefy OTU tables. The rarefied read depths for each study, categorized by microbial domain (bacteria or fungi), are listed in Table S1. Then, we compared single time point (microbial OTU richness at one decomposition time) with cumulative (cumulated OTU richness for all incubation times combined) bacterial and fungal OTU richness across the four types of organic matter. First, we compared trends in OTU richness over time to estimate single time point variation in richness compared with cumulative richness. Subsequently, we calculated fold changes of cumulative over average single time point richness to assess the degree to which cumulative richness exceeded single time point richness. This fold change was compared across organic matter types for bacterial and fungal richness using a linear mixed model with the original study as a random factor combined with an analysis of variance (ANOVA), respectively using the 'lmer' and 'aov' functions from the R *lme4* package (Bates et al., 2015). We performed the same analysis on only the abundant bacterial and fungal OTUs (those representing >0.5 % of total sequence reads at least once during decomposition) to account for the possibility that some of the rare OTUs may result from factors such as aerial contamination, thereby artificially inflating microbial richness involved in the decomposition processes. Finally, we calculated the appearance rate of novel OTUs (defined as the number of OTUs not present in the previous time points appearing per day) and tested the relationships between the appearance rate of novel OTUs and the decomposition time for the four organic matter types using Pearson's correlation tests using the 'cor.test' function in R.

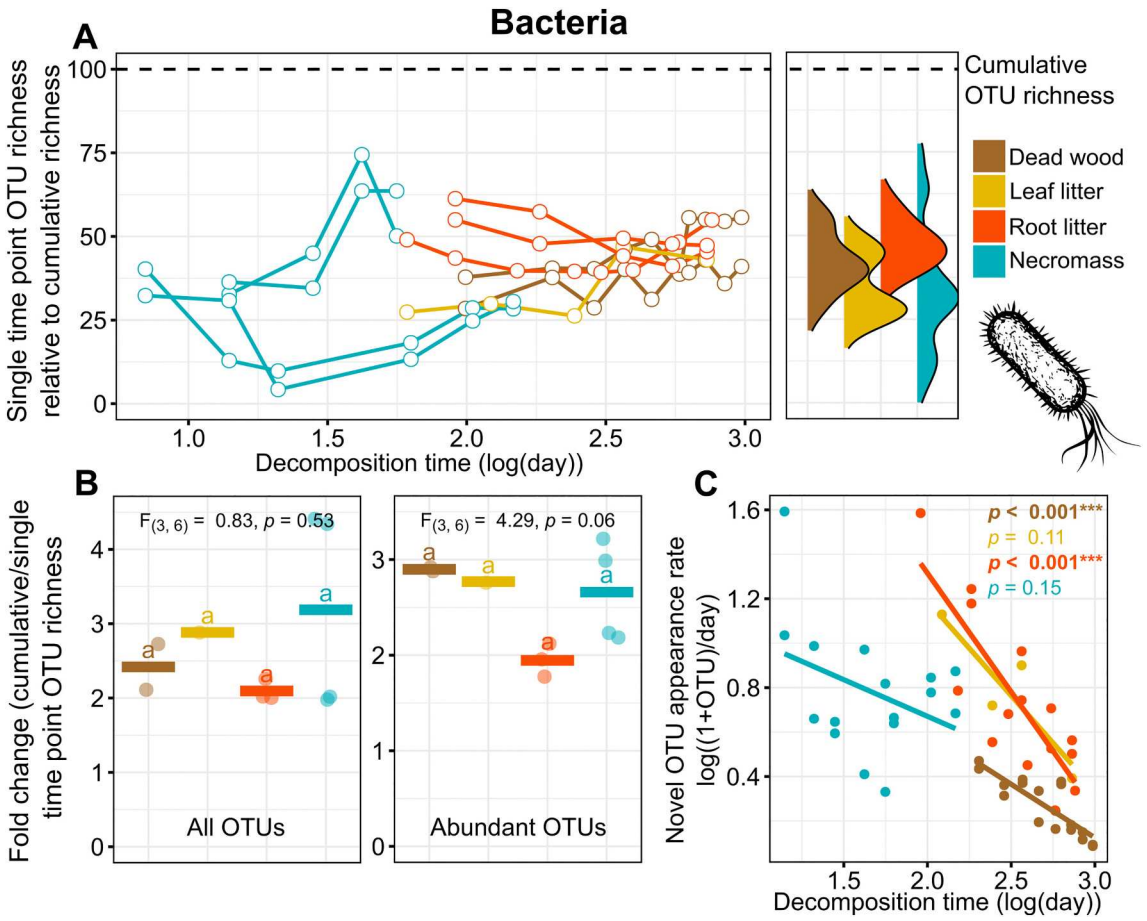

Fig. 1. Bacterial OTU richness analysis. (A) Relative bacterial OTU richness over decomposition time (log(day)) and organic matter type (dead wood, leaf litter, root litter, and fungal necromass) for each dataset. Density plots show the distribution of relative bacterial OTU single time point richness depending on organic matter type across all datasets. (B) Fold change of cumulative over single time point bacterial OTU richness for all OTUs and abundant OTUs only (<0.5 % in at least one decomposition time) per dataset (circles) and averaged across datasets (horizontal bar) based on organic matter type. (C) Linear regression between bacterial OTU appearance rate (log((1+ new OTU)/day)) and decomposition time (log(day)) for all datasets combined, separated by organic matter type. The impact of organic matter type on bacteria OTU richness was analyzed using a mixed linear model, with the originating study as a random factor. Statistical significance was assessed by one-way ANOVA and Tukey's HSD test for pairwise comparisons. Pearson's correlations evaluated the link between bacterial OTU appearance rate and decomposition time. Significance levels are indicated (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Bacterial silhouette image is from https://www.phylopic.org/.

3. Results and discussion

Bacterial (Fig. 1a) and fungal (Fig. 2a) single time point OTU richness varied over time, but rarely exceeded 50 % of the cumulative richness for each dataset. This indicates that no clear period exists at any stage of organic matter decomposition to recover the maximum microbial richness. Instead, studies including different sampling times from early to late degradation stages are necessary to exhaustively describe the microbial diversity involved in the degradation process. The cumulative microbial richness, irrespective of microbial domain and type of organic matter, was found to be 2–5 times greater than the average single time point richness (Fig. 1b and Fig. 2b). These results are not due to rare OTUs potentially contaminating samples, as the results constrained to just the abundant bacterial (Fig. 1b) and fungal (Fig. 2b) OTUs yielded similar findings. Collectively, these findings suggest that the microbial decomposer communities in forest ecosystems are highly dynamic and exhibit relatively swift turnover rates. This pattern was consistent across the four organic matter types studied here for bacteria, as no organic matter effect on the fold change between cumulative and single time point richness was found. Conversely, fungi demonstrated significantly lower fold changes between cumulative and single time point richness in belowground organic matter types (fine root litter and necromass) compared to those degrading aboveground, like leaf litter, and to a lesser degree, dead wood. This divergence may highlight that organic matter decomposing aboveground, such as dead wood and leaf litter, contains relatively less rich fungal communities due to a greater reliance on colonization from fungal spores than vegetative growth (Komonen and Müller, 2018; Peay and Bruns, 2014).

The appearance rates of novel OTUs decreased significantly over time for microorganisms across all organic types, except bacterial communities in necromass and fungal communities in dead wood that we discuss in the following paragraph (Fig. 1c and Fig. 2c). Ecologically, the overall decline in novel microbial OTU appearance rates might correlate with the resource levels and quality of organic matter. As decomposition advances, the chemical composition of organic matter becomes less diverse due to microorganisms' preference for labile over recalcitrant compounds (Fernandez et al., 2019; Maillard et al., 2021, 2023a, 2023b; Ryan et al., 2020). This is especially demonstrated for plant residues from studies included in our meta-analysis, where decay rates slow down over time, and a relative enrichment in lignin—an aromatic polymer generally regarded as resistant to microbial breakdown—is observed as decomposition advances (Herzog et al., 2019; Kohout et al., 2021; Maillard et al., 2023a). In the case of fungal residues, similar enrichment patterns involving aromatic molecules, such as melanin, have been previously documented (Fernandez et al., 2019; Ryan et al., 2020). Consequently, resource-depleted organic matter might reduce the chances for new colonizers to establish (Debray et al., 2022). Additionally, as organic matter becomes more resistant to degradation, decomposer communities might become more specialized in feeding on the remaining recalcitrant compounds, likely increasing inter- and intra-domain competition for C and nutrients (Hättenschwiler et al., 2005). Further, the limited number of new microbial OTUs appearing in the late stages of decomposition indicates that our estimate that cumulative microbial richness is 2–5 times higher than average single time point richness would not drastically increase with longer decomposition times for leaf and root litters as well as fungal necromass.

Regarding exceptions to the aforementioned general patterns, unlike for the other substrates, the appearance rate of novel bacterial OTUs on fungal necromass was found to decrease at a slow, insignificant rate over time. We suggest this may indicate that bacteria are particularly well-suited to access recalcitrant compounds present in fungal residues, as already proposed elsewhere (López-Mondéjar et al., 2018). The more striking exception was that new fungal OTUs continued to accumulate in dead wood at a comparatively high rate as time progressed. We posit this pattern is related to a number of non-mutually exclusive factors: dead wood's slower decay rate compared to the three other organic matter types studied, a possible increase in microbial carrying capacity due to the detoxification of wood chemicals by fungi (Valette et al., 2017), increased access to resources such as holocellulose as lignin is modified or degraded by specialized wood-decaying fungi (brown-rot and white-rot fungi; Maillard et al., 2022), and the accumulation of microbial necromass that generates new resources for decomposition (Prescott and Vesterdal, 2021).

Though our study is the first attempt to aggregate microbial richness across decomposition time series, significant limitations are crucial to note. Among the most notable is the overall limited number of studies characterizing microbial community successions during plant and microbial residue decomposition using high-throughput amplicon sequencing technologies, particularly for bacteria. Additionally, temperate forests are overrepresented in our meta-analysis compared with boreal and tropical ecosystems, suggesting more studies are needed in other biomes to confirm the generality of the observed patterns. Further, it is also important to note the heterogeneity in the time series included in our meta-analysis, both in terms of total decomposition time and sampling frequency, which might be sources of bias. As an example for wood decomposition, Viotti et al. (2021) had 10 sampling points over 971 days for fungal communities, while Brabcová et al. (2022) had only six sampling points for a longer incubation period of 2190 days. Consequently, future studies, including long-term organic matter decomposition time series with high-frequency sampling across a broader range of forest ecosystems, will be important to either reinforce or contrast the initial trends observed here regarding cumulative microbial richness during organic matter decomposition.

In conclusion, our results suggest that organic matter decomposition processes in forest ecosystems are associated with a high, yet relatively underappreciated, number of microbial taxa. Additionally, our findings indicate that when attempting to estimate the cumulative microbial richness involved in decomposition, it will be important to consider different microbial domains and various organic matter types, as they present specific patterns of richness accumulation over time. Moreover, while forest soil is often considered the reservoir of microbial diversity, it also seems essential to include plant and fungal residues at different decay stages as additional reservoirs when assessing global terrestrial microbial richness. Finally, from a microbial conservation perspective, it is not just crucial to preserve organic matter types like dead wood in harvested forests, but also to uphold the asynchronicity in dead wood production (i.e. maintain both fresh and old residues), which will foster microbial diversity and its ability to multiply and disperse through various decay stages.

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CRediT authorship contribution statement

Conceptualization: F. M.; Data curation: F. M., Y. C., C. V., M. B., I. B., P. B., and P. K.; Data analysis: F. M. and Y. C.; Original draft preparation: F. M.; Reviewing and editing the manuscript: Y. C., C. V., M. B., I. B., V. B., P. K., P. B., and P. K. All authors have revised and agreed to the published version of the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

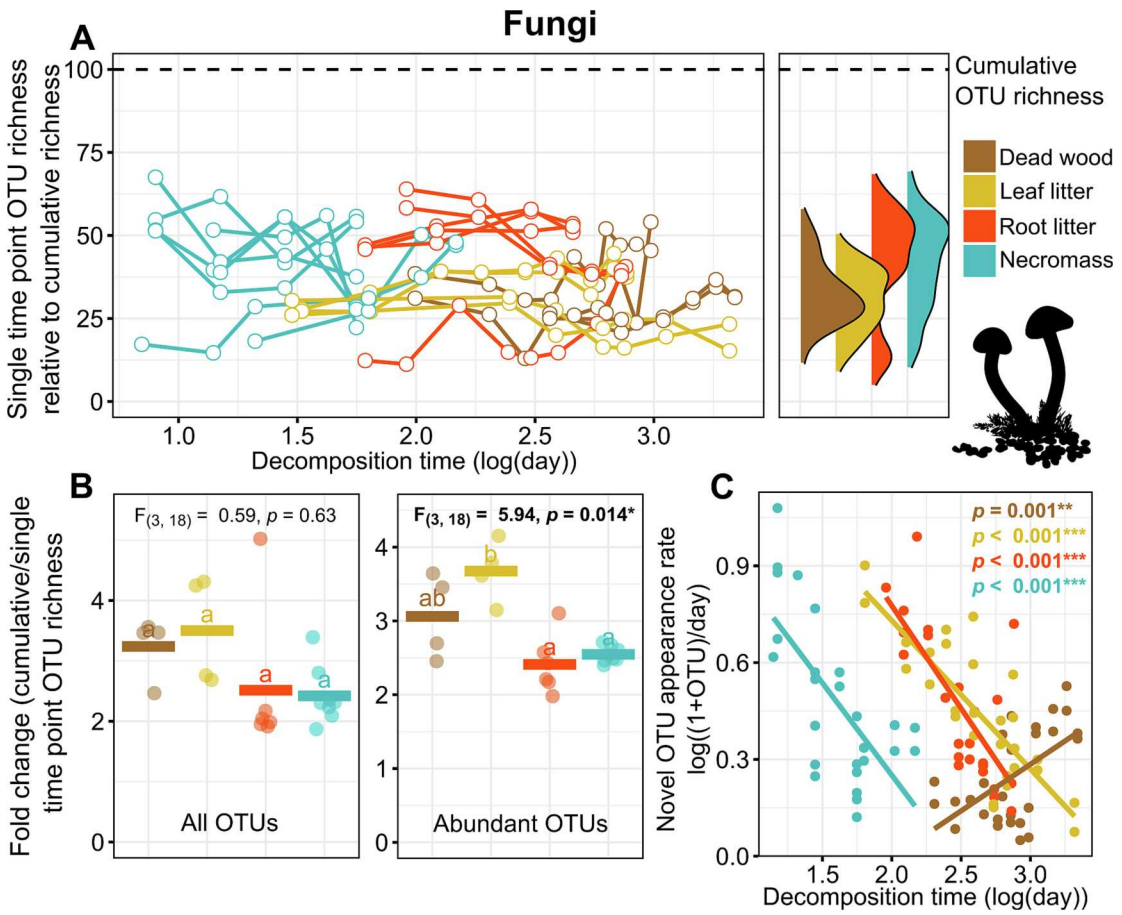

Fig. 2. Fungal OTU richness analysis. (A) Relative fungal OTU richness over decomposition time (log(day)) and organic matter type (dead wood, leaf litter, root litter, and fungal necromass) for each dataset. Density plots show the distribution of relative fungal OTU single time point richness depending on organic matter type across all datasets. (B) Fold change of cumulative over single time point fungal OTU richness for all OTUs and abundant OTUs only (<0.5 % in at least one decomposition time) per dataset (circles) and averaged across datasets (horizontal bar) based on organic matter type. (C) Linear regression between fungal OTU appearance rate (log((1+ new OTU)/day)) and decomposition time (log(day)) for all datasets combined, separated by organic matter type. The impact of organic matter type on fungal OTU richness was analyzed using a mixed linear model, with the originating study as a random factor. Statistical significance was assessed by one-way ANOVA and Tukey's HSD test for pairwise comparisons. Pearson's correlations evaluated the link between fungal OTU appearance rate and decomposition time. Significance levels are indicated (*P < 0.05; **P < 0.01; ***P < 0.001). Fungal silhouette image is from https://www.phylopic.org/.

Data availability

Data will be made available upon reasonable request to the corresponding author.

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